Evaluation of suitable nursery areas for penaeid shrimps in shallow water systems in Southern Mozambique

Daniela Carvalho de Abreu

Doctoral Thesis

UNIVERSITY OF GOTHENBURG

Department of Marine Sciences
Faculty of Sciences
Sweden

2017

Cover Photographs Composition: Daniela C. de Abreu
Cover Photographs by: Daniela C. de Abreu and Per-Olav Moksnes

ISBN 978-91-629-0304-6 (PRINT)
ISBN 978-91-629-0305-3 (PDF)
Available at http://hdl.handle.net/2077/53628

Printed in Gothenburg, Sweden 2017
By BrandFactory AB

To my parents, Brígida and João, and to my dear Hugo

" ...You raise me up, so I can stand on mountains..."
(Secret Garden, 2001)

Abstract

Tropical shallow water habitats such as estuaries, mangrove forests and seagrass beds are important nursery areas for juveniles of many commercially important species including penaeid shrimp. Penaeids are one of the most important fishery resources worldwide, and in Mozambique they are the basis of a profitable commercial fishery, landing hundreds of tons per year. Ecological knowledge concerning habitat use and factors driving the distribution and abundance of shrimp in nursery areas, and regarding the successful movement of juveniles from the nurseries to adult grounds, are critical to characterize productive nurseries for penaeid shrimp and provide important information for a sustainable management of their fishery. In this thesis I used a combination of stable isotope methods, ecotoxicology techniques and extensive field studies to assess feeding behaviour and factors affecting density and distribution of four shrimp species (*Metapenaeus monoceros, M. stebbingi, Penaeus indicus* and *P. japonicus*) in three estuaries (Espírito Santo, Maputo River and Incomati River) and two coastal marine areas (Bembe and Inhaca Island) in Maputo Bay, the second greatest shrimp fishing ground in Mozambique, to assess their values as nursery areas for the fishery.

Stable isotope analyses showed that the assessed shrimp species were mainly using seagrass beds and shallow sand and mud flats as feeding grounds, whereas only *P. indicus* appeared to also feed within the mangrove habitat. The analysis of metals concentration in shrimp showed no indication of elevated levels, and although levels for pesticides in the water exceed environmental thresholds in some of the nursery areas, only a localized effect of insecticides was detected in *P. indicus* in Espírito Santo estuary.

In Maputo Bay, juvenile shrimp were found to use many different types of coastal environments as nursery areas, including both estuarine and coastal marine areas, where different environmental and landscape factors appeared to control shrimp densities in seemingly similar nursery areas. Overall, the amount of benthic microalgae, turbidity and the extent of shallow water habitats appeared to be the most important factors explaining variation in shrimp density within and between nursery areas, whereas the extent of mangroves and contamination in the nursery areas was found to be less important. This caused the surprising results that the most exploited and contaminated nursery area, Espírito Santo estuary, showed the overall the highest abundance of juvenile shrimp. Taking all in consideration, productive mud- and sand flats, with or without fringing mangroves, appear to constitute key nursery habitats for penaeid shrimp in the study area, where the Bembe area, Espírito Santo and Maputo River estuaries were identified as the most

important nursery areas for the dominant fishing ground of penaeid shrimp in Maputo Bay. This information could guide conservation and provide support for an ecosystem management approach of the shrimp fishery in southern Mozambique.

Keywords: Tropics; Southeast Africa; Shallow water; Estuaries; Nursery ground value; Decapods; Penaeidae; Carbon and nitrogen isotopes; Diet; Acetyl cholinesterase, Butyryl cholinesterase, Metals.

Populärvetenskaplig sammanfattning

Grunda kustmiljöer i tropiska områden, som estuarier, mangroveskogar och sjögräsängar, är kända för att vara mycket viktiga uppväxtområden för unga stadier av många kommersiellt betydelsefulla arter, inklusive räkor inom familjen Penaeidae (tigerräkor på svenska). Dessa så kallade "barnkammarhabitat" förser de unga stadierna både med skydd från rovdjur samt riklig tillgång till olika sorters föda, och har en nyckelfunktion i arternas livscykel där de utgör en förutsättning för de vuxna populationerna och de fiske som baseras på dem. Alla grunda kustområden är dock inte lika viktiga som uppväxthabitat, och det kan vara stor variation i mängden unga fiskar och kräftdjur mellan tillsynes liknande kustmiljöer. Det är därför viktiga att identifiera och skydda de viktigaste uppväxtmiljöerna i ett område för en hållbar förvaltning av de arter som växer upp där. Studier har visat att den viktigaste aspekten för att bedöma värdet av ett uppväxtområde är antalet unga individer, samt hur många av dessa som migrerar framgångsrikt till den vuxna populationen. Detta har dock endast studerats i ett fåtal arter, och aldrig för tigerräkor i Afrika.

Betydelsen av att skydda grunda uppväxtområden är speciellt viktigt i fattiga delar av världen där stora delar av befolkningen längs kusten kan vara beroende av produktionen i dessa områden. I Maputo-bukten, i södra Moçambique utgör fisket efter tigerräkor en viktig källa till mat och inkomst, både för det småskaliga, traditionella fisket i grunda områden, samt för det kommersiella fisket i bukten som årligen landar hundratals ton. Landningarna av flera arter har dock minskat under senare år samtidigt som mangrove skogar minskat och föroreningar ökat i vissa områden. Det är idag dåligt känt om dessa miljöförändringar har påverkat produktionen av räkor, samt vilka uppväxtområden som är de viktigaste för fisket i Maputo-bukten.

Avhandlingens syfte var att öka förståelsen om vilka faktor som bestämmer hur många unga tigerräkor som hittas i ett uppväxtområde, vad de äter och var de hittar sin föda, hur de påverkas av olika miljöfaktorer som t.ex. salthalt, mängden mat i sedimentet, mängden rovfiskar, föroreningar eller utbredningen av mangrove i området, för kunna karaktärisera vad som utgör viktiga barnkammarhabitat för tigerräkor. Denna information, tillsammans med kunskap om hur unga räkor migrerar till viktiga fiskeområden, har sedan användas för att identifiera de viktigast uppväxtområdena i Maputo-bukten, vilket skulle kunna utgöra viktig information för en hållbar förvaltning av kustekosystemen och räkfisket i södra Moçambique.

Fyra arter av tigerräkor (*Metapenaeus monocero*, *M. stebbingi*, *Penaeus indicus*, *P. japonicas*) har studerats i de tre estuarierna Espírito Santo, Maputo river and Incomati river samt i två marina kustområdena vid Bembe och ön Inhaca. Avhandlingen bygger på fältundersökningar och insamling av prover för analyser i laboratoriet av olika biologiska parametrar, samt mätningar av stabila kol- och kväveisotoper (δ^{13}C and δ^{15}), med vars hjälp både födoval, födohabitat, samt migration från uppväxtområden till fiskeplatser i Maputo-bukten skattades. Vidare utfördes ekotoxikologiska analyser av miljöfaktorer som pesticider och metaller. Undersökningar analyserade också så kallade landskapsfaktor (t.ex. närhet till mangrove och utbredning av grunda lerbottnar) baserade på geografiska/geometriska värden.

Analyserna av de stabila isotoperna visade att räkorna främst använde sjögräsängar, grunda sand- och lerbottnar för att söka föda, men att bara en art (*P. indicus*) verkade söka föda också i mangroven. Metallkoncentrationerna i räkorna visade ingen indikation på förhöjda värden i något uppväxtområde. Även om pesticidhalterna överskred tröskelvärdena i flera uppväxtområden, påvisade bioindikatorer endast lokala effekter från insektsgifter i en art från estuariet Espírito Santo. I Maputo-bukten visade det sig att de juvenila tigerräkorna utnyttjade flera olika typer av kustområden, både utsötade estuarier och fullt marina kustområden, som uppväxtområden. Tätheten av räkor kontrollerades där sannolikt av olika miljöfaktorer i olika områden, inkl. landskapsfaktorer, även om uppväxtområdena till synes såg likvärdiga ut. De övergripande mest betydande faktorerna som kunde förklara variationerna i antalet unga räkor, inom och mellan uppväxtområdena, var mängden bottenlevande mikroalger, grumligheten i vattnet samt utbredningen av grunda mjukbottnar. Däremot var utbredningen av mangrove eller föroreningar i uppväxtområdena av mindre betydelse. Det sistnämnda var överraskande, särskilt som det mest exploaterade och förorenade uppväxtområdet fanns i estuariet i Espírito Santo, som trots detta hade den största mängden räkor.

Med allt inräknat, verkar produktiva ler- och sandbottnar, med eller utan omgivande mangrove, utgöra nyckelhabitat som uppväxtområden i Maputo-bukten. De uppväxtområden som kunde identifieras som de viktigaste för rekryteringen av räkor till fiskebankarna i den södra delen av bukten var det marina området vid Bembe samt estuarierna vid Espírito Santo och Maputo-floden. Informationen som tagits fram i avhandlingen kan användas för att skydda viktiga uppväxtområden för räkor i Maputo-bukten, där man hittills mest tagit hänsyn till områden där det finns vuxna räkor. Med hjälp av denna nya information skulle man kunna utveckla en ekosystembaserad förvaltning av räkfisket i södra Moçambique. Ett mål som många länder i världen skulle behöva nå för att bevara sina marina resurser.

Resumo em Português

Habitats costeiros tropicais, tais como estuários, mangais e tapetes de ervas marinhas, são importantes áreas de viveiro para muitas espécies de importância comercial, incluindo as espécies de camarões penaídeos. Estes camarões constituem um dos mais importantes recursos pesqueiros a nível mundial, e em Moçambique são a base de actividades de pesca lucrativas, que rendem milhares de toneladas anualmente.

O conhecimento ecológico sobre os habitats utilizados como área de viveiro, sobre os factores que influenciam a distribuição e abundância de juvenis nestas áreas, e sobre o valor de cada área, indicado pelo movimento de juvenis para habitats onde se encontra camarão adulto, é essencial para a caracterização das áreas de viveiro produtivas, e fornecer informação importante para a gestão sustentável da pesca de camarão.

Tendo em conta a importância deste conhecimento, usei, nesta tese, uma combinação de análises laboratoriais (métodos de isótopos estáveis e técnicas de ecotoxicologia) com trabalho de campo extenso para estudar os comportamentos alimentares e os factores que afectam a densidade e distribuição de quatro espécies de camarão: *Metapenaeus monocero, M. stebbingi, Penaeus indicus* e *P. japonicus.* O estudo incidiu sobre quatro estuários (Espírito Santo, Rio Maputo, Rio Incomati) e duas zonas costeiras (Bembe e Inhaca) da Baía de Maputo, a segunda maior área de pesca de camarão em Moçambique, e teve como objectivo estimar o valor de cada área de estudo como área de viveiro para a actividade pesqueira.

As análises de isótopos estáveis mostraram que as espécies de camarão estudadas usam maioritariamente os tapetes de ervas marinhas e as zonas arenosas ou lodosas de baixa profundidade como áreas de alimentação, sendo que apenas *P. indicus* faz também uso da floresta de mangal como área de alimentação.

As análises à concentração de metais no camarão não indicou níveis elevados destes contaminantes, e embora o nível de pesticidas na água exceda os limites ambientais estabelecidos em algumas das áreas de estudo, foi apenas detectado um efeito localizado de insecticidas em *P. indicus*, no estuário de Espírito Santo.

Na Baía de Maputo, o camarão juvenil demonstra utilizar diferentes tipos de habitats costeiros como área de viveiro, incluindo zonas estuarinas e zonas costeiras, onde diferentes factores ambientais e geográficos parecem afectar a densidade de camarão em áreas aparentemente comparáveis. No geral, a quantidade de microalgas no sedimento, a turbidez da água e o tamanho dos habitats marinhos de baixa profundidade são os factores que mais influenciam a variação da densidade de camarão em cada área em entre diferentes áreas, enquanto que a

extensão da floresta de mangal e a contaminação das áreas de viveiro têm menos relevância.
Surpreendentemente, a área de viveiro mais explorada e mais contaminada da Baía de Maputo, o estuário de Espírito Santo, mostrou ter a maior abundância de camarão juvenil.
Tendo em consideração estes resultados, as áreas arenosas e lodosas de baixa profundidade, com a presença ou não de mangal contíguo, constituem as principais áreas de viveiro das espécies de camarão penaídeo na região de estudo, sendo que Bembe e os estuários de Espírito Santo e do Rio Maputo foram identificados como as mais importantes áreas de viveiro para as espécies pesqueiras de camarão na Baía de Maputo.
As conclusões desta tese podem servir de base para delinear estratégias de conservação de habitats e de gestão de ecossistemas para a actividade da pesca do camarão em Moçambique.

List of Papers

This thesis is based on the papers listed bellow, which are referred to in the text by roman numerals as follows:

I. **de Abreu DC**, Paula, J, Macia, A (2017) Tropical seascapes as feeding grounds for juvenile penaeid shrimps in southern Mozambique revealed using stable isotopes. Estuar Coast Shelf S. *In press.* Advanced online publication. doi:10.1016/j.ecss.2017.08.040

II. **de Abreu DC**, Vetina AA, Matsombe J, Conceição K, Verão C, Macia A and Moksnes P-O. Assessment of factors affecting juvenile penaeid shrimp distribution in nearshore nursery areas in Maputo Bay reveals substantial variation in habitat use. *Manuscript.*

III. Sturve J, **de Abreu DC**, Gustavsson M and Moksnes P-O. Exposure and effects of pesticides and metals on penaeid shrimps in Maputo bay, Mozambique. *Manuscript.*

IV. **de Abreu DC**, Abrantes KGS, Vetina AA, Matsombe J, Mabilana H, Macia A and Moksnes P-O. Penaeid shrimps movement from nursery areas to adult fishing grounds in southern Mozambique: A stable isotope approach. *Manuscript.*

The article and manuscripts respective supplementary material are appended at the end of each of the article and each respective manuscript.
The Paper 1 is reproduced with permission from the respective journal.

Publications not included in the thesis:

Machava V, Macia A and **de Abreu D** (2014) By-catch in the artisanal and semi-industrial shrimp trawl fisheries in Maputo Bay. In: Bandeira, S. and Paula, J. (Eds.). *The Maputo Bay Ecosystems*. WIOMSA, Zanzibar Town, pp. 291- 295.

de Abreu D, Samussone D and Scarlet MP (2014) Heavy metal contamination of penaeid shrimps from the artisanal and semi-industrial fisheries in Maputo Bay, In: Bandeira S and Paula J (Eds). *The Maputo Bay Ecossystems.* WIOMSA, Zanzibar Town, pp. 377- 381.

Macamo C, Bandeira S, Muando S, **de Abreu** D, and Mabilana H (2015) Mangroves of Mozambique. In: Bosire JO, Mangora MM, Bandeira S, Rajkaran A, Ratsimbazafy R, Appadoo C and Kairo JG (Eds.). *Mangroves of the Western Indian Ocean: Status and Management*. WIOMSA, Zanzibar Town, pp. 161

My contribution to the papers

Paper I: ***Tropical seascapes as feeding grounds for juvenile penaeid shrimps in southern Mozambique revealed using stable isotopes.***
D.C.A design and planned all parts of the study, carried out all field sampling, and all laboratory activities and wrote the paper with comments from the co-authors.

Paper II: ***Assessment of factors affecting juvenile penaeid shrimp distribution in nearshore nursery areas in Maputo Bay reveals substantial variation in habitat use.***
D.C.A was involved in the design and planning of all parts of the study, coordinated and carried out all field sampling, and all laboratory activities with support from A.A.V., J.V., K.C., C.V., Sabina Manhique and Ana Gledys da Conceição, and wrote the papers with contributions from P-O.M. and comments from other co-authors.

Paper III: ***Exposure and effects of pesticides and metals on penaeid shrimps in Maputo bay, Mozambique.***
D.C.A was involved in the design and planning of the study, all field sampling and part of the laboratory activities, and contributed to the writing possess (J.S. wrote the paper).

Paper IV: ***Penaeid shrimps movement from nursery areas to adult fishing grounds in southern Mozambique: A stable isotope approach.***
D.C.A was involved in the design and planning of all parts of the study, coordinated and carried out all field sampling, and all laboratory activities with support from A.A.V., J.V., Kelvin da Conceição, Carlos Verão, and Ana Gledys da Conceição, and wrote the papers with contributions from P-O.M., and comments from other co-authors.

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Background

Nursery areas

Estuaries and mangrove forests, seagrass mats, mud and sand flats and other shallow coastal ecosystems are noticeable tropical nearshore systems with a variety of ecological functions and economic services, ranging from shoreline protection to highly productive fisheries (Moberg and Rönnbäck 2003, Barbier et al. 2011). Acting as nursery area for a variety of juvenile nektonic and benthonic groups, particularly fish, shrimp and crab, is one of the most important functions of these nearshore systems (Beck et al. 2003, Gillanders et al. 2003).
The relationship between tropical nearshore systems and some of the species important to the fisheries is based on high densities and increased survival of juvenile of fish and shrimp species in these habitats in different parts of the world. The proposed explanations for this relationship are the not mutually exclusive hypotheses of refuge (the high turbidity and high structural complexity of the habitats provide low predation risk) and food supply (these areas are highly productive; Nagelkerken 2009). For example, Rönnbäck et al. (1999) and Macia et al. (2003) indicated the role of mangroves as a refuge habitat penaeid shrimp with protection against predation being provided by the mangrove roots, and Chong et al. (2001) and Macia (2004a) evaluated the contribution role of mangrove detritus nutrition to these organisms.
The nursery value of these habitats is highly complex and presents spatial and temporal variations (Sheaves et al. 2015). Still, as most studies have only compared density and survival of juveniles in these shallow water habitats, their true nursery value is generally not clear. The successful movement of juveniles to adult habitats is usually not considered in most studies assessing nursery function, yet is given most important measure of nursery value (Beck et al. 2001, 2003, Dahlgren et al. 2006). Any habitat with a nursery function for fish and invertebrates imply being a particular important environment for juveniles, where their densities, growth and survival are enhanced and they successfully migrate into the adult habitats (Beck et al. 2001, Sheridan and Hays 2003) and by definition a true nursery habitat makes a greater than average contribution to adult populations on a per unit area basis (Beck et al. 2001).
Although there is a handful of studies on the nursery value of shallow water habitats and the factors governing juvenile production, in the tropics, these studies are still scarce, limiting the understanding of the nursery function of these habitats in this region (Adams et al. 2006), particularly the juvenile migration to adult

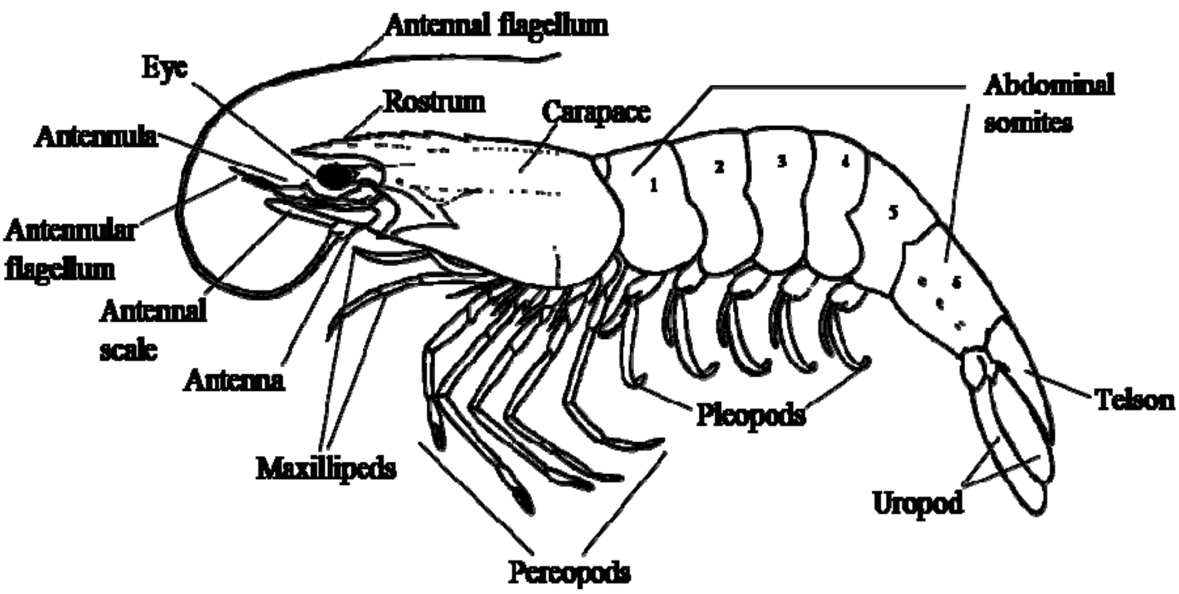
habitats. The complex interaction of biotic, abiotic and landscape factors generates large geographical variation of the nursery value (Beck et al. 2003, Sheaves et al. 2015). It is therefore critical to assess the nursery value of the available nursery habitats in specific areas for an efficient conservation of coastal ecosystems and management of fishery resources.

Penaeid Shrimp

Penaeid shrimps (Box 1) inhabit shallow and inshore habitats and are mainly distributed in the tropical and subtropical region with their distribution limited to around the latitudes 40° North and South by being essentially tropical stenotherms (only few species surviving below 15°C). Penaeids are benthonic and many burry themself in the sediment, but they don't occupy permanent burrows and are not territorial. Many species forage and are more active after sunset, and stay buried during the day (Dall et al. 1990). Sediment (detritus), benthic microalgae, epiphytic algae, seagrasses, plankton and polychaetes, are among the food items described on penaeid shrimp diet (Rodelli et al. 1984, Zieman et al. 1984; Stoner and Zimmerman 1988; Primavera 1996; Loneragan et al. 1997; Chong et al. 2001; Macia 2004a). From the more than 500 penaeid shrimp species identified, at least 22 species are described to occur in East Africa (Dall et al. 1990).
With a high number of commercially important species, this group of shrimps composes one of the most important fishery resources in the world with annual catches of about 2 million ton (FAO 2016). Presently 12 species of penaeids of commercial interest occur in Mozambican waters, and 8 in Maputo Bay, the second largest fishing ground in the country, where *Penaeus indicus* (H. Milne Edwards, 1837), *Metapenaeus monoceros* (Fabricius, 1798) and *M. stebbingi* (Nobili, 1904) compose presently a great percentage of the captures (IIP 2013).

Box 1. ***Penaeid shrimp characteristics***

Penaeid shrimps are decapods belonging to the suborder Dendrobranchiata, family Penaeidae. Penaeids are distinguished from other decapods by having their first three pairs of pereopods chelated, by having the pleuron of the second abdominal somite overlapping the anterior portion of the third somite, and by the females releasing the eggs into the water instead of caring the developing eggs in the abdomen pleopods (Dall et al. 1990, Fisher et al. 1990). Many species become sexually mature within six months from spawning and present well developed secondary sexual structures: petasma on the males (for spermatophore implantation) and thelycum on the females (for reception).



Penaeid shrimp morphology (Illustration from Fisher et al. 1990)

The large-sized genera *Penaeus* and *Metapenaeus*, with several species of commercial interest, have in general a life cycle where the adult shrimp spawn at the sea (offshore) and after some weeks of planktonic larval development stages (nauplius, protozoe, mysis), the postlarval shrimps settle in shallow inshore (e.g. mangroves and seagrass beds) and estuarine waters, which they use as nurseries and where they develop into benthic juveniles. After spending some months in their nursery areas, the sub-adult shrimps start their emigration offshore to complete their life cycle (Dall et al. 1990; Fig. 1).

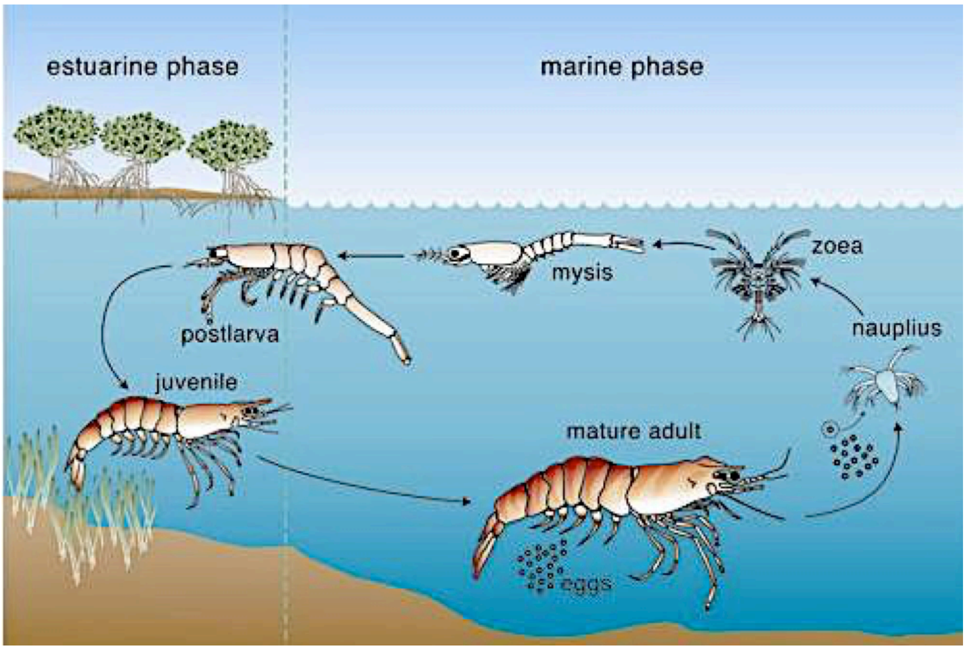
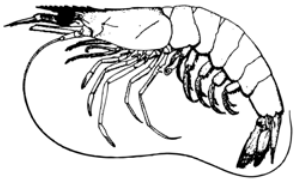
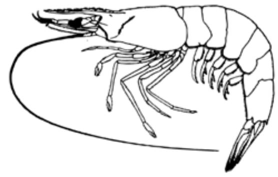
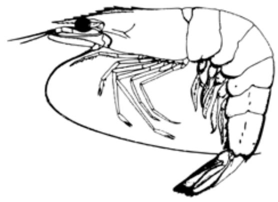


Fig. 1. General life cycle of penaeid shrimps. The estuarine phase indicates the nearhore habitats available in the tropical and subtropical region and the marine phase indicates the offshore adult habitats. (Illustration Source: https://csiropedia.csiro.au/prawn-fishing-industry-in-the-gulf-of-carpentaria/)

Juvenile penaeids are euryhaline and able to cope with the continuous or temporarily low salinities of their shallow water nursery areas, and are often concentrated in low saline areas such as estuaries (Dall et al. 1990). However, there are reports of high densities of juvenile penaeids also in fully marine shallow water habitats (e.g. Rönnbäck et al. 2002, de Freitas 2004), although fewer studies have been carried out in these potential nursery areas. Juveniles of many penaeid shrimp species are reported to have a preference for mangroves as nursery habitat, e.g. *Penaeus indicus* and *P. merguiensis,* (Rönnbäck et al. 2002, Vance et al. 1990), whereas other are more widespread occurring on mud flats, e.g. *Metapenaeus monoceros*; mud and sand-flats, e.g. *M. stebbingi,* and on vegetated habitats like seagrass beds, e.g. *P. semisulcatus* (de Freitas 1986; Rönnbäck et al. 2002, Macia 2004b; Table 1).

The daily cyclical unavailability of intertidal habitats, characteristics of macrotidal rage areas like southeastern African coast, imposes a well known tidal migration on the species using mangroves and adjacent intertidal areas at high tide as feeding ground and/or refuge, forcing them to find alternative habitats while these areas are unavailable. Although less is known in East African penaeid species, this tidal migration is described for some penaeids species (Dall et al. 1990) that stay within the mangrove forest until the water level and the amount of available habitat is very low (Vance et al.1996).

Table 1. *Habitat preference of penaeid shrimp present in Maputo Bay*. Habitats based on earlier studies in Maputo Bay (de Freitas 1986; Rönnbäck et al. 2002, Macia 2004b). Shrimp illustrations adapted from Fisher et al.1990).

Species	*Metapenaeus monoceros*	*Metapenaeus stebbingi*	*Penaeus indicus*
Common name	Speckled shrimp	Peregrine shrimp	Indian White Prawn
Illustration			
Habitat preference	Mud Flats (More widespread)	Mud and sand-flats	Muddy areas in mangroves

Several studies reported a positive relationship between the extension of the mangrove habitat and the penaeid shrimp catches (Vance et al. 1990, Manson et al. 2005; Meynecke et al. 2008, Sheaves et al. 2012), and because of this, mangrove habitats have been considered crucial nursery habitat for many penaeid shrimp species (e.g. Staples et al., 1985; Primavera, 1998, Rönnbäck et al. 2002). However, there is surprisingly little support for shrimp feeding in mangroves or from food sources provided by this habitat (Loneragan et al. 1997, Abrantes and Sheaves 2009, Kruitwagen et al. 2010), and recent studies suggest that the abundance of some penaeid shrimp species are more dependent on the presence of extensive areas of shallow, organically rich, muddy habitats than the presence of mangroves themselves (Lee, 2004, Sheaves et al. 2012). In Southeast Africa, little is known regarding the direct use of mangroves for shelter and food by penaeid shrimp species (but see Rönnbäck et al. 2002, Macia 2004a), or whether they mainly use the adjacent mud and sand flats.

The temporal and spatial variation of juvenile penaeid shrimp distribution in different shallow water habitats is relatively well described (e.g. Hughes 1966, Dall et al. 1990 and references therein, Vance et al. 1996, Primavera 1998, Rönbäck et al. 2002, Macia 2004b). However, factors controlling juvenile shrimp abundance and distribution within and between coastal areas are still poorly known (Lee 2004, Sheaves et al. 2012), particularly; very few studies have assessed how the availability of prey affects the distribution of shrimp (Dall et al.1990, Sheaves et al. 2012). Previous studies have found factors such like subtract types, turbidity, salinity, Chlorophyll-a, temperature, as well as landscape factors such as the position in the estuary or the extent of mangroves and intertidal area, to affect penaeid shrimp distribution, but the results have varied between studies, also within the same species (e.g. Haas et al. 2001, Macia 2004b, Sheaves et al. 2012, Mosha and Gallardo 2013, Munga et al. 2013, Jamizan and Chong 2017) suggesting complex relationships. For Southeast African penaeid species little is known regarding the most important factors for juvenile growth and survival, making it difficult to identify the most important nursery areas. Few have attempted to directly assess the movement of subadult shrimp from nurseries to adult habitats. Many key studies on penaeid shrimps movement and migration have been carried out in the Gulf of Mexico on *Penaeus aztecus* and *Penaeus duorarum* (Fry et al. 1999, Fry 2008, 2011). As far as we know, no similar study of penaeid shrimp movements to adult habitats has been performed in Southeast Africa, although fishery recruitment may have been inferred by shrimp size distribution (Brinca and Palha de Sousa 1984, Brito and Pena 2007).

Threats to coastal ecosystems and so to shrimp

The increasing human population, urbanization and industrialization are some of the causes to the escalated deterioration of coastal areas and shallow water systems, including estuaries, which are among the most used and threatened in the world (Barbier et al. 2011, Sheaves et al. 2016). Anthropogenic activities are degrading or depleting all dominant ecosystems in the tropics (which includes, mangroves, seagrass bed, among others habitats; Gladstone 2009). Both land based anthropogenic activities, like agricultural runoff and urban effluents discharge, and harbor and shipping activities, introduce to estuaries and coastal habitats, toxic compounds (Khan et al., 2014) including a wide range of pesticides and metals. These activities result in the degradation of these coastal ecosystems, affecting the functions and services they provide as maintaining viable fisheries, supplying nursery habitat and functioning as a filtering system (Worm et al. 2006). The toxic compounds, especially in shallow estuarine areas, can affect the health of aquatic organisms and since the estuarine environment already imposes stressful conditions to the organisms that inhabit it, this situation can alter their sensitivity to many pollutants (Monserrat et al. 2007). The toxicity of metals towards crustaceans is well documented (Marsden and Rainbow, 2004) and land based used pesticides (mainly organophosphates) for pest control in agriculture are considered to be a major threat to many non-target organisms, such as fish and crustaceans, due to their low target-species specificity and relatively high toxicity (Fulton and Key, 2001). Considering that the life cycle of most penaeid shrimp depends on estuaries and coastal habitats, their populations are threatened by several anthropogenic activities in these systems.

Aim of this thesis

Penaeid shrimps and their nursery areas are of major research interest since they are important fishery resources with very strong connections to nearshore habitats and estuaries, which are increasingly impacted by anthropogenic activities. Increased ecological understanding and baseline knowledge useful for the management of these resources and their habitat are in high demand, particularly for developing countries like Mozambique. To promote and facilitate this, the present thesis addresses both basic ecological questions regarding the environmental requirements for a "good" nursery area for penaeid shrimp, and also more applied question regarding how contaminants may affect the juvenile shrimp, and the contribution from different nursery areas to the shrimp fishery. This way, the overall aim was to increase our understanding on how biological and environmental elements determine shrimp distribution and abundance within and between nursery areas, and to identify important nursery areas in Maputo Bay. The specific aim of each paper was:

Paper I: to identify (1) main food sources and (2) feeding grounds within nursery areas for species of juvenile penaeid shrimps.

Paper II: (1) to investigate spatial and temporal pattern of three commercially important penaeid shrimp species (2) to identify environmental factors that influence juvenile shrimp distribution and abundance within nursery areas.

Paper III: (1) to investigate possible negative effects of pesticides and metals on juvenile penaeid shrimps in four nursery areas in Maputo bay.

Paper IV: (1) to assess the individual movement of juvenile penaeid shrimps from nursery habitats to adult habitats. (2) to investigate which nursery areas contribute with juvenile shrimp to the fishing grounds in Maputo Bay.

Methods

Study system

Located in southern Mozambique, Maputo Bay (26° 04' S, 32° 45' E) is a 90 km long, 32 km wide freshwater influenced inlet. The bay is well mixed in most parts with an average salinity and temperature of 31 and 26°C, respectively, in the central parts. Tides are semidiurnal with amplitudes of up to 3 m (Hoguane 1998), resulting in a southward transport of water during flood tides with maximum velocities of 0.8-1.0 m s^{-1} in the central part of the bay. Only 175 km^2 of the bay are deeper than 10 m and about 250 km^2 of its area becomes exposed on low spring tides (de Freitas 1986). Five main rivers discharge freshwater into the bay through three larger estuaries (Incomati, Espírito Santo, and Maputo Estuary), where Incomati and Maputo rivers present the main discharges into the bay (Fig. 2). The maximum discharge occurs in February during the wet season, when the horizontal salinity gradients from the estuaries into the bay are intensified, and a weak vertical stratification is observed in the bay. During the dry season in May-October the bay is well mixed and the circulation mainly driven by the tides (Canhanga and Dias 2014). The three estuaries are shallow (in general <10 m) with turbid water, variable salinity (5-40 PSU) and are fringed by mangrove forests in most parts (Kramer et al. 2003, Kuijper and Rjin 2011, Scarlet 2015). Extensive mangrove forests also line the southeastern part of Maputo Bay, from the mouth of Maputo River to the Bembe area, which is a shallow coastal embayment with little influence of fresh water (Fig. 2). Mangroves are also found in part of Inhaca Island that also have large seagrass meadows (de Boer 2002; Table 1). The common dominating mangrove species in the estuaries and along the coast are *Avicennia marina*, *Rhizophora mucronata*, *Bruguiera gymnorrhiza* and *Ceriops tagal* (Paula et al. 2014).

The estuaries present different levels of development activities. All are used for intensive agricultural practices, particularly the upstream reaches, being vulnerable to the input of fertilizers and pesticides. The Espírito Santo estuary is located next to Maputo City and is extensively developed and affected by industrial and harbour activities, particularly in the north margin of the estuary (Scarlet and Bandeira 2014). Previous studies in Mozambique have shown elevated levels of pesticides in estuarine environments with negative effect of pesticides reported for fish and shrimp (Sturve et al. 2016). Analyses of metals in the sediment from the same area also showed elevated levels (Scarlet 2015). However, little is still known regarding contamination from pesticides and metals in the other areas of the same region

(Maputo Bay) and how levels of contaminants reflect and influence shrimp production. Analyses of aerial photographs suggest that the distribution of mangroves has decreased with over 90% in this area, and overall with 37% in the whole estuary between 1958 and 1991 (de Boer 2002). In contrast, no losses of mangroves were indicated in the other estuaries and in the Bembe area in the same study. However, recent studies suggest that that a majority of the mangroves in the Incomati estuary, which is located just north of Maputo City, are degraded due to cutting (Macamo et al. 2015). It is not known, as well, if these anthropogenic impacts have also affected the nursery value and production of penaeid shrimp. Based on available data, the areal extent of mangroves in the three estuaries and in the Bembe area and southern Inhaca varies between 1354-2170 ha (Table 2).

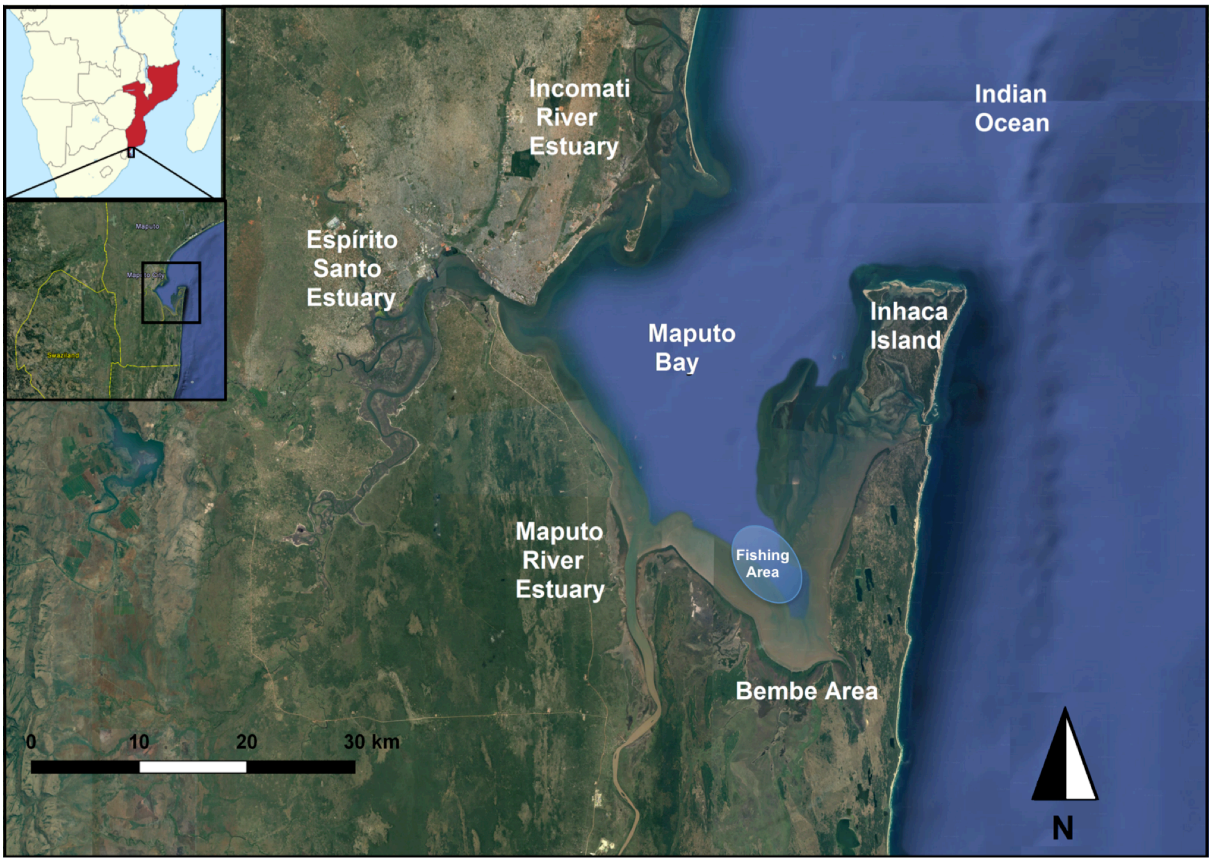


Fig 2. Map of the study area showing the estuarine and the marine coastal areas considered. (Images ©2017 Google)

Table 2. *Nursery areas characteristics and estimated shrimp abundance.* Average values from the wet and dry season of biotic, abiotic and landscape descriptive characteristics of the investigated nursery areas in the thesis. Mangrove area denotes the total areal extent of mangrove forest in each estuary and within the marine coastal areas Bembe and Saco Bay on Inhaca Island in 1991 (de Boer 2002). Sampling area denotes the estimated areal extent of the shallow, subtidal and intertidal sand and mudflats available for sampling during neap tides in each of the four nursery areas. The estimated mean density (no. 100 m^{-2}), and the estimated total abundance (no. 10^3) of the three shrimp species in each nursery area are based on sampling with trawls and estimates of the total sampling area (see **Paper IV** for details). The Saco Bay sampling area is based on the total area defined by de Boer and Longamane (1996) and the shrimp density is extracted from Macia (2004b).

			Nursery area		
	Saco	Incomati	Espírito Santo	Maputo	Bembe
Descriptive Factors					
Temperature (^{o}C)		23.7	23.5	23.8	22.3
Salinity (PSU)		10.9	31.8	20.0	34.5
Turbidity (NUT)		17.3	39.4	88.1	114.0
Chl-a Sediment (µg/g)		0.44	0.54	0.31	0.45
Silt and Clay (%)		3.4	69.4	56.7	38.3
T.P.Fish (ind/100m^2)		14.8	40.4	21.6	3.1
Distance Mg (m)		159	249	155	539
Mangrove area (ha)	209	2170	1354	1741	2009
Sampling area (ha)	66	895	2539	1080	4062
Shrimp Species					
Densities (n^o. 100 m^{-2})					
P. indicus	22	1.8	6.9	0.6	2.6
M. monoceros	14	4.6	8.4	3.1	2.7
M. stebbingi	11	6.7	11.7	0.9	7.6
Tot. Abundance (n^o. 10^3)					
P. indicus	145	162	1,753	64	1,038
M. monoceros	92	406	2,132	333	1,096
M. stebbingi	73	600	2,956	98	3,071

(Chl-a Sediment - Chlorophyll-a in the sediment; T.P.Fish –Total predatory fish; Desistance Mg – Distance to closest mangrove fringe; Tot. Abundance – Total Abundance)

Fishing activity is performed in the estuaries and in most parts of the bay. Artisanal and semi-industrial fishery for penaeid shrimp has been documented in Maputo Bay since the 1960's (Macia 1990) and it is today the second most important and profitable shrimp fishery in the country, landing hundreds of tons annually (IIP 2007) to a value of about 68 million $US per year (FAO 2007) that

supports near 3000 families of fishermen, merchants and naval carpenters (Michaque cited in Samucidine et al. 2015). Three species, *Penaeus indicus*, *Metapenaeus monoceros* and *Metapenaeus stebbingi* comprise together a great proportion of the captures from the shrimp fisheries in the bay and estuaries (IIP 2013). *Penaeus indicus* and *M. monoceros* attaining total lengths (TL) of about 236 mm and 195 mm, respectively, and *M. stebbingi* only about 139 mm TL (FAO 1980), are also the target species of the semi-industrial trawl fishery for shrimp, which is carried out outside of the estuaries, in particular in the south-eastern part of Maputo Bay (Fig. 2).
Juvenile and sub-adult shrimp (here defined as shrimp ≤24 mm carapace length; CL; approximately <60 mm TL) are concentrated within the estuaries and in shallow mangrove areas in Maputo Bay (Rönnbäck et al. 2002, Menomussanga 2003, Cassamo 2005). Most studies on juvenile stages of these species within the bay have been carried out at Inhaca Island. Studies on *M. monoceros* and *P. indicus* in Maputo Bay and Pungué River estuary in central Mozambique suggest that juvenile and subadult shrimp emigrate from nursery areas to the adult habitats and fishing grounds at around 13-25 mm CL (Brinca and Palha de Sousa 1984, Brito and Pena 2007). Although the estuaries in Maputo Bay are considered nursery areas by national authorities, less is known regarding the abundance of juvenile shrimp in these nurseries, or regarding movements from nursery areas to adults' habitats, and there is no information on which nurseries supports the important offshore fishery populations. Overall, there is a lack of understanding regarding factors that can control the juvenile abundance of these species, and determine what constitute suitable nursery areas.

Methodology applied

This thesis is based on an intense fieldwork effort using standard sample collection and measurement methods in marine sciences. I used a consistent shrimp collection method throughout the studies within this thesis based on trawling (**Paper I** to **IV**, as used and tested by Macia 2004b), and small seine net gears (**Paper I**). **Paper I** is based on biological samples collected over adjacent intertidal and subtidal habitats within two costal shallow water areas, Saco and Sangala bays on Inhaca Island (to collect shrimp and potential food sources for stable isotope analyses). In **papers II**, **III** and **IV**, I used the same biological samples and environmental factors collected and measured in two months representing the Mozambican wet (March) and dry (July) seasons, in the three main estuaries in Maputo Bay (Incomati, Espírito Santo and Maputo estuaries) and the mangrove fringed coastal areas in the southern part of the bay, Bembe area (Fig. 2). For **Paper II** and **IV**, a random sampling design was used to make possible the estimate of juvenile shrimp densities in the studied areas. The neap tide condition in which the sampling events took place ensured the majority of juveniles with potential preference for the mangrove habitat would be available for sampling. To assess how the distribution of juvenile shrimp in shallow habitats varies in relation to physical and biological variables, sampling of potential shrimp predators and food sources, the estimate of distance to mangrove habitats and other biological and physical variables were carried out in the same four nursery areas, coincident with the shrimp sampling (Fig. 2; **Paper II**). For **Paper IV**, juvenile shrimp from the adult fishing ground were acquired from the captures of the semi-industrial fishery.

To test for differences and assess correlations between variables in each particular paper of this thesis, I have used general statistical approaches: analyses of variance (ANOVA) and multiple regression analysis.

Stable Isotope Analysis

Along the thesis I have used carbon and nitrogen stable isotope analytic methods to identify food items and feeding habitats for juvenile shrimp (**Paper I**) and to detect juvenile shrimp movements from nursery areas to the dominant fishing ground in the south-eastern part of Maputo Bay to infer on nursery area contribution to the fishery (**Paper IV**). Stable isotopes (Box 2) are incorporated in animal tissues through their diet, reflecting the assimilation of organic matter rather than only what is ingested. As the diet is usually habitat specific, movement between isotopic distinct habitats will be reflected in the animal tissue within a certain time frame. The incorporation of dietary stable isotope signature into animal tissue makes it possible to reconstruct their diet, define the food web structure and trophic level, identify the habitat used as feeding ground, and tracking of movements between isotopically distinct food webs (Fry et al. 2003, McKechnie 2004, Herzka 2005).

Movement of juveniles from nursery areas to adult habitats is difficult to measure, in particular in crustaceans where small sizes, rapid growth rates that involves multiple moults, very high abundances and high mortality rates complicate the use of external tagging techniques. Stable isotope analysis can be used to track juvenile movements from nursery grounds into adult habitats (Gillanders et al. 2003, Sheaves et al. 2015). Most movement studies in the marine environment based on stable isotopes have focused on fish species (Herzka 2002, Lugendo et al. 2006, Vinagre et al. 2011), but fewer have focussed on shrimp migration and none have been carried out in Southeast Africa.

BOX 2. ***Stable Isotope Analysis: theory and terminology***

Isotopes are atoms of the same element that have a different number of neutrons in their nucleus, therefore present a different mass (number mass = number of protons + number of neutrons). All elements occur as different isotopes. The stable isotopes, unlike radioactive isotopes, do not decay with time (Fry 2006).

The most used stable isotopes in ecological studies are for example: ^{13}C:^{12}C (carbon) and ^{15}N:^{14}N (nitrogen) where ^{13}C and ^{15}N are the heavy isotopes and ^{12}C and ^{14}N the light. The isotope ratio is determined by a mass spectrometer that measures the ratio between the heavy and the light isotopes in a given sample and compares it against universal standards, PeeDee Belemnite (PDB) for carbon and atmospheric nitrogen for nitrogen. The values are reported in delta (***δ***) units as parts per thousand (‰) and calculated according to the following equation:

$$\delta R = \left[(X_{sample} / X_{standard}) - 1\right] \times 1000 \quad [‰]$$

R is the isotopic ratio in delta units related to the standard; *X* is the absolute isotope ratio of the sample or standard. The isotopic composition is expressed in relation the heavy isotope, where an increase or decrease in δR reflects respectively an increase or decrease in the relative proportion of the heavy isotope (Fry 2006).

Natural/biological processes affect the relative abundance of stable isotopes. If the isotopic ratio of a reaction products differs from the isotopic ratio of the substrate of that reaction, than is said that a fractionation has occurred. Fractionation generates unequal portioning of the isotopes between the substrate and the products formed by a reaction. This way, fractionation is the base for natural variation in biological materials; making it possible to use this tool to determine trophic interactions (Fry 2006). E.g. the food item and the animal isotopic ratio differ as result of the fractionation process along the trophic chain due to biochemical reactions, resulting in varying degree of trophic enrichment.

Based on the premise that shrimp stable isotope ratios would reflect those of their diet, with an average of 1‰ carbon enrichment and 3‰ of nitrogen enrichment (Abrantes and Sheaves 2009), the potential food sources to peaneid shrimps were analyzed and the proportion of the contributing sources for their diet was calculated by using a stable isotopic mixing model (**Paper I**). In **Paper IV**, to assess shrimp movement from the nursery areas to the fishing ground, reflecting the contribution of each nursery with juvenile shrimp to the fishery, I used a more recent application of the stable isotope method, the determination of the isotopic niche overlap. Once the isotopic niche represents what shrimp would be assimilating from its diet on their specific nursery, their isotopic niche approximates the trophic niche in each area (Bearhop et al. 2004, Newsome et al. 2007). By comparing the overlap of the isotopic niche area of shrimp from the nurseries and the fishing area, it was possible to infer on the origin of the shrimp present on the adult fishing area by calculating the standard ellipse areas (SEA; expressed as ‰^{2}) and their overlap (expressed as ‰^{2}).

Eco-toxicological Analysis

Eco-toxicological methods were used in **Paper III** to analyse the effect of pesticides and metals on juvenile penaeid shrimp in nursery areas. There, shrimp and water samples were collected from the three estuaries and the Bembe area and analyzed for metals and pesticides using standardized methods. The two pesticide biomarkers Acetyl cholinesterase (AChE) and Butyryl cholinesterase (BChE) were analysed in hepatopancreas, gill and muscle tissues from collected shrimp. In addition, Glutathione S-transferase activity was analysed as biomarker for compounds generally found in harbour areas.

Factors affecting shrimp distribution and nursery area value

In this thesis I used a combination of stable isotope, contaminants assessments techniques and extensive fieldwork studies to assess the factors affecting penaeid shrimp distribution in their nursery areas and the potential value of these nurseries. The studies showed that the nursery areas considered in Maputo Bay were clearly different regarding their salinity, sediment composition, and predator abundance, to mention some of the factors analyzed (Table 2), and the results suggest that different factors were affecting the distribution of shrimp in each nursery area. A complex interactions of abiotic, biotic and landscape factors seemed to be driving juvenile penaeid shrimp distribution, turning it into a difficult task to define what constitutes a good nursery area for *Penaeus indicus*, *Metapenaeus monoceros* and *Metapenaeus stebbingi* in general terms. In Maputo Bay the results suggest that these species can use many different coastal environments as nursery areas, including both estuarine and marine areas from which they successfully migrate to the adult habitat.

Below, I discuss the most important variables identified in the thesis work to affect shrimp abundance and the value of the nursery areas considered.

Salinity

Penaeid shrimp are well adapted to a wide range of salinities, with their juvenile phase coping very well with their nursery areas variable salinity levels, often very low in estuarine nurseries (Dall et al 1990). In Maputo Bay, salinity seems to influence very little of the shrimp densities both within and between nursery areas. The highest densities of shrimp were reported in nursery areas with the highest salinities in both estuarine, Espírito Santo estuary, and marine coastal nursery areas, Bembe (**Paper II**) and Saco Bay, Inhaca Island (Macia 2004b, 2004c). Yet, the overall shrimp abundance in Maputo Bay did not correlate with salinity. In **Paper II**, Incomati estuary presented the lowest salinity of all assessed estuaries (Table 2), and it was there where consistently smaller average size of all three species were found, compared to the other nursery areas, and the few adult *P. indicus* collected only found at higher salinity reaches at the mouth of the estuary. This results provide some support to the concept that smaller juvenile shrimp is better at coping with very low salinity conditions (Dall et al. 1990). Although *M. monoceros* density was inversely related to salinity in this same estuary and was present in higher abundances in its upper reaches, early studies have found the opposite distribution of juvenile shrimp where higher densities of all species were found at the mouth of the estuary (Menomussanga 2003). The shrimp density in

Maputo River estuary followed a similar distribution with higher densities of juvenile shrimp at the mouth of the estuary. However, the results of **Paper II** suggest that the distribution of shrimp in this estuary was not driven by salinity, but by the concentration of Chlorophyll-a in the sediment, and the extent of the mud flats.

Sediment composition

Different juvenile penaeids shrimp species have been described to show different substrate type preference (de Freitas 1986; Rönnbäck et al. 2002, Macia 2004b), usually associated to their ability to burrow (Dall et al. 1990). In **Paper II** the results only showed limited support for this habitat preference among species both within and between nursery areas, as all species were found in high densities in both very muddy and sandy nursery areas (Table 2).

In general, the sediment composition was weakly correlated with the density of shrimp within the three estuaries. However, in the coastal nursery area Bembe, *P. indicus* and *M. monoceros* densities correlated positively with the percentage of fine sediment particles, but *M. stebbingi* showed a negative correlation, consistent with earlier studies regarding species subtract preferences (Huges 1966, de Freitas 1986 Macia 2004b). In Bembe, species-specific distribution was clearly observed, where *M. stebbingi* preferred the larger grain size sediment sorted by higher wave or current condition on the eastern shore, while *P. indicus* and *M. monocero* preferred the fine sediment and less hydrodynamic west coast. However, *P. indicus* and *M. monoceros* showed relatively high densities in Incomati estuary where the sediment had an even lower silt and clay content than on the sandy eastern shore of Bembe (Table 2), suggesting that other factors or combination of factors than the sediment composition per se likely explain the low densities of these species in the sandy area. A possible complementary explanation for the species-specific distribution in Bembe is that these species have difference preference regarding the hydrodynamic environment, rather than the sediment composition. Thus, *P. indicus* and *M. monoceros* may have avoided the higher wave or current condition on the eastern shore, whereas *M. stebbingi* may have preferred these conditions, which would be consistent with observations of *M. stebbingi* often occurring in the swash zone on sandy beaches (de Freitas 1986).

Feeding habitats, sources and bottom-up effects on shrimp densities

The results in **Paper I** suggest that sand and mud flats, and particularly seagrass constitute important feeding habitats for the juvenile penaeid shrimp in this study, whereas evidence of feeding within the mangrove habitat was only found in one location for *P. indicus*, a species highly connected to mangroves (de Freitas 1986, Rönnbäck et al. 2002). These results are consistent with earlier studies showing that juvenile shrimp don't feed directly on sources from the mangrove habitat (Primavera 1996, Loneragan et al. 1997; Macia 2004b). Other taxa like polychaetes and fish have also been report to have low or no contribution at all from mangrove sources on their diets (Connolly et al. 2005, Lugendo et al. 2006). Based on the low contribution of the mangrove habitat with food sources and feeding habitat, it is believed that the shrimp presence within the mangrove habitat may be related to the protection against predators, this habitat may provide through the complex structure of the vegetation, such as the roots system (Dall et al. 1990; Primavera 1996; Macia et al. 2003). In **Paper I,** the identification of feeding areas was based on the origin of the shrimp's probable food sources in relation to actual occurrence of shrimp. The results suggested a movement of the shrimp between the habitats where they feed and the habitats where they were caught, which may result from the imposed tidal migration due to the semi-diurnal tidal cycle in Inhaca Island. This tidal migration forces the shrimp to migrate from the mangrove to the nearest adjacent habitats for a long period. Confined to the shelter of seagrasses habitat, shrimp have the chance to forage there, which may explain the great importance of this habitat as a feeding area. One alternative explanation to the high contribution of sources from the seagrass habitat to shrimp diet could be the export of seagrass leaves and other material to the other habitats as shown by de Boer (2000). However, the lack of mangrove sources as food items to shrimp collected in the mangroves would then imply that the shrimp was selectively feeding only on seagrass material in the mangrove, which appears unlikely.

Plankton, polychaetes, mangrove leaves, seagrasses, epiphytic algae, benthic microalgae and sediment (detritus) have been previously described as possible food sources to penaeid shrimp (Rodelli et al. 1984, Zieman et al. 1984; Stoner and Zimmerman 1988; Primavera 1996; Loneragan et al. 1997; Chong et al. 2001; Macia 2004a). In Inhaca Island, similar food items were identified as food source for the studied juvenile penaeid shrimp, where their diet seemed to be composed mainly by seston (proxy for plankton), sediment (detritus and other unidentified sources associated to the sediment), polychaetes, seagrass and in lesser extent and only for *P. indicus*, by benthic microalgae (Fig. 3). Seagrasses are not generally referred as direct food sources for penaeid shrimp, but some studies have described Them as important for the diet for *Penaeus esculentus* (Wassenberg 1990, O'Brien 1994) and *P. semisulcatus* and *Metapenaeus spp.* (Loneragan et al. 1997) in Australia, where seagrasses seeds and starch bodies are reported to be present on shrimp foreguts.

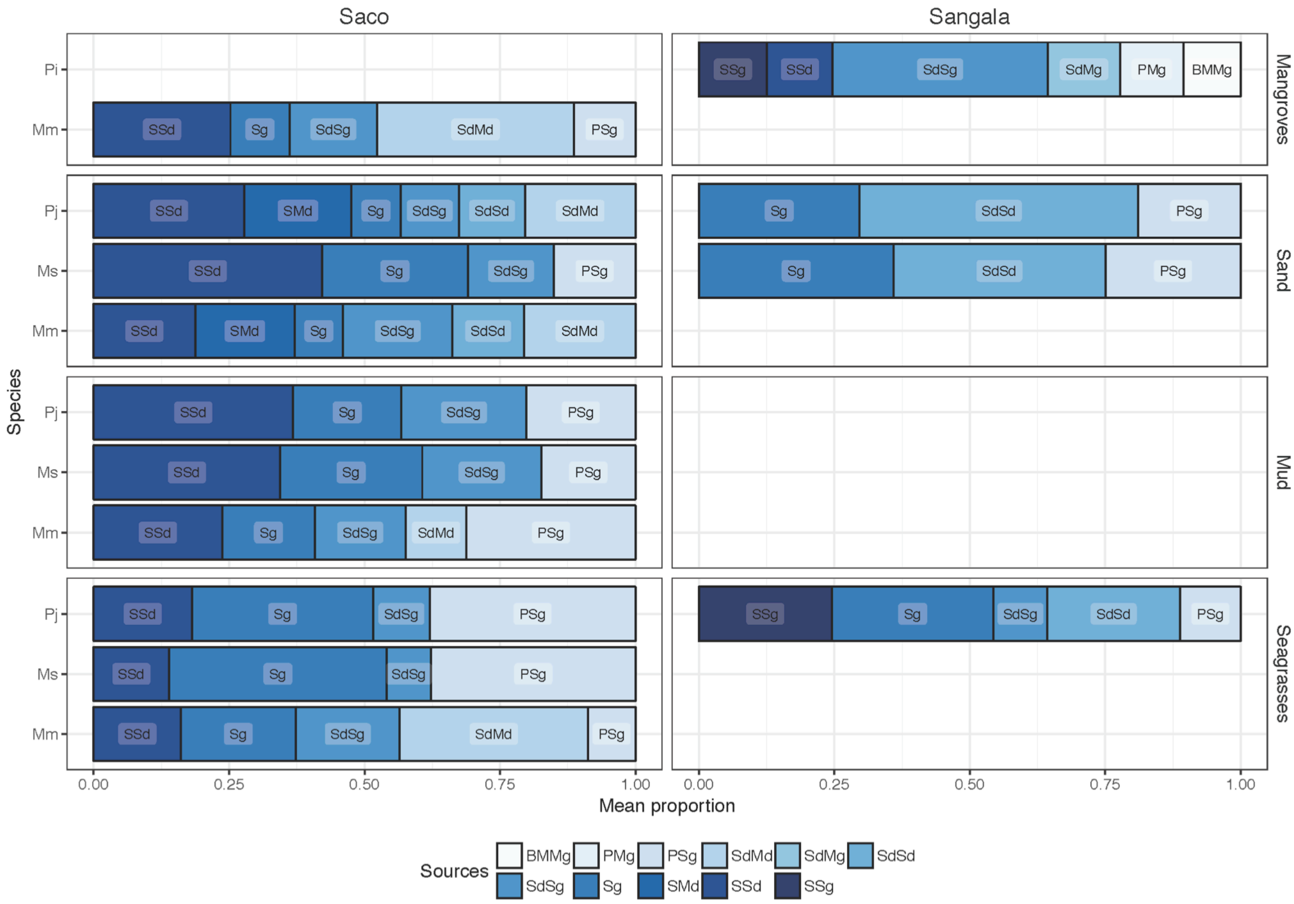


Fig. 3. Mean proportion of food sources contribution to the diets of *Metapenaeus monoceros* (Mm), *Penaeus japonicus* (Pj), *Metapenaeus stebbingi* (Ms) and *Penaeus indicus* (Pi) at Saco and Sangala bays, estimated by Stable Isotope Mixing Models in R ('simmr'). Proportion distribution and standard deviations present in Table A4 and Table A5 in the Appendices (**Paper I**). (Sources: BMMg – benthic microalgae in mangrove habitat SSd – seston in sand habitat; SMd - seston in mud habitat; SSg - seston in seagrass habitat; PMg – polychaetes in mangrove; PSg – polychaetes in seagrass; SdMg - sediment in mangrove; SdMd - sediment in mud; SdSd - sediment in sand; SdSg - sediment in seagrass; Sg - seagrass).

In Maputo Bay estuaries and Bembe area, food sources associated to the sediment (detritus, benthic microalgae and other unidentified sources associated to the sediment) and polychaetes seem to be the most important food sources for juvenile penaeids, and in lesser extent seston (Fig. 4). However the contribution and importance of the food sources varied among estuaries, possible associated with the composition of the benthic community and productivity in each estuary. Similarly to Inhaca Island, sources associated to the sediment (detritus and benthic microalgae) were important in Maputo River estuary and Bembe, and polychaetes were important in Espírito Santo estuary. At the same time, sources dominance was less clear in the shrimp diet in Incomati estuary (Fig. 4). The results in **Paper II** showed a positive correlation between shrimp densities and the levels of Chlorophyll-a in the sediment (primarily representing the presence of benthic microalgae; Moreno and Niell 2004) for all shrimp species in Maputo River and for *M. monoceros* and *M. stebbingi* in Bembe. These results together with importance of food sources associated to the sediment in these nurseries (Fig. 4), give support a "bottom-up" control of shrimp densities in particular in Maputo River estuary. This bottom-up effect is consistent with the overall lower levels of Chlorophyll-a in Maputo River (29-43% lower compared to the other nursery area) and its lower density of shrimp, which may explain the stronger correlation with benthic microalgae in the area, and possibly the overall lower density of shrimp in this estuary.

Turbidity and top-down effects

Many penaeid shrimp species have been described to occur in higher numbers in turbid environments (Macia 2004b, Johnston et al. 2007, Munga et al. 2013). Turbidity affects light penetration, which is a factor that penaeids respond very clearly to and to which their burrowing behaviour and ability is also related (Dall et al. 1990), and field and experimental studies suggest that turbid environments confer protection against predators to some penaeid shrimp species (Macia et al. 2003, Sheaves et al. 2012). However, there is some uncertainty regarding the direct effect of turbidity on the distribution of shrimp as turbidity may interact with factors such as substrate type (connected to burrowing ability) and predatory fish assemblages (Minello et al. 1987, Macia et al. 2003). In **Paper II,** the effect of turbidity on shrimp density was assessed both within and between four nursery areas, but didn't explain much of the variation in shrimp density between nursery areas, given that shrimp showed high and low densities in both low and high turbidity nurseries, indicating that turbidity may interact with other factors. However, in one of the estuaries, Espírito Santo, there was a strong positive correlation between the densities of all shrimp species and turbidity, which was possible related to the estimated higher densities of predatory fish in this estuary (Table 2). If so, the high density of fish could have had a top-down effect on shrimp distribution causing higher shrimp mortality in less turbid areas of the estuary, or result in shrimp behavioural response to fish presence by moving to turbid areas for protection. However, we did not find any support of a direct effect of predation on the distribution of shrimp, since shrimp densities of all species showed a positive correlation with shrimp predator densities in Espírito Santo estuary, and no correlation at all in the other nursery areas. The lack of support of a top-down effect in Espírito Santo estuary should be interpreted with caution considering the fish sampling limitations presented in **Paper II**. Nevertheless, the

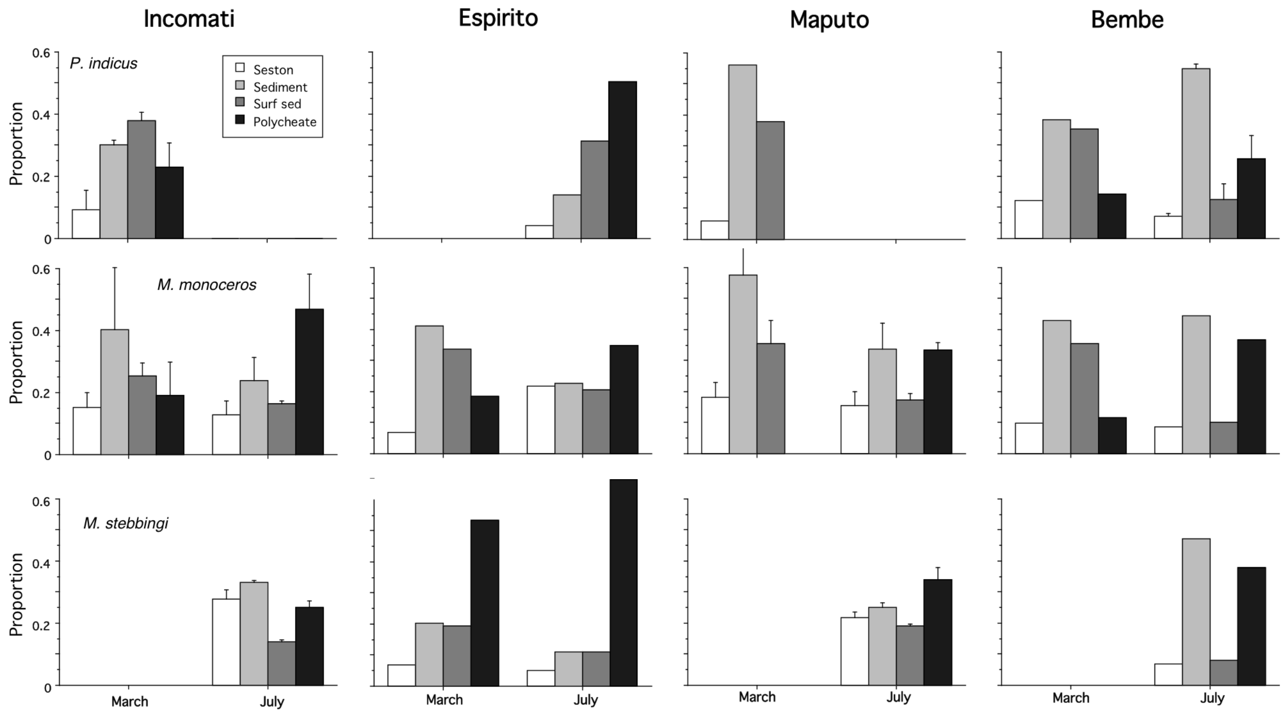


Fig. 4. Mean proportion of food sources contribution to the diets of *Penaeus indicus*, *Metapenaeus monoceros* and *Metapenaeus stebbingi* at Incomati, Maputo and Espírito Santo estuaries and the coastal area, Bembe, in Maputo Bay, in the wet (March) and dry (July) seasons estimated by Stable Isotope Mixing Models in R (de Abreu *unpublished data*). Food sources (seston, sediment, surface sediment and polychaetes) and the shrimp isotopic data in each nursery is the same as **Paper IV**.

high diversity and abundance of predator fish species in Maputo Bay indicates that predation is an important source of mortality for juvenile penaeid shrimp, similar to what has been found in Australian estuaries (Baker and Sheaves 2006, 2009).

Importance of mangroves, mud and sand flats as nursery habitats

Although, many studies indicated a direct positive relationship between penaeid shrimp captures and mangrove extent (Manson et al. 2005, Meynecke et al. 2008), the importance of this habitat as a nursery area for shrimp still debatable (Nagelkarken et al. 2008) and its nursery value is not the same in all mangrove occurring areas (Lee et al. 2014). Recent studies suggest that many penaeid shrimp species may not use the mangroves directly for food or shelter but instead use the shallow, organically rich, muddy habitats that are often found adjacent to mangroves (Lee 2004, Sheaves et al. 2012).

In the present studies, I found only limited evidence that the penaeid shrimp in Maputo Bay use the mangrove habitat directly for food or shelter, and no positive effect of mangroves on densities shrimp in the studied nursery areas. As indicated in **Paper I**, mangroves provided very limited nutritional support and composed a limited feeding habitat to most of the studied penaeid shrimp. *Penaeus indicus* may constitute a possible exception, as it was found to feed in one of the assessed mangrove habitats, in contrast to the other shrimp species (**Paper I**). These results are consistent with earlier studies on Inhaca Island showing that *P. indicus* enters the mangrove habitat in high numbers at high tide, whereas other penaeid species did not (Rönnbäck et al. 2002). Thus, the ecological function of mangroves for most penaeid shrimp seems to be other than providing food and shelter. This lack of direct effect of the mangrove habitat is also supported by the results in **Paper II** that showed a positive relation or the absence of one, between the density of penaeid shrimp and the distance to the closest mangrove fringe between and within nursery areas. An inverse relationship could be expected if the shrimp had used the mangrove habitat during high tide. Instead, we often found very high densities of shrimp next to extensive mud- and sandflats at the mouth of the estuaries, for example at the mouth of Espírito Santo estuary, which is not fringed by mangroves and the nearest mangrove patch is 1.7 km away. Support is also provided by the results in **Paper IV**, where the highest estimated abundance of shrimp from the assessed nursery areas, were presented in Espírito Santo estuary (over 50% of the total abundance of juvenile shrimp in the assessed nurseries); an estuary with the lowest mangrove area (Table 2), and which undertook extensive losses of mangroves in the past years due to a variety of anthropogenic pressures (de Boer 2002).

Lee (2004) indicates that rather than the mangrove area, the extension of intertidal areas in tropical nearshore systems has a greater importance to penaeid shrimp abundance. In support of this suggestion, **Paper I** showed that penaeid shrimp acquire most of their nutrition from a mosaic of shallow water habitats contiguous to the mangroves. In **Paper II,** higher densities of shrimp species were found at the mouth of the three estuaries, which also contained the largest areas of shallow water mud and sand flat, although in Incomati this pattern was only found for *M. stebbingi*. In Maputo River estuary, this pattern resulted in a positive correlation with the distance to the mangrove fringe and juvenile shrimp densities. Since the water depth was very similar in all sampling occasions in the study, and Maputo

River estuary had continuous mangroves along its shores, the distance to mangroves is also a proxy for the extent of shallow water mud and sand flats in the nursery area, which thus correlated positively with shrimp densities. The importance of shallow water mud and sand flats was also indicated when comparing shrimp densities between nursery areas, where the greatest total abundance of shrimp were present in the estuary with the largest extent of the mudflats in its inner reaches (Espírito Santo estuary) and in the coastal area (Bembe) with large mud and sand flats (**Paper II** and **IV**, Table 2). However, it's important to emphasize that mangroves are still important for penaeid shrimp even for species that do not utilize the habitat directly, by their contribution to the development and maintenance of the muddy, shallow water habitats used by the penaeids.

Anthropogenic impact on shrimp - Pesticides and metals

Shallow coastal nursery areas are impacted by several anthropogenic activities (Barbier et al. 2011). However, there is limited information on how pollutants affect juvenile shrimp in tropical estuaries. **Paper III** addressed possible negative effects of pesticides and metals on *Penaeus indicus* and *Metapenaeus monoceros* in Maputo Bay during the wet and dry seasons. Metal analyses of abdominal muscle tissue of shrimp collected from all nursery areas in the wet season, when the effect of contaminants was expected to be highest, suggested no elevated level of metals in any of the species and assessed nursery areas in the bay. This indicates that metal pollution does not constitute a problem to the juvenile shrimp in Maputo Bay. Yet, previous studies have shown elevated metal levels in the sediment in Espírito Santo estuary (Scarlet 2015), suggesting that further research should be undertaken regarding this matter.

During the wet season, three of the studied nursery areas in Maputo Bay presented herbicide levels over environment accepted thresholds (**Paper III**). Although herbicides may have no direct effect on penaeid shrimps, these chemicals may affect the base of the food web in these nurseries, with an indirect effect on shrimp via impacting microphytobenthic production. Sediment associated non-identified sources and benthic microalgae are important food sources for shrimp in Maputo Bay (**Paper I**, Fig. 3 and 4), and, in **Paper II**, shrimp densities showed a positive correlation with microalgae in the sediment in several nursery areas, indicating their dependence on microalgae as a food source.

Very high levels of the organophosphate Malathion (insecticide) were measured in the northern part of Espírito Santo estuary (by Infulene River). There, significant lower AChE activity (which is a bioindicator for organophosphate effect) was detected in *P. indicus*, suggesting a negative effect of pesticides in the shrimp. Curiously, densities of juvenile shrimp were very low in this area of the estuary in the wet season, >25x lower than in Matola River area, in a less developed southern part of the estuary, where no inhibition in AChE activity was indicated in the shrimp (Fig. 5). Even if other reasons than pollutants could explain the low density of shrimp in this highly exploited and heavily populated northern part of the estuary, these results still suggest a need for further studies evaluating the impact of pesticides on the benthic community. The indicated negative effect of contaminants on juvenile shrimp in this estuary is important considering that Espírito Santo showed the highest abundance of shrimp of all assessed nursery areas in Maputo Bay, and constituted an important source of juveniles to the fishing ground for both *P. indicus* and *M. monoceros* (**Paper IV)**. This indicates a need to keep a watchful eye on the levels of contaminants in this estuary to maintain its high shrimp production. However, with the exception of the local effect in Espírito Santo, pesticide and heavy metal did not seem to constitute a large problem for juvenile shrimp in Maputo Bay today.

Migration from nursery area to adult habitat and contribution to fisheries

The successful movement of juveniles from a nursery area to shrimp adult habitat is possibly the most important aspect when evaluating the nursery value of a habitat or area (Beck et al. 2001, 2003, Dahlgren et al. 2006), and this movement has never been directly assessed for penaeid shrimp in Southeast Africa. In **Paper IV**, the analysis of the isotopic niche of penaeid shrimp within nursery areas and the adult habitat suggested a significant movement of juvenile *P. indicus, M. monoceros,* and *M. stebbingi* from three of the four assessed nursery areas to the adult habitat and fishing ground in the southern part of Maputo Bay. The coastal area (Bembe) and, to a lesser extent, Maputo River estuary, both located close to the adult ground considered in the study, contributed with juveniles of all three species to the commercial fishery. Espírito Santo estuary contributed with juveniles for *M. monoceros* and *P. indicus,* but not for *M. stebbingi*, despite its high abundance, suggesting a different survival and/or migration pattern from the estuary to adult habitats, in comparison with the other species. On the other end, the results don't indicate any movement of juvenile shrimp from Incomati River estuary in the northern part of the bay towards the studied fishing area, possibly associated to unfavorable hydrology for juvenile migration or by the presence of closer preferable adult grounds (**Paper IV)**.

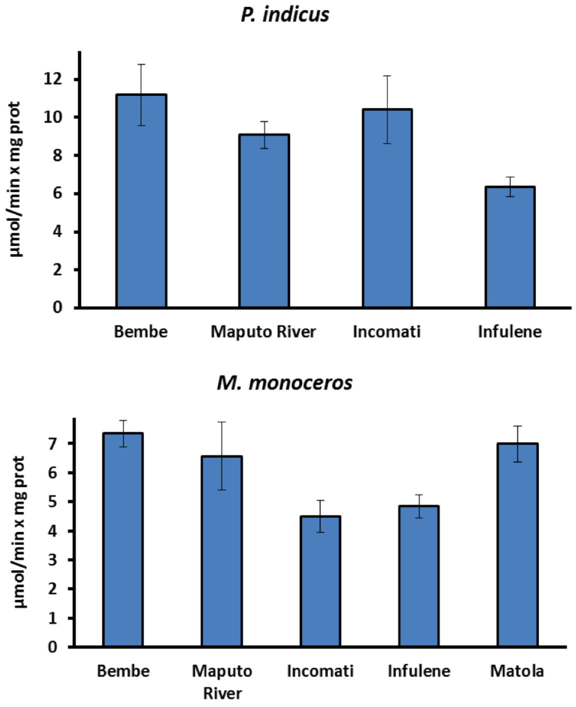


Fig. 5. Acetylcholine esterase activity (µmol/min x mg protein) in hepatopancreas from *Penaeus indicus* and *Metapenaeus monoceros* sampled at four different estuaries in Maputo bay. The sites Infulene and Matola are within the Espírito Santo estuary. Shrimps were sampled in March. Charts show mean ± SE.

Taken together with the estimated shrimp abundance, the results suggest that Bembe and Espírito Santo estuary constitute the most important nursery areas for the fishery for *P. indicus* and *M. monoceros* in southern Maputo Bay, with a minor contribution from Maputo River estuary. Bembe appears to be the main nursery area for the fishery for *M. stebbingi*. Despite the fact that Incomati estuary didn't contribute with juvenile shrimp to the fishing ground in the southern part of Maputo Bay in the present study period, the relatively high abundance of juvenile shrimp in the estuary suggests that this nursery area may be important for the shrimp fishery in other areas, e.g. in the northern part of the bay, which was not assessed in this study.

In summary, the results suggest that the distribution of juvenile penaeid shrimp is driven by complex interactions of abiotic, biotic and landscape factors that may differ between apparently similar nursery areas, making it challenging to identify important nursery areas and their values. In Maputo Bay, juvenile shrimp were found to use many different types of coastal environments as nursery areas, including both estuarine and coastal marine areas, where the amount of benthic microalgae, turbidity and the extent of shallow water habitats appear to be the most important factors that explain variation in shrimp density within and between nursery areas, whereas the extent of mangroves and contamination in the nursery areas found to be less important. This culminated in the surprising results that the apparently most exploited and contaminated nursery area, Espírito Santo estuary, showed the overall the highest shrimp densities, and constituted one the most important nursery areas for the fishery. Taking all in consideration, productive mud- and sand flats, with or without fringing mangroves, appear to constitute key nursery areas for penaeid shrimp in the study area.

Implication for management and conservation of shrimp in Maputo Bay

For a long period of time worldwide fisheries managers overlooked the identification and conservation of the critical juvenile habitats (Beck et al. 2003), but for fishery resources conservation and management purposes, it is important to known whether habitats are suitable and important nursery. The results presented in this thesis, including the identification of the most important nurseries supporting the shrimp fishery in Maputo Bay, have direct management applications and can support a sustainable management of the penaeid shrimp fishery in the area.

The semi-industrial fishery catches of *M. monoceros* and *P. indicus* in Maputo Bay have been decreasing for the last 5 years, and the stocks are considered intensely exploited (Samucidine et al. 2015). To maintain a sustainable fishery of penaeid shrimp in Maputo Bay it is important not only to regulate the fishery, but also to protect important shallow water nursery areas, both in estuaries and along the coast of the bay. The results from this thesis demonstrate that juvenile shrimp can use different shallow water habitats as nurseries, including also sand and mudflats outside estuaries and without extensive mangroves along the shore line, e.g. along the eastern shore of Bembe, which constituted an important habitat for *M. stebbingi*. This type of areas may traditionally not have been view as nurseries for penaeid shrimp, but as shown in **Paper IV**, it constituted the most important nursery area for the fishery of this species in Maputo Bay during the study period.

The suggested lack of a direct relationship between penaeid shrimp and mangroves (**Paper I**, **II** and **IV**) must not be taken as an indication that mangroves are not important. Quite the reverse, mangroves provide important ecosystem functions, including stabilization of shorelines (Gedan et al. 2011), so the presence of mangroves is critical to the development and maintenance of the important muddy, shallow water habitats (Sheaves et al. 2012, Lee et al. 2014). The large losses of mangroves in Espírito Santo (>90% in the northern part; de Boer 2002) and the degradation of the mangrove in Incomati due to cutting (Macamo et al. 2015) suggest that there is an urgent need to improve management and reinforce the existing regulation concerning these coastal habitats. It is critical as well to protect the remaining shallow water habitats from destructive exploitation and disturbing activities, so that the nursery function of these nursery areas can be maintained, ensuring continuing recruitment to and profitability of the Maputo Bay shrimp fishery.

In **Paper I**, seagrass beds were identified as being a very important feeding habitat for penaeid shrimp species. This habitat should as well be protected, not only by their given relevance to shrimp, but also by their already small coverage area Maputo Bay (38.75 km^2) and the already existing threats to this habitat (anthropogenic, by trampling, motorboat activity, and excavation for invertebrate collection and natural sedimentation; Bandeira et al. 2014).

It is also important to reduce and stop fishing for shrimp in these shallow nursery areas, especially during the wet season given that juvenile densities are the highest during this period (**Paper II**). Presently, the regulation of the shrimp fishery in Maputo Bay prohibits fishing in the nursery areas (Samucidine et al. 2015). Yet, commercial fishing activity occurs regularly in these shallow areas as (de Abreu pers. obs.) indicating the regulation needs to be better enforced.

In **Paper III**, the found pesticide levels above the environmental threshold in Espírito Santo estuary, and the detected localized effect of organophosphates on *P. indicus*, are consistent with earlier studies (Sturve et al. 2016) and suggest that the shrimp, in the northern part of the estuary are negatively affected by pesticides. *Penaeus indicus* is the most captured species reported for the shrimp fishery in the Maputo Bay, and warning signs support the need of an improved regulation of pollutants and management of this highly productive nursery.

Concluding Remarks

The present thesis aimed to bring some light and increase the understanding on how biological and environmental elements determine shrimp distribution and abundance within and between nursery areas, and to identify important nursery areas in Maputo Bay. The results presented in my thesis indicate that complex interactions of biological and environmental factors drive juvenile penaeid shrimp distribution and different nurseries present distinct driving factors. Consequently the identification of these factors should be expanded to other potential nursery areas in the Bay to properly construct locally oriented management plans.

Here I identified Bembe estuary, Espírito Santo and Maputo River estuaries as important nursery areas for the dominant fishing ground of penaeid shrimp in Maputo Bay. This information should guide conservation and provide support for an ecosystem management approach to the fishery of penaeid shrimps in southern Mozambique. Nevertheless, the nursery value of areas not included in this thesis should be further investigated and their contribution to the fishery integrated in management actions. As an example, the high densities of shrimp at Inhaca Island (Macia 2004b), which were not included in the juvenile migration study within this thesis (**Paper IV**), indicate this area as an important nursery for shrimp. More studies are equally needed to assess the importance of the nursery areas to other potential adult habitats by expanding the studies to other less productive fishing grounds. Incomati estuary did not contribute to the fishery in southern part of Maputo Bay, but this nursery area may be important for the shrimp fishery in other areas of the Bay.

Financial Support

This thesis was only possible to materialize thanks to the financial support from Swedish International Development Cooperation Agency (Sida) through the bilateral program with Eduardo Mondlane University (Mozambique), to which I am very grateful.

I am forever grateful to the Western Indian Ocean Marine Sciences Association (WIOMSA) for the financial support of the stable isotope analysis in Paper IV.

Acknowledgements

Through a roller coaster of emotions, experiences and deep learning that were these last 5 years, there are now several people who are present in my collage of moments and memories that I will keep in my heart with all affection. To all of you I owe profound thanks.

First I would like to express all my gratitude to my supervisor, **Per-Olav Moksnes** who embraced this project, helped me polish it and make it shine. Your confidence, critical thinking and honest enthusiasm encouraged me to keep on going. I learned from you that in research we don't face problems, we only face challenges and they make things more fun. Oh man, we had fun with this one. It was an honor and an amazing experience to work side-by-side with you to put together this Maputo Bay shrimp puzzle. It was an amazing team effort. Thank you for believing in me, for all your support during the ups and downs and for your friendship. The Tropics are down there whenever you wish to go back and start our "ultra scientific project" on which penaeid species is the most tasteful.

Joachim Sturve, my awesome Portuguese speaking Swedish co-supervisor, thank you so much for giving me the opportunity to keep collaborating with you, for being available for the so needed brain storm long distance telephone calls in the early phases of this thesis and for your words of encouragement and "it will be fine's" that always made me believe I would be fine. Thank you for the dinners with your family. Those were precious moments. Looking after so you don't forget you Portuguese: Muito obrigado por tudo.

Adriano Macia, my co-supervisor in Mozambique, thank you very much for having accepted, once more, this task and for having fought for my chance to be here with this thesis and writing these words today. About 14 years ago you planted the shrimp and nursery areas "bug" on my brain by suggesting a super exciting undergraduate project on mangrove detritus as food sources for shrimp. Since then we have always worked together, forming a team that I have always been very proud to belong to. This thesis has now brought light to some of your and our long time questions, but I have no doubt that we will keep on going and pushing to complete the Maputo Bay shrimp puzzle. Thank you for your support and creating the conditions in our home institution so I could be in Sweden focusing on writing this thesis when I needed the most.

Thank you **Anna Godhe** for being my examiner and for your availability whenever I needed your help. **Kristina Sundbäck**, my former examiner, thanks so much for your

support, availability and kindness. Our meetings were always very comforting and reassuring.
Inger Wallentinus, there are no words to express my gratitude for what you have done for me along the years we have been sharing office. You are an inspiration, a true friend; you were my family away from home.
I thank **Dr. Almeida Guissamulo**, for all your effort ensuring the smooth progression of this project. A special thanks goes to "Dona" **Liliana**, "Dona" **Amélia**, Eng. **Benedito**, Sr. **Chissano** for taking care of all paperwork and fund release during all these years, ensuring the completion of my project. I want to express my gratitude to **Professors Aidate Mussagy** and **Sandra Sílva** for your friendship and support. **Eunice Ribeiro**, thank you for always being there for me, for your encouragement, for your contagious laugh and for letting me work at your office so I could use your A/C after long hours of laboratory work. **Dra**. **Perpétua Scarlet**, thank you for being my partner in many adventures abroad during great courses and conferences in amazing locations. To my colleagues, **Ivan Nerantzoulis** and **Mizeque Mafambisse**, thank you for all your support and encouragement. **Damboia Cossa**, thank you very much for taking care of my courses and for giving the needed support to our students when I was away. **Hugo Mabilana**, thank you agreeing in embarking in a collaboration with me. I'm sure we will keep collaborating in the future. I would like to thank all colleagues and personnel from the Department of Biological Sciences and from the Faculty of Sciences of Eduardo Mondlane University in Maputo that directly or indirectly contributed to the completion of this thesis.
A special thanks goes to my collaborators **Alvaro Vetina**, **Julia Matsombe**, **Kelvin da Conceição**, **Carlos Verão**, **Ana Gledys da Conceição**, **Mery Rodrigues** and **Sabina Manhique**. Through your drive and enthusiasm you turned our intense field and laboratory works in moments that I will treasure forever. I extend my thanks to **Sr. Jotamo Mazive** for your great driving skills and always ensuring a timely start of our samplings and to **Walter Pimentel** for being the greatest skipper I have ever worked with and for your easy going personality always up for new challenges. **Estação Nhaca**, é espetacular como sempre fizeste as capturas de camarão parecerem simples. *Kanimambo* por estares sempre pronto me para ajudar nas minhas aventuras em busca de camarão.
I extend my gratitude to **Mr. Carlos Silva** from the Mozambican fishing company Pescas do Sul, for allowing me and my collaborators on board of the fishing vessels and providing the semi-industrial shrimp specimens.
I thank **John Lanham** and **Ian Newton** for all their support during the stable isotope analysis at the Stable Light Isotope Unit from the Department of Archaeology from Cape Town University, South Africa. You are my heroes. **Alberta**, **Bruna**, **Micaela** and **Nick**, thank you for always finding room for me and for taking your time to show me your Cape Town during my visits along the years.
Dear, **Sussi**, **Maria**, **Lisa**, **Malin**, **Emma**, **Anders**, **Mikael** and **Justine**, it was always heartwarming to see your friendly smiles every time I was back at the "5th Floor"; it was a pleasure to meet you all. **Louise**, thank you for all the nice chats, for the great moments at Inhaca and for the awesome short "road trip" in Portland, I had a great time. **Christian**, it was a pleasure getting to know you, thank you for the awesome time in Portland (and no, you didn't manage to change my mind about beer) and then in Germany/France. **Josefin**, what a great time we had in Greenland and, of course, Germany/France. I'm still counting on seeing you someday down in Maputo. No snakes, no peas, I promise. **Fabian**, thank

you very, very, very much for your support, reassurance, mega hugs and for your true friendship. My dear **Jenny** thanks for all the great memories from our fantastic times in Greenland, Portland and Lisbon. Thank you for your friendship and support. **Gurpreet**, you are the ultimate writing partner and companion of the long days and nights in Botan. Thank you very much for being there when I needed, thank you for our long chats about "whatever", during dinnertime and thank you for your friendship. **Olga**, muito obrigado pela nossas conversas agradáveis e pela tua amizade (I know you can read that). **Christy**, thank you for being the best officemate one can have wile writhing a thesis. **Monica**, **Ylva**, and **Sven**, thank you so much for your support along all this time.

Annalisa, **Ida**, **Nurun**, **Andrei**, **Trirantra**, **Somnath**, **Thomas**, **Karine**, **Brigitte**, **Zizka**, **Ivana**, **Josué** and **Wiebke**, thank you all for the great times during this past few years, you are all fantastic. Agradeço imenso à **Graziele**, **Beatriz**, **Cíntia**, **Angela**, **Maria do Céo** e **Marcela**, por todo o apoio e carinho que essas maravilhosas amigas e cientistas me deram durante este doutoramento. **Victor** e **Ivan**, muito obrigado pela vossa linda amizade e pelos momentos maravilhosos que passamos nesta grande Gotemburgo. **Filipe**, there are no words to express my gratitude for the awesome hours of silent contemplation of the outside "world" from the big window of the lunch room on the 4th floor and for the spontaneous and impossible to contain laughing attacks in the most inappropriate times. Thank you for being the very good friend you are. F., obrigado por me teres mostrado Gotemburgo, obrigado pelas conversas sem fim e sem tema em particular, pelos conselhos e dicas que tornaram mais fácil o meu percurso. Ah, e viva o pastel de nata. **Camila**, oh como vou ter saudades tuas. A pessoa mais generosa que alguma vez conheci. Muito obrigada pela tua amizade e companheirismo ao longo destes anos. Divertimo-nos muito e também "sofremos" de mais, dinâmica normal de doutoramento. Porém, tudo foi sempre mais fácil porque sabia que estavas por perto.

I thank all my colleagues at Escuela Cubana de Danza "Yassballet" for the fantastic atmosphere during the classes. **Yassel**, your amazing energy and enthusiasm and your fantastic dance routines always gave me drive to keep working on my thesis. It was an honor to learn from you.

Agradeço à **Dra. Alexandra Rodrigues** por todo o apoio e por acreditar que isto seria possível. **Kânya**, obrigada por me acolheres em tua casa durante as minhas amostragens e aguentares com as minhas amostras de poliquetas no teu congelador. **Kátya**, our collaboration is a dream come true. Who wouldn't like to collaborate in a scientific paper with a childhood friend, with whom I used to go to school holding hands in the early hours of the morning? Thank you for your support and for brainstorming over Skype. **Ivana**, mais uma vez provamos que esta amizade não tem tempo nem distância. Como era no berço assim ficou. Cristalizou no tempo. Não há palavras que agradeçam todo o apoio que me deste e as certezas que tiveste antes mesmo que eu. Love you, sempre.

Leonor, nunca tiveste dúvidas e isso sempre foi uma grande motivação para mim. Obrigado pelo carinho, obrigado por tudo.

Como toda a compreensão, carinho e suporte, o **meu pai** e **aminha mãe** tornaram esta minha odisseia numa viagem mais suave. Muito obrigado por estrem sempre presentes e por acreditarem incondicionalmente em mim. Seria muito complicado sem o vosso apoio. **Hugo**, obrigado por me acompanhares sempre e disposto a ajudar com o necessário e constantemente a encontrar formas de me mostrar que eu iria conseguir. Deste-me força e vontade de ir mais além. Finalmente chegou a hora de voltar para casa.

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