UiT The Arctic University of Norway

Norwegian College of Fishery Science

The challenges of understanding the biogeography of commercially important crustacean species of the Southwestern Indian Ocean

— Separating what we know from what we think we know

Bernadine Everett

A dissertation for the degree of Philosophiae Doctor January 2020

Abstract

Demersal trawl fisheries play an important role in providing income and protein to the people of the countries in the Southwestern Indian Ocean (SWIO) where they operate. These fisheries are, however, very destructive to the habitats in which they operate and have an impact on the associated biodiversity. Three crustacean species, the knife prawn (*Haliporoides triarthrus*), African langoustine (*Metanephrops mozambicus*) and pink geryon crab (*Chaceon macphersoni*) are the most important to these soft sediment fisheries and their management is crucial to securing sustainable fisheries. These species occur across boundaries in the SWIO so understanding their biogeography is an important component of formulating effective management strategies. This understanding is, however, hampered through inadequate species identifications despite the occurrence of many research surveys and the retention of these species for trade. Species identities have been allocated based on outdated and/or inappropriate taxonomic and distribution information. Without the availability of voucher specimens from research surveys it is impossible to determine if these species were correctly identified. Despite these three species having important commercial value to the region, there is little known about their reproduction strategies. This combined with limited information on the availability of suitable habitats thwarts understanding their distribution in the region. Previous researchers have proposed the existence of a limited recruitment area for knife prawns that seed the remaining habitat in the region, but this theory has, to some extent, been refuted through genetic testing that discovered isolated subpopulations in the region. The African langoustine showed a similar distribution of subpopulations, which is not surprising given their short larval phases and subsequent settlement very close to where the eggs hatched. It could be that the pink prawns have similar larval phases or that there are other barriers to their dispersal. The reproductive biology of pink geryon crabs is also unknown and so far, no genetic research has been conducted on them. In order to maximise the sustainability of the demersal trawl fisheries that target these three species, it is imperative that taxonomic research be undertaken to determine conclusive distributions of these populations to inform their transboundary management in the region. There is a need to train researchers from the SWIO in the science of taxonomy to ensure confidence in species identifications. There is also a great need to compile an up to date comprehensive species identification guide to assist in the identification of species trawled in the region.
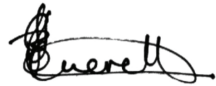
"The only true wisdom is in knowing you know nothing."
― Socrates

Declaration

I, **Bernadine Irene Everett**, declare that:

1. The research reported in this thesis, except where otherwise indicated, is my original research.

2. This thesis has not been submitted for any degree or examination at any other university.

3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.

4. This thesis does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:

   a) Their words have been re-written, but the general information attributed to them has been referenced;
   b) Where their exact words have been used, then their writing has been placed in italics and inside quotation marks and referenced.

5. This thesis/dissertation does not contain text, graphics or tables copied and pasted from the Internet, unless specifically acknowledged, and the source being detailed in the thesis and in the References sections.

Signed: _____   Date: 21 January 2020

Bernadine Irene Everett

Contents

1 **Acknowledgements**

Durban, January 2020

Bernadine Everett

2 List of papers and authors contributions

Name of candidate:
Bernadine Irene Everett

Papers:
The following papers are included in my D. Philos. dissertation.

Paper 1:
ROBEY, J., FENNESSY, S.T., EVERETT, B.I., SANTOS, J. & GROENEVELD, J.C. 2013. Patterns in abundance, population structure and biology of knife prawn *Haliporoides triarthrus* on deep-water trawl grounds off eastern South Africa. Journal of Marine Science, 35:4, 565-577.

Paper 2:
ROBEY, J., FENNESSY, S.T., EVERETT, B.I., SANTOS, J. & GROENEVELD, J.C. 2013. Abundance and biology of langoustine *Metanephrops mozambicus* (Nephropidae) on deep-water trawl grounds in eastern South Africa. Journal of Crustacean Biology, 33(6), 760-771.

Paper 3:
GROENEVELD, J.C., EVERETT, B.I., FENNESSY, S.T., KIRKMAN, S.T., SANTOS J. & ROBERTSON, W.D, 2013. Spatial distribution patterns, abundance and population structure of deep-sea crab *Chaceon macphersoni*, based on complementary analyses of trap and trawl data. Marine and Freshwater Research - http://dx.doi.org/10.1071/MF12263

Paper 4:
EVERETT BI, FENNESSY ST, VAN DEN HEEVER N. SUBMITTED. Using hotspot analysis to track changes in the crustacean fishery off KwaZulu-Natal, South Africa.

Paper 5:
EVERETT BI, GROENEVELD JC, FENNESSY ST, DIAS N, FILIPE O, ZACARIAS L, IGULU M, KUGURU B, KIMANI E, MUNGA CN, RABARISON GA, RAZAFINDRAKOTO H, YEMANE D. 2015. Composition and abundance of deep-water crustaceans in the Southwest Indian Ocean: Enough to support trawl fisheries? Ocean and Coastal Management 111: 50 – 61.

Paper 6:
EVERETT BI, GROENEVELD JC, FENNESSY ST, PORTER S, MUNGA CN, DIAS N, FILIPE O, ZACARIAS L, IGULU M, KUGURU B, KIMANI E, RABARISON G, RAZAFINDRAKOTO H. 2015. Demersal trawl surveys show ecological gradients in Southwest Indian Ocean slope fauna. Western Indian Ocean Journal of Marine Science 14(1 & 2): 73-92.

Contributions (alphabetical order)

	Paper 1	Paper 2	Paper 3	Paper 4	Paper 5	Paper 6
Concept and idea	JG, RJ	JG, RJ	BE, JG	BE	BE, JG, SF	BE, JG, SF
Study design and methods	JG, RJ	JG, RJ	BE, JG	BE	BK, BE, CM, DY, EK, GR, HR, JG, LZ, MI, ND, OF, SF	BK, BE, CM, EK, GR, HR, JG, LZ, MI, ND, OF, SF, SP
Data gathering and interpretation	BE, JG, JR, JS, ST	BE, JG, JR, JS, ST	BE, JG, JS, SF, SK, WR	BE, NH, SF	BK, BE, CM, DY, EK, GR, HR, JG, LZ, MI, ND, OF, SF	BK, BE, CM, EK, GR, HR, JG, LZ, MI, ND, OF, SF, SP
Manuscript preparation	BE, JG, JR, JS, ST	BE, JG, JR, JS, ST	BE, JG, JS, SF, SK	BE, SF	BK, BE, CM, DY, EK, GR, HR, JG, LZ, MI, ND, OF, SF	BK, BE, CM, EK, GR, HR, JG, LZ, MI, ND, OF, SF, SP

BK = Baraka Kuguru; BE = Bernadine Everett; CM = Cosmas Munga; DY = Dawit Yemane; EK = Edward Kimani; GR = Guy Rabarison; HR = Herimamy Razafindrakota; JG = Johan Groeneveld; JR = James Robey; JS = Jorge Santos; LZ = Lourenço Zacarias; MI = Mattias Igulu; ND = Nilza Dias; NH = Neil van den Heever; OF = Osvaldo Filipe; SF = Sean Fennessy; SK = Steve Kirkman; SP = Sean Porter; WR = Wendy Robertson (deceased).

With my signature I consent that the above listed articles where I am a co-author can be a part of the D. Philos. dissertation of the D. Philos. candidate.

Baraka Kuguru   Cosmas Munga   Dawit Yemane   Edward Kimani
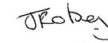
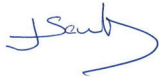Guy Rabarison   Herimamy Razafindrakota   Johan Groeneveld   James Robey

3

Jorge Santos

Lourenço Zacarias

Mattias Igulu

Nilza Dias

Neil van den Heever

Osvaldo Filipe

Sean Fennessy

Steve Kirkman

Sean Porter

3 Introduction

3.1 Description of the fishery

It is uncertain exactly when the South African deep-water crustacean trawl fishery off the province of KwaZulu-Natal (KZN) began. The earliest catch records date back to 1961 (Berry 1972) but the fishery could well have begun before then. The trawl grounds were discovered in the 1920s during a survey conducted with the SS Pickle (Gilchrist 1921). The surveys carried out in KwaZulu-Natal were aimed at discovering finfish resources but documented large catches of the deep-water lobster, *Palinurus delagoae*. It was this resource that the early fishers targeted. While the fishery targeted lobsters, other crustaceans such as knife prawns (*Haliporoides triarthrus*) and African langoustines (*Metanephrops mozambicus*) were also caught. The catches of lobsters started to decline during the 1960s and fishers diversified their fishing activities to also target the prawns and langoustines. In present times, along with prawns and langoustines, the fishers target the pink geryon crab, *Chaceon macphersoni* and do still catch some lobsters as bycatch.

The trawl grounds are located off the east coast of South Africa between 28°S and 31°S with a break in the grounds where the substrate is not suitable for trawling (Figure 1). For the most part, the continental shelf along this coastline is very narrow with a steep drop-off except for the central area, known as the Natal Bight, where the shelf is up to 50 km wide. The width of the trawl grounds varies from 15 km off St Lucia to 40 km off Durban (Oceanographic Research Institute, unpublished data). The trawlable area is approximately 1 750 km^2 and ranges in depth from 100 to 600 m (Fennessy and Groeneveld 1997). Berry (1969) described the substrate as variable with organic and mineral detritus and ranging from mud to hardened deposits of sediment, foraminifera and spicules. The water temperature drops from 20°C to 10°C as depth increases (Guastella and Roberts 2016) The strong Agulhas Current flows down the coast at rates up to three knots (Berry 1969) in a south-westerly direction, often with its core over the continental slope and with large scale meanders (Lutjeharms 2006). The current forms a formidable barrier to trawlers wanting to operate in depths greater than 600 m.

In terms of effort and production, the KZN crustacean trawl fishery is relatively small in comparison to the finfish trawl fisheries that operate off the Western Cape Province of South Africa (Warman 2017). The fleet is very small with only three to four vessels operating each year. In the early 1980s there were 21 vessels from 12 companies in the fleet, but it is very unlikely that they all fished at the same time (Fennessy and Groeneveld 1997). The vessels used are 25-35 m stern trawlers with approximately 30 t hold capacities. They utilise otter trawls, and mostly deploy a single net off the stern. Footropes vary between 26 and 60 m. Total retained catches range between 200 and 400 t/year with an average annual catch of 255 t (Groeneveld and Everett 2015). The three target species of knife prawn, African langoustine and pink geryon have contributed almost 75% towards the total retained catch since 2011 (DEFF Unpublished data).

Despite the importance of the contribution of the three target species to the overall catch, very few investigations have been conducted into their biology, particularly in recent years. In the late 1960s and early 1970s, scientists at the Oceanographic Research Institute undertook studies on African langoustines (Berry 1969) and knife prawns (Berry et al 1975). In the 1980s, de Freitas (1980) described all the Penaeoidea, including the knife prawn, of southeast Africa and Brinca et al (1983) documented knife prawns caught during four research surveys off Mozambique. In the 1990s Tomalin et al (1997) finalised research on the knife prawns, African langoustines and pink geryons of the KwaZulu-Natal (KZN) trawl grounds. They looked at catch trends, size distributions, sex ratios and maturity. After this there was no research conducted into these three species in KZN. There was, however, some research conducted in Mozambique but the results are mostly only available in unpublished reports of the Instituto Nacional de Investigação Pesqueira (Dias et al. 1999, Dias et al 2005, Dias and Caramelo 2007, Sobrino et al. 2007a, Sobrino et al. 2007b, Dias et al 2008, Dias et al. 2009, Dias et al. 2011). After the passage of time, it is necessary to repeat studies on species to establish current status. Further, it is well

documented that trawling has many effects on the environment in which it operates (Rijnsdorp 2016, Hiddink et al 2017, Kaiser 2019). These effects can include altered habitats, reduced biodiversity, and changes in the demographics of the species affected by trawling. The demographic changes include abundance, size and sex distributions (Jennings et al. 2005; Tillin et al. 2006, Hiddink et al 2017).
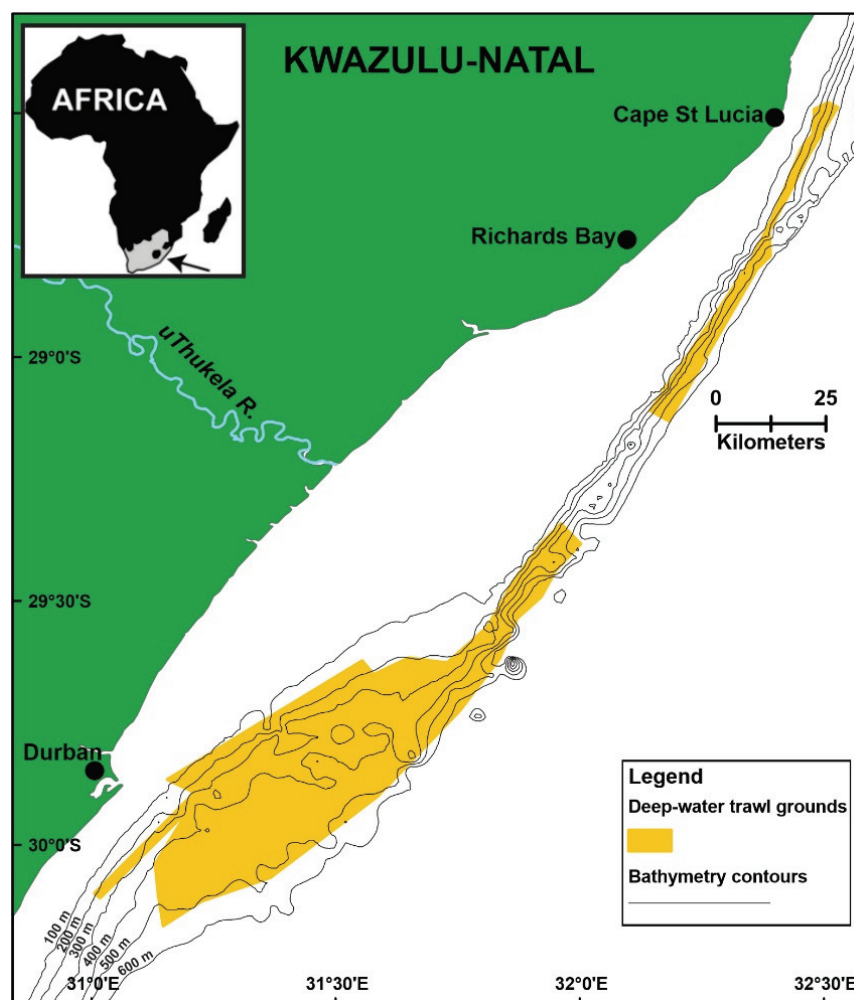
Figure 1: *Map of the study area showing the deep-water crustacean fishing grounds off the east coast of South Africa.*

3.2 Management of the fishery

Permits were first issued for the trawl fishery in 1972 but there were no restrictions on where the trawlers could fish (Fennessy and Everett 2015). Current permit conditions state that offshore fishing is not allowed within 7 nm of the highwater mark and must be between 28° 30.9'S 32° 24.0' E and 30°15.0'S 30° 46.8'E (DAFF 2018). In the late 1980s permit conditions stipulated that catch information in the form of trawling and landings logbooks were to be submitted to the then Department of Sea Fisheries (formally Department of Agriculture, Forestry and Fisheries, DAFF, and now Department of Environment, Forestry and Fisheries - DEFF) and this remains a permit condition (DAFF 2018). Logbooks consist of information about each trawl including date, time, depth, position and duration of the trawl along with the catch information. The management strategy in terms of catch and effort for this fishery has remained mostly unchanged for the last three decades. The fishery is managed through input control: Total Allowable Effort (TAE) in the form of the number of vessels allowed to operate per year (DAFF 2018). This limit has been set at seven vessels (including a maximum of four inshore (shallow water <50 m depth) vessels) although this is not based on any fisheries or biological analyses

of data to support the limit. Vessel numbers currently range between three and four, so the TAE is not currently being met. Besides spatial restrictions on the operations of the fleet, the only other restriction is on mesh size in the codend. Stretched mesh sizes in the codend are regulated by the fishing permit conditions and have changed over time from 38 mm in the 1990s (Fennessy and Groeneveld 1997) to 50 cm at present (DAFF 2018). There are no catch (output) controls in place.

3.3 A regional perspective

The KwaZulu-Natal (KZN) crustacean trawl fishery is the southern-most crustacean trawl fishery in the Southwestern Indian Ocean (SWIO). Nine countries' exclusive economic zones are in the SWIO: Kenya, United Republic of Tanzania, Mozambique, Madagascar, Mauritius, Seychelles, Comoros, France and South Africa (Figure 2). Deep-water trawling (industrial or for research purposes) has occurred in five of these countries: Kenya, United Republic of Tanzania, Mozambique, Madagascar and South Africa (Groeneveld and Everett 2015). This region is dominated by the presence of two western boundary current systems dividing the area into two large marine ecosystems (LME). The Somali Current LME extends from Dar es Salaam in the United Republic of Tanzania to just south of Socotra Island off Somalia and it includes the East African Coastal Current (EACC) and the Somali Current (Alexander 1998). The Agulhas Current LME stretches from the northern part of the Mozambique Channel down to Cape Agulhas, South Africa. It incorporates the Mozambique Current and the Agulhas Current (Lutjeharms 2006). The currents of the SWIO arise from the South Equatorial Current which forms two divergent currents when it divides on reaching the African coast. The EACC flows north along the Kenyan coast and the Mozambique Current flows southwards (Okemwa 1998). During the Southeast Monsoon (April to October) the EACC strengthens and during the Northeast monsoon (November to March) it weakens. This gives rise to the reversing Somali Current (Schott and McCreary 2001). The Mozambique Current morphs into a series of anticyclonic eddies before becoming a tributary to the Agulhas Current (Lutjeharms et al. 2012). The Agulhas Current is characterised by warm, fast-flowing water that hugs the continental shelf (Lutjeharms 2006).

In the SWIO, most crustacean trawling occurs in shallow water less than 50 m in depth, from South Africa to Kenya, and targets *Penaeus indicus* and *Metapenaeus monoceros*. These shallow species are more accessible than the deep-water resources (van der Elst et al. 2009). The deep-water trawl fisheries are of a multi-species nature and include catches of prawns (*Haliporoides triarthrus, Aristaeomorpha foliacea, Aristeus antennatus, Aristeus virilis*), langoustines (*Metanephrops andimanicus, African langoustines*), slipper lobsters (*Nephropsis stewarti*), spiny lobster (*Palinurus delagoae*) and geryonid crabs (*Chaceon macphersoni, C. crosnieri, C. somaliensis*) (Manning and Holthuis 1989, Manning 1993, Groeneveld and Everett 2015). These fisheries also retain a diversity of finfish and cephalopods categorised as bycatch. Non-valuable invertebrates, fish and elasmobranchs are discarded (Groeneveld and Everett 2015). Only two countries in the SWIO have well established deep-water crustacean trawl fisheries: South Africa and Mozambique. Kenya has a few vessels licenced to operate in deep-water but effort and catch statistics are not readily available (Fulanda et al. 2011, WIOFish 2019). In Madagascar and Tanzania there have been irregular attempts at deep-water trawling, but it is assumed that these attempts are not sustained due to the limited area of the grounds and unsuitable trawling conditions that possibly limit viability (Groeneveld and Everett 2015).
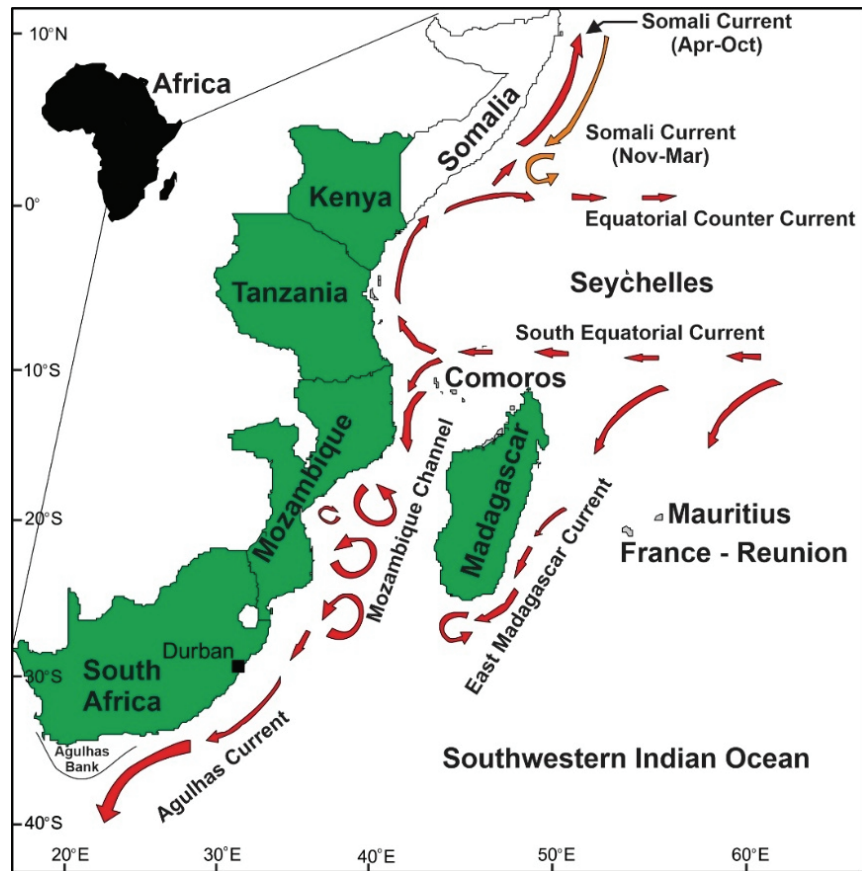
Figure 2*: Map showing the countries and ocean currents of the Southwestern Indian Ocean (adapted from van der Elst 2009).*

4 Objectives

The main objective of this thesis is to improve the understanding of the KwaZulu-Natal crustacean trawl fishery and how it fits in with a Southwestern Indian Ocean regional perspective of deep-water trawl fisheries catching crustaceans.

Specific questions raised were:

1) What is the abundance, distribution, size and growth of the knife prawn, *Haliporoides triarthrus*?

2) What is the abundance and biology of the African langoustine, *Metanephrops mozambicus*?

3) What is the spatial distribution, abundance and population structure of the deep-water crab *Chaceon macphersoni*?

4) What areas are the most important to the fishery in terms of effort and productivity of the three target species?

5) How does the KwaZulu-Natal fishery fit in with other trawl fisheries of the Southwestern Indian Ocean region and are the resources targeted by trawl fisheries adequate to sustain these fisheries?

6) How do the faunae targeted by deep-water trawl fisheries in the Southwestern Indian Ocean differ regionally and can any inferences be made regarding their biogeography in the region?

5 Materials and brief summary of methods

Catch and effort data for the KwaZulu-Natal crustacean trawl fishery used in **Paper 1**, **Paper 2**, **Paper 3, Paper 4** and **Paper 5** were from a long-term database (1988-2017) comprising logbook drag sheet data. Permit conditions make it mandatory that skippers complete these drag sheets for every trawl haul and submit the information to the Department of Environment, Forestry and Fisheries (DEFF). The data collected include date, time, depth and position of trawl haul as well as the retained catch species in kilograms. Anomalous records for which trawl localities, depth, trawl duration and catch compositions were obviously incorrect were excluded from the analyses. Catch and effort information for **Paper 3** was also provided by data collected by an onboard observer on a longline trapping vessel. The observer collected effort data such as numbers of longlines and traps set, date and time of setting and hauling, position and depth of sets and catch per trap. Catch and effort for **Paper 1**, **Paper 2** and **Paper 3** were explored using generalised linear models in R software. **Paper 5** and **Paper 6** utilised the catch and effort data from four research surveys conducted in Kenya, Tanzania, southern Mozambique and Southwestern Madagascar, between October 2011 and March 2012, in addition to the KwaZulu-Natal commercial trawl data. Nominal catch densities in **Paper 5** were standardised using a modelling framework to account for effects of depth, area and day/night differences.

Biological sampling for **Paper 1** was undertaken on six quarterly observer trips during normal fishing activities on a commercial trawler. An unsorted random sample of catch of 10-20 kg was collected for each trawl. All knife prawns were removed from this sample for further investigation. They were sexed, carapace lengths measured, and moult stage recorded. Numbers of reproductively active females were recorded, and macroscopic staging of their ovaries was undertaken. Length-weight relationships were determined in the laboratory by measuring and weighing samples purchased from the vessel. During the sampling trips mentioned for **Paper 1**, African langoustines were also collected for **Paper 2**. The langoustines were sexed, measured, moult stage recorded, and the eggs of berried (gravid) females were staged. Packed langoustines were purchased and measured and weighed in the laboratory to determine length-weight relationships. Biological sampling for **Paper 3** was conducted by observers on commercial trawlers in 1997 and 2012 and on the longline trapping vessel from 2004 to 2007. Carapace widths of pink geryons were measured and they were sexed. Numbers of berried females were recorded, and immature and mature females were distinguished. A carapace width: whole weight relationship was determined through measuring and weighing a range of crab sizes.

Analyses in **Paper 4** made use of spatial analyses routines available in ArcGIS Desktop 10.7.1 to determine clustering of fishing effort and target species catch per unit effort (CPUE). Space time cubes were created on which emerging hotspot analyses were conducted. These analyses showed the importance of various areas on the fishing grounds to the fishery.

Data in **Paper 6** were analysed for species richness, Chao2 estimator, Shannon's diversity, Pielou's index, multivariate, non-metric, multi-dimensional scaling and three-factor permutational multivariate analysis of variance.

6 Summary of results

6.1 Abundance, distribution, size and growth of the knife prawn, *Haliporoides triarthrus* (Paper 1)

© Oceanographic Research Institute
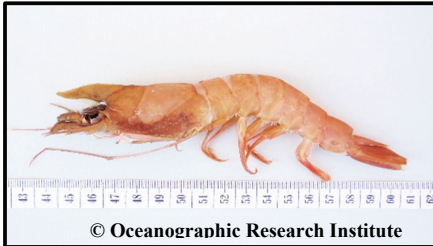
Knife prawns occurred in 85% of all trawls recorded in the database and retained catches averaged 125 t.y⁻¹ for the period 1990-2010. Standardisation of the catch per unit effort (CPUE) values showed that year, month, depth and vessel were significant in determining catch probability. Standardised CPUE declined gradually (with fluctuations) from 1990 to 2001 after which it increased to a peak in 2008. Monthly CPUE peaked in March with a decline to November before rising from December onwards. CPUE was highest between 200 and 599 m, peaking between 200 and 299m and 400 and 499m. The prawns sampled ranged in size (carapace length CL) from 13.0 to 59.8 mm. Significant predictors in the CL size model were sex, month and depth. March and November were when larger prawns were caught while December and February were when there were smaller prawns in the catches. There were very small differences in size across depth, but the larger prawns were mainly found between 450 and 474 m. Overall, the number of males were equal to that of females but the probability of catching a male was higher in March and August whereas the likelihood of catching a female was higher in November and December. Females were on average larger than males. Reproductive seasonality could not be assessed as only 20 females out of 2 991 showed any form of ovarian development and they were mostly in the developing stage. Cohorts for males and females were easily identifiable for all months sampled. The youngest female cohort (25 mm CL) was detected in November and it dispersed after approximately two years at 39 mm CL. Male cohorts appeared at similar times to females but were smaller. Estimates of growth parameters L_∞ and K were made using the standard von Bertalanffy growth function. Female values were 40.6 mm CL and 1.06 y⁻¹ while males were 35.2 mm CL and 1.27 y⁻¹ respectively.

6.2 Abundance and biology of the African langoustine, *Metanephrops mozambicus* (Paper 2)

© Oceanographic ResearchInstitute

African langoustines were present in 80% of trawl hauls. Most langoustines were caught in October and in depths between 400 and 499 m. Year, month, depth and vessel were significant in the catch probability models. CPUE increased between 1989 and 1994, declined until 2003 and increased again with fluctuations until it peaked at 2010. CPUE was lowest during the first four months of the year, increasing to a peak in July before decreasing gradually for the remainder of the year. The highest CPUEs were between 300 and 599 m. There was a negative correlation between standardised CPUE and fishing effort. Sampled langoustines ranged in carapace length (CL) from 17.5 to 72.6 mm. Month and depth were significant variables in the size models. Mean CL was smallest in March and November while size decreased consistently with depth. Males marginally outnumbered females (1:0.89) and month was the only significant variable in the sex model. The likelihood of encountering equal numbers of males and females was the same in all months except November when males were more prevalent. Female maturity was determined by size, month and depth. The probability of catching ovigerous females was highest in December and at depths between 325 and 350 m. The high proportion (72%) of eggs with well-developed embryos or about to hatch embryos seen in May suggests that this is the main hatching period. Distinct size cohorts were seen for intermediate-sized langoustines. Monthly samples were unimodal

except for March when two peaks were observed. These peaks represented males and females individually and March was the only month where there was a distinction between the sexes. Male and female length frequencies did not differ significantly (Pearson's χ^2 test of independence, P > 0.05) and sexes were therefore combined for growth analyses. Standard von Bertalanffy growth function estimated L_∞ at 65.5 ± 4.4 mm and K at 0.7 ± 0.1 y^{-1}.

6.3 Spatial distribution patterns, abundance and population structure of the pink geryon, *Chaceon macphersoni* (Paper 3)

© Oceanographic Research Institute
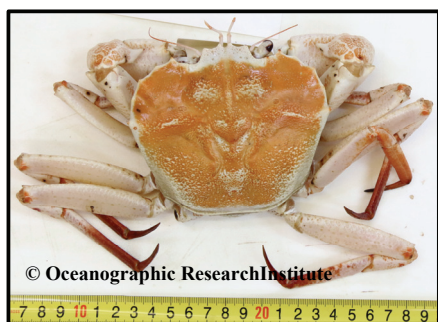
Pink geryons were recorded in 58% of trawl hauls and 16% of longline trap sets. Significant variables in the catch probability models for the trawl catch rates were year, month, depth and vessel while for the trap catch rates, they were season, depth and latitude for the binomial model and year, depth and latitude for the gamma model. Trawl CPUE peaked in the early 1990s and thereafter declined to its lowest in 2002. While some recovery was observed after 2002, the 2010 CPUE was only 17% of the maximum in 1992. November to January were the months with the highest CPUEs and they increased with depth from 100 to 499 m. CPUE values for the trap fishery declined between 2004 and 2007, they increased with depth, from September to November and between 29.5°S and 30.49°S. Significant variables in the size model were sex and year. Males were significantly larger than females and those caught in traps were smaller in 2004 and 2005 than those caught in 2006 and 2007. Female crabs attained sexual maturity at smaller sizes than males. Females outnumbered males by a ratio of 1:0.29. Month was the only significant variable in the sex model and the probability of encountering male crabs in the traps was highest from July to September and lowest in November. Reproductively active females were scarce in the overall catches of trawl hauls (6%) and traps (8%).

6.4 Determining areas of importance to the KwaZulu-Natal crustacean trawl fishery using hotspot analyses (Paper 4)

Autocorrelation analyses (Global Moran I statistic) indicate that overall fishing effort and CPUE of the three target species - knife prawns, African langoustines and pink geryons - in the KZN crustacean trawl fishery occurred in non-random clusters. Downward trends of the z-scores for all four aspects show that clustering is becoming less pronounced with time. A space-time cube was developed on which to conduct analyses that included both space and time. The Mann-Kendall trend test showed that effort in terms of sum and mean of hours fished per locality has a significant declining trend. This trend is particularly noticeable for the locations further away from Durban where the trawlers are based. The same test for the three species separately showed that neither the knife prawns nor the pink geryons have any significant trends over the study period but the langoustines had a significantly increasing trend. The emerging hotspot analyses show how the fishing effort has become more concentrated over time to a relatively small area directly off the Durban Harbour. Hotspots for the CPUE of the three target species were similarly concentrated in the southern section of the Durban Deep grounds showing that this area has persistently remained the most productive area for the fishery despite having the most effort concentrated there. Over time there have been contractions in the most productive areas for each species and the knife prawns experienced the tightest contraction.

6.5 Composition and abundance of trawl resources in the Southwestern Indian Ocean (SWIO) and are they enough to support fisheries (Paper 5)

This paper is based on four trawl surveys conducted in Mozambique, Madagascar, Tanzania and Kenya. Teleosts were the dominant catch group in all countries (59-74% of total catches) and depths. Crustaceans made up 15% of the catch in Mozambique and Madagascar, but only 6% in Kenya and Tanzania, where elasmobranchs (18%) and other invertebrates (11-15%) were more abundant. Country and depth were significant variables in the standardisation of catch data. Abundance of knife prawns and African langoustines declined from south (Madagascar, Mozambique) to north (Kenya, Tanzania), but the Indian nylon shrimp, *Heterocarpus woodmasoni*, was more abundant in Madagascar, Tanzania and Kenya. Pink geryon and knife prawn abundance increased up to 600 m depth, whereas African langoustines and Indian nylon shrimp peaked shallower, at 350-500 m. Crustacean catch composition in Mozambique was strikingly similar to commercial landings in eastern South Africa but differed markedly across the Mozambique Channel. Deep-water crustaceans were less abundant in Kenya and Tanzania, and at depths shallower than 400 m.

6.6 Ecological gradients of trawl resources in the Southwestern Indian Ocean (Paper 6)

This paper is based on the four trawl surveys conducted in Mozambique, Madagascar, Tanzania and Kenya used in Paper 5. A total of 243 genera were identified. Teleosts were the most dominant group (55%), followed by crustaceans (18%), elasmobranchs (12%) molluscs (10%), and other invertebrates (5%). Knife prawns (14%), greeneye fishes *Chlorophthalmus* (13%) and drift-fishes *Cubiceps* (12%) were the genera with the highest frequencies of occurrence in the trawls. Knife prawns were, however, rare in Tanzania and completely absent in Kenya. Highest species richness was found in Mozambique, and in the 300-399 m depth stratum where most of the fishing effort was directed. When the Chao2 non-parametric estimator of species richness was used, Kenya had the highest species richness and Tanzania the lowest. Tanzania had the highest evenness and Mozambique the lowest. Shannon's diversity was greatest in Kenya, decreasing southwards along a latitudinal gradient to Mozambique. Chao2 estimated that species richness was highest between 200 and 299 m and lowest between 500 and 599 m. Shallower depths showed more evenness than the deeper depths. Shannon's diversity was highest between 200 and 299 m. PERMANOVA and PERMDISP showed that differences between Kenya and Tanzania versus Mozambique and Madagascar were only a result of location effects. Differences between Kenya and Tanzania were due to location and differences between Madagascar and Mozambique were due to location and dispersion. PERMANOVA found significant differences between all depth strata while PERMDISP found significant differences in most pairwise comparisons with the exception of the two most shallow depth strata (200 - 299 and 300 - 399 m) and between 300 - 399 and 400 - 499 m strata. Genera contributing most to the dissimilarity between the north and south were greeneyes, knife prawns and the fish *Acropoma*. By country, Madagascar and Tanzania were most dissimilar, with blackchin fishes *Neoscopelus*, greeneyes, and nylon shrimps *Heterocarpus*, the main drivers. By depth, the 200-299 m and 500-599 m strata were most dissimilar, based on blackchin fishes, knife prawns and greeneyes. Our study shows a clear difference in community structure of slope fauna across the Mozambique Channel, reflecting sampling of two ecologically different soft-sediment communities.

13

7 Discussion

7.1 The importance of deep-water trawl fisheries in the Southwestern Indian Ocean

By 2017, the total marine catches for the western Indian Ocean (Fishing Area 51) documented on the Food and Agriculture Organization of the United Nations (FAO) Global Capture Production Dataset were over 5.3 million tons (FAOa 2019). Catches by the nine countries of the Southwestern Indian Ocean accounted for only 13% of the total. Crustaceans contributed about 7% towards the total catch and Southwestern Indian Ocean countries caught 13.5% of the total crustacean catches. Figure 3 confirms that catches by the SWIO countries form a very small part of the overall catches of the western Indian Ocean. This does not necessarily indicate that the fisheries of the SWIO countries are not important to the countries which operate them, particularly since catches from small-scale fisheries are known to be underreported for the region (van der Elst et al. 2005). Population estimates for the SWIO are over 107 million people with 47% living within 100 km of the coast (Kimani et al. 2009). The fisheries contribute to vital issues such as food security and poverty alleviation in countries that have the lowest gross incomes per capita (Cunningham and Bodiguel 2005, Obura et al. 2017).
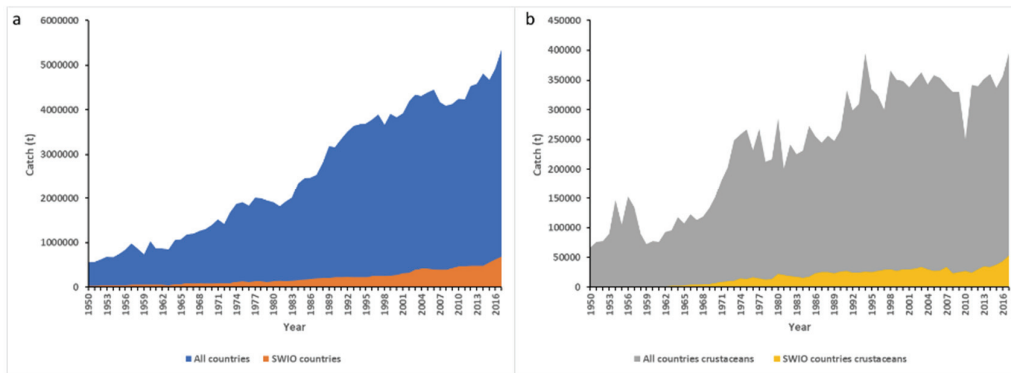
Figure 3: Marine catches recorded in the FAO Global Capture Production Dataset by all countries and countries of the Southwestern Indian Ocean fishing in the western Indian Ocean for total catch (a) and total marine crustacean catches (b).

Fisheries in the SWIO generate 9% of the gross marine product with 87% of this value coming from industrial fisheries, particularly for tuna (Obura et al. 2017). Industrial fishing provides an important source of foreign exchange revenue through exports to markets in developed countries (Kimani et al. 2009). Catches from the SWIO deep-water trawl fisheries include high-value prawns, langoustines and crabs as well as teleosts and elasmobranchs that have lower values (Groeneveld and Everett 2015). The only long-term deep-water crustacean trawl fisheries in the SWIO are found off the east coast of South Africa and off Mozambique. Both of these fisheries began in the 1960s and continue at present. The South African fishery is relatively small with a cap of seven vessels allowed to fish (DAFF 2013) with only three or four operating. The fishery off Mozambique has had a declining trend in the number of vessels operating from around 40 vessels in the 1980s to 16 in 2012 (Dias and Caramelo 2013) but has since expanded markedly to over 25 (IIP, unpubl. data). Tanzania and Madagascar have had sporadic, short-lived deep-water fisheries that have not been very successful (Groeneveld and Everett 2015) and Kenya has, since 2018, permitted two vessels to fish in the deep (N. Wambiji pers. com, nwambiji@kmfri.co.ke).

There is some difficulty in separating the various fisheries' catches in the FAO Fishery Commodities Global Production and Trade Dataset where shrimps and crabs are all combined without any distinction between shallow or deep fisheries. The total crustacean catch in 2017 for Mozambique, United Republic

of Tanzania, Kenya and Madagascar, however, brought in almost US$ 172 million to these countries (FAOb 2019). Deep-water langoustines (*Metanephrops* spp.) on their own were responsible for US$ 515 000 in foreign income, and the recent annual export value of Mozambican deep-water crustaceans was around US$ 8 million (IIP unpubl. data). While these amounts may not seem substantial, for these developing countries and the fisheries that catch these species, they are significant amounts of foreign revenue. Catch statistics provided by national fisheries departments show that for the SWIO crustacean catches are relatively small (53 000 t in 2017) in comparison to other fisheries such as those targeting tuna (192 000T in 2017) (FAOa 2019) and the South African crustacean trawl fishery averages 255 t/year and its counterpart in Mozambique averages over 2000 t/year in recent years (IIP unpubl. data). Kenya's catch statistics have not yet been published (N. Wambiji pers. com, nwambiji@kmfri.co.ke).

7.2 Taxonomic issues with crustaceans in the SWIO

Marine biodiversity has been affected by a combination of human impacts including ocean warming, pollution, biological introductions and overfishing (Sala and Knowlton 2006, Lehtiniemi et al. 2015, Hilborn 2016). Fishing in its specific targeting of biological resources has a very direct impact on ecosystem biodiversity (Norse 1993) while trawling is recognised as one of the most destructive forms of fishing. Along with the target species, it removes a large number of species caught as bycatch and results in the physical disruption of the environment in which it operates (Alverson 1997, Gage et al 2005, Kaiser et al. 2002, Kelleher 2005, Bellido et al. 2011). The effects of trawling differ between habitats, especially the various types of substrate, and between the species targeted by the trawlers (Ryan and Moloney 1988, Riemann and Hoffman 1991, Hamre 1994, Kaiser et al. 2002). Increases in the number of vessels operating and the harvesting efficiency with the introduction of new technologies has resulted in decreases of target species and subsequent changes in the ecosystems (Vecchione 1987).

According to Vecchione et al. (2000) there are two methods for determining the effects of fishing on biodiversity. First, it involves the discovery and description of the species living in the ecosystem of interest and their relationship with similar species globally (baseline information). Second, is to assess the current and historical (if possible) status of the biodiversity of the ecosystem and to establish if there have been any changes. Understanding and monitoring an ecosystem's biodiversity is completely reliant on the proper identification of species within that ecosystem (Vecchione and Collette 1996).

Taxonomic information is not only essential for understanding biodiversity, it also addresses many critical conservation issues particularly regarding transboundary matters (McNeely 2002). With a move to an ecosystem approach to fisheries in terms of multiple target species (Murawski 1993) and/or large marine ecosystems (Sherman et al. 1990) it is essential for management to have adequate information on all abundant and ecologically significant species (McNeely 2002).

Crustacean fisheries in the SWIO are multi-target fisheries that share transboundary resources to various extents (Table 1) (Paper 5, Groeneveld and Everett 2015). Surveys conducted by the *RV Dr Fridtjof Nansen* showed that crustaceans were the only regional resources that showed any potential to sustain demersal trawl fisheries (Fennessy et al. 2017). The question is, though, how certain are we that species were correctly identified?

Table 1: *Main species caught by deep-water trawls in the SWIO, showing transboundary species (Paper 5, Groeneveld and Everett 2015).*

Species	Kenya	Tanzania	Mozambique	South Africa	Madagascar
Aristaeomorpha foliacea	X				
Aristeus antennatus			X		X
Aristeus sp			X		
Aristeus virilis					X
Chaceon macphersoni	X	X			
Haliporoides triarthrus		X	X	X	X
Heterocarpus woodmasoni	X	X	X		X
Linuparus somniosus	X	X	X		
Metanephrops mozambicus	X	X	X	X	X
Palinurus delagoae		X	X	X	
Penaeopsis balssi	X	X	X		X

Surveys conducted from the 1970s to the 1990s in the western Indian Ocean by the Norwegian vessel the *RV Dr Fridtjof Nansen* were focused on exploring the potential of resources for fisheries, and crustacean species were mostly recorded simply as crustaceans, shrimps, lobsters and crabs (Groeneveld and Koranteng 2017) without an attempt to classify them to species level (Figure 4). Voucher specimens were not collected, and this was a lost opportunity to store samples in museum collections that could be referred to later. Very few data from other surveys that occurred in the region, such as those undertaken by the USSR, are readily available (van der Elst and Everett 2015). It would, however, be valuable to be able to compare the results of those surveys with those of the RV *Dr Fridtjof Nansen* but due to costs of repatriating the data, it is not possible (Romanov 2012).
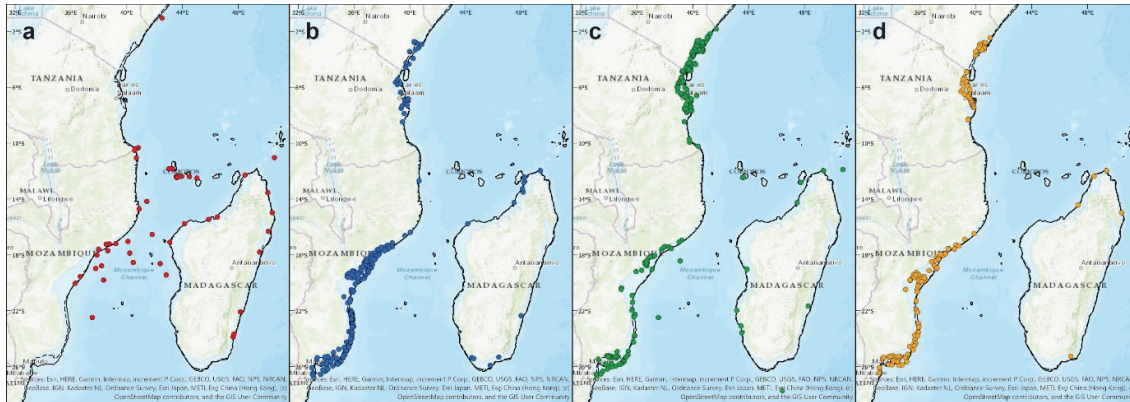
Figure 4: *Stations sampled by the RV Dr Fridtjof Nansen where crustaceans were only identified as a) Crustaceans unidentified, b) Crabs unidentified, c) Shrimps unidentified, and d) Lobsters unidentified (see Groeneveld and Koranteng 2017 for the full list of survey reports from which these figures are derived).*

More recently, during the South West Indian Ocean Fisheries Project (SWIOFP), the opportunity to validate species identifications was lost once again when voucher specimens were not collected during the deep-water trawl surveys (Paper 5). In Paper 6, which analysed these data, a conservative approach was adopted in the community analyses, and genus rather than species level was used after discovering mismatches of species recorded beyond their known depth and latitudinal ranges. Furthermore, examination by two crustacean taxonomists (Prof. Tin-Yam Chan, National Taiwan Ocean University and Prof. Peter Ng Kee Lin, National University of Singapore) of photographs of three of the most abundant species of crustaceans found that these species had been misidentified (Figure 5).

Figure 5: *Incorrectly identified species from the SWIOFP surveys a) Metapenaeus monoceros initially identified as Fenneropenaeus indicus, b) Penaeopsis balssi initially identified as F. indicus, and c) Chaceon somaliensis initially identified as C. macphersoni.*

Unfortunately, these misidentifications are not overly surprising since species identification guides for deep-water taxa in the SWIO are incomplete, outdated or not appropriate for the regions in which they are used. Scientists without taxonomic experience can very easily misidentify species while using these guides. An example is that of the African langoustine, *Metanephrops mozambicus* which was previously thought to be the same species as the Andaman lobster, *M. andamanicus*. These species are very similar and difficult to distinguish from each other and while they occur in different areas, guide users might think that they have identified the species correctly based on the incorrect distributions given. Macpherson (1990) identified the differences between the two species as well has their distributions but lobster guides such as the Marine Lobsters of the World (Holthuis 1991) and FAO species identification sheets (Fischer and Bianchi 1984), which are still in widespread use in the SWIO, describe the distribution range of the Andaman lobster to include East Africa. Macpherson (1990) and Chan (2010) limit its distribution to the Andaman Sea, Philippines and Indonesia. Even if researchers use electronic guides such as the World Register of Marine Species, they will be led astray when looking at the species distribution for the Andaman lobster (Figure 6) which also includes South Africa in its distribution range (WoRMS 2019). This brings into question the identification of the langoustine in publications such as Fulanda et al. (2011) and Zacarias (2013) that list the Andaman lobster as an East African species.
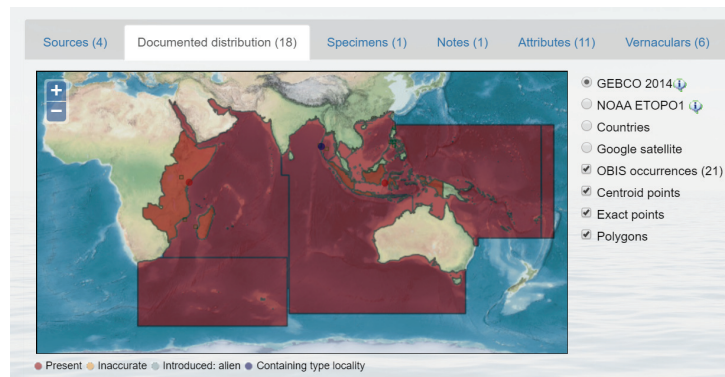
Figure 6: *Species distribution of Metanephrops andamanicus as provided by the World Register of Marine Species (WoRMS 2019a).*

The African langoustine is not the only target crustacean species with identification issues. *Chaceon macphersoni*, the pink geryon crab that is found from the border between Namibia and South Africa (Atkinson and Sink 2018) to Mozambique (Manning and Holthuis 1988, 1989) has been identified in Kenyan and Tanzanian deep-water trawls. During the trawl surveys of the SWIOFP it came to light through photographs that the crab species identified as *C. macphersoni* was actually *C. somaliensis* (see above and Figure 5c). Manning 1993 described *C. somaliensis* from a single specimen that was collected off Somalia in 1991. It is very similar to the pink geryon but differs in having slender legs, a comparatively greater gap between the first and second anterolateral teeth of the carapace, a smoother carapace, and a different shape to the orbital margin. These minor differences are not easily recognised particularly when they are not specifically being looked for. In Paper 5, after considering the decreasing

catch rates with decreasing latitude for pink geryons, we speculated that the transition from pink geryons to *C. somaliensis* occurs somewhere off Tanzania and that in all likelihood, all *Chaceon* caught from Tanzania northward are *C. somaliensis*. Photographs of the crabs provided during the SWIOFP surveys, and of specimens obtained more recently, certainly appear to collaborate with this theory. Without actual samples though, absolute certainty is difficult to establish.

The irregularities in the identification of the target species leave a lot of concern for the bycatch species which are even less well known. Two examples are presented below but there are probably many others, and the extent of taxonomic issues concerning the many discarded species are completely unknown. The greeneye (*Chlorophthalmus* cf. *punctatus*), a very common retained bycatch species of the KwaZulu-Natal and Mozambican deep-water crustacean trawl fishery, is thought to be a species complex in the SWIO and will most likely be re-described as a new species (Dr Barry Russell, Charles Darwin University, 2019 pers. comm. 16 August) but for now there is uncertainty regarding their identity and distribution. Another difficult bycatch species group are the dogfish sharks of the *Squalus* genus which are discarded rather than retained. Observers on the KZN deep-water trawlers have struggled to identify these species at sea, even after retaining some for further identification in the laboratory (Oceanographic Research Institute Unpublished Observer Data). In 2017, the genus was revised to include two new species, *Squalus margaretsmithae* and *Squalus mahia* (Viana et al. 2017) leaving uncertainty regarding the species that were previously identified as *S. megalops* and *S. mitsukurii*. The species in this genus share morphological characteristics that makes their distinction from one another almost impossible at sea (Myagkov and Kondryurin 1986).

The misidentification of species is not limited to survey and fisheries data. On investigation of the FAO Fishery Commodities Global Production and Trade Dataset to calculate the total marine resource exports from South Africa and Mozambique, it was found that African langoustines were listed under the categories of "Norway lobsters (*Nephrops norvegicus*), dried, salted or in brine, smoked" and "Norway lobsters (*Nephrops norvegicus*), whether in shell or not, frozen" for both countries (FAO 2019b). *Nephrops norvegicus* is a Northern Hemisphere species that is found in the Eastern Atlantic and Mediterranean Sea (Holthuis 1991). Furthermore, a search on the Alibaba trade website (www.alibaba.com) listed langoustines from Mozambique as *M. andamanicus*, the Andaman lobster, (https://www.alibaba.com/product-detail/Langoustine-Scampi-Metanephrops-Andamanicus_122757920.html?spm=a2700.7724838.2017115.14.7bd27456lzr0cL). Holthuis (1991) stated that the Andaman lobster does not occur in Mozambique but presumably the use of inappropriate guides or misinformation is being used in the labelling of the species. Seafood mislabelling, whether done intentionally or unintentionally, can occur at any stage in the supply chain. Often this is not intentional because species are difficult to identify and because species sometimes have more than one common name and common names may vary between countries or regions (Buck 2010). When mislabelling is done intentionally it can be to either sell illegally caught fish on the legal markets or to command a higher price for a lower value species (Ogden 2008). Given the issues regarding the identification of African langoustines as Andaman lobsters as discussed above, it is likely that the langoustines sold on the Alibaba website are more likely not intentionally mislabelled. Seafood mislabelling is a global issue and needs to be addressed (Jacquet and Pauly 2007, 2008). A study of seafood samples from wholesalers and retailers in South Africa found 9% and 31% respectively had been mislabelled (Cawthorn et al. 2012). In the South African crustacean trawl fishery, some bycatch species are being reported under incorrect common names in the trawl logbooks that are provided to the Department of Environment, Forestry and Fisheries (DEFF). These include finfish such as the false kingklip (*Hoplobrotula gnathopus*) which is reported as kingklip, internationally known as ling (*Genypterus capensis*). Kingklip is a very popular eating fish in South Africa and it commands a high price in restaurants but according to Smith and Smith (1966) it has been mislabelled for a very long time, as they wrote in 1966 "as it is nowhere abundant, far more fish named 'kingklip' on menus is eaten than is ever caught".

May (1990) proposed that species that have not been correctly identified, do not receive adequate protection under legal management regimes. Mace (2013) stresses that conservation of species is near impossible because without knowing the species we cannot understand their relationships within their

ecosystems and how they will react to environmental change and degradation. Morrison et al. (2009) found that changes in taxonomy had mixed results in conservation for various species. The habitats and communities of the benthic soft sediments are the most predominant along the continental shelf and slope of the SWIO (Fennessy and Green 2017) yet these remain the least known and understood. Improving our taxonomic understanding of the species affected by deep-water trawl fisheries (both target and bycatch) can go a long way towards formulating management plans that address resources on both national and regional scales. This can be done through re-evaluating species caught by the deep-water crustacean trawl fisheries that are currently operational in South Africa, Mozambique and Kenya. Any further surveys that are undertaken in the region should be specifically tasked with the collection of voucher specimens to improve identification of species. It is concerning when researchers on surveys, who often do not have any experience using taxonomic keys, rely solely on using pictorial species guides when assigning species names. These pictorial guides may not even be from the correct area where the species are being collected and species names are assigned based on the closest resemblance between the specimen and an image. Therefore, in order to make sure that the correct taxonomies are assigned, there is an urgent need for scientists to be trained in the use of taxonomic keys so that they become comfortable with their use. Hopefully this will encourage researchers to turn to the keys before relying on identification guides that do not always provide the best identification characteristics and, as discussed above, outdated or misleading distribution information.

7.3 Importance of understanding species distributions

As with taxonomy, species distributions play an important role when applying the ecosystem approach to fisheries (Monk 2013), managing transboundary stocks (Levin et al. 2018), understanding effects of fishing pressure on biodiversity and monitoring ecosystems to external drivers such as climate change (Perry et al. 2005, Lucey and Nye 2010). Mesoscale distribution patterns for many commercially important species and their associated ecosystems are lacking even though knowing this information is particularly important (Mackinson 2001). Regardless of the awareness of the importance of accurately identifying essential fish habitats and their inhabitants for effective spatial fisheries management, current knowledge of species distributions is qualitative and uncertain (Moreno et al. 2014). Species distribution data can be collected through fisheries-dependent data from commercial fisheries or through fisheries-independent data consisting of dedicated research surveys. Determining species distributions on local scales with the use of fisheries-dependent data which is collected consistently is more easily undertaken than using data collected during research cruises. Research cruises may only provide snapshots of distributions in both time and space. Fisheries-dependent data is, however, limited by data credibility, vessel capabilities and by economic considerations of the fishers (Pennino et al. 2016).

Complete coverage of the Southwestern Indian Ocean continental shelf and slope by demersal trawl surveys is hampered by seabed geology and oceanography in various areas along the coastline which do not allow for bottom trawl fishing (Groeneveld and Everett 2015). The continental shelf is mostly narrow, and the slope is in parts very steep, with the substrate rough and rocky and the currents too strong for correct operation of the trawl (Groeneveld and Everett 2015, UNEP-Nairobi Convention and WIOMSA 2015). Survey coverage is also not complete when spatial variations are taken into account, and is compounded by the focus of the early research programmes on fisheries species, which led to inadequate species identifications (see above discussion). The most complete survey dataset available is that of the Mozambique shelf and slope by the RV *Dr Fridtjof Nansen* but these surveys were also temporally inconsistent. Other surveys conducted by the RV *Dr Fridtjof Nansen* were conducted either as once-off surveys in several countries several decades ago, or as incomplete coverage of the country's coastline, for example Madagascar (Everett 2017). Surveys such as those of the RV *Vizconde de Eza* in Mozambique focused specifically on known trawl grounds (Diaz et al. 2009). This patchiness combined with inadequate identification of species in the catches (as discussed above) has contributed to an incomplete understanding of the distributions of species, particularly crustaceans, that are important to fisheries in the SWIO. Once-off research surveys do not provide any indication of factors affecting distributions, such as seasonality, and can produce outcomes that are biased and imprecise (Hilborn and Walters, 2013). Pennino et. al. (2016) suggest that using a combination of fisheries-dependent and fisheries-independent data can provide a more comprehensive outcome than using data sets on their

own. There is, therefore, scope for future work in combining the data from the three currently operating deep-water fisheries in the SWIO with data collected during the South West Indian Ocean Fisheries Project (SWIOFP), RV *Vizconde de Eza* and RV *Dr Fridtjof Nansen* surveys. Careful attention will however need to be paid to the species identifications from each data set.

Papers 1, 2, 3 and 4 dealt with distributions of knife prawns, African langoustines and pink geryons within the trawl grounds off the eastern coast of South Africa. These studies have provided a better insight into the local distributions of these three species within the confines of the relatively small trawl grounds there. We now know that knife prawns are more available to the fishery at depths of 200-299 m and 400-499 m while African langoustines CPUEs were highest in the depth range of 300-399 m. These two species have difference preferences for the substrate in which they live, with the former preferring soft substrata composed of sticky muds (Berry et al. 1975) and the later preferring soft muddy substrata into which they presumably burrow as other *Metanephrops* species do (Bell et al. 2013). McArthur et al (2010) found that there are often complex relationships between benthic diversity and sediment variables, and percentage mud, percentage gravel, rugosity and compaction are the most dominant characteristics in determining what species are found. Variations in the distributions of these two species are most likely underpinned by the spatial distribution of the varying habitats over the trawl grounds. Unlike the prawns and langoustines, the pink geryons did not appear to show spatial/habitat preferences and changes in distribution were linked to depth and season. There were no significant distribution differences in the crab sizes over the trawl grounds, but females were found all over the grounds whereas males tended to be found deeper on the grounds. This suggests that the majority of males are found in areas that are too deep for the trawlers to operate (because of the influence of the strong Agulhas Current).

7.4 Difficulties in assessing species distributions due to inadequate reference materials

While species determinations should not be based solely on distribution information, particularly in the face of climate-change induced distribution changes (Perry et. al. 2005, Pinsky et al. 2013, Poloczanska et al. 2013), published distributions do aid in preventing assigning of incorrect species names. There are some factors to consider when using species distributions. These include the age of the document in use, the area/region covered by the source and the credibility of the source. It is important to consult more than one source, but this can be confusing when sources provide conflicting information. The prawn, langoustine and crab species discussed in Papers 1, 2, 3 and 4, and in the discussion above, are good examples of cases in which distribution information is confusing.

Online species catalogues are very popular as they save researchers from having to carry vast quantities of hard copy species descriptions when going into the field and they provide a valuable service in allowing quick checks into the validity of species names and their distributions. These sources include among others the World Register of Marine Species (www.marinespecies.org), SeaLifeBase for invertebrate species (www.sealifebase.org) and FishBase for fish and elasmobranchs (www.fishbase.org). These sources of information of very convenient but they have some challenges. For knife prawns, WoRMS lists the distribution as occurring in the South West Indian Ocean, East Africa, Kenya, Tanzania, Mozambique, South Africa (Cape of Good Hope, East London and the whole country) and Madagascar. Not one of the references provided to substantiate these occurrences are from taxonomic monographs of the species. The distributions for Kenya, Tanzania, Mozambique and South East Africa are from Dore and Frimodt (1987) who provide a basic map and description of the distribution, with no supporting references as to where this distribution was sourced, while the reference for the East Africa region is from Ivanov and Hassan (1976) who collected a single male specimen off Mozambique. The description for knife prawns given by SeaLifeBase is given as "Southeast Atlantic and Western Indian Ocean: from Kenya and Madagascar to Cape of Good Hope, South Africa" without any reference provided (SeaLifeBase 2019a). It is confusing since the main reference given for the overall species description is Holthuis (1980) which gives the distribution as South and Southeast Africa which would by convention exclude Tanzania and Kenya. Currently there are two subspecies of knife

prawns recognised from the SWIO region - these are *Haliporoides triarthrus triarthrus* from South Africa and Mozambique, and *Haliporoides triarthrus vniroi* from Madagascar and Mozambique (Kensley et al. 1987; Pérez-Farfante and Kensley 1997; De Grave and Fransen 2011). *Haliporoides* does not occur in Tanzania and Kenya.

The African langoustine is another species for which the distribution provided by WoRMS is baffling to website users (Figure 7). It shows the species to occur in the Mediterranean Sea as well as the South Pacific Ocean, the East Atlantic as well as the SWIO. The reference for these distributions is Holthuis (1991). According to Holthuis (1991), however, the distribution for African langoustines is "Indo-West Pacific region: off E. Africa (from Kenya to Natal), Madagascar". SeaLifeBase states that besides being found from Kenya to Natal, it is also found in the Southwest Atlantic. Similar to the knife prawn, there is no specific reference for the distribution and the main reference is Holthuis (1991) which does not mention the occurrence of African langoustines in the Atlantic. The maintenance of these databases is without a doubt an extremely challenging task with each taxonomic editor responsible for an average of 805 species (WoRMS 2019c). Bearing that in mind, researchers should be encouraged to validate species with which they are familiar with to ensure that the distributions and other biological data presented are accurately reflected on the species pages (van Zyl and Willemse 2000).

Figure *7: Species distribution of* <u>*Metanephrops mozambicus*</u> *as provided by the World Register of Marine Species (WoRMS 2019b).*

The use of identification guides that are not appropriate for the area in which a study is being conducted can very easily result in the misidentification of species. Because there are no comprehensive and up to date guides for the deep-water soft-sediment demersal fauna of the Southwestern Indian Ocean, the South West Indian Ocean Fisheries Project (SWIOFP) onboard researchers used an informal identification guide developed by the Oceanographic Research Institute in Durban, based on observer information from the South African crustacean trawl fishery. As discussed in Paper 6, this led to the identification of species in the trawls that were subsequently shown to not be previously described from the study areas. Because the areas where the surveys were being conducted had not had much attention in terms of taxonomic work, it was uncertain if these species were misidentifications or if these species had merely been overlooked previously and their ranges did in fact cover those areas. Without voucher specimens from the surveys it was impossible to distinguish which situation applied or if it was a combination of both. For paper 6, the process of deciding to use genus as the taxon level for analysis was done after determining that there were other congeneric species of the "misidentified" species in the area. This at least provided some confidence that analyses would not be skewed.

Another example whereby inappropriate guides may cause misidentifications is when guides are for specific areas and only give distributions within that area rather than the whole range of the species. In

Atkinson and Sink (2018), which is titled as a guide to deep-water invertebrates of South Africa, only distributional ranges for the West and South coasts of South Africa are provided, and East coast are not mentioned. This has not been made apparent in the guide, so users might not realise that the species distributions do not include to the entire country. For both knife prawns and pink geryons, the distributions are given as "West and South coasts of South Africa" with no mention of the East coast where these species are of commercial value. Similarly, African langoustines do not feature at all because the species does not occur within the geographic scope of this particular guide.

The use of outdated guides also needs to be mentioned although it has to some extent been covered in the discussion about the misidentification of the Andaman lobster above. Researchers should make an effort to trace the latest species reviews before embarking on surveys were species identifications will be undertaken and used to describe distributions. This applies also to species that are caught regularly as these species may have been reclassified, such as the *Chlorophthalmus* and *Squalus* genera mentioned above. A further example of a species that may have been perpetually misidentified is that of *C. somaliensis* which has been recorded as pink geryons in Kenya (Paper 5 and Figure 5c) when in all likelihood it is *C. somaliensis*.

Undoubtedly there are numerous obstacles in determining the correct distributions of species of the Southwestern Indian Ocean. Of course, one of the most important challenges is that taxonomy seems to be a dying science with few scientists training in this discipline (Drew 2011). It is becoming increasingly difficult to find taxonomic experts to include on research surveys and the importance of collecting taxonomic samples seems to be overlooked more often.

7.5 Biogeographic considerations in the context of ocean circulation and dispersal

The three focal species, knife prawns, African langoustines and pink geryons, are generally found along the eastern African coast from South Africa northwards and on the western coast of Madagascar. But what has led to these distributions, how the distributions are maintained and are these single stocks/populations, are questions whose answers are required to develop or maintain sustainable fisheries. This requires an understanding of their biogeography. Biogeography is the investigation into the patterns and processes that direct the distributions of species. Factors that need to be considered include the species' life history traits, environmental factors and evolutionary influences.

Species' diversity and distribution is determined by their biological and behavioural traits. These traits include the characteristics of their life stages such as egg, larval, juvenile and adult phases with their specific requirements and adaptations. When egg and larval stages are longer, the gene flow of a population can be increased (White et al. 2009) or decreased when eggs are demersal rather than pelagic, or if the larvae are large, or the planktonic larval phase is short (McCusker and Bentzen 2010). Migration also plays a role in distributions and if adult benthic marine organisms show limited or no migratory behaviour, it is expected that gene flow occurs via larval movements which may be active or passive (Hellberg 2009). Distributions may also be influenced by habitat preferences, for example size distributions differing over depths or females inhabiting shallower areas than males (Hastie 1995, Gutiérrez et al. 2011). Environmental factors that may contribute to distributions include habitat topography, salinity, temperature and food availability, all of which may affect the separate life stages differently (Ayre et al. 2009). Ocean currents and counter-currents also influence the gene flow by either limiting or enhancing connectivity (Gonzalez and Zardoya 2007, Berntson and Moran 2009, Viñas et al. 2010) and historical events such as continental drift, climate change, sea level rise and sedimentation can have contributed to the evolutionary developments of species (Martínez et al. 2006, Gonzalez & Zardoya 2007, Provan & Bennett 2008, Hoareau et al. 2012). The population genetic structure and history of species, particularly those that are of commercial importance and where conservation and management of the species is required, can be and have been analysed using molecular markers (Hauser & Ward 1998, Ovenden et al. 2009, Kiper 2014, Healey et al. 2017).

The links between biogeography and population genetics of Southwestern Indian Ocean (SWIO) marine species has only fairly recently started to become a research focus and most studies focus on shallow-water teleosts such as *Otolithes ruber* (Kiper 2014), *Lethrinus nebulosus* (Healey et al. 2018) and *Pristipomoides filamentosus* (Mzingirwa et al. 2019) and shallow-water invertebrates such as *Neosarmatium meinerti* (Ragionieriet al. 2010), *Uca annulipes* (Silva et al. 2010), *Panulirus homarus* (Singh et al. 2018) and penaeid prawns (Mkare et al. 2014, Mkare et al. 2017). Zacarias (2013) explored the population genetics of *Haliporoides triarthrus* and *Metanephrops mozambicus* from South Africa and Mozambique in his MSc thesis but his work was not published due to concerns that the genetic markers used were not appropriate. *Chaceon macphersoni* has so far not been subjected to any biogeographical studies.

One of the oldest recognised patterns of biodiversity is the increase in biodiversity with decreasing latitude (Rosenzweig 1995, Gaston 1996a, Gaston 1996b, Brown and Lomolino 1998, Willig 2001). According to Schemske (2002) these gradients are due to historical, geographic, biotic, abiotic and stochastic influences. Latitude is, however, a proxy for other environmental gradients such as temperature, solar radiation and seasonality. While there are some exceptions to these gradients, they are true for most marine fishes (Barbour & Brown 1974) and for decapod crustaceans (Steele 1988). During the South West Indian Ocean Fisheries Project (SWIOFP), crustacean trawl surveys were conducted in Mozambique, Tanzania, Kenya and Madagascar. The catches from these surveys were used in Paper 6 to determine if there were gradients in composition of demersal fauna of the region. Due to limitations in the identification of species, genus level was used for the analyses (see above). Willig et al. (2003) state that patterns based on higher taxonomic levels than species may repeat those at species level, but caution must be used when assuming that the relationship is quantitative. Using genera for the SWIOFP data (Paper 6) it was possible to determine that there were indeed gradients in distributions from north to south along the coast of the mainland, and differences between deep-water fauna found off the African mainland and off the West coast of Madagascar. There was an overall dissimilarity of 90% between the northern (Kenya and Tanzania) and the southern (Mozambique and Madagascar) sampling sites. While this marked dissimilarity supports the theory of a latitudinal gradient there is some caution required in interpreting the results. Two commercial trawl vessels were used for the surveys, one based in the south and the other based in the north. Catches were standardised using a ratio of the area sampled by the nets and the smaller vessel's catch was scaled up by this ratio to equate them to that of the larger vessel. There were also more trawls undertaken in the south than in the north so the species in the southern area were deemed to be better represented. Even with these constraints, Kenya had the highest diversity while Mozambique had the lowest. Gradients of species diversity can inform fisheries managers from the region as to which resources are more important to which areas and which genera are the drivers of similarities and dissimilarities between benthic communities. Albeit hampered by problems with species identification and distribution information, Paper 6 showed that there is at very least a broad scale pattern against which to compare future catch information. This will be of importance in the consideration of changes in diversity due to climate change, as some species or phases of their life cycles may not be able to survive (Orr et al. 2005, Fabry et al. 2008, Fogarty et al. 2008, Cheung et al. 2011).

Previous studies have shown that the availability of physical habitat is not evenly distributed over space and spatial clusters, and long stretches of unsuitable habitat can be a limiting factor in determining dispersal (Pearson and Dawson 2005), range limits (Sexton et al. 2009) and biogeographical regions (Whitton et al. 2012). The current knowledge on the distributions of the three species of this study is closely linked to the grounds on which trawls, either commercial or research, have been deployed and, in the case of the crabs some experimental trap fisheries that were conducted over a limited time frame (Groeneveld and Everett 2015, Paper 3 and 4). It is highly probable that these species are also found in areas where trawlers are unable to operate because they may be beyond the vessels' operational capabilities or are too risky to trawl. The absence of detailed maps of the seafloor of the SWIO limits the interpretation of biogeography for the three species, making it difficult to predict the full extent of the population distributions. It also cannot be determined if areas such as the northern continental slope of Mozambique have unsuitable habitat that is extensive enough to form effective barriers to the northward dispersal of African langoustines and pink geryons (Figure 8). Furthermore, Fenberg and

Rivadeneira (2019) hypothesise that species that have low dispersal potential (i.e. short or non-pelagic larval phases) would be more directly affected by regional patterns of habitat continuity compared to those with a longer pelagic phase. Thus, ecological dynamics of any marine species is affected by its life history.

With regards to the individual species distributions, Figure 8 provides the localities of catches of knife prawns, African langoustines (with Andaman lobsters included) and pink geryons from the surveys conducted during the South West Indian Ocean Fisheries Project (SWIOFP) and from the RV *Dr Fridtjof Nansen* surveys (Groeneveld and Koranteng 2017, EAF Nansen Programme Unpublished data). The Andaman lobster has been included since this is considered a misidentification of the African langoustine. These maps show that all three species occur off the East coast of mainland Africa and on the West coast of Madagascar. As discussed above there are substantial gaps in our knowledge of these three species but by using information from other closely related species, it may be possible to infer how these distributions came about and how they are maintained.
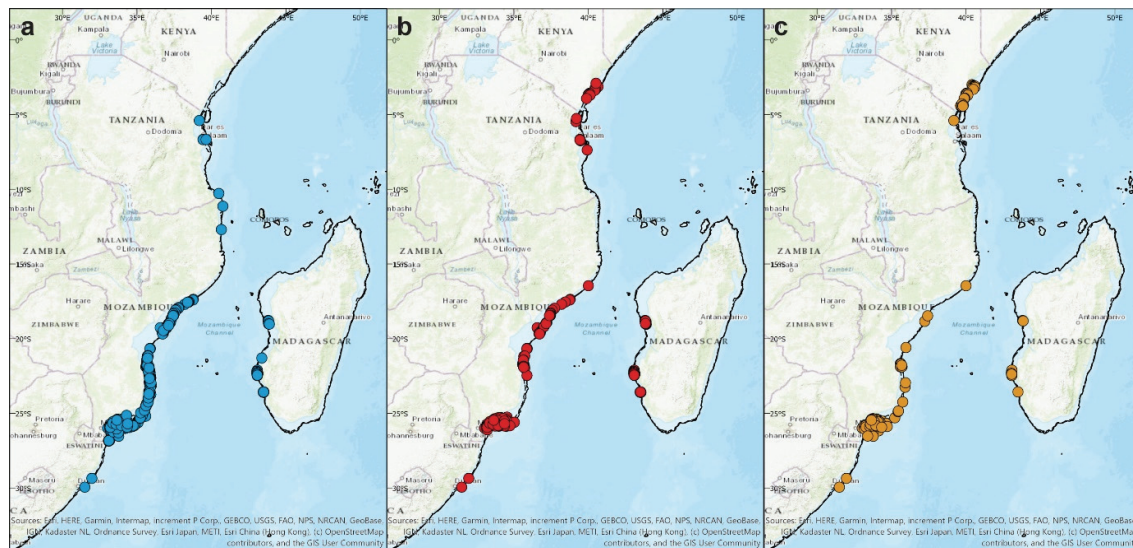

Figure 8: *Maps showing position of trawled catches of a) Haliporoides triarthrus, b) Metanephrops mozambicus and M. andamanicus, and c) Chaceon macphersoni from surveys conducted during the South West Indian Ocean Fisheries Projects (Papers 5 and 6) and by the RV Dr Fridtjof Nansen (Groeneveld and Koranteng 2017, EAF Nansen Programme Unpublished data).*

Different population dynamics can occur for species with long-lived, far-dispersing larvae as opposed to species with short-lived larvae (Eckert 2003, Kinlan and Gaines 2003; Weersing and Toonen 2009). Likewise, natural and anthropogenic disturbances will affect species that have highly dispersive larvae rather than species with larvae that spend a very short time in the water column (Levin 1984). Oceanographic transport systems are thought to facilitate genetic connections between remote ecosystems (Marsac et al. 2014) such as those seen in Figure 8 where species distributions are separated by the Mozambique Channel and the extensive northern Mozambique coastline. The effectiveness of these modes of connectivity by meso and sub-mesoscale circulations has however been debated with proponents (Rosenblatt and Waples, 1986; Shulman and Bermingham, 1995; Doherty et al., 1995) and opponents (Cowen et al., 2000; Warner and Cowen, 2002). In terms of the SWIO and its predominant southward flow of water, it is not surprising that species that occur in Mozambique are also found off the East Coast of South Africa. Not so easily explained though is the co-occurrence of a range of species that occur off the African mainland and Madagascar (Marsac et al. 2014). The success of egg and larval transport is dependent on the duration of these stages in the species' life cycles and also on the ability of larvae to control their movement within the water column. The eggs and larvae of invertebrates need to reach their settlement destinations before metamorphosis occurs, to ensure their survival (Marsac et al. 2014). Some species, such as the spiny lobster *Panulirus homarus rubellus*, have no contemporary gene flow across the Mozambique Channel and yet the Madagascar clade originated on the coast of the

African mainland from the ancestral lineage (Reddy et al. 2014). An explanation provided by Pollock (1992) is that colonization events occurred initially through larval dispersal and exchange, followed by isolation resulting from sea level changes during glacial periods.

It is possible that eggs and larvae of species that do cross the Mozambique Channel are doing so through entrainment by the mesoscale eddies that are characteristic of the area (Ockhuis et al. 2017). This strategy is only successful for species with long pelagic egg and larval stages as, depending on the origin of the propagules, the crossing could take between five and seven months (Marsac et al. 2014). For benthic organisms, the settlement destination must be reached before metamorphosis occurs. A quicker alternate route for crossing suggested by Marsac et al. (2014) was through the regions of the contra-rotating eddies where current speeds would allow a channel crossing of 50 days (Hancke et al. 2014). Schleyer et al. (2019) through the use of the South-West Indian Ocean Model distinguished five transport categories for crossing the Mozambique Channel. These are: (1) transport within eddies, (2) advection towards/onto the continental shelf by eddies in the narrowest part of the channel, (3) almost direct cross-channel transport (probably in interstitial waters between eddies), (4) particles caught up in southward travelling eddies and (5) fast transport in interstitial waters between westward propagating eddies. Understanding the feasibility of transport of genes for the various species across the geographic barriers of the SWIO therefore requires knowledge of the egg and larval stages of the species.

African langoustine females are ovigerous, like many decapod species. Egg-bearing females are found in trawl catches all year round, but it is more probable to catch them in December (Paper 2). Mating is estimated to occur around August with hatching occurring around May (Paper 2). Eggs, therefore, hatch after 9 to 10 months and the larvae are in an advanced developmental state with limited swimming abilities, a short or no natatory period and settle within days to hours after hatching (Robey and Groeneveld 2014). With such a short larval stage, probably close to the seabed, it appears that the langoustines do not make use of ocean currents to either move along the African coast or across the Mozambique Channel. Without other factors such as adult migration, it is expected that these life history traits will result in unique genetic structures within subpopulations that have developed in isolation. Zacharias (2013) found genetic partitioning between six sample sites (three from Mozambique, one from South Africa and two from Madagascar) using mitochondrial DNA analyses. As with *P. homarus rubellus*, population expansion was interpreted as having occurred after the Last Glacial Maximum period, approximately 19 000 – 20 000 years ago (Yokoyama et al. 2000), at the end of the Pleistocene era, and gene flow between subpopulations was interrupted by sea level fluctuations – as suggested for other species by Daniels et al. (2002), Ragionieri et al. (2009) and Daniels (2011).

Pink geryon females are ovigerous but unlike African langoustines there is very little further information available on the biology of this crab, particularly for the egg and larval stages. Despite catches on the trawl grounds in both South Africa (Paper 3) and Mozambique (Paula e Silva 1985) being dominated by females, very few egg-bearing females were encountered during the studies for Paper 3 with only 6% and 8% of females caught in the trawls and traps, respectively, being ovigerous. Haefner (1978) and Wigley et al. (1975) suggested that hatching of eggs occurred in depths of 200 to 400 m for *Chaceon* species. This is an unlikely strategy for pink geryons as we would then expect to see a higher amount of ovigerous females on the trawl grounds that occur at these depths. It is possible though that the females do move to shallower areas to release their eggs, but possibly not on the trawl grounds. The decline in the proportion of female crabs caught during the austral winter months (Paper 3) suggest that gravid females move off the trawl grounds and aggregate where they are unavailable to the fishery. A similar scenario was described by Melville-Smith (1987) for *C. maritae* off Namibia. This unavailability of egg-bearing females to the trawls and traps has compounded the difficulty in studying their reproductive biology. In the absence of information on pink geryons, information on other *Chaceon* species can be used in the assumption that species in the same genera exhibit the same life history traits. It has been suggested that the eggs are carried for 9 months by *C. quinquedens* (Haefner 1977, 1978), *C. maritae* (Melville-Smith 1987) and *C. fenneri* and *C. quinquedens* (Erdman and Blake 1988, Erdman et al. 1991). Larval development of *C. quinquedens* was estimated at between 23 and 125 days with duration dependent on temperature and food availability (Kelly et al. 1982). As larvae mature, there is decline in swimming activity, particularly in the later stages, and their sinking rates increase. Thus, the larval

distribution in the water column becomes deeper as they mature towards metamorphosis (Kelly et al. 1982). With temperature being an important factor in the duration of the larval stage, and the larvae being exposed to a variety of temperatures as they rise in the water column, there is a resultant wide range in dispersion potential (Kelly et al. 1982). In the SWIO context, should pink geryon larvae exhibit the same larval development and behaviour, the larvae released nearer to the tropics will have shorter larval stages due to the higher water temperatures and settle closer to the reproductively active adults while those further south will have the potential to settle in more distant sites. Since pink geryons are likely to inhabit a similar range of habitats to other *Chaceon* species (Manning and Holthuis 1989, Wenner and Barans 1990, Hastie 1995), there is less risk of the megalopa not finding a suitable habitat on which to settle as may happen with the African langoustines that require soft sediments into which they burrow. As previously discussed, knowledge of the distribution of pink geryons is very much limited to where trawling (and to a smaller extent trapping) can occur while the crabs live in much more diverse habitats, so their distributions could be vastly underestimated by this limited fisheries-based source of information. No genetic studies have as yet been conducted on the pink geryons but morphological studies on North Atlantic species of *Chaceon* hypothesised that speciation was relatively recent (Weinberg et al. 2003).

Despite the commercial importance of knife prawns to fisheries (de Freitas 1985, Paper 1), there is almost no information available on its reproductive biology. From a literature search this lack appears to be common in the other *Haliporoides* species: *H. cristatus, H. diomedeae* and *H. sibogae*, as well as in most deep-water prawns. There have also been no reports of studies on the culture of any deep-sea Penaeoid species (Carretón et al. 2010). But, *Haliporoides* belongs to the Dendrobranchiata suborder so some assumptions can be made regarding its life history based on other species in the suborder. Eggs hatch into larvae that go through the following moults: nauplii, protozoea, and mysis (Carretón et al. 2010). It is assumed that ripe females spawn on the sea floor and the egg and nauplius stages have the ability to move to the water surface through buoyancy and swimming abilities (Clavel-Henry et al. 2019). From there it can be assumed that hydrodynamic processes will determine if the larvae are dispersed or retained. Duration of the planktonic phases of knife prawns is unknown so the extent of dispersal is unknown. Reproductively active females are scarce on SWIO trawl grounds except for Bazaruto, Mozambique (Brinca et al. 1983). Females dominated catches deeper than 450 m which may suggest that the spawning population is found at depths beyond the capabilities of the trawlers (Paper 1). The hypothesis presented by Brinca et al. (1983) that Bazaruto was the primary spawning ground for knife prawns was refuted by genetic studies conducted by Zacarias et al. (2013), who indicated that the subpopulations found in South Africa, Madagascar and Mozambique were genetically distinct. While some caution is required interpreting the results of this study due to the use of pseudogenes in the analyses (ORI unpubl. data), a reviewer felt that the subpopulation separation results were not in question. From these separations we can carefully draw the conclusions that Bazaruto is not the single source for recruitment to all the trawl grounds of the SWIO, because the larval phases may not be long enough to take advantage of the ocean currents in the region and that there are most likely other barriers to the dispersal of the larvae between regions. These barriers may include the presence of a strong thermocline that inhibits water mixing (Thorpe 2007) or food availability in the later larval stages (Fortibuoni et al. 2010).

Species distributions are not based on the dispersal abilities of eggs and larvae alone but rather through complex interactions between biotic and abiotic factors to which each species is subjected. Abiotic factors include temperature, salinity, oxygen concentration and solar radiation (Lomolino et al. 2006). Abiotic factors in the SWIO that may affect species distributions include low oxygen zones (Sæterdal et al. 1999, Halo et al 2017) and the general oligotrophic nature of the region due to very little cold-water upwelling (Huggett and Kyewalyanga 2017). This explains limited food availability to organisms of the SWIO, but food availability on its own is not a predictor of life histories. Marshall and Burgess (2014) found that the relative proportion of species occurring in a habitat that have a planktonic (versus a non-planktonic) larval phase was associated with temperature and seasonality. Where food availability is more seasonal, Marshall and Burgess (2014) also found that the proportion of species with a planktonic phase is higher. Biotic factors that influence home ranges include competition, predation, parasitism and availability of prey or mutualistic species (Vance 1973, Wiens 2011, Marshall and

Burgess 2014). The role of biotic factors in large-scale biogeographic patterns remains largely unexplored (Wiens 2011). While all these factors on their own or through interactions may limit species ranges, it is also the failure of the species to adapt to changes in conditions at the edges of their distributions that limits range expansions (Kirkpatrick and Barton 1997, Gaston 2003, Gaston 2009).

A dispersal barrier appears to exist for crustaceans off northern Mozambique as can be seen in Figures 4 and 8. Very few crustaceans were recorded here during the RV *Dr Fridtjof Nansen* surveys between 1977 and 2018 (Groeneveld and Koranteng 2017, EAF Nansen Programme Unpublished data) – albeit that few demersal trawls could be deployed in this region of the SWIO. The separation of demersal communities found in Paper 6 identified significant differences between the north (Kenya and Tanzania) and the south (Mozambique and Madagascar) and this separation was also found for the shallow-water teleost *Otolithes ruber* with very low levels of genetic mixing between Kenya and Tanzania in the north and Mozambique, South Africa and Madagascar in the south (Kiper 2014). This separation of populations is speculated to have come about through a combination of historical factors such as sea level changes (Daniels et al. 2002, Ragionieri et al. 2009, Daniels 2011), biological differences and oceanographic features (Kiper 2014). The historical development of three "oceanic" large marine ecosystems (LME) discussed by Pollock (1998) may account for the differences between habitat suitability for some species with a central truly tropical LME off the coasts of northern Mozambique, northern Madagascar, Tanzania and Kenya, flanked on each side by subtropical LMEs. The tropical conditions of this LME may have been beyond the adaption capabilities of these and other species of the region. The hydrodynamic energy associated with the division of the South Equatorial Current to the north and south in the vicinity of the border between Mozambique and Tanzania (Figure 2) may also provide a barrier to the dispersal of fauna that reproduce to the south of this area, but this needs further investigation.

8 Further work

The work described in this thesis has answered some questions related to the biology of three commercially important crustacean species as well as their place in the deep-water trawl fisheries of the Southwest Indian Ocean (SWIO). It has also raised a number of concerns and suggestions for future activities and research. A fundamental problem that faces the region is the lack of taxonomists or even biologists with some experience in taxonomy. This extends beyond the deep-water crustaceans, but is perhaps especially prominent in these faunae, and in deep-water fauna in general, owing to their being less often encountered. As Forges et al. (2013) state, "good taxonomic work at species level is a prerequisite for any meaningful analysis on ecology or biogeography". It is, therefore, extremely important to promote the development of this area of expertise in the SWIO and in particular for the crustacean species that form the core of the deep-water trawl fisheries.

Taxonomic monographs are generally difficult to access (Gill 1999) and it would be very useful to develop a repository for them so that researchers may access them with relative ease. This could be accomplished through the Nairobi Convention Clearinghouse that is currently under development. The Nairobi Convention Clearinghouse will be a central repository that provides accurate and relevant data and information for improved management and protection of the coastal and marine environment in the western Indian Ocean (UNEP 2019).

Another useful resource to have would be a definitive guide to the deep-water, soft-sediment species. Guides can be inaccurate and oversimplified (Gill 1999) so it would be imperative to make the guide as accurate as possible with sufficient information to make it a worthwhile resource. This would need the cooperation of researchers from all countries in the region that have or have the potential for these fisheries.

Developing this guide would require that the uncertainties in the identifications of species be addressed. As a first step the data collected from all sources, both fisheries and fisheries independent data, could be combined to establish a baseline off which to work. Validation of the distributions established from this step would require the collection of specimens from as many localities as possible. Of great interest would be from areas where species overlap, where it is speculated that there are transitions of one species to another and the outer limits of distributions. Sampled specimens would need to be subjected to traditional morphometric analyses as well as genetic methods.

Supplementary to this would be the development of maps of the soft-sediment habitats of the continental shelves and slopes. This can be achieved through the analyses of acoustic data from various sources such as research vessels and from ships of opportunity that have passed through the region. Having knowledge of the availability of appropriate habitats will allow for informed decision-making regarding the extent of stocks and for the appropriate placement for the development of Marine Protected Areas.

With specific regard to the three species discussed in this study, it is important to understand the distributions since all three have transboundary distributions which has management implications. Species uncertainties need to be understood as well as population dynamics. The genetic studies of knife prawns and African langoustines should be repeated using genetic markers that are better understood than those of mitochondrial DNA. Mitochondrial DNA analyses are open to interpretation biases due to the occurrence of pseudogenes which are known to be common in crustaceans (Schneider-Broussard et al. 1997, William and Knowlton 2001, Song et al. 2008, Buhay 2009, Baeza and Fuentes 2013, Kim et al. 2013). Genetic markers whose mode of evolution that is better understood (microsatellites, genome-wide single nucleotide polymorphisms, etc.) would be more appropriate (Lemopoulos et al. 2018). It is also recommended that other species, such as the pink geryon, be subjected to these analyses to provide a better understanding of their phylogeny. Even simple barcoding of specimens from different regions could provide an indication as to whether species are as widely distributed as recorded.

A further suggestion is that the diversity studies undertaken for Paper 6 be expanded to incorporate the effects of abiotic factors on the species richness, diversity and community structures. This will contribute towards providing more comprehensive understanding of the driving forces behind the latitudinal gradients of the SWIO. Factors for exploration should include ocean circulation (Marsac et al. 2014), water temperature, productivity, and seasonality (Ricklefs and Schluter 1993, Marshall and Burgess 2014). Currents, temperature and productivity data are available from the RV *Dr Fridtjof Nansen* surveys (Groeneveld and Koranteng 2017) and these data can be supplemented with data from satellite programs such as Ocean Color Web (https://oceancolor.gsfc.nasa.gov/). Understanding the relationships between species diversity and community structures with regard to abiotic factors will provide a necessary understanding of changes that will occur due to the influences of pollution and climate change (Ormond et al. 1998, Harley et al. 2006).

Paper 4 provides a first step towards the designation of trawl footprints (the seabed area trawled at least once in a specified location and time period) for the trawl grounds of the East Coast of South Africa. Amoroso et al. (2018) described the trawl footprint for 24 continental shelves and slopes down to 1000 m. For the East Agulhas Current, data were combined for the southern Agulhas Banks trawl fisheries as well as the east coast crustacean trawl fishery and included a large area in between the two as part of available trawl grounds even though trawling is not possible. This study did not provide an indication of a possible trawl footprint specifically on the habitats where trawling is possible. In terms of management this provides an underestimation of the impact that trawling is having considering the limited amount of habitat that is actually available for trawling. It will also be advisable to develop trawl footprints for other SWIO countries where trawling occurs such as Mozambique, Madagascar and Kenya. These trawl footprints will provide a better indication of the extent of impacts that the industry is having on the ecosystems.

The final suggestion for further work applies to developing space time analyses of the various commercial size categories of packed target species in the South African crustacean trawl fishery, similar to the methodology used in Paper 4. Knowing which areas are predominantly occupied by the smallest and largest individuals and when they frequent these areas can have implications for enhancing the sustainability of the resources and for maximising the fisheries profits. When juvenile habitats are protected, they can increase exploitable biomass by subsidising unprotected areas (Gell and Roberts 2003, Kerwath, et al. 2013). Fisheries receive higher returns for larger specimens, so for this fishery that has only limited potential (based on the rapid negative response of catch per unit effort to increased effort described in Papers 1, 2, 3 and 4), it may be possible to discover areas that are more favourable at certain times to harvesting larger individuals. If fishers are informed about where to find these individuals, they can expend less energy to find them while at the same time reducing growth overfishing on the smaller specimens. Currently there is no protection for any of the size classes of the resources but by providing maps of areas where larger individuals can be caught, the harvesting of individuals that are smaller than the size that would produce the maximum yield per recruit (Caillouet et al. 2008) would be reduced.

9 **Concluding remarks**

The purpose of the studies described in this thesis was to explore the biology and distribution of three commercially important crustacean species in the deep-water trawl fisheries of the Southwestern Indian Ocean (SWIO). The studies also investigated the potential for deep-water trawl fisheries in the SWIO and the diversity gradients that exist in these soft sediment habitats. The papers have provided updated information on various aspects of the deep-water trawl fisheries but at the same time it has highlighted the inconsistencies and gaps in what is known of the three species specifically and also the limited scientific resources available to researchers in the SWIO. In order to better manage and conserve these transboundary resources, it is necessary to understand their biogeography. Biogeographic information has the potential to enhance systematic conservation planning but such information for marine ecosystems is difficult to define (Lourie and Vincent 2004) as highlighted in this thesis. Species misidentifications can compromise sustainable management measures by leading to overestimation of stock abundances or inappropriate management measures based on incorrect biological parameters such as age at maturity (Griffiths and Heemstra 1995). They can also contribute to underestimates of species richness of areas and cause inaccuracies in the understanding of biological, ecological and evolutionary processes (Garcia-Vazquez et al. 2012). The understanding of biogeography and gene flow has implications when developing marine reserves (Shanks et al. 2003) and managing the resources, be they single populations or a collection of subpopulations. Inspection of the marine protected areas on the Protected Planet website (https://www.protectedplanet.net/) showed that for the countries of the SWIO, very few deep-water soft sediment habitats have received any protection. This excludes the island states of Seychelles, Mauritius and Comoros where trawling is banned. Understanding the biogeography of the SWIO species will advance the identification and implementation of effective marine protected areas in these specific habitats.

This study has exposed the need for improved taxonomic skills and better understanding of the biology of the species concerned. Regional bodies such as the South West Indian Ocean Fisheries Commission, the Western Indian Ocean Marine Science Association and the Sapphire Project of the Nairobi Convention should be persuaded to invest in addressing these issues in order to protect the resources themselves and in so doing, secure a long-term source of income and food in a region where many people rely on the sea for their economic, social and cultural security (Standing 2009, FAO 2010, Cox 2012).

10 References

Alexander LM. 1998. Somali Current large marine ecosystem and related issues. In: Sherman K, Okemwa E, Ntiba M. (eds). Large marine ecosystems of the Indian Ocean: Assessment, sustainability, and management. (pp 327-331) Cambridge, MA: Blackwell Science.

Alverson, D. L., 1997. Global assessment of fisheries bycatch and discards: a summary overview, global Trends. Fisheries Management 20: 115–125.

Amoroso RO, Pitcher CR, Rijnsdorp AD, McConnaughey RA, Parma AM, Suuronen P, … Althaus F. 2018. Bottom trawl fishing footprints on the world's continental shelves. Proceedings of the National Academy of Sciences 15(43): E10275–E10282. doi:10.1073/pnas.1802379115

Atkinson LJ, Sink KJ. (Eds). 2018. Field Guide to the Offshore Marine Invertebrates of South Africa, Malachite Marketing and Media, Pretoria, pp. 498.

Ayre DJ, Minchinton TE, Perrin C. 2009. Does life history predict past and current connectivity for rocky intertidal invertebrates across a marine biogeographic barrier? Molecular Ecology, 18: 1887-1903.

Baeza JA, Fuentes MS. 2013. Exploring phylogenetic informativeness and nuclear copies of mitochondrial DNA (numts) in three commonly used mitochondrial genes: mitochondrial phylogeny of peppermint, cleaner, and semi-terrestrial shrimps (Caridea: *Lysmata*, *Exhippolysmata*, and *Merguia*). Zoolog J Linnean Soc. 168: 699–722.

Barbour CD, Brown JH. 1974. Fish species diversity in lakes. Am. Nat. 108:473–89

Bell MC, Tuck ID, Dobby H. 2013. *Nephrops* species, pp. 357-413. In, Phillips BF. (ed.), Lobsters: Biology, Management, Aquaculture and Fisheries. Wiley-Blackwell, Hoboken, NJ.

Bellido JM, Santos MB, Pennino MG, Valeiras X, Pierce GJ. 2011. Fishery discards and bycatch: solutions for an ecosystem approach to fisheries management. Hydrobiologia 670: 317 - 333. https://doi.org/10.1007/s10750-011-0721-5

Berntson EA, Moran P. 2009. The utility and limitations of genetic data for stock identification and management of North Pacific rockfish (*Sebastes* spp.). Reviews in Fish Biology and Fisheries, 19: 233–247.

Berry PF. 1969. The Biology of *Nephrops andamanicus* Wood-Mason (Decapoda, Reptantia). Investigational Report, Oceanographic Research Institute, 22, 1–55. Durban.

Berry PF. 1972. Observations on the fishery for *Palinurus delagoae*. Unpublished Report 72, Oceanographic Research Institute, 1–5. Durban.

Berry PF, Heydorn AEF, Alletson DJ. 1975. The biology of the knife prawn, *Hymenopenaeus triarthrus* off the Natal coast. Unpublished Report, Oceanographic Research Institute, 1–29. Durban.

Brinca L, Cristo M, Silva C. 1983. Camarão de profundidade: Relatorio dos cruzeiros realizados com o N/I "Ernst Haeckel" em. Revista de Investigação Pesqueira, 5, 1–99.

Brown JH, Lomolino MV. 1998. Biogeography. Sunderland, MA: Sinauer. 2nd ed.

Buck EH. 2010. Seafood marketing: combating fraud and deception. [Internet document] URL: https://www.everycrsreport.com/files/20100702_RL34124_761e664dbcd4f2e9f3bd2c7261aa003192e7e479.pdf. Accessed 25/11/2019. Food Research International 46: 30–40.

Buhay JE. 2009. "COI-like" sequences are becoming problematic in molecular systematic and DNA barcoding studies. J Crust Biol. 29: 96–110.

Caillouet CW, Hart RA, Nance JM. 2008. Growth overfishing in the brown shrimp fishery of Texas, Louisiana, and adjoining Gulf of Mexico EEZ. Fisheries Research, 92(2-3): 289–302. doi:10.1016/j.fishres.2008.01.009

Carretón M, Company JB, Planella L, Heras S, García-Marín J-L, Agulló M, et al. 2010. Morphological identification and molecular confirmation of the deep-sea blue and red shrimp *Aristeus antennatus* larvae. PeerJ. 2010; 7: e6063.

Cawthorn D-M, Steinman HA, Witthuhn RC. 2012. DNA barcoding reveals a high incidence of fish species misrepresentation and substitution on the South African market.

Chan T-Y. 2010. Annotated Checklist of the World's Marine Lobsters (Crustacea: Decapoda: Astacidea, Glypheidea, Achelata, Polychelida). The Raffles Bulletin of Zoology 2010 Supplement No. 23: 153–181

Cheung WWL, Dunne J, Sarmiento JL, Pauly D. 2011. Integrating ecophysiology and plankton dynamics into projected maximum fisheries catch potential under climate change in the Northeast Atlantic, ICES Journal of Marine Science 68: 1008-1018.

Clavel-Henry M, Solé J, Bahamon N, Briton F, Rotllant G, Company JB. In review. Influence of the summer deep-sea circulations on passive drifts among the submarine canyons in the Northwestern Mediterranean Sea. Ocean Sci. Discuss. doi: 10.5194/os-2019-61

Cowen RK, Lwiza KMM, Sponaugle S, Paris CB, Olson DB. 2000. Connectivity of marine populations: open or closed? Science 287: 857–859.

Cox J. 2012. Assessment Report on Small-Scale Fisheries in Africa. Masifundise Development Trust for AU-IBAR

Cunningham S, Bodiguel C. 2005. Subregional review: Southwest Indian Ocean. In: de Young C (ed). Review of the state of world marine capture fisheries management: Indian Ocean. FAO Fisheries Technical Paper. No. 488. Rome, FAO. 2006. 458p.

DAFF. 2013. Draft revised KwaZulu-Natal prawn trawl policy on the allocation and management of fishing rights: 2013. Department of Agriculture, Forestry and Fisheries, Cape Town, South Africa.

DAFF. 2018. Permit Conditions: KwaZulu-Natal Prawn Trawl Fishery, Fishing Season: 2019. Department of Agriculture, Forestry and Fisheries, Cape Town, South Africa.

Daniels SR. 2011. Reconstructing the colonisation and diversification history of the endemic freshwater crab (*Seychellum alluaudi*) in the granitic and volcanic Seychelles Archipelago. Molecular Phylogenetics and Evolution 61: 534-542.

Daniels SR, Stewart BA, Gouws G, Cunningham M, Matthee CA. 2002. Phylogenetic relationships of the southern African freshwater crab fauna (Decapoda: Potamonautidae: *Potamonautes*) derived from multiple data sets reveal biogeographic patterning. Molecular Phylogenetics and Evolution 25: 511-523.

De Freitas AJO. 1980. The Penaeoidea of Southeast Africa. PhD thesis. University of Witwatersrand, Johannesburg: 480p.

De Grave S, Fransen CHJM. 2011. Carideorum Catalogus: the recent species of the dendrobranchiate, stenopodidean, procarididean and caridean shrimps (Crustacea: Decapoda). Zoologische Mededelingen, 85(9). NCB Naturalis: Leiden. 195-588 pp.

Dias ML, dos Santos MN, Pinto MA, Jardim E, Rodrigues MJ, Santos A, Dove V. 1999. Relatório da 1a Campanha de Investigação Pesqueira Luso – Moçambicana do " NI CAPRICORNIO" nas Aguas de Moçambique – IPIMAR / IIP – Marco / Abril 1999. Instituto Nacional de Investigação Pesqueira, Maputo, Junho 1999. 90pp.

Dias N, Caramelo AM. 2005. Avaliação do estado dos stocks de gambas em Moçambique. Instituto Nacional de Investigação Pesqueira, Maputo, 15 de Novembro de 2005, 25pp.

Dias N, Caramelo AM. 2007. Avaliação do estado do stock de Haliporoides triarthrus e o estado de exploração da pescaria de gamba. Instituto Nacional de Investigação Pesqueira, Maputo, Janeiro 2007, 16pp.

Dias N, Sobrino I, Balguerias E, Palha de Sousa L, Burgos C, Varela D. 2008. Relatório do cruzeiro de investigação de recursos de profundidade realizado a bordo do b/o Vizconde de Eza de 13 de Março a 9 de Abril 2008. Instituto Nacional de Investigação Pesqueira, Maputo, 11 Agosto 2008, 116pp.

Dias N, Sobrino I, Garcia E, Silva L, Burgos C, Muñoz I. 2009. Relatório do cruzeiro de investigação de recursos de profundidade realizado a bordo do b/o Vizconde de Eza de 13 de Março a 9 de Abril 2009. Instituto Nacional de Investigação Pesqueira, Maputo, 15 de Outubro 2009, 148pp.

Dias N, Zacarias L, Caramelo AM. 2011. Análise de pescaria de gamba e perspectivas de gestáo. Instituto Nacional de Investigação Pesqueira, Maputo, 4 de Fevereiro de 2011, 15 pp.

Dias N, Zacarias L, Caramelo AM. 2013. Avaliação da Pescaria Industrial de arrasto de Camarão de profundidade. Instituto Nacional de Investigação Pesqueira, Maputo, 4 de Fevereiro de 2011, 30 pp.

Doherty PJ, Planes S, Mather P. 1995. Gene flow and larval duration in seven species of fish from the Great Barrier reef. Ecology 76: 2373–2395.

Dore I, Frimodt C. 1987. An Illustrated Guide to Shrimp of the World. Van Nostrand Reinhold Company, New York, 1-229.

Drew LW. 2011. Are We Losing the Science of Taxonomy? BioScience, 61(12), 942–946. doi:10.1525/bio.2011.61.12.4

Eckert GL. 2003. Effects of the planktonic period on marine population fluctuations. Ecology 84: 372–83.

Erdman RB, Blake NJ. 1988. Reproductive ecology of female golden crabs, *Geryon fenneri* Manning and Holthuis, from southeastern Florida. J. Crust. Biol. 8: 392–400.

Erdman RB, Blake NJ, Lockhart FD, Lindberg WJ, Perry HM, Waller RS. 1991. Comparative reproduction of the deep-sea crabs *Chaceon fenneri* and *C. quinquedens* (Brachyura: Geryonidae) from the northeast Gulf of Mexico. Invertebr. Repr. Dev. 19: 175–184.

Everett BI. 2017. Study area, vessels and surveys. In: Groeneveld, J.C. & Koranteng, K.A. (Eds). 2017. The RV Dr Fridtjof Nansen in the Western Indian Ocean: Voyages of marine research and capacity development. FAO. Rome, Italy: 23 – 35.

Fabry VJ, Seibel BA, Feely RA, Orr JC. 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. ICES Journal of Marine Science 65: 414-432.

FAO. 2010. The state of world fisheries and aquaculture. Food and Agriculture Organization of the United Nations, Rome.

FAOa. 2019. Global Capture Production 1950-2017. http://www.fao.org/fishery/statistics/global-capture-production/query/en Accessed on 15 November 2019.

FAOb. 2019. Fishery Commodities Global Production and Trade Dataset 1976-2017. http://www.fao.org/fishery/statistics/global-commodities-production/query/en Accessed on 19 November 2019.

Fenberg PB, Rivadeneira MM. 2019. On the importance of habitat continuity for delimiting biogeographic regions and shaping richness gradients. Ecology Letters. DOI: 10.1111/ele.13228

Fennessy ST, Everett BI. 2015. Crustacean shallow-water trawl fisheries. In: van der Elst RP, Everett BI. (eds). Offshore fisheries of the Southwest Indian Ocean: their status and the impact on vulnerable species. South African Association for Marine Biological Research Special Publication (10): 19-66.

Fennessy ST, Groeneveld JC. 1997. A review of the offshore trawl fishery for crustaceans on the east coast of South Africa. Fisheries Management and Ecology 4, 135–147. doi:10.1046/J.1365-2400.1997.00104.X

Fennessy ST and Green A. 2017. Shelf sediments and biodiversity. In: PAULA J (ed.). The Regional State of the Coast Report: Western Indian Ocean. UNEP and WIOMSA, Nairobi, Kenya. p. 103-114.

Fennessy S, Krakstad J-O, Groeneveld J, Bianchi G, Everett B. Demersal resources based on bottom trawl and other sampling methods. In: Groeneveld JC. & Koranteng KA. (Eds). 2017. The RV Dr Fridtjof Nansen in the Western Indian Ocean: Voyages of marine research and capacity development. FAO. Rome, Italy: 23 – 35.

Fischer W, Bianchi G. (Eds.) 1984. FAO Species Identification Sheets for Fishery Purposes. Western Indian Ocean (Fishing Area 51). Prepared and Printed with the Support of the Danish International Development Agency (DANIDA). FAO, Rome, Vol. 1-6.

Fogarty M, Incze L. Hayhoe K, Mountain D, Manning J. 2008. Potential Climate Change Impacts on Atlantic cod (*Gadus Morhua*) off the Northeastern USA. Strategies of Global changes 13: 452–466.

Fortibuoni T, Bahri T, Camilleri M, Garofalo G, Gristina M, Fiorentino F. 2010. Nursery and spawning areas of deep-water rose shrimp, *Parapenaeus longirostris* (Decapoda: Penaeidae), in the strait of Sicily (central Mediterranean Sea). Journal of Crustacean Biology, 30(2): 167-174.

Fulanda B, Ohtomi J, Mueni E, Kimani E. 2011. Fishery trends, resource-use and management system in the Ungwana Bay fishery Kenya. Ocean & Coastal Management 54(5): 401-414. https://doi.org/10.1016/j.ocecoaman.2010.12.010

Gage JD, Roberts JM, Hartley JP, Humphery JD. 2005. Potential impacts of deep-sea trawling on the benthic ecosystem along the Northern European continental margin: a review. In Barnes PW, Thomas JP. (Eds.). Benthic Habitats and the Effects of Fishing (pp. 503-517). American Fisheries Society Symposium; Vol. 41. American Fisheries Society.

Garcia-Vazquez E, Machado-Schiaffino G, Campo D, Juanes F. 2012. Species misidentification in mixed hake fisheries may lead to overexploitation and population bottlenecks. Fisheries Research 114: 52–55.

Gaston KJ. 1996a. Biodiversity: A Biology of Numbers and Difference. Oxford: Blackwell Sci.

Gaston KJ. 1996b. Biodiversity—latitudinal gradients. Prog. Phys. Geogr. 20: 466–76

Gaston KJ. 2003. The structure and dynamics of geographic ranges. Oxford, UK: Oxford University Press.

Gaston KJ. 2009. Geographic range limits: achieving synthesis. Proc. R. Soc. B 276, 1395–1406. (doi:10.1098/rspb.2008.1480)

Gell FR, Roberts CM. 2003. Benefits beyond boundaries: The fishery effects of marine reserves. Trends in Ecology & Evolution, 18(9): 448–455. https://doi.org/10.1016/S0169-5347(03)00189-7

Gilchrist JDF. 1921. Fisheries and Marine Biological Survey Report No. 1 for the Year 1920. Cape Times Limited, Government Printers, Cape Town, 1–113.

Gill AC, 1999. Subspecies, geographic forms and widespread Indo-Pacific coral reef species: a call for a change in taxonomic practice. In: Seret B, Sire JY. (eds). Fifth Indo-Pacific Fish Conference. Société Français D'Ichthyologie and Institut de Recherche pour le Dévelopment, Paris. 79-87.

Gonzalez EG, Zardoya R. 2007. Relative role of life history traits and historical factors in shaping genetic population structure of sardines (*Sardina pilchardus*). BMC Evolutionary Biology, 7: 197-209.

Griffiths MH, Heemstra PC. 1995. A contribution to the taxonomy of the marine fish genus *Argyrosomus* (Perciformes: Sciaenidae), with descriptions of two new species from southern Africa. Ichthyological Bulletin 65: 1–40.

Groeneveld JC, Everett BI. 2015. Crustacean deep-water trawl fisheries. In: van der Elst RP, Everett BI. (eds). Offshore fisheries of the Southwest Indian Ocean: their status and the impact on vulnerable species. South African Association for Marine Biological Research Special Publication (10): 67-118.

Groeneveld JC, Koranteng KA. (Eds). 2017. The RV Dr Fridtjof Nansen in the western Indian Ocean: Voyages of marine research and capacity development. FAO. Rome, Italy.

Guastella LA, Roberts MJ. 2016. Dynamics and role of the Durban cyclonic eddy in the KwaZulu-Natal Bight ecosystem, African Journal of Marine Science, 38:sup1, S23-S42, DOI: 10.2989/1814232X.2016.1159982.

Gutiérrez, N. L., Masello, A., Uscudun, G., and Defeo, O. (2011). Spatial distribution patterns in biomass and population structure of the deep sea red crab *Chaceon notialis* in the Southwestern Atlantic Ocean. Fisheries Research 110: 59–66. doi:10.1016/J.FISHRES.2011.03.012

Halo I, Malauene B, Ostrowski M. 2017. Physical Oceanography. In: Groeneveld, J.C. & Koranteng, K.A. (Eds). 2017. The RV Dr Fridtjof Nansen in the Western Indian Ocean: Voyages of marine research and capacity development. FAO. Rome, Italy: 37 – 53.

Hamre J. 1994. Biodiversity and exploitation of the main fish stocks in the Norwegian-Barents Sea ecosystem. Biodiversity and conservation 3: 473-492.

Haefner PA. 1977. Reproductive biology of the female deep-sea red crab, *Geryon quinquedens*, from the Chesapeake Bight. Fish. Bull. 75 (1): 91–102.

Haefner PA. 1978. Seasonal aspects of the biology, distribution and relative abundance of the deep-sea red crab *Geryon quinquedens* Smith, in the vicinity of the Norfolk Canyon, Western North Atlantic. Proc. Natl. Shellfish Assoc. 68: 49–62.

Hancke, L., Roberts, M.J., Ternon, J.F., 2014. Surface drifter trajectories highlight flow pathways in the Mozambique Channel. Deep-Sea Res. II 100: 27-37.

Harley CDG, Randall Hughes A, Hultgren KM, Miner BG, Sorte CJB, Thornber CS, Rodriguez LF, Tomanek L, Williams SL. 2006. The impacts of climate change in coastal marine systems. Ecology Letters, 9(2): 228–241. doi:10.1111/j.1461-0248.2005.00871.x

Hastie LC. 1995. Deep-water geryonid crabs: a continental slope resource. Oceanography and Marine Biology – an Annual Review 33: 561–584.

Hastie, L. C., and Saunders, W. B. (1992). On the distribution and fishery potential of the Japanese red-crab, *Chaceon granulatus*, in the Palauan archipelago, Western Caroline Islands. Marine Fisheries Review 54: 26–32.

Hauser L, Ward RD. 1998. Population identification in pelagic fish: The limits of molecular markers. In: Advances in molecular ecology (ed. Carvalho GR), pp. 191-224. IOS Press, Amsterdam.

Healey AJE, Gouws G, Fennessy ST, Kuguru B, Sauer WHH, Shaw PW, McKeown NJ. 2018. Genetic analysis reveals harvested *Lethrinus nebulosus* in the Southwest Indian Ocean comprise two cryptic species. ICES Journal of Marine Science, 75(4): 1465–1472. doi:10.1093/icesjms/fsx245

Hellberg ME. 2009. Gene flow and isolation among populations of marine animals. In: Annual Review of Ecology, Evolution, and Systematics, 40: 291-310.

Hiddink JG, Jennings S, Sciberras M, Szostek CL, Hughes KM, Ellis N, Rijnsdorp AD, McConnaughey RA, Mazor T, Hilborn R, Collie JS, Pitcher CR, Amoroso RO, Parma AM, Suuronen P, Kaiser MJ. 2017. Effects of bottom trawling on seabed biota. Proceedings of the National Academy of Sciences Aug 2017, 114 (31) 8301-8306; DOI: 10.1073/pnas.1618858114.

Hilborn R. 2016. Marine biodiversity needs more than protection. Nature 535: 224-226.

Hilborn, R., and Walters, C. J. Eds. 2013. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Springer Science & Business Media, Dordrecht.

Hoareau TB, Boissin E, Berrebi, P. 2012. Evolutionary history of a widespread Indo-Pacific goby: The role of Pleistocene sea-level changes on demographic contraction/expansion dynamics. Molecular Phylogenetics and Evolution, 62: 566-572.

Holthuis LB. 1980 FAO Species Catalogue. Vol. 1. Shrimps and prawns of the world. An annotated catalogue of species of interest to fisheries. FAO Fish. Synop. 125(1):271 p. Rome: FAO.

Holthuis LB. 1991. FAO species catalogue. Vol. 13. Marine lobsters of the world. An annotated and illustrated catalogue of species of interest to fisheries known to date. FAO Fisheries Synopsis. No. 125, Vol. 13. Rome, FAO. 1991. 292 p.

Huggett J, Kyewalyanga M. 20107. Ocean productivity. In: Groeneveld, J.C. & Koranteng, K.A. (Eds). 2017. The RV Dr Fridtjof Nansen in the Western Indian Ocean: Voyages of marine research and capacity development. FAO. Rome, Italy: 55 – 80.

Ivanov BG, Hassan AM. 1976. Penaeid shrimps (Decapoda, Penaeidae) collected off East Africa by the fishing vessel 'Van Gogh'. 1. *Solenocera ramadani* sp. nov., and commercial species of the genera Penaeus and Metapenaeus.— Crustaceana 30: 241-251.

Jacquet, J. L., & Pauly, D. (2007). The rise of seafood awareness campaigns in an era of collapsing fisheries. Marine Policy, 31, 308–313.

Jacquet, J. L., & Pauly, D. (2008). Trade secrets: Renaming and mislabelling of seafood. Marine Policy, 32, 309–318.

Jennings, S., Freeman, S., Parker, R., Duplisea, D. E., and Dinmore, T. A. 2005. Ecosystem consequences of bottom fishing disturbance. American Fisheries Society Symposium, 41: 73-90.

Kaiser MJ. 2019. Recent advances in understanding the environmental footprint of trawling on the seabed. Canadian Journal of Zoology, 2019, 97(9): 755-762, https://doi.org/10.1139/cjz-2018-0248.

Kaiser MJ, Collie JS, Hall SJ, Jennings S, Poiner IR. 2002. Modification of marine habitats by trawling activities: prognosis and solutions. Fish and fisheries 3(2): 114 - 136.

Kelleher, K., 2005. Discards in the world's marine fisheries. An update. FAO Fisheries Technical Paper No. 470. FAO, Rome: 131 pp.

Kelly P, Sulkin SD, Van Heukelem WF. 1982. A dispersal model for larvae of the deep sea red crab *Geryon quinquedens* based on behavioral regulation of vertical migration in the hatching stage. Marine Biology. 72: 35–43.

Kensley B, Tranter HA, Griffin DJG. 1987. Deepwater decapod Crustacea from eastern Australia (Penaeidea and Caridea). Records of the Australian Museum 39, 263-331.

Kerwath SE, Winker H, Götz A, Attwood CG. 2013. Marine protected area improves yield without disadvantaging fishers. Nature Communications, 4: 2347. https://doi.org/10.1038/ncomms3347

Kim SJ, Lee KY, Ju SJ. 2013. Nuclear mitochondrial pseudogenes in *Austinograea alayseae* hydrothermal vent crabs (Crustacea: Bythograeidae): effects on DNA barcoding. Mol Ecol Res. 13: 781–787.

Kimani EN, Okemwa GM, Kazungu JM. 2009. Fisheries in the Southwest Indian Ocean: Trends and Governance Challenges. In: Laipson E, Pandya A. (eds). The Indian Ocean: Resource and governance challenges. The Henry L. Stimson Center, Washington, USA.

Kinlan BP, Gaines SD. 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. Ecology 84: 2007–2020.

Kiper IE. 2014. Phylogeography of the snapper kob *Otolithes ruber* (Bloch & Schneider 1801) from the South West Indian Ocean. MSc thesis. University of Pretoria, South Africa.

Kirkpatrick M, Barton NH. 1997. Evolution of a species' range. Am. Nat. 150, 1–23. (doi:10.1086/286054)

Lehtiniemi M, Ojaveer H, David M, Galil B, Gollasch S, McKenzie C, Minchin D, Occhipinti-Ambrogi A, Olenin S, Pederson J. 2015. Dose of truth—Monitoring marine non-indigenous species to serve legislative requirements. Marine Policy, 54, 26–35. doi:10.1016/j.marpol.2014.12.015

Lemopoulos A, Prokkola JM, Uusi-Heikkilä S, Vasemägi A, Huusko A, Hyvärinen P, Koljonen M-L, Koskiniemi J, Vainikka A. 2019. Comparing RADseq and microsatellites for estimating genetic diversity and relatedness—Implications for brown trout conservation. Ecol Evol.9: 2106–2120. https://doi.org/10.1002/ece3.4905

Levin LA. 1984. Life history and dispersal patterns in a dense infaunal polychaete assemblage: community structure and response to disturbance. Ecology 65: 1185–1200.

Levin N, Beger M, Maina J, McClanahan T, Kark S. 2018. Evaluating the potential for transboundary management of marine biodiversity in the Western Indian Ocean, Australasian Journal of Environmental Management, 25:1, 62-85. DOI: 10.1080/14486563.2017.1417167

Lomolino MV, Riddle BR, Brown JH. 2006. Biogeography, 3rd edn. Sunderland, MA: Sinauer Associates.

Lourie SA, Vincent ACJ. 2004. Using biogeography to help set priorities in marine Conservation. Conservation Biology 18(4): 1004-1020.

Lucey SM, Nye JA (2010) Shifting species assemblages in the Northeast US Continental Shelf Large Marine Ecosystem. Marine Ecology Progress Series 415:23-33.

Lutjeharms JRE. 2006. Three decades of research on the greater Agulhas Current. Ocean Science Discussions 3: 939-995.

Lutjeharms JRE, Biastoch A, van der Werf PM, Ridderinkhof H, de Ruijter WPM. 2012. On the discontinuous nature of the Mozambique Current. South African Journal of Science, 108(1-2), 01-05.

Mace GM. 2004. The role of taxonomy in species conservation. Phil. Trans. R. Soc. Lond. B (2004) 359, 711–719. DOI 10.1098/rstb.2003.1454

Mackinson, S. 2001. Integrating local and scientific knowledge: an example in fisheries science. Environmental Management, 27: 533–545.

Macpherson, E., 1990. Crustacea Decapoda: On a collection of Nephropidae from the Indian Ocean and Western Pacific. In: Crosnier A. (Ed.), Résultats des Campagnes MUSORSTOM. Volume 6. Mémoires du Muséum national d'Histoire naturelle, Paris, (A) 145: 289–329, Figs. 1–17.

Manning RB. 1993. A new deep-sea crab, genus *Chaceon*, from the Arabian Sea (Crustacea, Decapoda, Geryonidae). Pakistan Journal of Marine Sciences, Vol.2(1), 1-3.

Manning RB, Holthuis LB. 1988. South African species of the genus geryon (Crustacea, Decapoda, Geryonidae). Annals of the South African Museum 98: 77 – 92.

Manning RB, Holthuis LB. 1989. Two new genera and nine new species of geryonid crabs (Crustacea, Decapoda, Geryonidae). Proc. Biological Soc. Wash. 102, 50-77.

Marsac F, Barlow R, Ternon JF, Ménard F, Roberts M. 2014. Ecosystem functioning in the Mozambique Channel: Synthesis and future research. Deep Sea Research Part II: Topical Studies in Oceanography, 100, 212–220. doi:10.1016/j.dsr2.2013.10.028

Marshall DJ, Burgess SC. 2014. Deconstructing environmental predictability: seasonality, environmental colour and the biogeography of marine life histories. Ecology Letters, 18(2): 174–181. doi:10.1111/ele.12402

Martínez P, Gonzalez EG, Castilho R, Zardoya R. 2006. Genetic diversity and historical demography of Atlantic bigeye tuna (*Thunnus obesus*). Molecular Phylogenetics and Evolution, 39: 404-416.

May RM. 1990. Taxonomy as destiny. Nature 347, 129–130.

McArthur MA, Brooke BP, Przeslawski R, Ryan DA, Lucieer VL, Nichol S, McCallum AW, Mellin C, Cresswell ID, Radke LC. 2010. On the use of abiotic surrogates to describe marine benthic biodiversity. Estuarine, Coastal and Shelf Science, 88(1), 21–32. doi:10.1016/j.ecss.2010.03.003

McCusker MR, Bentzen P. 2010. Historical influences dominate the population genetic structure of a sedentary marine fish, Atlantic wolfish (*Anarhichas lupus*), across the North Atlantic Ocean. Molecular Ecology, 19, 4228–4241.

McNeely JA. 2002. The role of taxonomy in conserving biodiversity. Journal for Nature Conservation 10: 145 – 153.

Melville-Smith R. 1987. The reproductive biology of *Geryon maritae* (Decapoda, Brachyura) off South West Africa/Namibia. Crustaceana 53: 259–275. doi:10.1163/156854087X00358

Melville-Smith R. 1989. A growth model for the deep-sea red crab (*Geryon maritae*) off South West Africa/Namibia (Decapoda, Brachyura). Crustaceana 56: 279–292.

Mkare TK, von der Heyden S, Groeneveld JC, Matthee CA. 2014. Genetic population structure and recruitment patterns of three sympatric shallow-water penaeid prawns in Ungwana Bay, Kenya, with implication for fisheries management. Mar Freshw Res 65:255–266.

Mkare TK, Groeneveld JC, Teske PR, Matthee CA. 2017. Comparative genetic structure in two high-dispersal prawn species from the south-west Indian Ocean. Afr J Mar Sci 39:467–474.

Monk J. 2013. How long should we ignore imperfect detection of species in the marine environment when modelling their distribution? Fish and Fisheries. 15(2): 352–358. doi:10.1111/faf.12039

Moreno A, Lourenço S, Pereira J, Gaspar MB, Cabral HN, Pierce GJ, Santos AMP. 2014. Essential habitats for pre-recruit *Octopus vulgaris* along the Portuguese coast. Fisheries Research, 152: 74–85.

Morrison WR, Lohr JL, Duchen P, Wilches R, Trujillo D, Mair M, Renner SS. 2009. The impact of taxonomic change on conservation: Does it kill, can it save, or is it just irrelevant? Biological Conservation 142 (2009) 3201–3206.

Murawski SA. 1993. Climate change and marine fish distributions: Forecasting from historical analogy. Transactions of the American Fisheries Society 122: 647 – 658.

Myagkov NA, Kondyurin VV. 1986 Dogfishes, *Squalus* (Squalidae) of the Atlantic Ocean and comparative notes on the species of this genus from other regions. J Ichthyol 26(6):1–18

Mzingirwa FA, Mkare TK, Nyingi DW, Njiru J. 2019. Genetic diversity and spatial population structure of a deepwater snapper, *Pristipomoides filamentosus* in the south-west Indian Ocean. Molecular Biology Reports 46(5): 5079-5088. https://doi.org/10.1007/s11033-019-04962-w

Norse EA (Ed). 1993. Global marine biological diversity. A strategy for building conservation into decision making. Island Press, Washington, USA.

Obura D. et al. 2017. Reviving the Western Indian Ocean Economy: Actions for a Sustainable Future. WWF International, Gland, Switzerland. 64 pp.

Ockhuis S, Huggett JA, Gouws G, Sparks C. 2017. The 'suitcase hypothesis': Can entrainment of meroplankton by eddies provide a pathway for gene flow between Madagascar and KwaZulu-Natal, South Africa? African Journal of Marine Science 39(4): 435-451.

Ogden R. 2008. Fisheries forensics: The use of DNA tools for improving compliance, traceability and enforcement in the fishing industry. Fish and Fisheries, 9, 462–472.

Okemwa EN. 1998. Application of the large marine ecosystem concept to the Somali Current. In: Sherman K, Okemwa E, Ntiba M. (eds). *Large marine ecosystems of the Indian Ocean: Assessment, sustainability, and management*. (pp 73-99) Cambridge, MA: Blackwell Science.

Ormond RFG, Gage JD, Angel MV. Marine biodiversity: patterns and processes. Oceanographic Literature Review 45: 1-101.

Orr JC, Fabry VL, Aumont O, Bopp L, Doney SC, Freely RA, Gnanadesikan A, et al. 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms, Nature 437: 681-686.

Ovenden JR, Kashiwagi T, Broderick D, Giles J, Salini J. 2009. The extent of population genetic subdivision differs among four co-distributed shark species in the Indo-Australian archipelago. BMC Evolutionary Biology, 9.

Paula e Silva R. 1985. The deep crab – *Geryon quinquedens*. First notes on its biology off Mozambique. Revista de Investigação Pesquiera. Moçambique 13: 5–25.

Pearson RG, Dawson TP. 2005. Long-distance plant dispersal and habitat fragmentation: identifying conservation targets for spatial landscape planning under climate change. Biol. Conserv., 123: 389–401.

Pennino MG, Conesa D, López-Quílez A, Muñoz F, Fernández A, Bellido JM. 2016. Fishery-dependent and -independent data lead to consistent estimations of essential habitats. – ICES Journal of Marine Science, 73: 2302–2310

Pérez-Farfante I. & Kensley B. (1997) Penaeoid and sergestoid shrimps and prawns of the world. Keys and diagnoses for the families and genera. Mémoires du Muséum national d'Histoire naturelle 175.

Perry AL, Low PJ, Ellis JR, Reynolds JD. 2005. Climate Change and Distribution Shifts in Marine Fishes. Science, 308(5730): 1912–1915. doi:10.1126/science.1111322

Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL, Levin SA. 2013. Marine Taxa Track Local Climate Velocities. Science 341(6151): 1239-1242. DOI: 10.1126/science.1239352

Pollock DE. 1992. Palaeoceanography and speciation in the spiny lobster genus *Panulirus* in the Indo-Pacific. Bulletin of Marine Science 51: 133–146.

Pollock DE. 1998. Spiny lobsters in the Indian Ocean: Speciation in relation to oceanographic ecosystems. In: Sherman K, Okemwa EN, Ntiba MJ. 1998. Large Marine Ecosystems of the Indian Ocean. Assessment, sustainability, and management (pp 215-222) Cambridge, MA: Blackwell Science.

Poloczanska, E., Brown, C., Sydeman, W. et al. 2013. Global imprint of climate change on marine life. Nature Clim Change 3: 919–925. doi:10.1038/nclimate1958

Provan J, Bennett KD. 2008. Phylogeographic insights into cryptic glacial refugia. Trends in Ecology and Evolution, 23: 564-571.

Ragionieri L, Cannicci S, Schubart C, Fratini S. 2010. Gene flow and demographic history of the mangrove crab Neosarmatium meinerti: a case study from the western Indian Ocean. Estuar Coast Shelf Sci 86:179–188.

Ragionieri L, Fratini S, Vannini M, Schubart CD. 2009. Phylogenetic and morphometric differentiation reveal geographic radiation and pseudo-cryptic speciation in a mangrove crab from the Indo-West Pacific. Molecular Phylogenetics and Evolution 52: 825-834.

Reddy M, Macdonald A, Groeneveld J. 2014. Phylogeography of the scalloped spiny-lobster *Panulirus homarus rubellus* in the southwest Indian Ocean. Journal of Crustacean Biology 34: 773-781.

Ricklefs RE, Schluter D. 1993. Species diversity in ecological communities: historical and geographical perspectives. Chicago: University of Chicago, 416p.

Riemann B, Hoffman E. 1991. Ecological consequences of dredging and bottom trawling in the Limfjord, Denmark. Marine Ecology Progress Series 69: 171 – 178.

Rijnsdorp AD, Bastardie F, Bolam SG, Buhl-Mortensen L, Eigaard OR, Hamon K, Hiddink JG, Hintzen NT, Ivanovic A, Kenny A, Laffargue P, Nielsen JR, O'Neill FG, Piet GJ, Polet H, Sala A, Smith C, Van Denderen PD, Van Kooten T, Zengin M. 2016. Towards a framework for the quantitative assessment of trawling impact on the seabed and benthic ecosystem. Ices Journal of Marine Science, 73, 127-138. https://doi.org/10.1093/icesjms/fsv207

Robey J, Groeneveld JC. 2014. Fecundity of the langoustine *Metanephrops mozambicus* Macpherson, 1990 (Decapoda, Nephropidae) in eastern South Africa. Crustaceana, 87(7): 814–826. doi:10.1163/15685403-00003311

Romanov E. 2012. Survey of historical data sets on past fisheries research and exploratory cruises in the SWIOFP region. Report prepared for the South West Indian Ocean Fisheries Project, 232p.

Rosenblatt RH, Waples RS. 1986. A genetic comparison of allopatric populations of shore fish species from the eastern and central Pacific Ocean: dispersal or vicariance? Copeia, 275–284.

Rosenzweig ML. 1995. Species Diversity in Space and Time. Cambridge, MA: Cambridge Univ. Press

Ryan PG, Moloney CL. 1988. Effect of trawling on bird and seal distributions in the southern Benguela region. Marine Ecology Progress Series 45: 1 – 11.

Sætersdal G, Bianchi G, Strømme T, Venema SC. 1999. The Dr Fridtjof Nansen Programme 1975 – 1993. Investigations of fishery resources in developing regions. History of the programme and review of results. FAO Fisheries Technical Paper 391 FAO, Rome Italy.

Sala E, Knowlton N. 2006. Global marine biodiversity trends. Annu. Rev. Environ. Resour. 2006. 31:93–122. doi: 10.1146/annurev.energy.31.020105.100235

Schemske DW. 2002. Ecological and evolutionary perspectives on the origins of tropical diversity. In Foundations of Tropical Forest Biology: Classic Papers with Commentaries, ed. R Chazdon, T Whitmore, pp. 163–73. Chicago, IL: Univ. Chicago Press

Schott FA, McCreary JP. 2001. The monsoon circulation of the Indian Ocean. Prog. Oceanogr. 51: 1-123.

Schleyer MH, Downey-Breedt NJ, Benayahu Y. 2019. Species composition of Alcyonacea (Octocorallia) on coral reefs at Europa Island and associated connectivity across the Mozambique Channel. Marine Biodiversity (2019) 49:2485–2491. https://doi.org/10.1007/s12526-019-00975-7

Schneider-Broussard R, Neigel JE. 1997. A large-subunit mitochondrial ribosomal DNA sequence translocated to the nuclear genome of two stone crabs (*Menippe*). Mol Biol Evol. 14: 156–165.

SeaLifeBase. 2019a. *Haliporoides triarthrus* Stebbing, 1914.
https://www.sealifebase.ca/summary/Haliporoides-triarthrus.html Accessed online 29 November 2019.

Sexton JP, McIntyre PJ, Angert AL, Rice KJ. 2009. Evolution and ecology of species range limits. Annu. Rev. Ecol. Evol. Syst. 40: 415–436.

Sherman K, Alexander LM, Gold BD. (Eds) 1990. Large Marine Ecosystems: Patterns, Process and Yields. American Association for the Advancement of Science. Washington DC, USA.

Shulman MJ, Bermingham E, 1995. Early life histories, ocean currents and the population genetics of Caribbean reef fishes. Evolution 49: 897–910.

Silva IC, Mesquita N, Paula J. 2010. Lack of population structure in the Fiddler crab *Uca annulipes* along an East African latitudinal gradient: genetic and morphometric evidence. Mar Biol 157:1113–1126.

Singh SP, Groeneveld JC, Hart-Davis MG, Backeberg BC, Willows-Munro S. 2018. Seascape genetics of the spiny lobster *Panulirus homarus* in the Western Indian Ocean: Understanding how oceanographic features shape the genetic structure of species with high larval dispersal potential. Ecology and Evolution, 8(23): 12221–12237. doi:10.1002/ece3.4684

Smith JLB, Smith MM. 1966. Fishes of the Tsitsikama Coastal National Park. National Parks Board, Pretoria. 161 pp, 233 figs.

Sobrino I, Dias N, Balguerias E, Santana Afonso P, Burgos C, Palha de Sousa B, Palha de Sousa L. 2007a. Volume 1: Relatório do cruzeiro de investigação de recursos de profundidade realizado a bordo do b/o Vizconde de Eza de 13 de Março a 14 de Abril 2007. Instituto Nacional de Investigação Pesqueira, Maputo, 30 Agosto 2007, 63pp.

Sobrino I, Dias N, Balguerias E, Ramil F, Santana Afonso P, Burgos C, Palha de Sousa B, Palha de Sousa L. 2007b. Volume 2: Relatório do cruzeiro de investigação de recursos de profundidade realizado a bordo do b/o Vizconde de Eza de 13 de Março a 14 de Abril 2007. Instituto Nacional de Investigação Pesqueira, Maputo, 30 Agosto 2007, 62pp.

Song H, Buhay JE, Whiting MF, Crandall KA. 2008. Many species in one: DNA barcoding overestimates the number of species when nuclear mitochondrial pseudogenes are coamplified. Proc Nat Acad Sci USA. 105: 13486–13491. 10.1073/pnas.0803076105

Standing A. 2009. The Growth of Marine Fisheries Ecolabelling in Southern and Eastern Africa. 18. Institute for Security Studies, Pretoria, South Africa.

Steele DH. 1988. Latitudinal variations in body size and species diversity in marine Decapod Crustaceans of the continental shelf. Int. Rev. Hydrobiol. 73: 235–46

Tillin, H. M., Hiddink, J. G., Jennings, S., and Kaiser, M. J. 2006. Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. Marine Ecology Progress Series, 318: 31-45.

Thorpe SA. 2007. An introduction to ocean turbulence. 1st ed. Cambridge University Press.

UNEP. 2019. About the Nairobi Convention Clearinghouse.
http://staging1.unep.org/emunyao/ncchm/about Accessed online on 18 December 2019.

UNEP-Nairobi Convention and WIOMSA. 2015. The Regional State of the Coast Report: Western Indian Ocean. UNEP and WIOMSA, Nairobi, Kenya, 546 pp.

Van der Elst RP, Everett BI. 2015. (Eds). Offshore fisheries of the Southwest Indian Ocean: their status and the impact on vulnerable species. South African Association for Marine Biological Research Special Publication (10): 448pp

Van der Elst, R.P., Everett, B.I., Jiddawi, N., Mwatha, G., Afonso, P.S, Boulle, D. 2005. Fish, fishers and fisheries of the Western Indian Ocean: their diversity and status, a preliminary assessment. Philosophical Transactions of the Royal Society of London A 363: 263-284.

van der Elst RP, Groeneveld JC, Baloi AP, Marsac F, Katonda KI, Ruwa RK, Lane WL. 2009. Nine nations, one ocean: A benchmark appraisal of the South Western Indian Ocean Fisheries Project (2008–2012). Ocean Coastal Management, 52(5), 258–267.

Van Zyl, B., & Willemse, N. (2000). FishBase: a database and fisheries management-orientated tool for the 21st century. African Journal of Aquatic Science, 25(1): 225–226. doi:10.2989/160859100780177703

Vance RR. 1973. On reproductive strategies in marine benthic invertebrates. Am. Nat. 107: 339–52.

Vecchione M. 1987. Commercial fishing for gulf butterfish, *Peprilus burti*, in the Gulf of Mexica. Marine Fisheries Review 49: 14 – 22.

Vecchione M, Collette BB. 1996. Fisheries agencies and marine biodiversity. Annals of the Missouri Botanical Garden 83(1): 29 – 36.

Viñas J, Gordoa A, Fernández-Cebrián R, Pla C, Vahdet Ü, Araguas RM. 2010. Facts and uncertainties about the genetic population structure of Atlantic bluefin tuna (*Thunnus thynnus*) in the Mediterranean: Implications for fishery management. Reviews in Fish Biology and Fisheries, 21: 1-15.

Warman G. 2017. Fishing industry handbook. South Africa, Namibia & Mozambique, 45 (pp. 1-454). Gorge Warman Publications. Cape Town.

Warner RR, Cowen RK. 2002. Local retention of production in marine populations: evidence, mechanisms and consequences. Bull. Mar. Sci. 70 (Suppl. 1): 245–249.

Weersing K, Toonen RJ. 2009. Population genetics, larval dispersal, and connectivity in marine systems. Mar. Ecol. Progr. Ser. 393: 1–12.

Weinberg JR, Dahlgren TG, Trowbridge N, Halanych KM. 2003. Genetic differences within and between species of deep-sea crabs (*Chaceon*) from the North Atlantic Ocean. The Biological Bulletin 204: 318-326.

Wiens JJ. 2011. The niche, biogeography and species interactions. Phil. Trans. R. Soc. B (2011) 366, 2336–2350 doi:10.1098/rstb.2011.0059

Wenner EL, Barans CA. 1990. In situ estimates of density of golden crab, *Chaceon fenneri*, from habitats on the continental slope, southeastern US. Bulletin of Marine Science 46: 723–734.

White TA, Stefanni S, Stamford J, Hoelzel AR. 2009. Unexpected panmixia in a long-lived, deep-sea fish with well-defined spawning habitat and relatively low fecundity. Molecular Ecology, 18, 2563-2573.

Wigley RL, Theroux RB, Murray HE. 1975. Deep sea red crab, *Geryon quinquedens*, survey off northeastern United States. Marine Fisheries Review. 37(8): 1–21.

Williams ST, Knowlton N. 2001. Mitochondrial pseudogenes are pervasive and often insidious in the snapping shrimp genus *Alpheus*. Mol Biol Evol. 18: 1484–1493.

Willig MR. 2001. Common trends with latitude. In: Levin SA. (ed.) 2001. Encyclopaedia of Biodiversity. San Diego: Academic pp. 701–714.

Willig MR, Kaufman DM, Stevens RD. 2003. Latitudinal Gradients of Biodiversity: Pattern, Process, Scale, and Synthesis. Annu. Rev. Ecol. Evol. Syst. 2003. 34:273–309 doi: 10.1146/annurev.ecolsys.34.012103.144032

WIOFish. 2019. Industrial nets, offshore, crustaceans – Kenya (updated 30 March 2016). In: WIOFish: Western Indian Ocean Fisheries Database. Accessed online at http://www.wiofish.org/fishery/industrial-nets-offshore-crustaceans on 1 November 2019.

Whitton FJ, Purvis A, Orme CDL, Olalla-Tárraga, MÁ. 2012. Understanding global patterns in amphibian geographic range size: does Rapoport rule? Global Ecol. Biogeogr. 21: 179–190.

WoRMS. 2019a. *Metanephrops andamanicus* (Wood-Mason, 1892). Accessed at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=220230 on 23 November 2019.

WoRMS. 2019b. *Metanephrops mozambicus* (Macpherson, 1990). Accessed at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=241290#distributions on 29 November 2019.

WoRMS. 2019c. World Register of Marine Species. Accessed at: http://www.marinespecies.org/index.php on 30 November 2019.

Yokoyama Y, Lambeck K, Deckker PD, Johnston P, Fifield LK. 2000. Timing of the last glacial maximum from observed sea level minima. Nature 406: 713-716.

Zacarias LD. 2013. Genetic population structure of deep-water prawns *Haliporoides triarthrus* and langoustines *Metanephrops mozambicus* in the South West Indian Ocean: use of mitochondrial DNA to investigate metapopulation structure. MSc thesis. University of KwaZulu-Natal, South Africa.

Paper 1

Paper 2

Paper 3

Paper 4

1 **Using hotspot analysis to track changes in the crustacean fishery off KwaZulu-Natal, South Africa**

2 Everett BI[1*], Fennessy ST[1] and van den Heever N[2]

3 [1]Oceanographic Research Institute, PO Box 10712, Marine Parade, 4045, South Africa

4 [2]Department of Environment, Forestry and Fisheries, Private Bag x9087, Cape Town, 8000

5 *Corresponding Author, email: bernadine@ori.org.za

6

7 **Abstract**

8   This study focuses on the KwaZulu-Natal deep-water crustacean trawl fishery located off the east coast of
9   South Africa. It investigates the spatiotemporal changes in fishing effort and catch per unit effort of three
10 target species (knife prawns (*Haliporoides triarthrus*), African langoustine (*Metanephrops mozambicus*) and
11 pink geryon (*Chaceon macphersoni*) using a space-time cube and hotspot analysis in ArcGIS Pro. This
12 analysis shows the contraction of the fishing effort over time and the confining of the most productive
13 localities to a relatively small area directly off the vessels' home port of Durban. This provides invaluable
14 information on a fishery that has not been subjected to any formal stock assessments.

15

16 **Keywords**: spatiotemporal analysis, crustaceans, trawl fishery, hotspot analysis

17

18 **Introduction**

19 A deep-water crustacean trawl fishery operates off the province of KwaZulu-Natal on the coast of South
20 Africa. The trawl grounds were first discovered during exploratory research trawling in the 1920s when
21 large catches of spiny lobster, *Palinurus delagoae*, were made at times (Berry 1972). However, industrial
22 trawling for spiny lobster only appears to have commenced in the 1960s, with subsequent targeting of
23 deep-water prawns, langoustines and crabs as lobster catches declined (Berry 1972), although there are
24 few records from that time. The fleet size is small at present, with only three or four vessels operating, but
25 more vessels were fishing in the early 1980s (de Freitas 1995) although numbers are not certain owing to
26 poor records. Vessels utilised in the fishery are mostly stern trawlers with an overall length of 25-35 m with
27 a catch storage capacity of *ca.* 30 t, and they can remain at sea for up to 30 days. Otter trawls are used with
28 most deploying a single stern net (Fennessy and Groeneveld 1997), and trawl footrope lengths range from
29 26 to 60 m. Stretched mesh sizes in the codend have changed over time from 38 mm in the 1990s
30 (Fennessy and Groeneveld 1997) to 50 cm at present (DAFF 2018).

31

32 The current fishery targets predominantly knife prawns (*Haliporoides triarthrus*), African langoustine
33 (*Metanephrops mozambicus*) and pink geryon (*Chaceon macphersoni*)) (Groeneveld and Everett 2015).
34 These three species have different life history characteristics so most likely their catchability varies in space
35 and time. *Haliporoides triarthrus* inhabits a sticky mud substratum that is composed mostly of
36 foraminiferous remains located on the upper continental slope (Berry *et al* 1975), reportedly at depths of
37 300–800 m (Brinca et al. 1983; Torstensen 1989). Robey el al (2013a) confirmed that it is a fast-growing

38 species with a lifespan of 2 – 3 years. *Metanephrops mozambicus* lives in soft muddy substrata at depths of
39 200-750 m (Berry 1969). Its lifespan is 3 - 4 years (Robey et al 2013b), and it is assumed that it burrows as
40 other *Metanephrops* species do (Bell et al. 2013). *Chaceon macphersoni*, like other species of the genus, is
41 found on both soft and hard (untrawlable) substrates (Groeneveld *et al.* 2013). Most deep-water *Chaceon*
42 species are slow-growing and long-lived (Serchuk and Wigley 1982, Hastie and Saunders 1992) and it is
43 likely that *C. macphersoni* has these characteristics.

44

45 The KZN deep-water crustacean trawl fishery is not large with a total retained catch that ranges between
46 200 and 400 t/year and averages 255 t/year (Groeneveld and Everett 2015). Since 1988, permit conditions
47 require that the fishery submits catch logbooks. These logbooks are submitted by vessel captains and
48 provide information on each trawl such as the date, setting and hauling time of the trawl, position, depth
49 and catches in each trawl. These logbooks show that the nominal catch per unit effort (CPUE) of *H.*
50 *triarthrus* decreased in the 1990s with a small increase in 1999 and 2000 before declining in 2001, and then
51 increasing until 2008, after which there was a rapid decline until 2017 (the last year of available data). They
52 showed a recovery until 2014 but have since declined again. *Metanephrops mozambicus* had an increasing
53 nominal CPUE until 2000 after which there was a decline for three years followed since by an increasing
54 trend. The nominal CPUE for *C. macphersoni* was initially high in the 1990s but declined in the early 2000s,
55 remaining low until 2013. Catch rates have since been steadily increasing to approach the early high values
56 (Groeneveld and Everett 2015, Department of Agriculture, Forestry and Fisheries Unpublished data).

57 The fishery has not been formally assessed in terms of its sustainability, and there have been limited efforts
58 to interpret fishing patterns in the context of distribution of resources, since the initial work of Groeneveld
59 and Melville-Smith (1995). The use of Geographical Information Systems (GIS) in fisheries mapping can
60 provide useful insights into the resources that exist at specific locations, and possible explanations for the
61 distribution of spatial assemblages and changing catch trends that have occurred over time (Bordalo-
62 Machado 2006, Jalali 2015, Steves 2019). These observations can, where necessary, be incorporated into
63 fisheries policies and plans to manage fisheries more sustainably (Dineshbabu et al. 2016). For this study,
64 we investigated if fishing effort and catches of the three target species were randomly distributed on the
65 fishing grounds; if there had been any spatial-temporal changes in effort and CPUE; and if the CPUE of
66 target species differed spatially from one another.

67

68 **Methods**

69 *Study area*

70 Trawlers in the deep-water crustacean fishery are based in Durban and operate on the continental slope in
71 depths from 100m to 600m. There is a small shallow-water (<50 m) fishing ground closer inshore, but that
72 is not included in this study as very little trawling has occurred there for several years. The deep-water
73 trawl grounds extend from 28.5°S in the north to 30.2°S in the south with a break in the grounds where the
74 seabed is apparently untrawlable based on the distribution of trawl localities (Figure 1). For the purpose of
75 this study the northern section of the trawl grounds will be referred to as Richards Bay Deep while the
76 southern area will be Durban Deep. The grounds vary in widths of around 15 km off Saint Lucia to 40 km off
77 Durban (Oceanographic Research Institute, unpublished data). Trawlers are prevented from operating in
78 depths greater than 600 m due to the strong Agulhas Current which flows in a south-westerly direction,
79 with the current core often over the continental slope, but with large-scale meanders at times (Lutjeharms

80   2006). Guastella and Roberts (2016) reported that bottom water temperatures where the trawl grounds
81   are situated ranged from 20°C to 10°C as depth increased. This was confirmed separately during a survey
82   off the KwaZulu-Natal coast with the RV *Dr Fridtjof Nansen* in January and February 2018 (EAF-Nansen
83   Programme Unpublished Data). The trawl ground substratum was found by Berry (1969) to be a mixture of
84   organic and mineral detritus, foraminiferous remains, mineral grains and siliceous spicules.

85   *Data*

86   It has been mandatory since 1988 for skippers to complete and submit logbook data for every trawl to the
87   Department of Environment, Forestry and Fisheries (Fennessy and Groeneveld 1997). The information
88   collected includes the date, time, duration, trawl start position, depth and catch. From 1988 to 1999, trawl
89   positions were given according to a coarse-resolution grid reference, but in 2000, skippers began providing
90   more accurate global positioning system (GPS) coordinates. Therefore, only data from 2000 onwards have
91   been used in this study. Logbook data were selected for inclusion primarily on the availability and accuracy
92   of trawl start positions. Those entries that were clearly inaccurate were eliminated. Furthermore, records
93   were eliminated when trawl duration was less than 30 minutes, or longer than 8 hours, or if no catch
94   amounts were provided. A total of 1 313 (4.2%) trawls was discarded leaving 30 165 trawls for analysis.

95   *Data analyses*

96   Spatial statistical tools in ESRI ArcMap 10.5 software were used to analyse the spatial and temporal
97   patterns in the effort and CPUE data. Initially all trawl start positions were assigned to a 5km grid over the
98   fishing ground to provide an overview of fishing effort and CPUE of the target species, that occurred on the
99   trawl grounds over the entire 18-year period. Auto correlation was calculated using the global Moran I tool
100   for each year. Moran's Index was calculated using the distance trawled, position and values of each trawl
101   with the values of the index ranging between -1 (dispersed) and +1 (clustered), with values around zero
102   indicating a random pattern. This tool also provides the distance band threshold used in the hotspot
103   analysis (ESRI 2019a).

104

105   Having determined the overall patterns, the dataset was used to produce space-time cubes to be able to
106   explore the changes in effort and CPUE in both time and space. Space-time cubes allow for the display and
107   analyses of the data in three dimensions with the positions represented on the x and y axes and the years
108   represented on the z axis. All data points are aggregated into space-time bins which are packaged into a
109   NetCDF file with trend data created from the Mann-Kendall trend test. This test compares each bin value
110   with that of the previous year. Positive values indicate inter-annual increases, negative values show
111   decreases and zero indicates no change (ESRI 2019b).

112

113   The space-time cubes were analysed using the Getis Ord Gi* statistic of the emerging hotspot analysis tool
114   (ESRIb 2019). Emerging hotspot analysis examines neighbouring bins in both space and time and identifies
115   bins that have high and low values of effort and CPUE which are then designated as hot and cold spots
116   when there is significant clustering of high and low values respectively. Emerging hotspot analysis accounts
117   for the consistency and intensity of each time step in the classification of the significant hot and cold spots.
118   The tool also calculates the statistical significance of the autocorrelation and the dependence among the
119   neighbouring bins. A distance band of 4 241 m, derived from the autocorrelation (see Results), was used to
120   determine spatial neighbours, and one-year intervals were used for the neighbourhood time steps. Three-

121 dimensional hotspot analysis was used to provide the ability to view each time step at each locality. This
122 allows scrutiny of the changes in hotspots at each time-step and locality and was used to create 3D
123 animations (Supplementary data).

124

125 Two- and three-dimensional visualisations of the space-time cubes were produced to allow visual
126 identification of the spatial-temporal patterns. The 2D visualisation provides a useful display of overall
127 changes in the study period while the 3D visualisation shows each location's history and how it has changed
128 over the duration of the study period.

129

130 **Results**

131 *Summarisation of effort and catch*

132 Over the 18-year period of this study, nine different vessels have operated but not all at the same time. At
133 most in one year there were eight vessels and at the least there were two vessels. Total trawl hours ranged
134 from 4 100 to 12 400 per year (Figure 2). The total retained catch of the fleet (including non-targeted
135 species of fishes and cephalopods) was between 209 and 372 tons per year and that of the three targeted
136 species discussed here was between 164 and 282 tons per year. CPUE for the target species ranged
137 between 8.0 and 29.9 kg/h for knife prawns, 4.3 and 15.8 kg/h for African langoustines, and 2.1 and 11.8
138 kg/h for the pink geryons (Figure 2). Considering spatial distribution (Figure 3), trawling occurred over
139 almost all the trawl grounds except for a few parts of the Richards Bay Deep area where trawling is
140 presumably not possible. Most of the trawl effort was unsurprisingly on the gentlest sloping area of the
141 grounds between 400 m and 500 m in the Durban Deep area (Figure 3). The individual CPUE of the three
142 target species show very different patterns of distribution (Figure 3). The knife prawn CPUE had high
143 concentrations in the very southern part of Durban Deep and around 500 m depth; CPUE was also high in
144 the Richards Bay Deep area. African langoustine had higher CPUE in the northern part of the Durban Deep
145 area and to some extent in the Richards Bay Deep area, although less than that of the knife prawns. CPUE
146 for the pink geryon was concentrated in the Durban Deep area, most noticeably in the southern section,
147 and shallower than that of the knife prawns (Figure 3).

148 *Autocorrelation*

149 The results of the autocorrelation analyses (Figure 4), and specifically the Global Moran I statistic, indicate
150 that overall fishing effort and CPUE of the target species occurred in non-random clusters. There were,
151 however, three years when fishing effort appeared random and two years when CPUE of knife prawn and
152 pink geryon appeared random. Incremental spatial autocorrelation tested the Global Moran I statistic for a
153 series of distances to identify an appropriate neighbourhood distance for use in the space time cube. The
154 resulting distance bands and their corresponding z-scores indicate the scale at which the most pronounced
155 clustering is found for each year, and overall. Peak z-score distance bands ranged from 3 887 m to
156 15 535 m. The distance band calculated for all years was 4 241 m which was used as the maximum value to
157 create the bin sizes in the space-time cube to avoid losing patterns in reduced resolutions. The overall
158 downward trends of the linear z-scores show that, for all four aspects, clustering becomes less pronounced
159 over time.

160

Space-Time Cube

162   The space-time cube aggregated 30 165 data points into 1 520 hexagonally gridded (fishnet) locations over
163   18-time step intervals. Each bin is 4 241 m long by 4 241 m wide as calculated during the autocorrelation as
164   the appropriate distance band and each time step is equivalent to one year. Of the 1 530 total locations,
165   201 (13.14%) had at least one data point for at least one time-step interval. These 201 locations equate to
166   3 618 space-time bins of which 2 035 (56.25%) have point counts greater than zero. There was a statistically
167   significant decrease in data points over time indicating a decrease in the number of trawls over the study
168   period. Figure 5 shows the space time cube in its three-dimensional form, with the total annual effort in
169   hours for each locality and year. The space-time cube also incorporates the catch information for the three
170   target species and has been used for all further analyses.

171

172   *Mann-Kendall Trend Test*

173   The Mann-Kendall trend test shows the changes in the values of each bin for the overall period. Fishing
174   effort, in hours, showed a significant declining trend overall for both the sum of hours and the mean of
175   hours but there are locality variabilities in both (Figure 6). Figure 6a shows that the trend in sum of hours
176   fished increased in only 3 location bins while it decreased in 75 bins. The remaining bins showed no
177   significant trends. These declining trends are particularly noticeable in the Richards Bay Deep area and in
178   the northern and western portions of the Durban Deep grounds. Figure 6b shows that 33 bins showed
179   declining trends in the mean amount of time spent fishing in each locality, and 33 bins showed increasing
180   trends. The mean amount of time spent in the Richards Bay Deep grounds declined over the study period
181   but the central southern portion of Durban Deep saw an increase. There is also a small area in the north of
182   Durban Deep that has shown a local increase in mean fishing time but an associated decline in the sum of
183   fishing time. This indicates that fishing trips to this area have declined but the time spent there has
184   increased.

185

186   With regards to CPUE, the Mann-Kendall trend test showed that neither the knife prawns (Figure 7a) nor
187   pink geryons (Figure 7c) showed any overall trends with regards to changes in bins but, similarly to the
188   effort, there were localised increasing and decreasing trends. The knife prawns had 30 bins with decreasing
189   trends and 15 with increasing trends. The pink geryons had 17 decreasing and 8 increasing bins
190   respectively. The African langoustines, however, showed a significant increase overall, with 25 bins that
191   showed decreasing trends and 58 bins with very high confidence of increasing bins. Most of the bins with
192   increasing CPUE were located off Durban (Figure 7b).

193

194   *Hotspot Analyses*

195   The hotspot analysis showed locations that were more heavily fished and those where CPUE was higher
196   than surrounding locations. There are concentrations of hotspots of the sum of effort (Figure 8a) and the
197   mean of effort (Figure 8b) in the southern section of the Durban Deep grounds, where there are persistent
198   hotspots which have been statistically significant hotspots for 90% of the time-step intervals and oscillating
199   hotspots which are statistically significant in the final time-step but have also had statistically significant
200   cold spots during previous time-steps. The sum of effort also showed diminishing hotspots where total
201   trawl hours decreased over time while the mean of effort showed some intensifying hotspots. The Richards

202 Bay Deep grounds and the northern section of the Durban Deep grounds only have varying levels of cold
203 spots indicating that the trawl effort has diminished over time in these areas.

204

205 The CPUE maps for the target species (Figure 9) produced similar patterns in hotspots to those of effort in
206 that the hotspots were predominantly located in the southern portion of the Durban Deep grounds and the
207 northern section of the Durban Deep grounds, and the Richards Bay Deep grounds only showed areas with
208 cold spots. The contraction of the areas with high CPUE varied according to species, with the knife prawns
209 (Figure 9a) experiencing the tightest contraction. There were three locations in the Richards Bay Deep
210 grounds that showed that they had previously been hotspots. The Richards Bay Deep grounds had
211 intensifying cold spots for the pink geryons (Figure 9c) while the northern section of the Durban Deep
212 grounds have never been particularly successful areas for high crab CPUEs. There is a section in the central
213 Durban Deep area where historical CPUE hotspots are shown. These areas have been statistically significant
214 hotspots for more than 90% of the time-step intervals but the most recent time step was not hot. The
215 African langoustines (Figure 9b) have the most localities with persistent hotspots and some areas in the
216 north of the Durban Deep grounds with consecutive or sporadic hotspots. There was also an area in the
217 south that had intensifying hotspots.

218

219 The three-dimensional animations (Supplementary material) clearly show the variability in space and time
220 of hot and cold spots of effort and the target species' CPUE. From 2012 to 2015 the effort hotspots
221 concentrate into a very small area. During this time two vessels left the fishery and it was the start of an
222 increase in effort by the vessel that became the most prolific by the end of the time series. Similarly, the
223 contractions and expansions of the CPUE hot and cold spots can be visualised and the differences between
224 the species are very noticeable. The Richards Bay Deep area was very productive in the early 2000s for
225 knife prawns but by 2008 this area showed only cold spots, showing that productivity in this area was no
226 longer high. At the same time there was a very restricted area in the southern section of the Durban Deep
227 area that produced hotspots of knife prawn CPUE. This area gradually expanded up until 2009 when it filled
228 all the southern portion of the grounds. After 2009 the hotspots start to decrease in area becoming
229 confined to a very small section of the grounds in 2017. During this study period, the Richards Bay Deep
230 area was not of importance to the fishery and the Durban Deep area started off in 2000 as a small area in
231 the middle of the grounds. For two years, in 2003 and 2004, there were no hotspots where CPUEs were
232 higher than other areas but after that the hotspots reappeared in the centre where they expanded
233 outwards. Hotspots also started to appear in the northern section of the Durban Deep grounds. From 2010
234 to 2013 these two areas were joined. They became separated again in 2014 and gradually the middle
235 hotspot area expanded southwards. The hotspots associated with the pink geryon CPUEs are located only
236 in the southern portion of the Durban Deep area. The northern section and the Richards Bay Deep grounds
237 have not been very productive for these crabs. The hotspot area stays spread across the southern portion
238 of the Durban Deep grounds until it starts to shrink quite drastically from 2007. It reaches its smallest size
239 from 2010 to 2013 after which it dramatically increases again.

240

241 **Discussion**

242 By nature, fisheries have a strong spatial component due to their activities being directed at specific
243 resources in specific areas where catches can potentially be maximized (Booth 2000, Verdoit 2003). Fishing

244 grounds also do not necessarily cover the full portion of a species' distribution, or species may be
245 unavailable to the fishery in parts of the grounds due to gear incompatibities. Over time the KwaZulu-
246 Natal dee-water crustacean fishery has changed in the amount of effort and the catches and CPUEs of the
247 target species and whilst these changes can be seen in the traditional one-dimensional view of fisheries
248 information, the space-time analyses show a more comprehensive view of where and when fishing
249 pressure and catch rates changed. The spatial distribution of catch rates of the target species are clearly
250 different from each other, and areas that were once more productive are clearly highlighted.

251

252 Fishing effort has occurred in non-random clusters on the fishing grounds i.e. effort has not been
253 homogenous over either space or time. Generally, clustering of fishing effort can be attributed to several
254 factors that may include distance from port, resource availability, skipper knowledge, fuel and other
255 running costs, and number of vessels in the fleet among others (Steves 2019). For the KwaZulu-Natal
256 fishery, while all years showed clustering of effort, there has been a reduction in the strength of the
257 clustering. This is probably a result of fewer vessels fishing, allowing them to disperse more (Table 2).
258 However, the trend may also be attributed to less experienced skippers entering the fishery. Fisher
259 experience has been widely recognised as playing a significant role in the performance levels of fisheries
260 (Vázquez-Rowe and Tyedmers 2013, Fuller and Schaefer 2014, Oliveira et al. 2016). This has not been
261 documented formally in the KwaZulu-Natal (KZN) crustacean fishery, but there are no other industrial trawl
262 fisheries in the province, so companies tend to bring in skippers from the Western Cape province where the
263 main South African trawl fisheries are based. When the fishing rights change hands, new companies enter
264 the fishery, and often bring in new skippers; or skippers fall out of favour with companies and are replaced.
265 New skippers are unfamiliar with fishing conditions off KZN and have to develop capacity as they do not
266 have much prior knowledge of species' distributions on the grounds, nor with the difficult fishing
267 conditions.

268

269 The results of the Mann-Kendall trend tests and the emerging hotspot analyses show that over time the
270 effort of the fleet has become focussed on an area relatively close to the Durban port in the Durban Deep
271 grounds. They also show that when the fishers do venture further from port, the mean fishing time spent in
272 that locality increased i.e. when the fishers steam further to a more distant fishing area, they tend to spend
273 more time once there as it is probably more economical to remain there rather than using more fuel to
274 move to another locality. This dynamic is complicated by the higher catch rates attainable in grounds more
275 distant from port, but with the risk that the powerful Agulhas Current frequently prevents trawling there
276 (Figure 3). Thus, areas such as the Richards Bay Deep ground and the northern section of the Durban Deep
277 ground have become less important to the fishery due to their distance from the home port of Durban, and
278 due to the risks entailed in steaming a long distance only to find that trawling cannot take place. The role of
279 external factors in changing in the distributions of fishing activities has been noted in other parts of the
280 world such as the United Kingdom (Abernethy et al. 2010) and Alaska (Brinkman et al 2014), and in these
281 cases were attributed to the rising costs of fuel which makes longer distances travelled less profitable.

282

283 CPUEs of the three target species occurred in non-random clusters. This is to be expected as marine benthic
284 species form heterogenous distributions on local and regional scales (Deng et al. 2005, McGarvey 2006).
285 Furthermore, these distributions may result from habitat preferences, population dynamics, species
286 behavioural traits and fishing strategies (Maynou 1998). There is limited information on such influences for

287   the KZN deep-water crustacean trawl grounds. In areas inshore of these grounds, Green and MacKay (2016)
288   showed the heterogenous nature of the shelf sediment and MacKay et al. (2016) provided insight into the
289   distributions of the associated macrobenthos. These studies showed that neither shelf sediments nor the
290   macrobenthos are homogenous, and it is reasonable to infer that the deep-water targeted benthic
291   organisms in this study likewise have heterogenous distributions. Albeit in the context of the influence of
292   depth, Groeneveld and Melville-Smith (1995) and Fennessy and Groeneveld (1997) showed how the
293   distribution of trawled crustaceans changed from shelf to slope.

294   Very little is known about the population dynamics of the three target species off KwaZulu-Natal and
295   changes in the hot and cold spots seen in this study could be related to the natural fluctuations in the
296   populations as well as fishing pressure. The congeneric *Chaceon quinquedens* is known to have irregular
297   and aperiodic recruitment pulses (Steimle et al. 2001) which may also be possible for *C. macphersoni*. This
298   recruitment strategy can result in considerable population size variability and it leaves the species
299   particularly vulnerable to overexploitation. This could explain the contraction of the hotspots on the trawl
300   grounds from 2000 to 2002 and again from 2007 to 2014. There is a strong negative correlation between
301   effort and CPUE when considering the data from 2000 to 2017 (r = -0.71, P = 0.001). The negative
302   correlation of CPUE with effort also holds for the African langoustine (r = -0.58, P = 0.001) and the pink
303   geryon (r = -0.30, P = 0.001) but to a lesser extent. Determining the ultimate cause of trends in CPUE can,
304   however, be confounded by factors other than those of a non-biological nature, such as improvements in
305   vessel power, the introduction of modern technology, increased knowledge of the fishing grounds, and
306   improved fishing methods particularly when targeting specific species (Bishop 2006; Quirijns et al. 2008;
307   Erisman et al. 2011).

308

309   The distribution of CPUE hotspots for the three target species shows that for all three species, the southern
310   portion of the Durban Deep grounds has been the most productive for the fishery. While the distributions
311   for each species change over time, the overall patterns differ for each, potentially indicating the different
312   preferences of the three species for various areas within the trawl grounds. Robey et al (2013a) found that
313   the CPUE for knife prawns was highest at depth greater than 400 m from 1990 to 2010. The emerging
314   hotspot analysis placed the highest CPUE in the 400 to 600m depth zone but in a relatively small area in the
315   southern portion of the Durban Deep grounds. Robey et al (2013b) found that the highest African
316   langoustine CPUE was between 400 and 499 m while the CPUE hotspots in the current analysis were
317   between 200 and 600 m in the central area of the Durban Deep grounds. While there were no persistent
318   hotspots, three other levels of hotspots occurred, including consecutive, sporadic and oscillating hotspots.
319   Pink geryons had highest CPUEs between 400 and 499 m according to Groeneveld et al (2013) whereas our
320   study found the CPUE hotspots from 100 m to 600 m, with persistent hotspots between 200 and 500 m.
321   There was some overlap of the three species' hotspots but the African langoustine and the pink geryon
322   hotspots were spread over a relatively larger area and the knife prawn and pink geryons hotspots occurred
323   further south than the langoustines. The geryons show an overlap with all the areas where the prawns and
324   the langoustines occur. This is expected as the geryons have a wider range of suitable habitats (Groeneveld
325   et al 2013) than both the prawns and the langoustines.

326

327   The hot and cold spots show localities in time where fishing effort has been successful for these
328   three species in relation to other areas on the trawl grounds. It is notable that despite experiencing
329   sustained effort, the southern portion of the Durban Deep ground remains the most productive.

This is surprising in the light of the concentration of effort in this area. While little is known about the reproductive strategies of the knife prawn and pink geryon, as few gravid females are encountered (Robey et al. Groeneveld), it could be surmised that this productive area is disproportionately benefitting from local recruitment of langoustines and crabs (Robey et al. 2013b, Groeneveld et al. 2013) from nearby areas where trawlers do not operate, or, in the case of prawns, from Mozambique where this species also occurs (Brinca 1983). Areas in which trawlers do not operate could effectively act as harvest refugia, potentially providing "spill-over" movement of target organisms from unfished to adjacent fished areas (Halpern et al. 2009, Sala et al. 2013).

The KwaZulu-Natal crustacean trawl fishery has had no formal stock assessments conducted on its resources and management continues to maintain a status quo Total Allowable Effort of seven vessels without adequate scientific supporting information for this level of fishing. The results of our study show that certain areas of the trawl grounds are more heavily fished than other areas, but these areas remain the most productive locations. This is, however, without the maximum of all seven permitted vessels currently operating. Management of this fishery needs to consider the relationship between effort and CPUE, the implications of possible effort saturation in a very small area of the fishing grounds, and the lack of biological information for the target species and the associated fauna. The recent (August 2019) declaration of a Marine Protected Area which excludes trawling in the northern part of the Durban Deep grounds may provide some mitigation for effects of fishing.

Acknowledgements

References

Abernethy KE, Trebilcock P, Kebede B, Allison EH, Dulvy NK. 2010. Fuelling the decline in UK fishing communities?, ICES Journal of Marine Science, Volume 67, Issue 5, July 2010, Pages 1076–1085, https://doi.org/10.1093/icesjms/fsp289Bell M. C., Tuck I. D., and Dobby H. 2013. Nephrops species, pp. 357–413. In, Phillips B. F. (ed.), Lobsters: Biology, Management, Aquaculture and Fisheries. Wiley-Blackwell, Hoboken, NJ.

Berry PF. 1969. The biology of *Nephrops andamanicus* Wood-Mason (Decapoda, Reptantia). Investigational Report 22: pp. 1–55. Durban.

Berry PF. 1972. Observations on the fishery for *Palinurus delagoae*. Oceanographic Research Institute, Durban, South Africa. Unpublished Report, 1-5.

Berry PF, Heydorn AEF, Alletson DJ. 1975. The biology of the knife prawn, Hymenopenaeus triarthrus Stebbing, off the Natal coast. Unpublished Report of the Oceanographic Research Institute of South Africa, pp. 1-29.

368 Bishop J. 2006. Standardizing fishery-dependent catch and effort data in complex fisheries with technology
369   change. Reviews in Fish Biology and Fisheries 16: 21-38.

370 Booth AJ. 2000. Incorporating the spatial component of fisheries data into stock assessment models. ICES J.
371   Mar. Sci., 57: 858–865.

372 Bordalo-Machado P. 2006. Fishing effort analysis and its potential to evaluate stock size. Reviews in
373   Fisheries Science 14: 369 – 393.

374 Brinca L, Cristo M, Silva C. 1983. Camarao de profundidade. Relat6rio dos cruzeiros realizados como N/1
375   "Ernst Haeckel''. Rev. Invest. Pesq. (Maputo) 5: 99 pp.

376 Brinkman, T., K. B. Maracle, J. Kelly, M. Vandyke, A. Firmin, and A. Springsteen. 2014. Impact of fuel costs
377   on high-latitude subsistence activities. Ecology and Society 19(4): 18. http://dx.doi.org/10.5751/ES-
378   06861-190418

379 DAFF. 2018. Permit Conditions: KwaZulu-Natal Prawn Trawl Fishery, Fishing Season: 2019. Department of
380   Agriculture, Forestry and Fisheries, Cape Town, South Africa.

381 De Freitas AJ. 1995. Shrimps and Prawns. In A. I. L. Payne & R. J. M. Crawford (Eds.), *Oceans of life off*
382   *southern Africa* (2nd ed., pp. 81–90). Cape Town: Vlaeberg.

383 Deng R, Dichmont C, Milton D, Haywood M, Vance D, Hall N, David D. 2005. Can vessel monitoring system
384   data also be used to study trawling intensity and population depletion? The example of Australia's
385   northern prawn fishery. Canadian Journal of Fisheries and Aquatic Sciences 62: 611–622.

386 Dineshbabu AP, Sujitha T, Dinesh AC. 2016. Handbook on Application of GIS as a Decision Support Tool in
387   Marine Fisheries, CMFRI special publication No.121. Central Marine Fisheries Research Institute, Kochi:
388   104.

389 Erisman BE, Allen LG, Claisse JT, Pondella DJII, Miller EF, Murray JH. 2011. The illusion of plenty:
390   hyperstability masks collapses in two recreational fisheries that target fish spawning aggregations.
391   Canadian Journal of Fisheries and Aquatic Sciences 68: 1705-1716.

392 ESRI. 2019a. Modeling spatial relationships. Accessed 13 February 2019. https://pro.arcgis.com/en/pro-
393   app/tool-reference/spatial-statistics/modeling-spatial-relationships.htm#GUID-F063A8F5-9459-42F9-
394   BF41-4E66FBBCC415.

395 ESRIb.   2019.   How   Emerging   Hotspot   Analysis   works.   Accessed   13   February   2019.
396   http://desktop.arcgis.com/en/arcmap/10.5/tools/space-time-pattern-mining-
397   toolbox/learnmoreemerging.htm

398 Fennessy ST, Groeneveld JC. 1997. A review of the offshore trawl fishery for crustaceans on the east coast
399   of South Africa. Fisheries Management and Ecology 4: 135–147.

400 Fuller DW, Schaefer KM. 2014. Evaluation of a fishing captain's ability to predict species composition, sizes,
401   and quantities of tunas associated with drifting fish-aggregating devices in the eastern Pacific Ocean.
402   ICES Journal of Marine Science 71: 1774–1780.

403 Groeneveld JC, Everett BI, Fennessy ST, Kirkman ST, Santos J, Robertson WD. 2013. Spatial distribution
404   patterns, abundance and population structure of deep-sea crab Chaceon macphersoni, based on

405   complementary analyses of trap and trawl data. Marine and Freshwater Research -
406   http://dx.doi.org/10.1071/MF12263

407   Groeneveld JC, Everett BI. 2015. Crustacean deep-water trawl fisheries. In: van der Elst RP, Everett BI. (eds).
408   Offshore fisheries of the Southwest Indian Ocean: their status and the impact on vulnerable species.
409   South African Association for Marine Biological Research Special Publication (10): 67-118.

410   Guastella LA, Roberts MJ. 2016. Dynamics and role of the Durban cyclonic eddy in the KwaZulu-Natal Bight
411   ecosystem, African Journal of Marine Science, 38:sup1, S23-S42, DOI: 10.2989/1814232X.2016.1159982

412   Halpern BS, Lester SE, Kellner JB. 2009. Spillover from marine reserves and the replenishment of fished
413   stocks. Environmental Conservation, 36: 268–276.

414   Hastie LC, Saunders WB. 1992. On the Distribution and Fishery Potential of the Japanese Red Crab *Chaceon*
415   *granulatus* in the Palauan Archipelago, Western Caroline Islands. Marine Fisheries Review 54(1): 26-32.

416   Jalali MA, Ierodiaconou D, Gorfine H, Monk J, Rattray A. 2015. Exploring Spatiotemporal Trends in
417   Commercial Fishing Effort of an Abalone Fishing Zone: A GIS-Based Hotspot Model. PLoS ONE 10(5):
418   e0122995.

419   Lutjeharms, J. R. E. 2006. Three decades of research on the greater Agulhas Current. Ocean Science
420   Discussions 3: 939-995.

421   Maynou F. 1998. The application of geostatistics in mapping and assessment of demersal resources.
422   Nephrops norvegicus (L.) in the northwestern Mediterranean: A case study. Scienta Marina 62: 117–133.

423   McGarvey R. 2006. Assessing survey methods for greenlip abalone in South Australia South Australian
424   Research and Development Institute (Aquatic Sciences), Adelaide: RD04/0152-2 SARDI Research Report
425   Series No 184 195 pp.

426   Oliveira MM, Camanho AS, Walden JB, Gaspar MB. 2016. Evaluating the influence of skipper skills in the
427   performance of Portuguese artisanal dredge vessels, ICES Journal of Marine Science 73 (10): 2721–2728,
428   https://doi.org/10.1093/icesjms/fsw103

429   Quirijns FJ, Poos JJ, Rijnsdorp AD. 2008. Standardizing commercial CPUE data in monitoring stock dynamics:
430   accounting for targeting behaviour in mixed fisheries. Fisheries Research 89: 1-8.

431   Robey J, Fennessy ST, Everett BI, Santos J, Groeneveld JC. 2013a. Abundance, distribution, size and growth
432   of knife prawn *Haliporoides triarthrus* on deep-water trawl grounds off eastern South Africa. Journal of
433   Marine Science, 35:4, 565-577.

434   Robey J, Fennessy ST, Everett BI, Santos J, Groeneveld JC. 2013b. Abundance and biology of langoustine
435   Metanephrops mozambicus (Nephropidae) on deep-water trawl grounds in eastern South Africa.
436   Journal of Crustacean Biology, 33(6), 760-771.

437   Sala E, Costello C, Dougherty D, Heal G, Kelleher K, Murray JH, et al. (2013) A General Business Model for
438   Marine Reserves. PLoS ONE 8(4): e58799. https://doi.org/10.1371/journal.pone.0058799

439   Steimle, F. W., Zetlin, C. A., and Chang, S. (2001). Essential fish habitat source document: red deepsea crab,
440   Chaceon (Geryon) quinquedens, life history and habitat characteristics. US Department of Commerce,
441   Woods Hole. NOAA Technical Memorandum NMFS-NE, 163, 27.

442 Serchuk FM, Wigley RL. 1982. Deep-sea red crab, Geryon quinquedens. In M.D. Grosslein and T.R. Azarovitz
443   eds. Fish distribution. p. 125-129. MESA New York Bight Atlas Monograph 15. N.Y. Sea Grant Institute,
444   Albany, NY.

445 Steves C. 2019. Trends in the Alaskan Bottom Trawl Fishery from 1993 to 2015: A GIS-based Spatiotemporal
446   Analysis. GI Forum 2019, Volume 7, Issue 1: 87 – 104. DOI: 10.1553/giscience2019_01_s87.

447 Torstensen E. 1989. Avaliação preliminar dos recursos de camario de profundidade em Moçambique. Rev.
448   Invest. Pesq. (Maputo) 18: 185-194.

449 Vázquez-Rowe I, Tyedmers P. 2013. Identifying the importance of the "skipper effect" within sources of
450   measured inefficiency in fisheries through data envelopment analysis (DEA). Marine Policy 38: 387–396.

451 Verdoit M, Pelletier D, Bellail B. 2003. Are commercial logbook and scientific CPUE data useful for
452   characterizing the spatial and seasonal distribution of exploited populations? The case of the Celtic Sea
453   whiting. Aquat. Living Resour., 16: 467–485.

454

Table 1: Definitions of the classification of emerging hot and cold spot analysis (ESRI 2019b).

Pattern Name	Definition
No Pattern Detected	Does not fall into any of the hot or cold spot patterns defined below.
New Hotspot	A location that is a statistically significant hotspot for the final time step and has never been a statistically significant hotspot before.
Consecutive Hotspot	A location with a single uninterrupted run of statistically significant hotspot bins in the final time-step intervals. The location has never been a statistically significant hotspot prior to the final hotspot run and less than ninety percent of all bins are statistically significant hotspots.
Intensifying Hotspot	A location that has been a statistically significant hotspot for ninety percent of the time-step intervals, including the final time step. In addition, the intensity of clustering of high counts in each time step is increasing overall and that increase is statistically significant.
Persistent Hotspot	A location that has been a statistically significant hotspot for ninety percent of the time-step intervals with no discernible trend indicating an increase or decrease in the intensity of clustering over time.
Diminishing Hotspot	A location that has been a statistically significant hotspot for ninety percent of the time-step intervals, including the final time step. In addition, the intensity of clustering in each time step is decreasing overall and that decrease is statistically significant.
Sporadic Hotspot	A location that is an on-again then off-again hotspot. Less than ninety percent of the time-step intervals have been statistically significant hotspots and none of the time-step intervals have been statistically significant cold spots.
Oscillating Hotspot	A statistically significant hotspot for the final time-step interval that has a history of also being a statistically significant cold spot during a prior time step. Less than ninety percent of the time-step intervals have been statistically significant hotspots.
Historical Hotspot	The most recent time period is not hot, but at least ninety percent of the time-step intervals have been statistically significant hotspots.
New Cold Spot	A location that is a statistically significant cold spot for the final time step and has never been a statistically significant cold spot before.
Consecutive Cold Spot	A location with a single uninterrupted run of statistically significant cold spot bins in the final time-step intervals. The location has never been a statistically significant cold spot prior to the final cold spot run and less than ninety percent of all bins are statistically significant cold spots.

Intensifying Cold Spot	A location that has been a statistically significant cold spot for ninety percent of the time-step intervals, including the final time step. In addition, the intensity of clustering of low counts in each time step is increasing overall and that increase is statistically significant.
Persistent Cold Spot	A location that has been a statistically significant cold spot for ninety percent of the time-step intervals with no discernible trend, indicating an increase or decrease in the intensity of clustering of counts over time.
Diminishing Cold Spot	A location that has been a statistically significant cold spot for ninety percent of the time-step intervals, including the final time step. In addition, the intensity of clustering of low counts in each time step is decreasing overall and that decrease is statistically significant.
Sporadic Cold Spot	A location that is an on-again then off-again cold spot. Less than ninety percent of the time-step intervals have been statistically significant cold spots and none of the time-step intervals have been statistically significant hotspots.
Oscillating Cold Spot	A statistically significant cold spot for the final time-step interval that has a history of also being a statistically significant hotspot during a prior time step. Less than ninety percent of the time-step intervals have been statistically significant cold spots.
Historical Cold Spot	The most recent time period is not cold, but at least ninety percent of the time-step intervals have been statistically significant cold spots.

Table 2: Number of trawl vessels operating in the crustacean trawl fishery off KwaZulu-Natal, South Africa from 2000 to 2017.

Year	No. of vessels
2000	6
2001	8
2002	6
2003	6
2004	5
2005	4
2006	4
2007	5
2008	3
2009	3
2010	4
2011	4
2012	4
2013	3
2014	3
2015	3
2016	2
2017	3
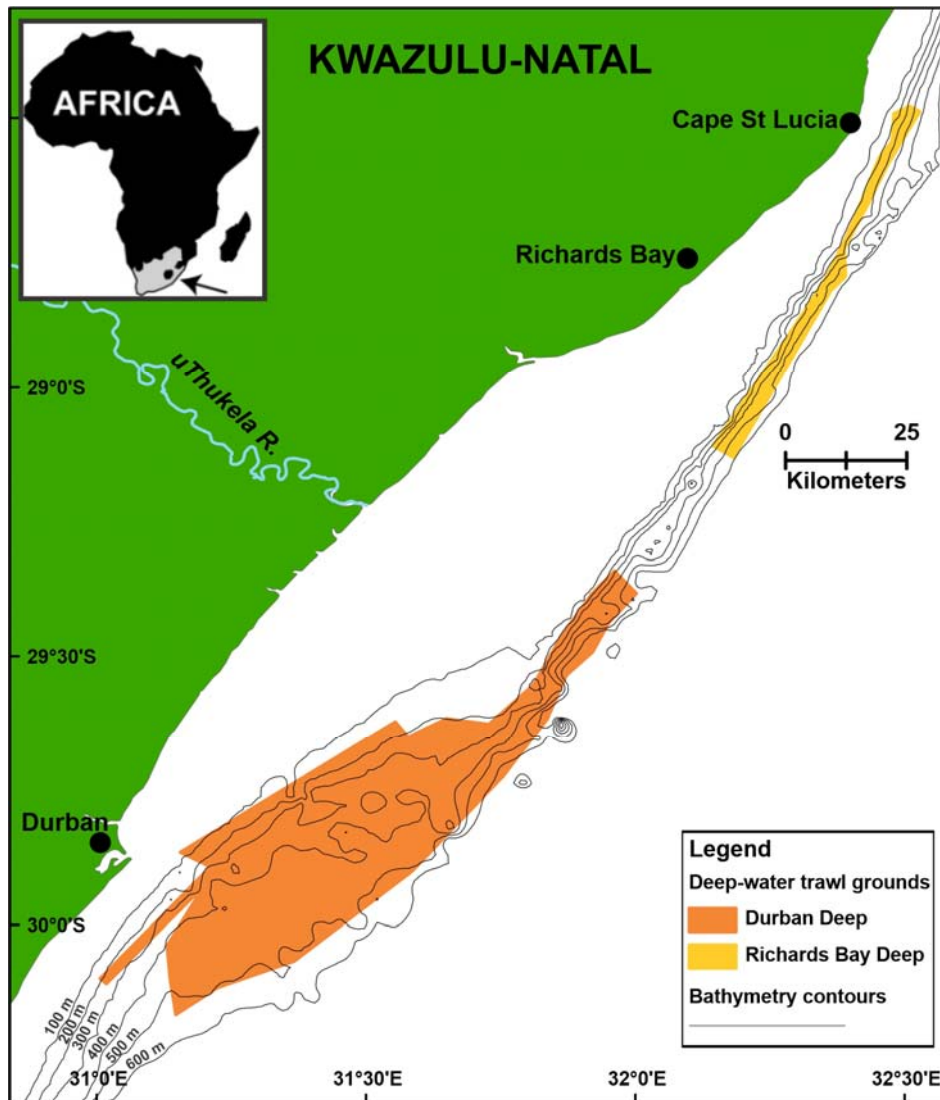
Figure 1: Map showing the study area with the two trawl grounds: Durban Deep in the South and Richards Bay Deep in the north.
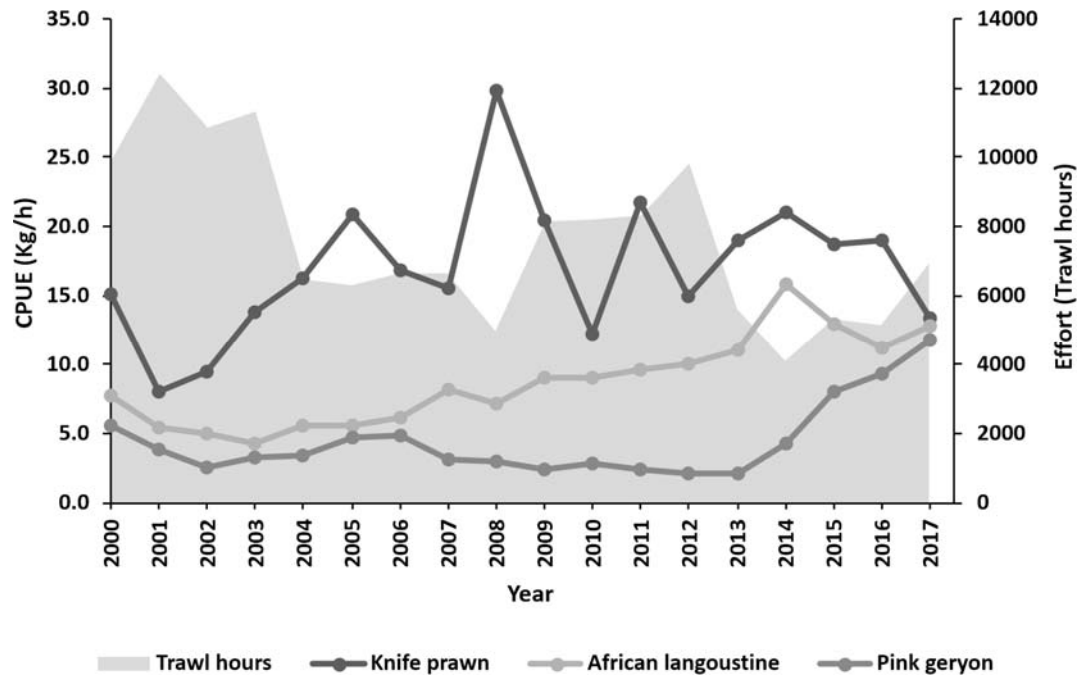
Figure 2: Overall trends in the effort and catch per unit effort of knife prawn (*Haliporoides triarthrus)*, African langoustine (*Metanephrops mozambicus*) and pink geryon (*Chaceon macphersoni*) of the KwaZulu-Natal crustacean trawl fishery
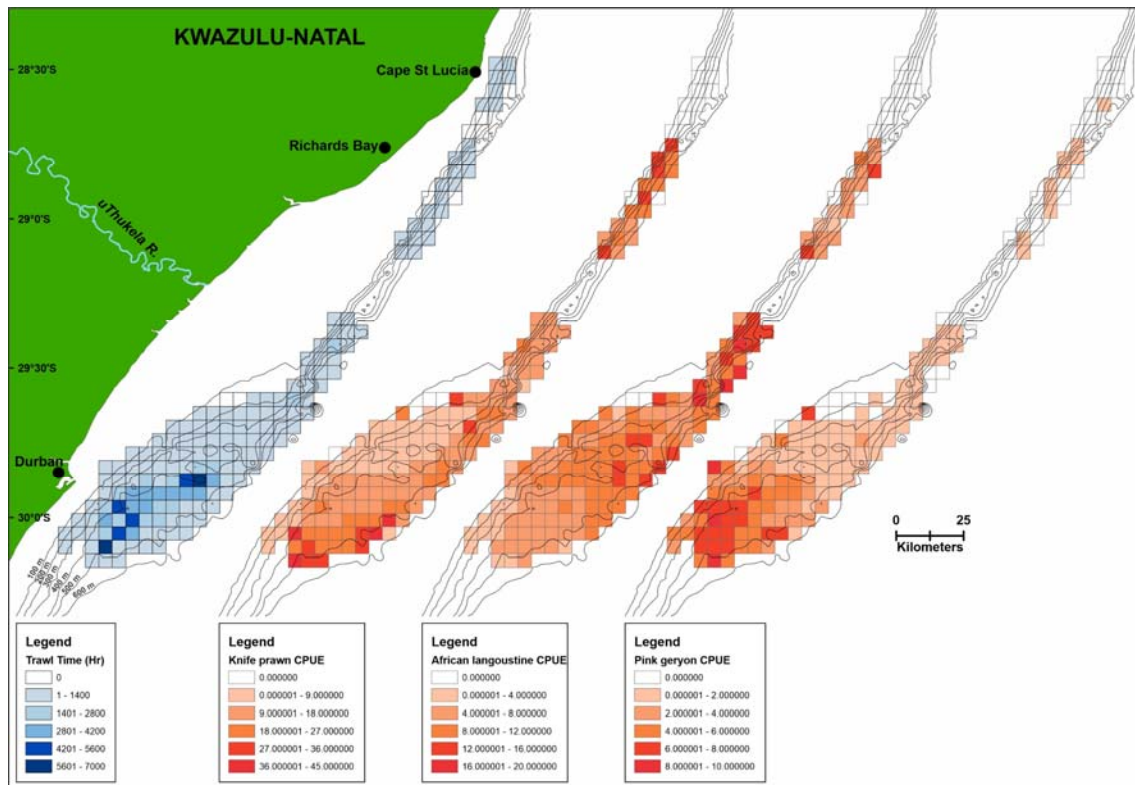
Figure 3: Spatial distribution of the KwaZulu-Natal deep-water crustacean trawl effort and mean CPUE for the three target species: knife prawn (*Haliporoides triarthrus)*, African langoustine (*Metanephrops mozambicus*) and pink geryon (*Chaceon macphersoni*).
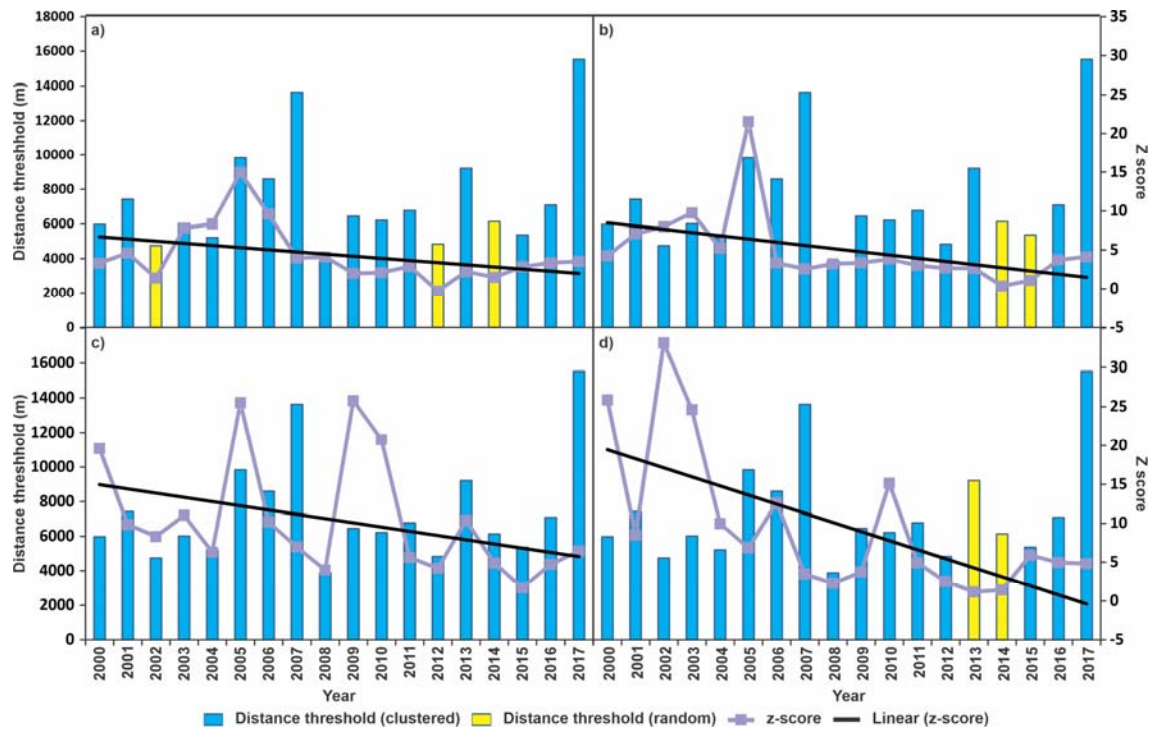
Figure 4: Results of the autocorrelation analyses showing peak z-score values and corresponding distance bands for a) the sum of effort in trawl hours, and the CPUEs of b) knife prawn (*Haliporoides triarthrus*), c) African langoustine (*Metanephrops mozambicus*), and d) Pink geryon (*Chaceon macphersoni*).
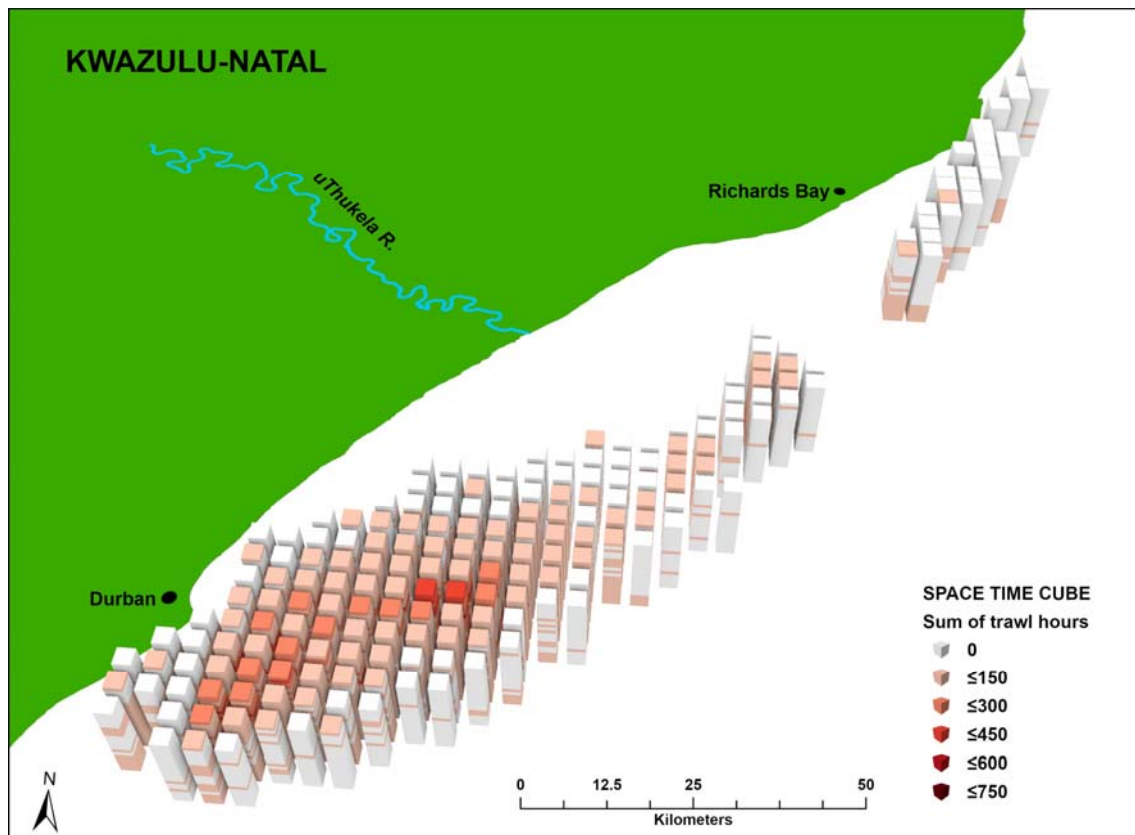
Figure 5: Space-time cube in three-dimensional format for the sum of trawl hours in each locality and each time step.
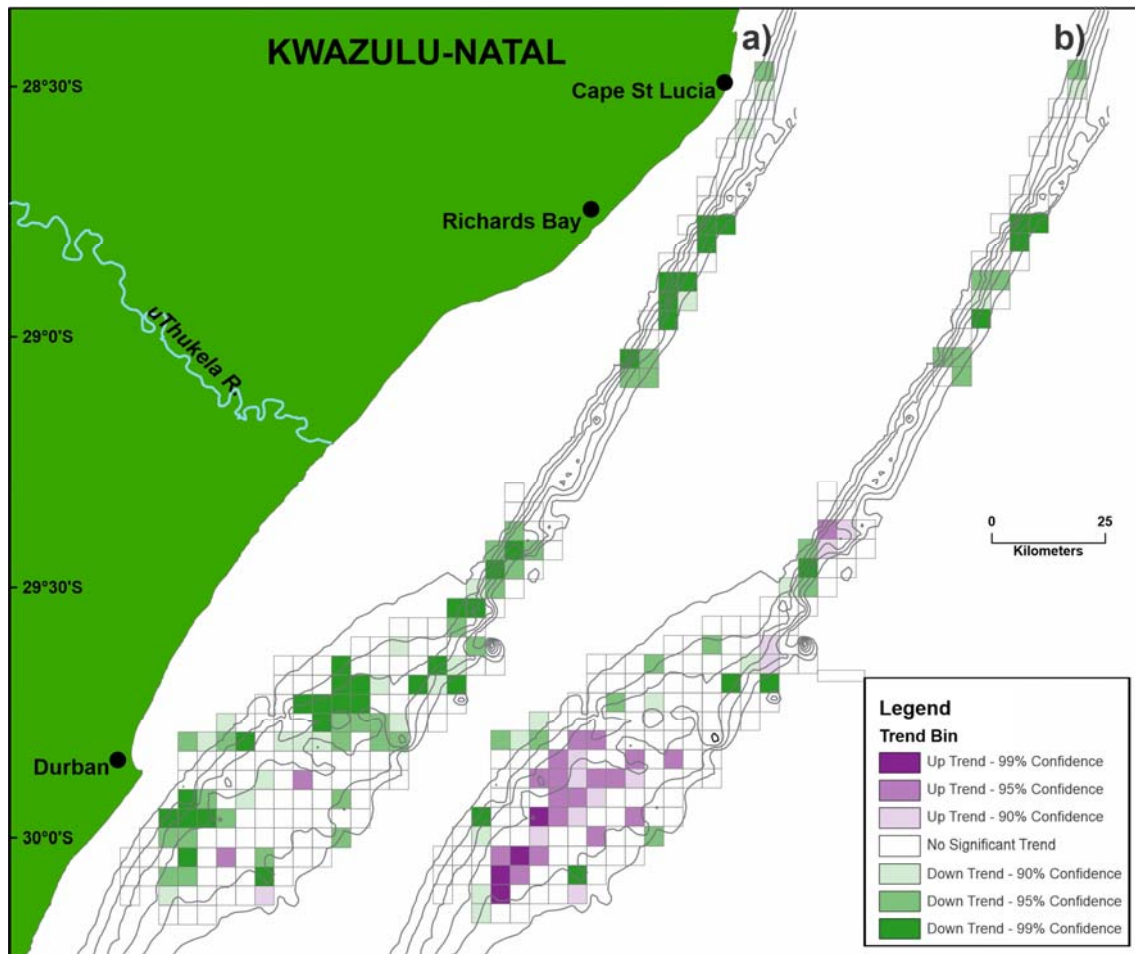
Figure 6: Results of the Mann-Kendall trend test for effort in a) sum of hours and b) mean of hours.
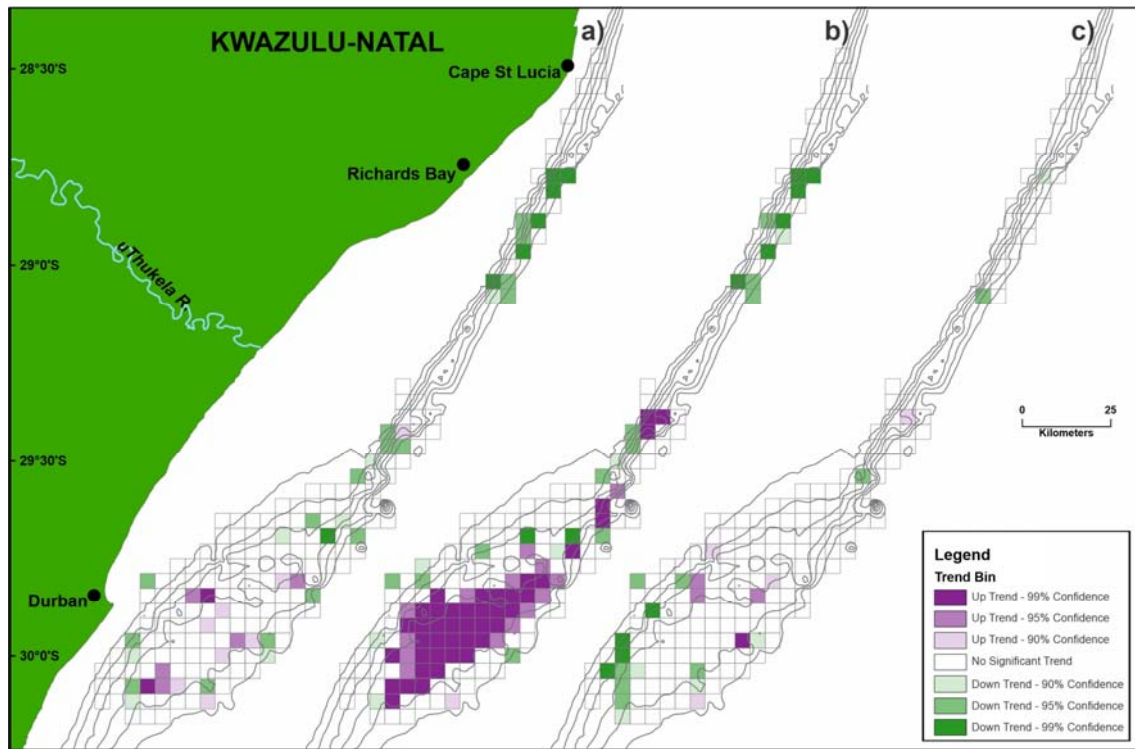
Figure 7: Results of the Mann-Kendall trend test for effort in a) knife prawn (*Haliporoides triarthrus*), b) African langoustine (*Metanephrops mozambicus*), and c) Pink geryon (*Chaceon macphersoni*).
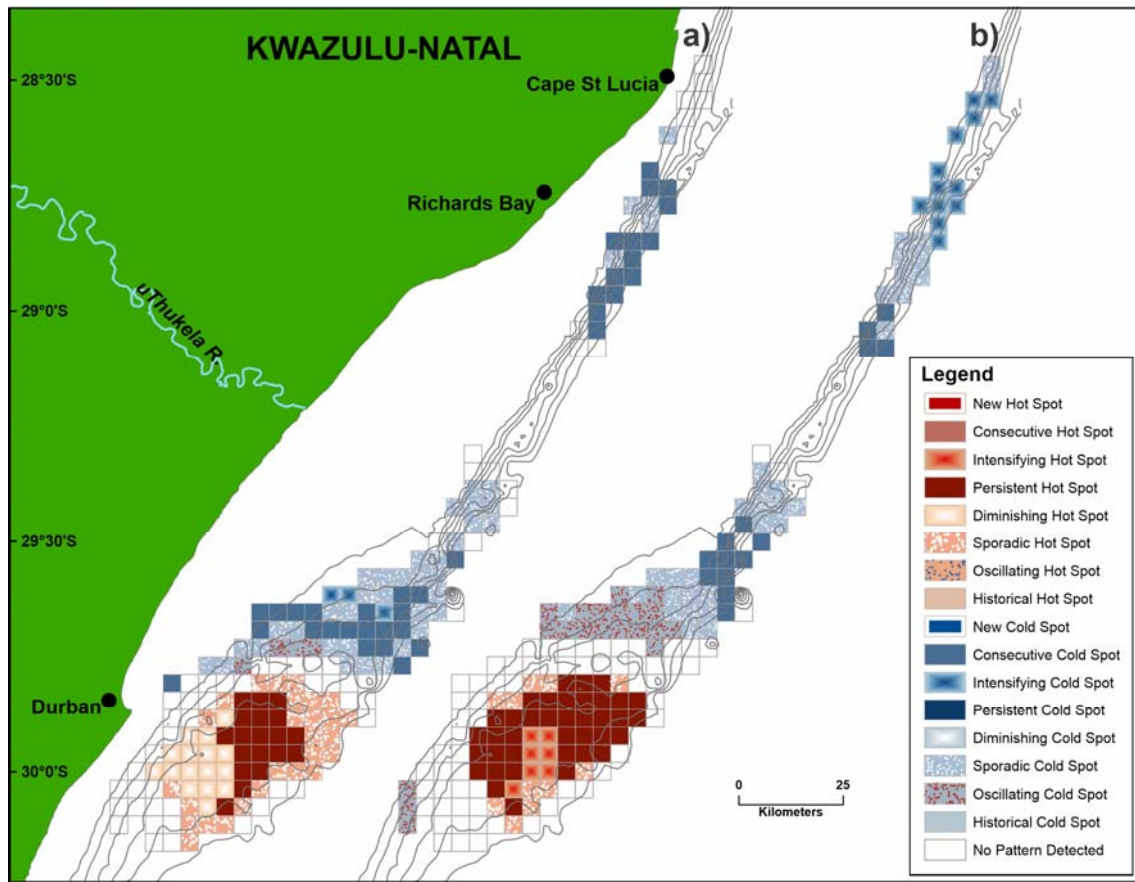
Figure 8: Results of the emerging hotspot analyses for effort in a) sum of hours and b) mean of hours
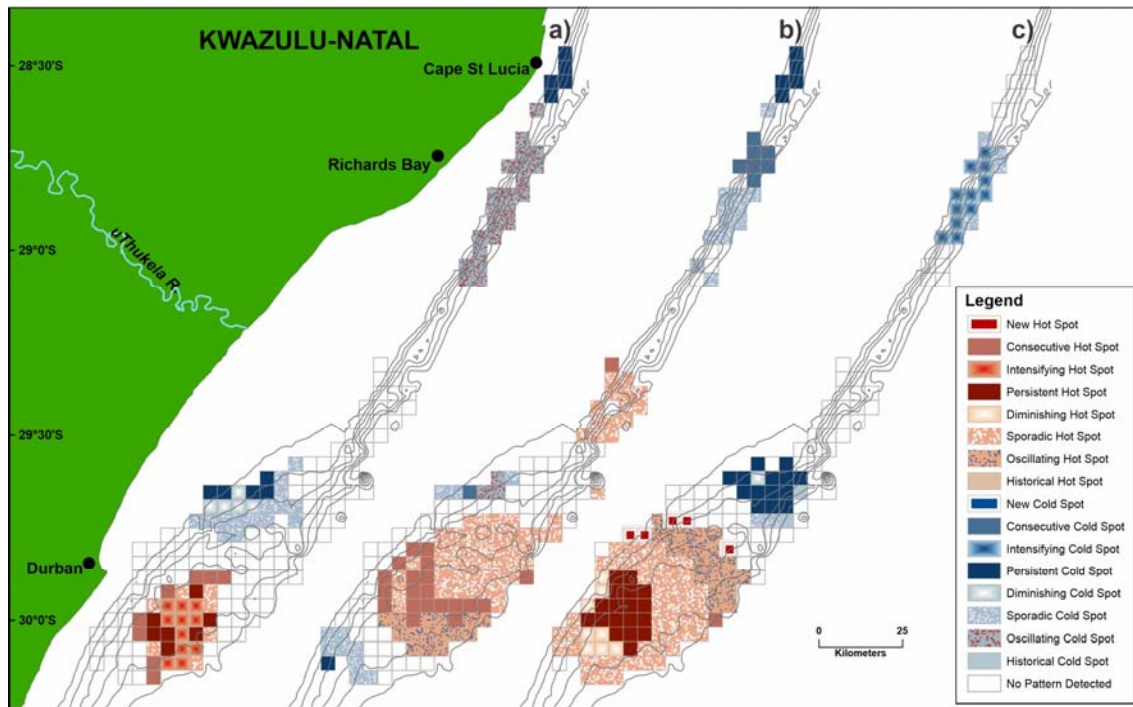
Figure 9: Results of the emerging hotspot analyses for effort in a) knife prawn (*Haliporoides triarthrus*), b) African langoustine (*Metanephrops mozambicus*), and c) Pink geryon (*Chaceon macphersoni*).

Paper 5

Composition and abundance of deep-water crustaceans in the Southwest Indian Ocean: Enough to support trawl fisheries?

B.I. Everett [a, *], J.C. Groeneveld [a], S.T. Fennessy [a], N. Dias [b], O. Filipe [b], L. Zacarias [b], M. Igulu [c], B. Kuguru [c], E. Kimani [d], C.N. Munga [d, e], G.A. Rabarison [f], H. Razafindrakoto [g], D. Yemane [h]

[a] Oceanographic Research Institute, PO Box 10712, Marine Parade, 4056 Durban, South Africa
[b] Instituto de Investigação Pesqueira, Av. Mao Tse Tung N° 389, Maputo, Mozambique
[c] Tanzania Fisheries Research Institute, PO Box 9750, Dar es Salaam, Tanzania
[d] Kenya Marine and Freshwater Fisheries Institute, PO Box 81651, 80100 Mombasa, Kenya
[e] Department of Environment & Health Sciences, Marine Sciences Section, Technical University of Mombasa, PO Box 90420, 80100 Mombasa, Kenya
[f] Centre National de Recherche sur l'Environnement, PO Box 1739, Fiadanana, 101 Antananarivo, Madagascar
[g] Centre d'Etudes et de Développement des Pêches, PO Box 373, Port Schneider, Mahajanga 401, Madagascar
[h] Fisheries Management, Department of Agriculture, Forestry and Fisheries, Private Bag X2, Rogge Bay 8012, South Africa

ARTICLE INFO

ABSTRACT

Expanding coastal fisheries into deeper waters is frequently tabled as an option to increase harvests from the sea in the Southwest Indian Ocean. In this region, only Mozambique and South Africa have established deep-water trawl fisheries for mixed crustaceans. To investigate the fishery potential of deep shelf waters over a broader geographical extent, four bottom trawl surveys were undertaken, in Madagascar, Mozambique, Tanzania and Kenya, respectively, in 2011—2012. Teleosts dominated catches in all surveys (59—74% of total catches) and depths. Crustaceans made up 15% of the catch in Mozambique and Madagascar, but only 6% in Kenya and Tanzania, where elasmobranchs (18%) and other invertebrates (11—15%) were more abundant. A generalized linear model was constructed to quantify the effects of country, depth and day/night on the abundance of four common crustacean species. Abundance of *Haliporoides triarthrus* and *Metanephrops mozambicus* declined from south (Madagascar, Mozambique) to north (Kenya, Tanzania), but *Heterocarpus woodmasoni* was more abundant in Madagascar, Tanzania and Kenya. *Chaceon macphersoni* and *H. triarthrus* abundance increased up to 600 m depth, whereas *M. mozambicus* and *H. woodmasoni* peaked shallower, at 350—500 m. Crustacean catch composition in Mozambique was strikingly similar to commercial landings in eastern South Africa, supporting a distinct sub-region for fisheries management, but differed markedly across the Mozambique Channel. Deep-water crustaceans were less abundant in Kenya and Tanzania, with limited commercial appeal. New deep-water trawl fisheries will have to contend with significant teleost bycatch.

© 2015 Elsevier Ltd. All rights reserved.

1. Introduction

The Southwest (SW) Indian Ocean region comprises developing nations that are among the poorest in the world, based on per capita gross domestic product (GDP) (World Bank, 2014). Most of these countries fall below the top 100 level on the UN development index (UNDP, 2013), and all face severe socio-economic challenges, with a growing need for employment opportunities and food security (van der Elst et al., 2005, 2009). Governments of these countries recognize that nearshore fisheries resources are under immense pressure from ever-increasing exploitation by coastal communities (van der Elst et al., 2009). Consequently, expansion of coastal fisheries into deeper waters is frequently mentioned as an option to increase harvests from the sea.

The assumption of abundant resources in deeper water is not necessarily valid, and historical surveys undertaken on the narrow shelf of Kenya and Tanzania have shown low densities of benthic organisms, with limited fishery potential (Sanders et al., 1988; Sætersdal et al., 1999; Groeneveld and Everett, 2015). The

* Corresponding author.
  E-mail address: bernadine@ori.org.za (B.I. Everett).

continental slope of western Madagascar is steep and irregular, and trawlable areas in deep water are sparse (Crosnier and Jouannic, 1973). Further south, in Mozambique and eastern South Africa, trawl grounds are more productive, and a mixture of crustaceans and fish are caught by established deep-water trawl fisheries (Fennessy and Groeneveld, 1997). These fisheries report landings of approximately 2200 tonnes of crustaceans per year, of which 85% originate from Mozambique (WIOFish, 2013).

Target species in Mozambique and eastern South Africa are deep-water prawns (*Haliporoides triarthrus*, *Aristeus virilis*, *Aristeus antennatus* and *Aristaeomorpha foliacea*), langoustines (*Metanephrops mozambicus*), spiny lobsters (*Palinurus delagoae*) and deep-sea crabs (*Chaceon macphersoni*) (Groeneveld and Everett, 2015). The species mix in catches varies by depth, season, latitude and bottom type trawled (Groeneveld and Melville-Smith, 1995; Dias et al., 2009; Sobrino et al., 2009). Significant quantities of teleosts, elasmobranchs, cephalopods and molluscs are also caught in trawl nets, and are retained if they can be sold, or discarded overboard if their commercial value is considered to be low (Fennessy and Groeneveld, 1997; Fennessy et al., 2004). Far less is known about crustaceans on deeper grounds in Madagascar, Tanzania and Kenya, with most information coming from historical surveys undertaken after the early 1970s. Crosnier and Jouannic (1973) found *H. triarthrus*, *A. foliacea*, two Aristeid species, and *M. mozambicus* in Madagascar trawl surveys. Survey reports from Kenya and Tanzania list deep-water prawns *Heterocarpus* sp., langoustine *Metanephrops andamanicus* and lobsters *Linuparus somniosus* and *Puerulus angulatus* (Birkett, 1978; Sanders et al., 1988). Some of the species names may have changed in the interim.

A recent review of historical trawl information suggested that aggregations of deep-water crustaceans, some with a high unit value, could potentially be exploited at several locations in the SW Indian Ocean (Groeneveld and Everett, 2015). Based on this, the South West Indian Ocean Fisheries Project (SWIOFP; van der Elst et al., 2009) funded a series of bottom trawl surveys to assess the fishery potential of deep-water grounds in Kenya, Tanzania, Mozambique, western Madagascar and eastern South Africa. We determined the relative importance of major taxa (crustaceans, teleosts, elasmobranchs, cephalopods, other invertebrates) represented in trawl catches, and investigated the abundance of crustacean species by country, day/night and depth stratum.

2. Materials and methods

2.1. Study area

The SW Indian Ocean extends along the African coast, from northern Kenya (2°S) to eastern South Africa (31°S), and around the island states of Madagascar, Mauritius, Comoros and Seychelles (Fig. 1). It is a low-latitude mainly tropical region influenced by large-scale oceanographic systems (Lutjeharms, 2006; Ternon et al., 2014a). Monsoon winds affect coastal flow in the north. The East Africa Coastal Current (EACC) off Kenya strengthens during the wet southeast monsoon (April to October), and weakens during the northeast monsoon (November to March), giving rise to a seasonally reversing Somali Current (Schott and McCreary, 2001). Upwelling and deep-water mixing makes the Somali Current region nutrient-rich and productive, compared to oligotrophic waters further south. Mozambique Channel circulation is influenced by seabed topography, including cyclonic and anti-cyclonic cells (Lutjeharms, 2006; Ternon et al., 2014b). The Agulhas Current originates near the southern end of the Mozambique Channel, and flows southwest along the shelf edge of eastern South Africa.

The shelf topography is narrow and steep along much of eastern Africa, widening in bights or near river deltas, such as the Natal Bight (South Africa), Maputo Bay and the Delagoa Bight (Mozambique), the Rufiji Delta (Tanzania) and Malindi-Ungwana Bay (Kenya). The shelf edge is mostly rocky and unsuitable for trawling. Deep trawl grounds in eastern South Africa comprise sand, mud, hardened sediment accretions, foraminifera and spicules (Berry, 1969). Sea surface temperatures are warmer near the equator (25–29 °C; World Sea Temperatures, 2014) than further south (22–27 °C; Smit et al., 2013), however bottom temperatures at >200 m in eastern South Africa have been reported as 9–12 °C (Berry, 1969) and 8–10 °C at 500–700 m depth in western Madagascar (Pripp et al., 2014).

2.2. Survey gear and strategy

Four trawl surveys were conducted in Kenya, Tanzania, Mozambique and western Madagascar, respectively, between October 2011 and March 2012 (Fig. 1). Two commercial fishing trawlers with their crew complement and fishing gear were leased. The FV Caroline (40 m length; 313 t GRT; 745 hp) towed a single otter trawl net deployed from the stern (net length 75 m; footrope length 60 m; mesh in codend 50 mm stretched), and was used in Mozambique and Madagascar. The FV Roberto (23 m length; 117 t GRT; 295 hp) also towed an otter trawl net from the stern (net length 26 m; footrope length 26 m; mesh in codend 38 mm stretched), and was used in Tanzania and Kenya. Both vessels were equipped with echo sounders, global positioning systems and track plotters, radar, and VHF/SSB radios. A team of scientists (minimum 4) accompanied each survey.

Detailed knowledge of existing fishing grounds (Mozambique), information from historical research surveys (Sætersdal et al., 1999), or anecdotal information obtained from fishing companies (Madagascar, Tanzania, Kenya) were used to define survey grounds, based on substrate type (trawlable muddy/sandy grounds) and depth range (100–700 m). Prospective grounds were stratified by depth and latitude (Table 1), and the surface area of individual blocks calculated, based on distance estimates obtained from British Admiralty Nautical Charts (760, 3855, 2930, 2931, 2939 and 2949) with scales of 1: 300 000 to 1: 1000 000. The calculated surface area of sampling blocks totalled 21 319 km^2 in Mozambique, 473 km^2 in Tanzania and 6034 km^2 in Kenya. Sampling effort (number of trawls) was allocated to blocks based on surface area except in Madagascar where the area was unknown and trawls were allocated equally. Given the imprecise geographical information available, it was foreseen that some blocks would be untrawlable. Remaining trawls at the end of each survey were redistributed at the discretion of the survey leader.

Trawls were undertaken roughly parallel to the coast, within the boundaries of each block. Start and end-time of trawls were recorded when the net reached the seafloor (winches stopped), and when hauling commenced. Nominal trawl speed (3 knots) and duration (60 min) could be adjusted based on sampling requirements (i.e., seafloor conditions; expected catch). Most trawls were conducted during daylight. Night trawls (set and hauled between sunset and sunrise) were undertaken so that day/night effects on CPUE could be assessed (Table 1).

No survey was conducted in eastern South Africa (28-31°S), but summarized information on the catch composition of crustaceans was obtained from commercial trawl logbooks (DAFF, 2014), as described in detail by Robey et al. (2013a; 2013b). Similar trawl vessels and nets were used to collect the survey and fisheries information, but in the commercial fishery, the proportions of target species may have been affected by targeting practices.
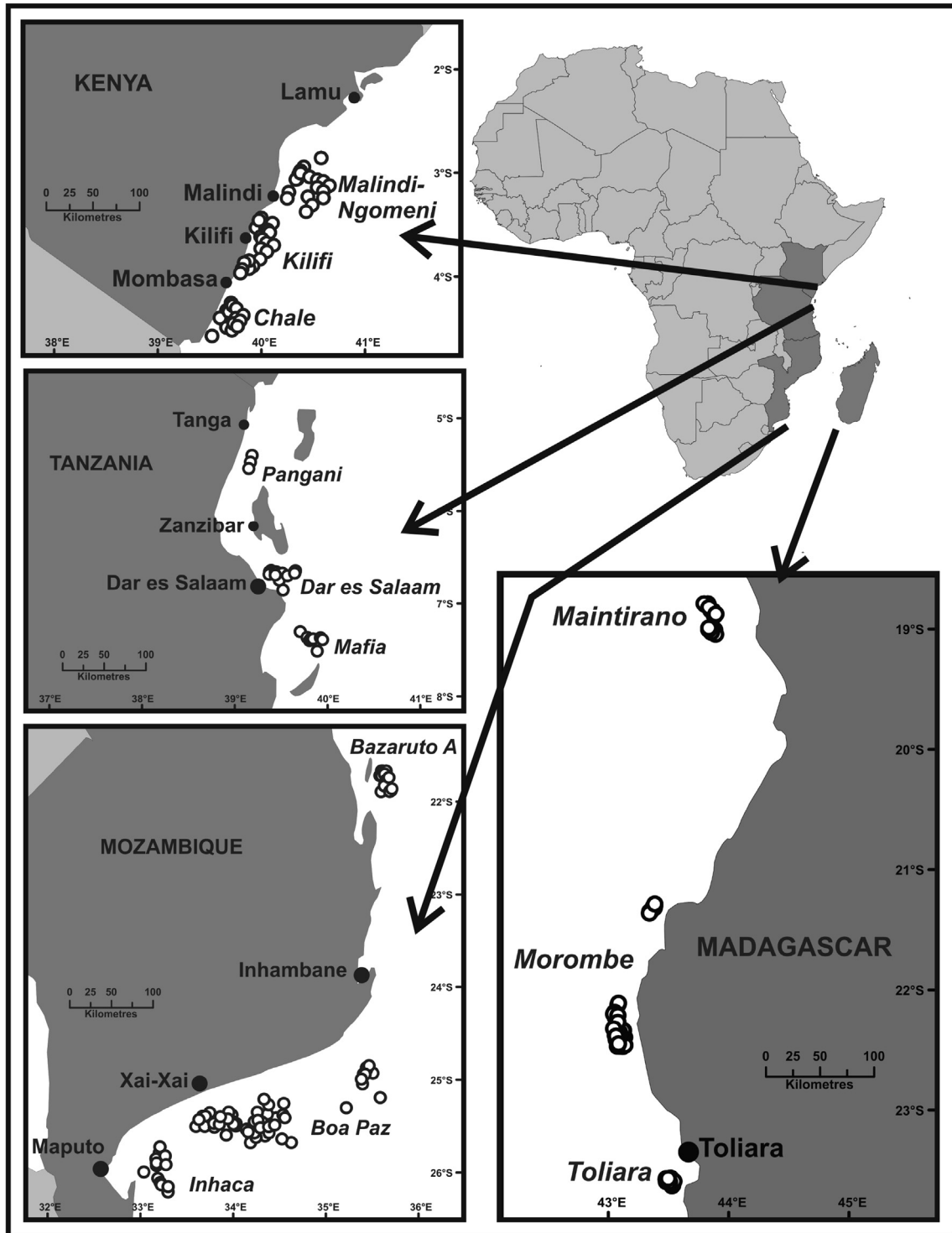
Fig. 1. Map of the areas trawled during the South West Indian Ocean Fisheries Project deep-water crustacean surveys. Symbols indicate actual positions where nets were set, trawl area names in italics.

2.3. Data collection

The entire catch brought up in each trawl was emptied into a holding pen, without releasing or discarding any organisms. The catch was weighed, or when too large, it was subdivided into randomly mixed equal subsamples in bins, of which one was selected and weighed. Large animals (mostly sharks and rays) were removed before subdividing the catch, and weighed separately. The total catch was estimated by multiplying the subsampled bin weight by the number of bins, and adding the weights of the large animals.

The total catch (or a randomly mixed representative sample) was sorted by species using standard species identification guides for the region (Barnard, 1950; Holthuis, 1980; Bauchot and Bianchi,

Table 1
Number of trawls set per country, latitude and depth.

Latitude	Country	Depth						Total
		100–299	200–299	300–399	400–499	500–599	600–699	
−3	Kenya	2	3					5
−4		8	9	9	10			36
−5			3	6	5	5		19
−6	Tanzania		1	2				3
−7			5	6	2	3		16
−8			3	3	2			8
−19	Madagascar			3	3	6	3	15
−20				3	2	1		6
−22		2	3	3				8
−22	Mozambique		5	7	2	3		17
−23	Madagascar	1	4	5	9	14	6	39
−24			5	2	2	8	4	21
−25	Mozambique				6	1		7
−26			9	32	18	2		61
−27					5			5
Total		13	50	81	66	43	13	

Shaded blocks indicate where some trawls were set at night. All other trawls were set during daylight hours. Depth categories show the shallowest points of their respective intervals, e.g. 100 = 100–299 m.

1984; Bianchi, 1985; Smith and Heemstra, 1986; van der Elst, 1993; Randall, 1995; Richmond, 1997) as well as unpublished identity photographs (Oceanographic Research Institute, Durban). Individual specimens were counted, and callipers used to measure the carapace length (CL, mm) or width (CW, mm) of crustaceans. Gender was determined visually using standard indicators for crustaceans (King, 1995).

2.4. Data analysis

Catches were categorized into five taxa, comprising crustaceans (larger species with present or potential commercial value, including *H. triarthrus*, *A. foliacea*, *Aristeus* sp. *Heterocarpus* sp., *Penaeopsis* sp., *Penaeus marginatus*, *M. mozambicus*, *P. delagoae*, *L. somniosus* and *C. macphersoni*), teleosts, elasmobranchs, cephalopods and other invertebrates (small crustaceans or species without commercial value, molluscs except for squid, cuttlefish and octopus that can potentially be sold, echinoderms and coral fragments).

Catches made by the two vessels could not be directly compared because of differences in vessel power, footrope length, net size, and mesh size in the codend. Catches were therefore converted to weight per unit swept area, which was determined for each haul as follows:

$$\text{Swept area}\left(m^2\right) = \text{footrope length(m)*vessel speed}\left(m \cdot s^{-1}\right)$$
$$*\text{trawl duration(s)}$$

Vessel speed used was the mean per vessel for all trawls. An average swept area per trawl was determined for each vessel, and the ratio of these was then used as a multiplication factor to raise catches made by the FV Roberto to the equivalent of those made by the FV Caroline.

Density of each species was then used as nominal CPUE (kg/km²), which was passed through a modelling framework (regression type models, variants of the Generalized Linear Models) to account for the effects of depth, area and day/night, while assessing the CPUE. Trawl stations were patchily distributed across the geographic domain of the study, partly due to untrawlable substrata, which precluded the use of finer spatial resolutions/latitudinal bins (Fig. 1; Table 1). Thus we used country, instead of latitude, and depth categories as factors in the models to assess broader spatial patterns in abundance, by species (Table 2). Time of

day (converted to a day/night factor) was not significant, except in a binomial model for *C. macphersoni*, but considering the biology of deep-sea crabs (Groeneveld et al., 2013) it was likely the result of the patchiness of the data, and was excluded from the final model.

The CPUE of crustacean species (*H. triarthrus*, *Heterocarpus woodmasoni*, *M. mozambicus* and *C. macphersoni*) that were present in catches in the majority of countries, and abundant in at least some locations, was standardised using a GLM. The delta method was applied as datasets comprised many zeroes (species absent in a trawl), and distributions were skewed to the right (Lo et al., 1992; Maunder and Punt, 2004). The delta method comprises a two-step model. In the first step, the probability of a non-zero catch is modelled, assuming a binomial error distribution (usually with a logit link), and in the second step, only the positive catch is modelled, assuming one of the different exponential family of distributions (e.g. gaussian, poisson, normal, log-normal, negative binomial, etc.). We used a gamma error distribution with a log link, because residuals were then randomly distributed, and it fitted the data best, based on the AIC (Fig. 2). In addition, the distribution of the residuals was also checked for biases that might have resulted from using two vessels, and the spreads were roughly comparable for the four species (Fig. 3). For the continuous part of the delta method the following GLM model was used for four species:

$$\log\left(C_{ijk}\right) = \mu + R_{ij} + D_{ik} + \varepsilon_{ijk}$$

where the $\log(C_{ijk})$ is the log of CPUE in trawl i, Region j, and Depth category k. The intercept term is μ, R_{ij} is the region factor for trawl i and region j, D_{ij} is the depth factor for trawl i and depth category k, and ε_{ijk} is the error term. The same model formulation was used for the binomial part with the exception that the logit link function was used and the response was presence/absence (1 or 0). Standardized indices for the continuous part were then obtained as canonical indices (Francis, 1999):

$$\bar{R} = \frac{\sum_{i=1}^{i=n} R_i}{n}$$

$$A_i = e^{R_i - \bar{R}}$$

where $\bar{R}$ is the mean of the region effect in log-space, R_i is the coefficient for Region i and A_i the standardized index for region i. The

Table 2
Summary of the best model used to standardise the catches of *Heterocarpus woodmasoni*, *Metanephrops mozambicus*, *Haliporoides triarthrus* and *Chaceon macphersoni*.

|	Models	R.DF	M.deviance	R.deviance	P.deviance	Species	Model
1	M1: WCatchStdVessel > 0 ~ CountryO + DepthInt	258	30.06	276.55	9.80	*H. woodmasoni*	Binomial
2	M1: WCatchStdVessel > 0 ~ CountryO + DepthInt	258	85.66	282.36	23.28	*M. mozambicus*	Binomial
3	M1: WCatchStdVessel > 0 ~ CountryO2 + DepthInt	199	61.51	223.11	21.61	*H. triarthrus*	Binomial
4	M1: WCatchStdVessel > 0 ~ CountryO + DepthInt	258	54.81	263.47	17.22	*C. macphersoni*	Binomial
5	M1: WCatchStdVessel ~ CountryO + DepthInt	62	94.94	152.09	38.43	*H. woodmasoni*	Gamma
6	M1: WCatchStdVessel ~ CountryO + DepthInt	132	46.18	173.48	21.02	*M. mozambicus*	Gamma
7	M1: WCatchStdVessel ~ CountryO2 + DepthInt	89	77.08	172.57	30.88	*H. triarthrus*	Gamma
8	M1: WCatchStdVessel ~ CountryO + DepthInt	68	8.55	49.80	14.65	*C. macphersoni*	Gamma
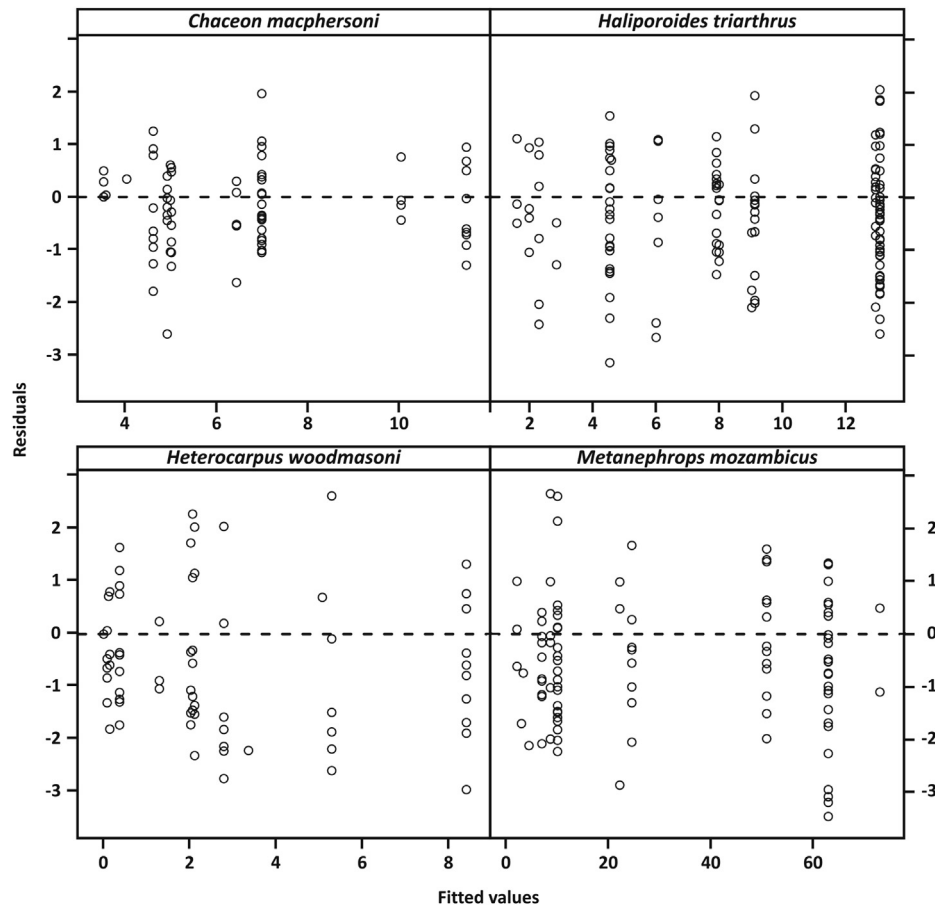
Fig. 2. Model diagnostic: residuals vs. fitted values of the GLM model applied for the non-zero catches.

canonical indices for the binomial models were also computed in the same way. The combined index of abundance was then obtained as follows (Vignaux, 1994):

$$C_i = \frac{R_i^c}{\left[1 - P_o \left[1 - \frac{1}{R_i^b}\right]\right]}$$

where C_i is the combined index of abundance (from the delta method) for region i, R_i^c is the index from the continuous model for region i, P_0 is the proportion of zero trawls for the reference region (it is added to reduce the impact of varying proportion of zero trawls across the factor level considered, in this case region), R_i^b is the index from the binomial model for region i. A similar procedure was applied to get a standardized index by depth classes. All

analyses, model fitting, model validation, and standardization of CPUE were done in R version 3.1.1 (R Development Core Team, 2011).

3. Results

3.1. Fishing effort and catch composition

A total of 231 day and 35 night trawls were undertaken over a period of 55 sampling days (Table 1). Trawl duration varied from ten minutes to two hours (0.82 ± 0.26 [SD] h). The shortest trawls were due to rough trawl grounds and the longer ones to increase sample size. Trawl depths ranged from 170 to 655 m, and were mostly between 300 and 399 m (81 trawls) and 400 and 499 m (66 trawls). Individual trawl catches ranged from zero to a maximum of
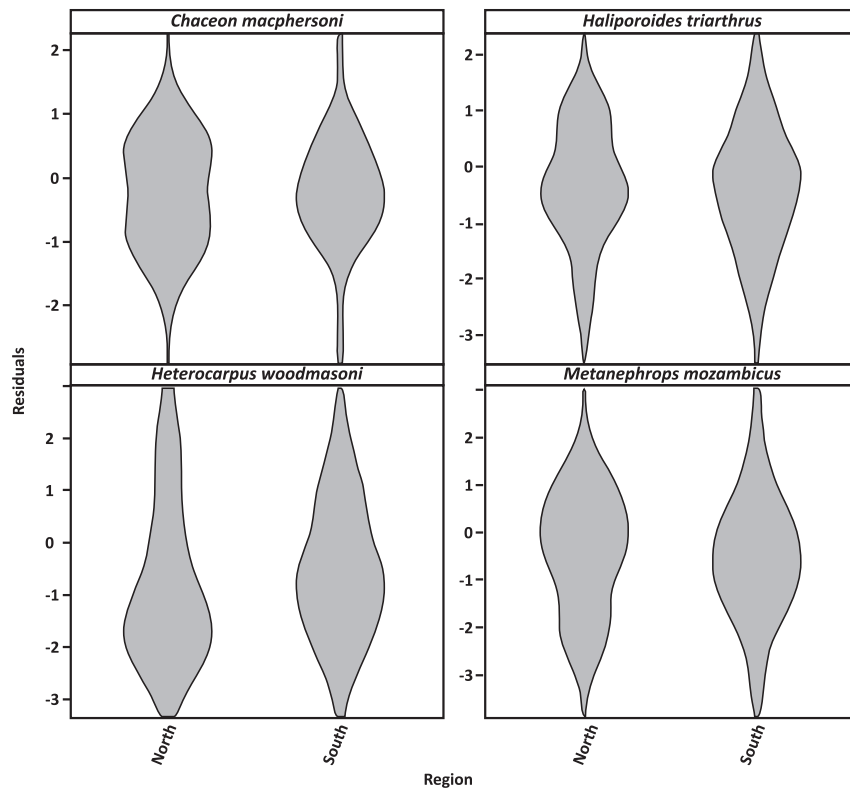
Fig. 3. Model diagnostic: comparison of the distribution of residuals from the GLM model applied to the non-zero catches for the northern (Kenya and Tanzania) and southern (Mozambique and Madagascar) regions.

1530 kg. Catches of all taxa combined were 29.2 t in Mozambique, 19.0 t in Madagascar, 5.5 t in Kenya and 1.3 t in Tanzania.

Teleosts dominated catches in all surveys (59—74% of total catches), irrespective of the depth trawled (Fig. 4a, b). Elasmobranchs were more commonly caught in Kenya (18%). Crustaceans made up around 15% of the catch in Mozambique and Madagascar, but only 6% in Kenya and Tanzania. Other invertebrates were relatively more abundant in Kenya and Tanzania (11—15%). Crustaceans made up <10% of catches between 200 and 399 m depth, but increased thereafter to a maximum of 29% at 600—699 m depth (Fig. 4b).

The penaeid prawn *P. marginatus* contributed most to crustacean catches in Kenya (36% by weight), and the spear lobster *L. somniosus* contributed most in Tanzania (61%) (Fig. 5). Kenyan catches included substantial quantities of *C. macphersoni* (19%) and the prawns *H. woodmasoni* (10%) and *Penaeopsis balssi* (18%), whereas *H. woodmasoni* (19%) and *M. mozambicus* (11%) were important in Tanzania. Two prawn species predominated in Madagascar: *A. foliacea* (31%) and *Aristeus* spp. (28%), with lesser amounts of *H. triarthrus* (12%), *M. mozambicus* (14%) and *C. macphersoni* (5%). The Mozambique survey caught mainly *H. triarthrus* (63%), followed by *M. mozambicus* (18%), *P. delagoae* (10%) and *C. macphersoni* (6%). The composition of crustacean catches in the Mozambique survey was strikingly similar to landings from the commercial trawl fishery in South Africa, where *H. triarthrus* contributes 60% by weight, *M. mozambicus* 23%, *P. delagoae* 10% and *C. macphersoni* 8% (DAFF Unpublished data).

3.2. Nominal biomass estimates

Nominal biomass estimates based on all trawls sampled were dominated by teleosts (771 kg/km²), followed by crustaceans

(142 kg/km²), elasmobranchs (84 kg/km²), other invertebrates (77 kg/km²) and cephalopods (47 kg/km²) (Table 3).

The biomass of *H. triarthrus* was estimated as 56 kg/km² over all trawls sampled, but highest concentrations occurred in Mozambique, where the estimate increased to 95 kg/km² (Table 3). *M. mozambicus* biomass estimates were similar for Mozambique (27 kg/km²) and Madagascar (28 kg/km²), compared to the lower regional estimate of 22 kg/km². Biomass of *A. foliacea* was concentrated in Madagascar (62 kg/km²), compared with 19 kg/km², regionally. The regional biomass estimate of *H. woodmasoni* was 4 kg/km² with the highest concentrations in Kenya (8 kg/km²). *C. macphersoni* biomass was also highest in Kenya (15 kg/km²), followed by Madagascar and Mozambique (both 9 kg/km²), but they were scarce in Tanzania (1 kg/km²).

3.3. CPUE models

The proportion of deviance explained by the best-fitting models (binomial and gamma) ranged from 9.8% to 38.4% for the four species (Table 3). The standardised CPUE indices mostly showed similar trends, by country, than the nominal values (Fig. 6). The standardised CPUE of *H. woodmasoni* was highest in Madagascar, lowest in Mozambique, and moderate in both Kenya and Tanzania. The opposite trend was observed for *M. mozambicus*, with the highest CPUE in Mozambique, followed by Madagascar, Tanzania and Kenya, suggesting declining abundance from south to north. Similarly *H. triarthrus* had the highest CPUE in Mozambique and Madagascar, declining towards the north. The standardized CPUE of *C. macphersoni* was highest towards the south and the north, and lowest in Tanzania.

The standardised and nominal CPUE indices by depth also showed similar trends (Fig. 7). For *H. woodmasoni* and *M. mozambicus*,
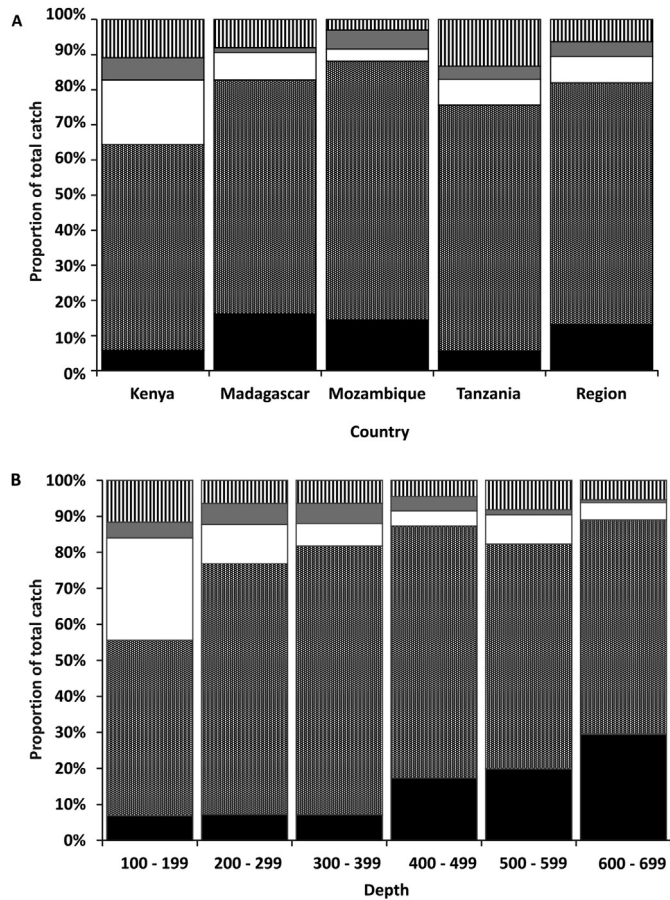
3.4. Biological information

The deep-water prawn species with the largest mean size (CL ± SD) were *A. foliacea* (48.5 ± 7.4 mm), *A. antennatus* (39.8 ± 9.1 mm) and *H. triarthrus* (35.6 ± 7.9 mm) (Fig. 8). *H. woodmasoni* (25.3 ± 3.5 mm) and *P. balssi* (22.7 ± 5.4 mm) were much smaller, presumably reducing their market value compared to the larger species. The mean CL of all five species remained relatively constant across the depth range sampled. Of all *H. woodmasoni* captured, only 3% were males. The skewed sex ratio suggests that at least a part of the population was not accessible to the trawl nets. Sex reversal as a possible cause for the skewed ratio was not considered (King and Moffitt, 1984). The percentages of male *P. balssi* (27%) and *A. antennatus* (33%) were also considerably lower than parity, suggesting that females were more accessible to trawl nets than males.

The mean CL of *M. mozambicus* was 47.1 ± 10.6 mm. Larger individuals were caught between 100 and 199 m depth (52.5 ± 3.8 mm), whereafter the mean CL decreased to 43.7 ± 7.6 mm between 500 and 599 m depth. The sex ratio remained relatively stable, near parity (Fig. 8). Some 116 *C. macphersoni* were measured, and they covered a broad CW range from 78 to 181.3 mm. The broad range is explained by the inclusion of both males (154 ± 12.5 mm) and much smaller females (118.6 ± 12.1 mm) in the same histogram. Males were dominant at all depths, but the dominance increased at depths ≥400 m, where the mean CW increased.

4. Discussion

A standard survey methodology was adhered to during the four trawl surveys, and the data were therefore comparable across the region. In theory, a regional dataset offers broader insights into the nature of shared or transboundary fish stocks, compared to smaller localized projects. A regional framework also allows for a more collective approach to fisheries and management challenges shared by SW Indian Ocean countries, for instance, user conflicts caused by competition among fishing sectors, discarding of trawl bycatch, or habitat degradation through use of damaging fishing practices. A collective approach is particularly useful in a developing region, such as the SW Indian Ocean, where pooling of resources can offset
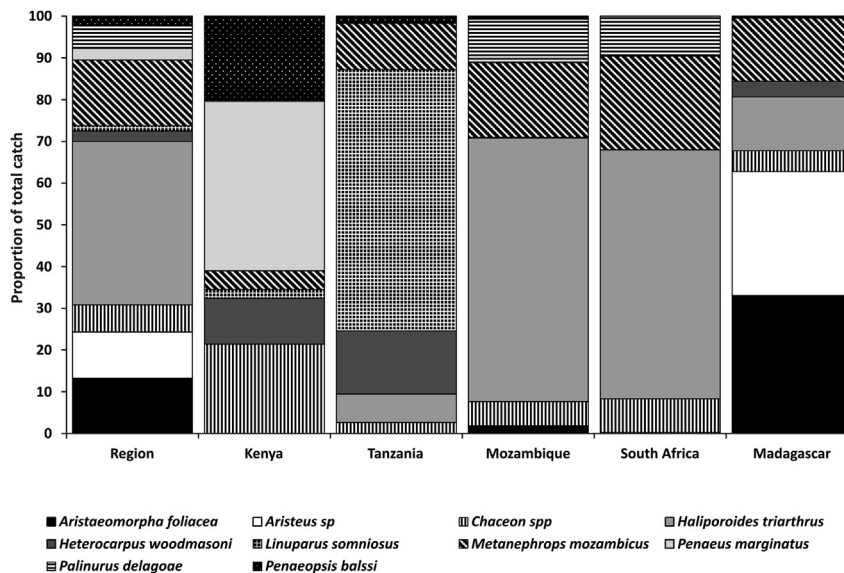
Fig. 4. Proportion of the catch made up of crustaceans, teleosts, elasmobranchs, cephalopods and other invertebrates by A) country and B) depth interval.

standardised CPUE peaked in the medium depths, declining towards shallow and deeper waters. The CPUE of *H. triarthrus* and *C. macphersoni* increased with increasing depth over the depth range sampled.

Fig. 5. Proportion of the selected crustaceans that were caught by country and for the region.

Table 3
Nominal biomass (kg/km^2) of selected crustaceans by country and for the region. Areas trawled were 7.78 km^2 (Kenya), 3.47 km^2 (Tanzania), 27.75 km^2 (Mozambique), 15.31 km^2 (Madagascar) and 54.31 km^2 (Region).

| Species or group	Kenya	Tanzania	Mozambique	Madagascar	Region
Teleosts	775.9	489.11	774.46	825.98	770.97
Elasmobranchs	243.65	50.98	37.02	96.78	84.35
Other invertebrates	152.6	93.77	32.95	113.36	76.64
Haliporoides triarthrus	0.00	2.57	94.78	23.97	55.35
Cephalopods	83.91	25.91	56.77	16.78	47.41
Metanephrops mozambicus	3.06	4.21	26.75	28.09	22.30
Aristaeomorpha foliacea	0.02	0.00	2.67	61.60	18.73
Aristeus spp.	0.00	0.00	0.15	55.32	15.67
Chaceon spp.	14.62	1.02	8.64	9.33	9.20
Palinurus delagoae	0.00	0.05	15.65	0.00	8.00
Penaeus marginatus	27.82	0.00	0.00	0.00	3.98
Heterocarpus woodmasoni	7.52	5.74	0.22	7.05	3.54
Penaeopsis balssi	13.94	0.59	1.07	0.90	2.84
Linuparus somniosus	1.48	23.76	0.00	0.00	1.73
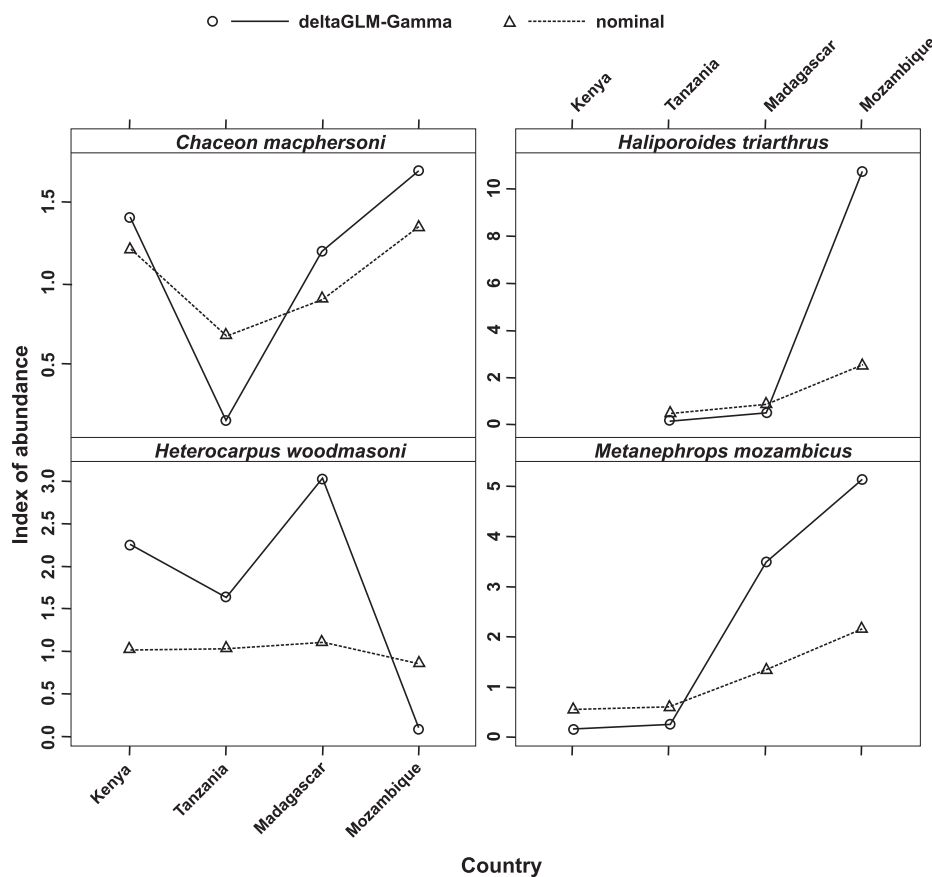
Fig. 6. Standardized CPUE indices for *Chaceon macphersoni*, *Haliporoides triarthrus*, *Heterocarpus woodmasoni* and *Metanephrops mozambicus* by country, based on the final delta models.

scarce manpower, infrastructure and economic resources (van der Elst et al., 2009). Some limitations of our approach were that only small portions of the shelf and upper slope could be sampled with the available resources, and that some variability in selectivity (i.e. use of different vessels and trawl nets) and sampling methods (use of different samplers in each country) may have been introduced.

The survey strategy was limited to a single set of surveys covering a large area, and therefore seasonal variability in abundance and catch composition could not be assessed. Environmental conditions in deep-water habitats are generally more stable than in shallow water (Gibson et al., 2003), and, at similar depths to those

covered in these surveys, little seasonal variation was observed in the abundance of South African commercial catches of *M. mozambicus* (Robey et al., 2013a), *H. triarthrus* (Robey et al., 2013b) and *C. macphersoni* (Groeneveld et al., 2013). Seasonal variation might, however, be more important in the northern part of the sampling area, where ocean conditions change dramatically during the Southeast and Northeast monsoons, at least in surface waters.

The large geographical area covered, and vessel security concerns in waters south of Somalia in 2010–2013, resulted in two vessels being used for the four surveys, instead of a single vessel.
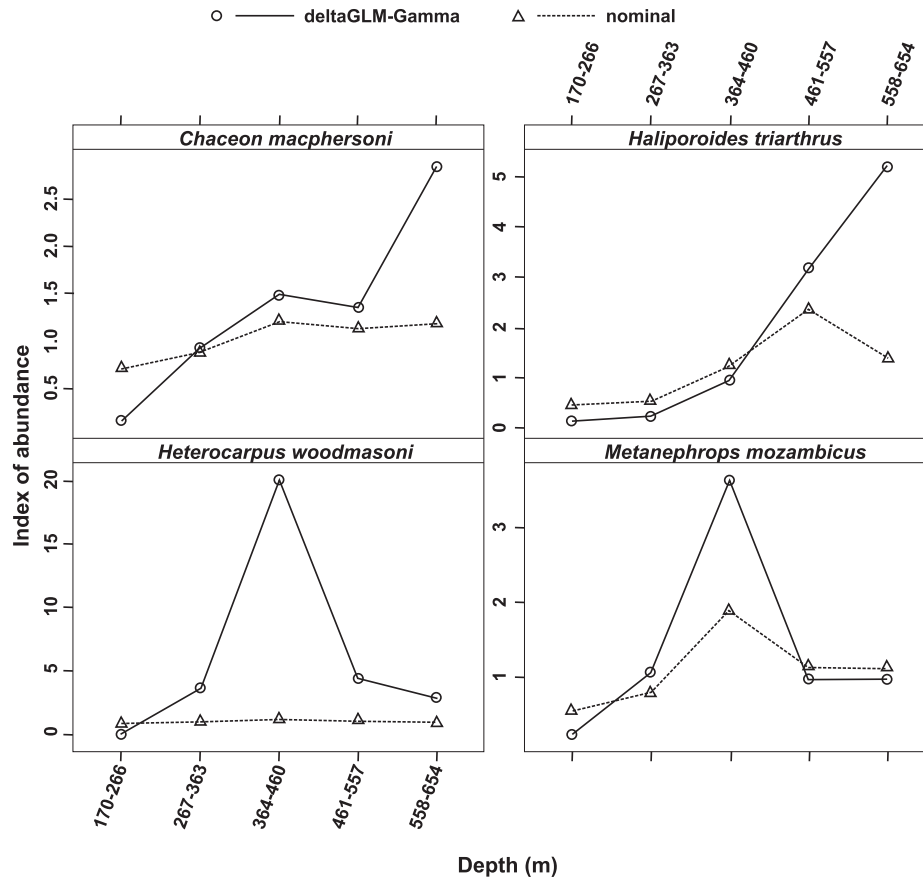
Fig. 7. Standardized CPUE indices for *Chaceon macphersoni*, *Haliporoides triarthrus*, *Heterocarpus woodmasoni* and *Metanephrops mozambicus* by depth interval, based on the final delta models.

The two vessels differed in size and engine power, and towed nets of different sizes and mesh. No inter-calibration trawls could be done, and *post-hoc* catch conversions were therefore required to render data compatible. The conversions took trawl speed, duration and footrope length into account to produce a swept area per trawl, but differences in mesh size could not wholly be accounted for. It was nevertheless assumed that the majority of organisms in the path of the net were caught, and that catches adequately represented the species and abundance available on the trawled substrata.

Although the initial survey strategy was to undertake representative trawls in all depth by latitude cells (Table 1), this could not be achieved because much of the seafloor in the targeted depth range was rocky or too steep to trawl. The resulting distribution of samples was therefore unbalanced, with many empty cells, and surplus trawls in other cells where trawl conditions were more favourable. By country, there were far fewer trawls undertaken in Tanzania. Trawls in the deepest stratum (600—699 m) were only undertaken by the larger of the two vessels, and only in Madagascar. To compensate for the unbalanced distribution of trawl samples, we grouped them by country (instead of latitude), and adjusted the boundaries of depth strata during analysis. The countries along the African shelf follow a latitudinal gradient from north (Kenya) to south (eastern South Africa), and therefore country could be used as a proxy for latitude.

Some difficulties in combining datasets across surveys stemmed from species identification. No up-to-date regional species identification guide exists for deep-water taxa in the SW Indian Ocean, although there are some dated FAO guides for species of

commercial interest. Species identification was therefore not always standard across surveys, and misidentification may have occurred in some species. *C. macphersoni* is well-known from the trawl grounds in South Africa and Mozambique, and its distribution is listed as 'southwestern Indian Ocean and South Africa' by Manning and Holthuis (1988, 1989). In Madagascar, it can be captured together with *Chaceon crosnieri* (Manning and Holthuis, 1989) and although these two species can be distinguished macroscopically, this was not attempted during the Madagascar survey. Similarly, deep-sea crabs caught on the Kenya survey might have been *Chaceon somaliensis* Manning, 1993 (see Davie, 2014), based on photographs, but unfortunately no specimens were retained for positive identification. Although speculative, the scarcity of deep-sea crabs in Tanzania (1 kg/km^2) may reflect the transition between *C. macphersoni* (to the south) and *C. somaliensis* (to the north) distribution ranges. This needs to be confirmed through collection and identification of more specimens.

The most abundant prawn species caught on the Kenya survey, but nowhere else, was identified as *P. marginatus* Randall, 1840 using photographs post-survey. That it was only reported from Kenya suggests that it has a more northerly distribution in the SW Indian Ocean than some of the other more widely-distributed species. It has previously been reported in Kenyan surveys (Kimani et al., 2012) as well as from Reunion, Mauritius, Madagascar and Tanzania, thus confirming a more tropical distribution pattern (Fransen and De Grave, 2014).

Teleosts made up the bulk of the catches in all surveys, suggesting that any deep-water trawl fishery targeting crustaceans would have a large fish bycatch to contend with. Most of this will
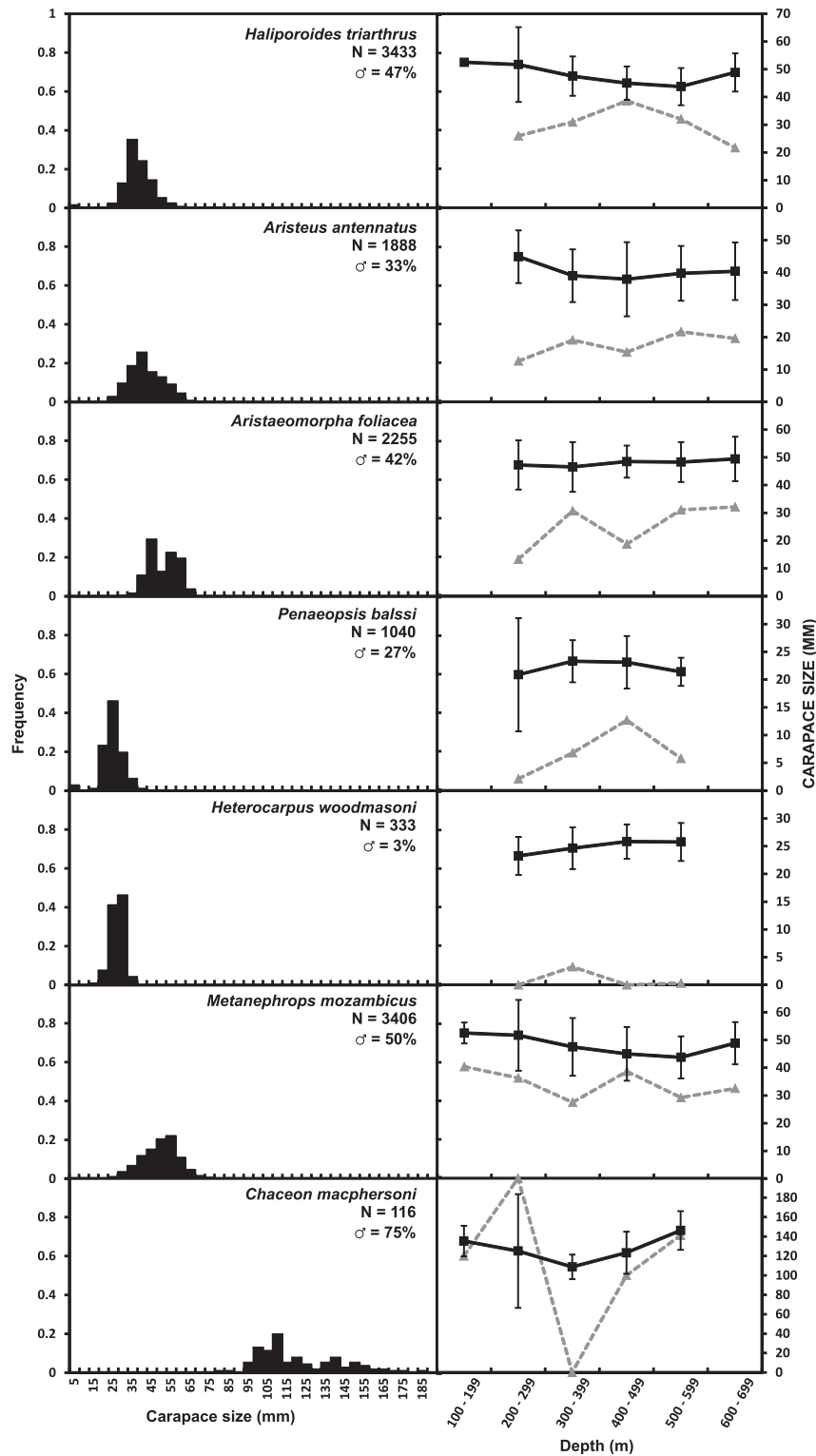
Fig. 8. Size distribution frequencies (left column) and mean size and proportion of males per depth category of the selected crustaceans.

likely be discarded overboard, because it cannot be sold, or has a low economic value (Fennessy et al., 2008). Crustaceans made up a much larger proportion of catches in Madagascar and Mozambique, compared with Tanzania and Kenya, thus confirming the fisheries importance of this group in the subtropical part of the region. The relative paucity of crustaceans in Kenya and Tanzania may alternatively be an artefact of using a different vessel and a smaller net

with smaller mesh size (36 mm vs. 50 mm mesh) − this may have affected the selectivity for crustaceans, such as via the vessels' relative abilities to trawl at greater depths (Table 1). Notwithstanding the differences in sampling gear, the varying proportions of faunal groups in trawl catches (Fig. 2) suggest that there may be important differences in benthic habitats over the wide latitudinal gradient considered here. Water temperature and other

environmental parameters are generally more stable at the depths trawled in our study than in shallower water, and therefore other habitat features, such as sediment type, might determine demersal catch composition (Demestre et al., 2000).

A south to north gradient in crustacean catch composition was apparent along the African coast, based on standardized CPUE indices and nominal biomass. *H. triarthrus* and *M. mozambicus* were most abundant in the south (Mozambique), but scarce in the north (Kenya and Tanzania). Conversely, *H. woodmasoni*, *P. balssi*, *P. marginatus* and *L. somniosus* were more abundant in the north. This gradient is supported by information from historical surveys undertaken in the 1970s and 1980s in Tanzania and Kenya by the RV Professor Mesyatsef, FV Unjuzi and the Nansen programme (Birkett, 1978; Iverson et al., 1984; Mutagyera, 1984; Sætersdal et al., 1999). These surveys reported *Heterocarpus* spp, *L. somniosus*, *P. angulatus* and smaller quantities of *M. andamanicus* (the previous name of *M. mozambicus* in the SW Indian Ocean; Holthuis, 1991).

The species composition and proportions of crustaceans caught in trawls in Mozambique (survey data) and South Africa (data from commercial fishery) were nearly identical, suggesting similar habitats and species aggregations across the geopolitical boundary. The two fisheries use similar trawl gear and fishing strategies, and some vessels fish in both countries. Earlier assumptions that stocks were therefore shared, have however not been validated, since genetic analyses have shown distinct populations of *M. mozambicus* and *H. triarthrus* over relatively short distances along the coast (Zacarias, 2013). Shallow genetic structure was also observed in populations of spiny lobster *P. delagoae* (Gopal et al., 2006), in which the split between populations coincided with the interface of the Mozambique channel eddies and upper Agulhas Current (i.e. near the South Africa/Mozambique border). Berry and Plante (1972) similarly recognized two varieties of *P. delagoae*; var. *natalensis* from eastern South Africa and var. *delagoae* from Mozambique.

Although at similar latitudes and depth, and separated by only a few hundred kilometres across the Mozambique channel, the catch composition of crustaceans in trawls differed substantially between Mozambique (dominated by *H. triarthrus*) and Madagascar (*A. foliacea* and *Aristeus* sp). *H. woodmasoni* was also more abundant in Madagascar than in Mozambique, where it was scarce. The habitats in the surveyed sites may be different, because trawling in Madagascar was restricted to a few enclaves with steep grounds, compared with much larger and flatter trawl grounds in Mozambique (Groeneveld and Everett, 2015). Crustacean assemblages in Madagascar and Mozambique may furthermore be isolated from each other, because intervening deep water precludes benthic migrations across the channel. Recent genetic studies suggest that the Mozambique Channel forms a formidable barrier to larval dispersal of some crustaceans, including *M. mozambicus* and *H. triarthrus* (Zacarias, 2013). *M. mozambicus* has a short drifting larval phase of only a few hours or days, so that recruits settle close to parent populations, rather than dispersing widely (Robey and Groeneveld, 2014). Crossing the channel appears to be unlikely even in some crustaceans with long-lived drifting larvae, such as spiny lobster *Panulirus homarus* (Reddy et al., 2014). Different habitats on the sampled trawl grounds and the relative isolation of Madagascar can therefore explain the differences in catch composition.

Standardized CPUE showed that *H. triarthrus* increased in abundance in waters >400 m. Based on commercial data from the South African trawl grounds, Robey et al. (2013b) showed high CPUE at depths >300 m, extending to at least 600 m, thus confirming that *H. triarthrus* extends deeper than the depth range presently fished. This conclusion is based on limited data, because few trawls were undertaken >600 m depth in this survey. The core

distribution of *C. macphersoni* appears to be deeper than the range trawled during the present surveys (i.e. >655 m), and this was also apparent from commercial data from South Africa (Groeneveld and Melville-Smith, 1995; Groeneveld et al., 2013). Paula e Silva (1985) and Dias et al. (2008, 2009) found high CPUE at 500–800 m depth in Mozambique from trawl survey data. *M. mozambicus* was most abundant at 350–500 m depth, and this result agrees with Robey et al. (2013a). The fact that the depth distribution of all of these species overlap between about 400 and 500 m allows trawlers to target this depth range to catch an economically valuable species mix (Groeneveld and Melville-Smith, 1995).

To conclude, the regional survey strategy was logistically complex to undertake, but conferred several important advantages, such as pooling of scarce resources, and establishing strong networks for future shared projects. Trends in catch composition and standardized CPUE, that may have been difficult to detect from separate surveys, could be readily discerned. Data from using two dissimilar trawl vessels, and inconsistent species identification, could be partially redressed after the surveys. Although these factors may have affected the results of this study, the broader trends in catch composition and abundance at a regional scale remain clear. These trends confirm that deep-water crustaceans were less abundant in Kenya and Tanzania, with limited commercial appeal, and that new deep-water trawl fisheries will have to contend with significant teleost bycatch. Therefore, the expansion of crustacean trawl fisheries into deeper water does not appear to be a viable option in the SW Indian Ocean region at the present.

Acknowledgements

References

Barnard, K.H., 1950. Descriptive catalogue of South African Decapod Crustacea. Ann. South Afr. Mus. 38, 1–837.

Bauchot, M.L., Bianchi, G., 1984. Fiches FAO d'identification des espéces pour les besoins de la péche. Guide des poissons commerciaux de Madagascar (espéces marines et d'eaux saumàtres). Avec le support du Programme des Nations Unies pour le Développement (Projet RAF/79/065). FAO, Rome.

Berry, P.F., 1969. Investigational Report of the Oceanographic Research Institute of South Africa. The Biology of *Nephrops andamanicus* Wood-Mason (Decapoda, Reptantia), vol. 22, pp. 1–55.

Berry, P.F., Plante, R., 1972. Revision of the spiny lobster genus *Palinurus*, in the south-west Indian Ocean. Trans. R. Soc. S. Afr. 40, 373–380.

Bianchi, G., 1985. Field Guide to the Commercial Marine and Brackish-water Species of Tanzania. In: FAO Species Identification Guide for Fishery Purposes. FAO, Rome.

Birkett, L., 1978. Western Indian Ocean Fishery Resources Survey. Report on the cruises of R/V Professor Mesyatsev December 1975-June 1976/July 1977-December 1977. Indian Ocean Program, Technical report No 21. FAO, Rome. August 1978.

Crosnier, A., Jouannic, C., 1973. Note d'information sur les prospections de la pente continentale Malgache effectuées par le N.O. Vauban. ORSTOM, Nosy-Bé, Document 42, p. 18.

DAFF, 2014. KwaZulu-natal Crustacean Trawl Fisheries Database [Data file]. Department of Agriculture, Forestry and Fisheries. Date Accessed 3.03.15.

Davie, P., 2014. *Chaceon somaliensis* Manning, 1993. Accessed through: World Register of Marine Species at. http://www.marinespecies.org/aphia.php?p=taxdetails&id=442711. on 2014-09-12.

Demestre, M., Sanchez, P., Abello, P., 2000. Demersal fish assemblages and habitat characteristics on the continental shelf and upper slope of the north-western Mediterranean. J. Mar. Biological Assoc. U. K. 80, 981–988.

Dias, N., Sobrino, I., Balguerias, E., Palha de Sousa, L., Burgos, C., Varela, D., 11 Agosto

2008. Relatório do cruzeiro de investigação de recursos de profundidade realizado a bordo do b/o Vizconde de Eza de 13 de Março a 9 de Abril 2008. Instituto Nacional de Investigação Pesqueira, Maputo, p. 116.

Dias, N., Sobrino, I., Garcia, E., Silva, L., Burgos, C., Muñoz, I., 15 de Outubro 2009. Relatório do cruzeiro de investigação de recursos de profundidade realizado a bordo do b/o Vizconde de Eza de 13 de Março a 9 de Abril 2009. Instituto Nacional de Investigação Pesqueira, Maputo, p. 148.

Fennessy, S.T., Groeneveld, J.C., 1997. A review of the offshore trawl fishery for crustaceans on the east coast of South Africa. Fish. Manage. Ecol. 4, 135–148.

(No. 734). In: Fennessy, S.T., Mwatha, G.K., Thiele, W. (Eds.), 2004. Report of the Regional Workshop on Approaches to Reducing Shrimp Trawl Bycatch in the Western Indian Ocean: Mombasa, Kenya, 13–15 April 2003. FAO.

Fennessy, S.T., Vincent, X., Budeba, Y., Mueni, E.M., Gove, D.Z., 2008. An update on initiatives to reduce prawn trawl bycatch in the Western Indian Ocean. West. Indian Ocean J. Mar. Sci. 7, 217–222.

Fransen, C., De Grave, S., 2014. *Penaeus marginatus* Randall, 1840. Accessed through: World Register of Marine Species at. http://www.marinespecies.org/aphia.php?p=taxdetails&id=210376. on 2014-09-12.

Francis, R., 1999. The Impact of Correlations on Standardized CPUE Indices. New Zealand Fishery Assessment Research Document 1999/42, p. 30 (Unpublished report held in NIWA library, Wellington, New Zealand).

Gibson, R.N., Barnes, M., Atkinson, R.J.A., 2003. A riot of species in an environmental calm: the paradox of the species-rich deep-sea floor. Oceanogr. Mar. Biol. An Annu. Rev. 40, 311.

Groeneveld, J.C., Everett, B.I., 2015. Crustacean deep-water trawl fisheries. In: van der Elst, R.P., Everett, B.I. (Eds.), Offshore Fisheries of the South West Indian Ocean their Status and the Impact on Vulnerable Species, South African Association for Marine Biological Research, vol. 10. Special Publication.

Gopal, K., Tolley, K.A., Groeneveld, J.C., Matthee, C.A., 2006. Mitochondrial DNA variation in spiny lobster *Palinurus delagoae* suggests genetically structured populations in the southwestern Indian Ocean. Mar. Ecol. Prog. Ser. 319, 191–198.

Groeneveld, J.C., Melville-Smith, R., 1995. Spatial and temporal availability in the multispecies crustacean trawl fishery along the east coast of South Africa and southern Mozambique, 1988–1993. South Afr. J. Mar. Sci. 15, 123–136.

Groeneveld, J.C., Everett, B.I., Fennessy, S.T., Kirkman, S.P., Santos, J., Robertson, W.R., 2013. Spatial distribution patterns, abundance and population structure of deep-sea crab *Chaceon macphersoni* based on complementary analyses of trap and trawl data. Mar. Freshw. Res. 64, 507–517.

Holthuis, L.B., 1980. FAO Species Catalogue. In: Shrimps and Prawns of the World. An Annotated Catalogue of Species of Interest to Fisheries, vol. 1. FAO, Rome, p. 261. FAO Fisheries Synopsis 125.

Holthuis, L.B., 1991. FAO Species Catalogue. In: Marine Lobsters of the World. An Annotated and Illustrated Catalogue of Species of Interest to Fisheries Known to Date, vol. 13. FAO, Rome, p. 292. FAO Fisheries Synopsis 125.

Iversen, S.A., Myklevoll, S., Lwiza, K., Yonazi, J., 1984. Tanzanian marine fish resources in the depth region 10–500 m investigated by R/V "Dr Fridtjof Nansen". In: The Proceedings of the NORAD-Tanzania Seminar to Review the Marine Fish Stocks in Tanzania (Mbegani, Tanzania, 6-8 March 1984). Tanzania Fisheries Research Institute, Dar es Salaam and Norwegian Agency for International Development, Bergen, pp. 45–83.

Kimani, E., Aura, C., Manyala, J., Ndoro, C., Agembe, S., Ochiewo, J. (Eds.), 2012. Technical report of the Malindi-Ungwana Bay prawn and fishery survey, December 2009. Kenya Coast Development Project, p. 45.

King, M. (Ed.), 1995. Fisheries Biology Assessment and Management. Blackwell, London.

King, M.G., Moffitt, R.B., 1984. The sexuality of tropical deepwater shrimps (Decapoda: Pandalidae). J. Crustacean Biol. 4, 567–571.

Lo, N.C.H., Jacobson, L.D., Squire, J.L., 1992. Indices of relative abundance from fish spotter data based on delta-lognormal models. Can. J. Fish. Aquatic Sci. 49, 2515–2526.

Lutjeharms, J.R.E., 2006. Three decades of research on the greater agulhas current. Ocean Sci. Discuss. 3, 939–995.

Manning, R.B., Holthuis, L.B., 1988. South African species of the genus *Geryon* (Crustacea, Decapoda, Geryonidae). Ann. South Afr. Mus. 98, 77–92.

Manning, R.B., Holthuis, L.B., 1989. Two new genera and nine new species of geryonid crabs (Crustacea, Decapoda, Geryonidae). Proc. Biological Soc. Wash. 102, 50–77.

Maunder, M.N., Punt, A.E., 2004. Standardizing catch and effort data: a review of recent approaches. Fish. Res. 70, 141–159.

Mutagyera, W.B., 1984. Distribution of some deep water prawn and lobster species in Kenya's waters. In: Iversen, S.A., Myklevoll, S. (Eds.), The Proceedings of the NORAD-Kenya Seminar to Review the Marine Fish Stocks and Fisheries in Kenya. Mombasa, Kenya, 13–15 March 1984. Marine and Fisheries Research Institute, Mombasa: Kenya, p. 210.

Paula e Silva, R (de), 1985. The deep crab — *Geryon quinquedens*. First notes on its biology off Mozambique. Rev. Investig. Pesquiera Moçambique 13, 5–25.

Pripp, T., Gammelsrød, T., Krakstad, J.O., 2014. Physical influence on biological production along the western shelf of Madagascar. Deep Sea Res. Part II: Top. Stud. Oceanogr. 100, 174–183.

R Development Core Team, 2011. R: a Language and Environment for Statistical Computing. The R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0. Available online at: http://www.R-project.org/.

Randall, J.E., 1995. The Complete Divers' & Fishermen's Guide to Coastal Fishes of Oman. Crawford House Publishing, Bathurst.

Reddy, M.M., Macdonald, A.H.H., Groeneveld, J.C., Schleyer, M.H., 2014. Phylogeography of the scalloped spiny-lobster *Panulirus homarus rubellus* in the Southwest Indian Ocean. J. Crustacean Biol. 34, 773–781.

Richmond, M.D. (Ed.), 1997. Field Guide to the Seashores of Eastern Africa and the Western Indian Ocean Islands. The Swedish International Development Cooperation.

Robey, J., Fennessy, S.T., Everett, B.I., Santos, J., Groeneveld, J.C., 2013a. Abundance and biology of the langoustine *Metanephrops mozambicus* (Nephropidae) on deep-water trawl grounds in eastern South Africa. J. Crustacean Biol. 33, 760–771.

Robey, J., Fennessy, S.T., Everett, B.I., Santos, J., Groeneveld, J.C., 2013b. Patterns in abundance, population structure and biology of knife prawn *Haliporoides triarthrus* on deep-water trawl grounds off eastern South Africa. Afr. J. Mar. Sci. 35, 565–577.

Robey, J., Groeneveld, J.C., 2014. Fecundity of the langoustine *Metanephrops mozambicus* Macpherson, 1990 (Decapoda, Nephropidae) in eastern South Africa. Crustaceana 87, 814–826.

Sætersdal, G., Bianchi, G., Stromme, T., Venema, S.C., 1999. The Dr. Fridtjof Nansen Programme 1975–1993: Investigations of Fishery Resources in Developing Regions: History of the Programme and Review of Results. FAO Fisheries Technical Paper 391. FAO, Rome, p. 434.

Sanders, M.J., Sparre, P., Venema, S.C., 1988. FAO/UNDP: RAF/79/065/WP/41/88/E. In: . Proceedings of the Workshop on the Assessment of the Fishery Resources in the Southwest Indian Ocean, p. 277.

Schott, F.A., McCreary, J.P., 2001. The monsoon circulation of the Indian Ocean. Prog. Oceanogr. 51, 1–123.

Smit, A.J., Roberts, M., Anderson, R.J., Dufois, F., Dudley, S.F.J., Bornmann, T.G., Olbers, J., Bolton, J.J., 2013. A coastal seawater temperature dataset for biogeographical studies: large biases between in situ and remotely-sensed data sets around the coast of South Africa. PLoS One 8, e81944. http://dx.doi.org/10.1371/journal.pone.0081944.

Smith, M.M., Heemstra, P.C., 1986. Smith's Sea Fishes. Macmillan, Johannesburg, p. 1047.

Sobrino, I., Dias, N., Muñoz, I., Salmerón, F., Varela, D., 2009. Distribution patterns and biological characteristics of *Aristeus antennatus* (Risso, 1816) and *Aristeus virilis* (Bate, 1881) in Mozambique waters of the Western Indian Ocean. West. Indian Ocean J. Mar. Sci. 8, 49–59.

Ternon, J.F., Bach, P., Barlow, R., Huggett, J., Jaquemet, S., Marsac, F., Ménard, F., Penven, P., Potier, M., Roberts, M.J., 2014a. The Mozambique Channel: from physics to upper trophic levels. Deep Sea Res. Part II: Top. Stud. Oceanogr. 100, 1–9.

Ternon, J.F., Roberts, M.J., Morris, T., Hancke, L., Backeberg, B., 2014b. In situ measured current structures of the eddy field in the Mozambique Channel. Deep Sea Res. Part II: Top. Stud. Oceanogr. 100, 10–26.

UNDP, 2013. http://hdr.undp.org/en/content/table-1-human-development-index-and-its-components.

van der Elst, R.P., 1993. A Guide to the Common Sea Fishes of Southern Africa. Struik, Cape Town.

van der Elst, R., Everett, B., Jiddawi, N., Mwatha, G., Afonso, P.S., Boulle, D., 2005. Fish, fishers and fisheries of the Western Indian Ocean: their diversity and status. A preliminary assessment. Philos. Trans. R. Soc. A 363, 263–284.

van der Elst, R.P., Groeneveld, J.C., Baloi, A.P., Marsac, F., Katonda, K.I., Ruwa, R., Lane, W.L., 2009. Nine nations, one ocean: a benchmark appraisal of the South Western Indian Ocean Fisheries Project (2008–2012). Ocean Coast. Manage. 52, 258–267.

Vignaux, M., 1994. Catch per unit effort (CPUE) analysis of west coast South Island and Cook Strait spawning hoki fisheries, 1987–93. N.Z. Fisheries Assessment Research Document 94/11, p. 29 (Unpublished report held in NIWA library, Wellington, New Zealand).

WIOFish, 2013. Western Indian Ocean Fisheries Database: a Catalogue of Small-scale Fisheries. www.wiofish.org. Accessed 25 April 2014.

World Bank, 2014. http://data.worldbank.org/data-catalog/GDP-ranking-table.

World Sea Temperatures, 2014. Kenya Sea Temperatures. http://www.seatemperature.org/africa/kenya/. Accessed 29 April 2014.

Zacarias, L.D., 2013. Genetic Population Structure of Deep-water Prawns *Haliporoides triarthrus* and Langoustines *Metanephrops mozambicus* in the South West Indian Ocean: Use of Mitochondrial DNA to Investigate Metapopulation Structure. MSc thesis. University of KwaZulu-Natal, Durban, South Africa, p. 93.

Paper 6