Ocean & Coastal Management 111 (2015) 50–61

Contents lists available at ScienceDirect

Ocean & Coastal Management

journal homepage: www.elsevier.com/locate/ocecoaman

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'Environment, PO Box 1739, Fiadanana, 101 Antananarivo, Madagascar
[g] Centre d'Etudes et de Développement des Pèches, 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

Article history:
Received 6 November 2014
Received in revised form
2 April 2015
Accepted 2 April 2015
Available online

Keywords:
Abundance index
Standardized CPUE
Crustaceans
Teleosts
Catch composition
Southwest Indian Ocean
Nominal biomass
Fisheries management
Shared resources
Trawl surveys

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.

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).

http://dx.doi.org/10.1016/j.ocecoaman.2015.04.003
0964-5691/

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.

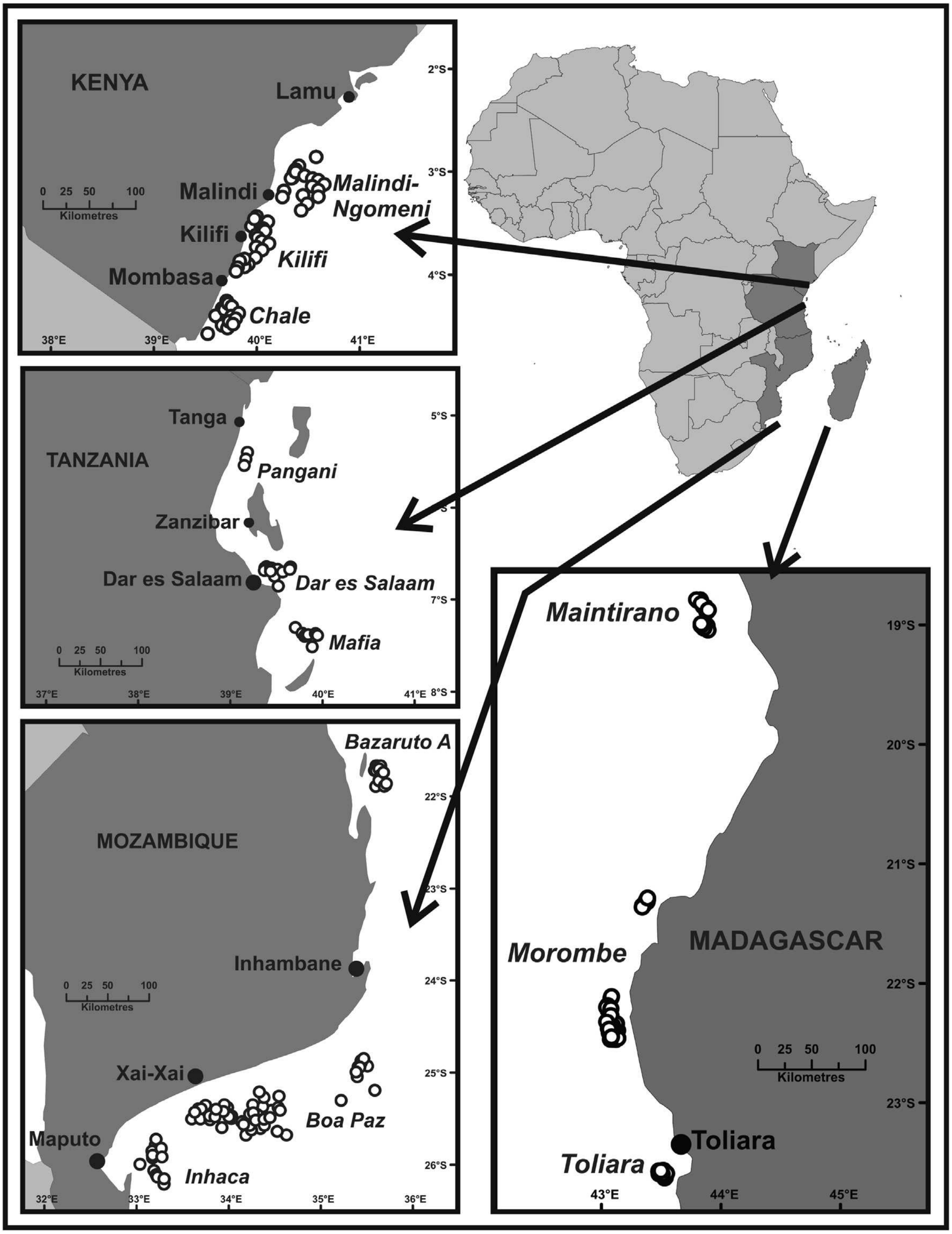

Fig. 1. Map of the areas trawled during the South West Indian Ocean Fisheries Project deep-water crustacean surveys. Symbols indicate actual positions where nets were set, trawl area names in italics.

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:

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

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/km^2), 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):

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

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

where $\overline{R}$ 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

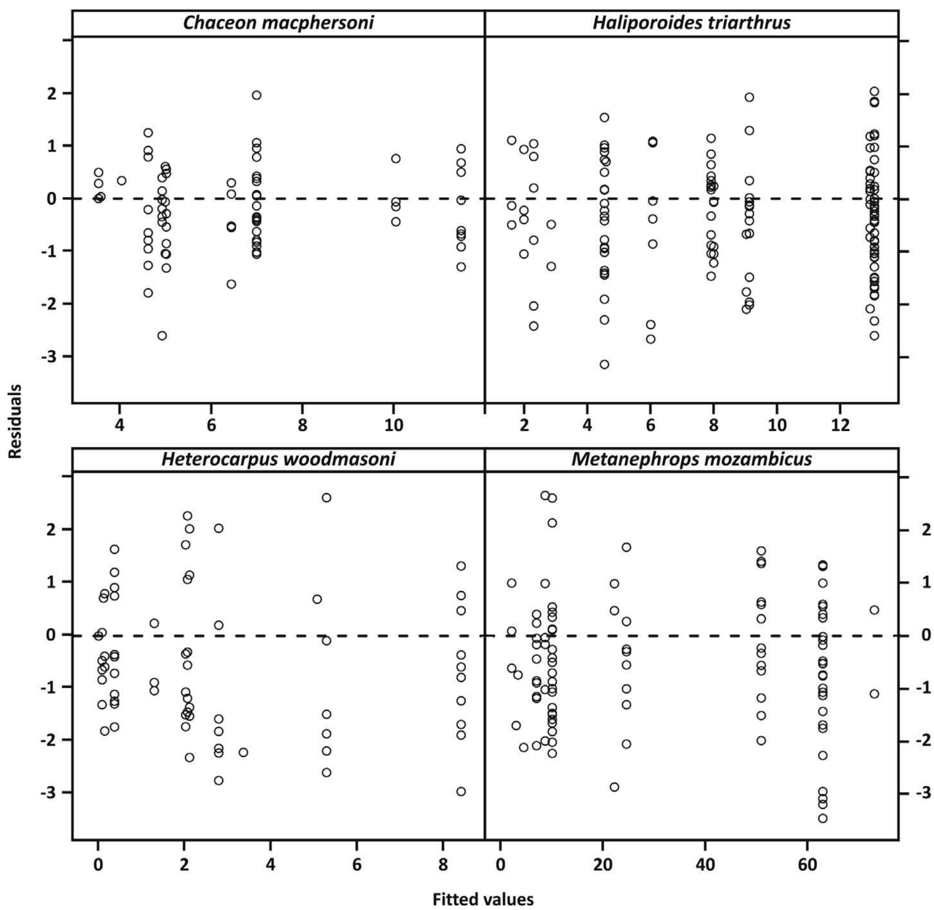

Fig. 2. Model diagnostic: residuals vs. fitted values of the GLM model applied for the non-zero catches.

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

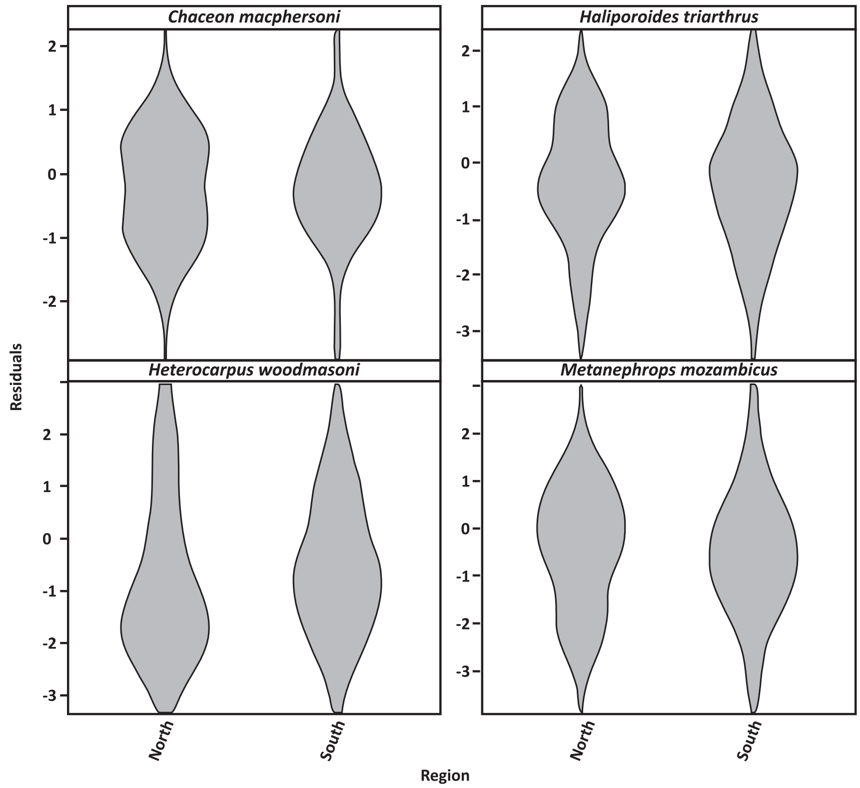

Fig. 3. Model diagnostic: comparison of the distribution of residuals from the GLM model applied to the non-zero catches for the northern (Kenya and Tanzania) and southern (Mozambique and Madagascar) regions.

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/km^2), followed by crustaceans (142 kg/km^2), elasmobranchs (84 kg/km^2), other invertebrates (77 kg/km^2) and cephalopods (47 kg/km^2) (Table 3).

The biomass of *H. triarthrus* was estimated as 56 kg/km^2 over all trawls sampled, but highest concentrations occurred in Mozambique, where the estimate increased to 95 kg/km^2 (Table 3). *M. mozambicus* biomass estimates were similar for Mozambique (27 kg/km^2) and Madagascar (28 kg/km^2), compared to the lower regional estimate of 22 kg/km^2. Biomass of *A. foliacea* was concentrated in Madagascar (62 kg/km^2), compared with 19 kg/km^2, regionally. The regional biomass estimate of *H. woodmasoni* was 4 kg/km^2 with the highest concentrations in Kenya (8 kg/km^2). *C. macphersoni* biomass was also highest in Kenya (15 kg/km^2), followed by Madagascar and Mozambique (both 9 kg/km^2), but they were scarce in Tanzania (1 kg/km^2).

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*,

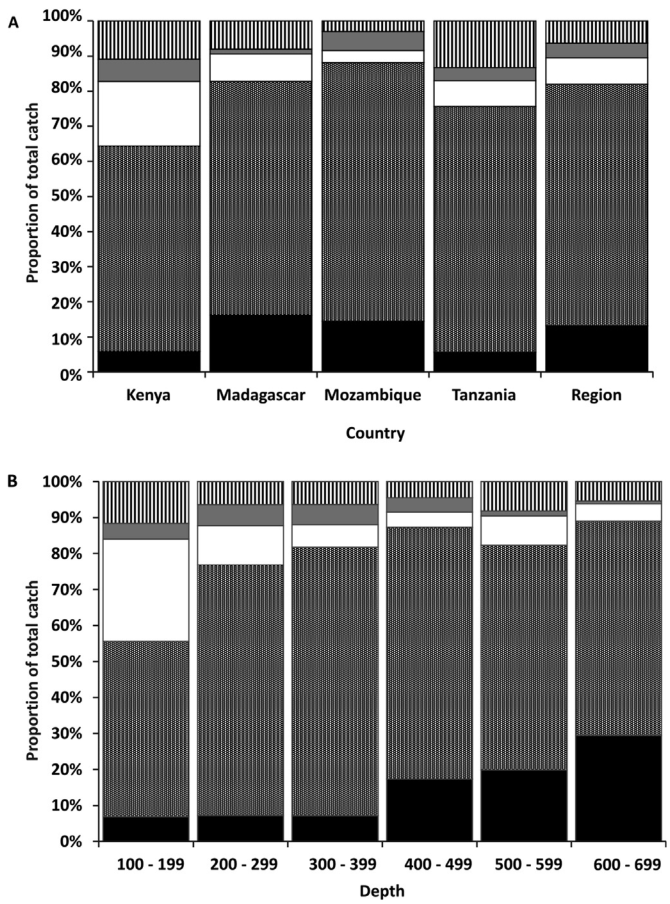

Fig. 4. Proportion of the catch made up of crustaceans, teleosts, elasmobranchs, cephalopods and other invertebrates by A) country and B) depth interval.

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.

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

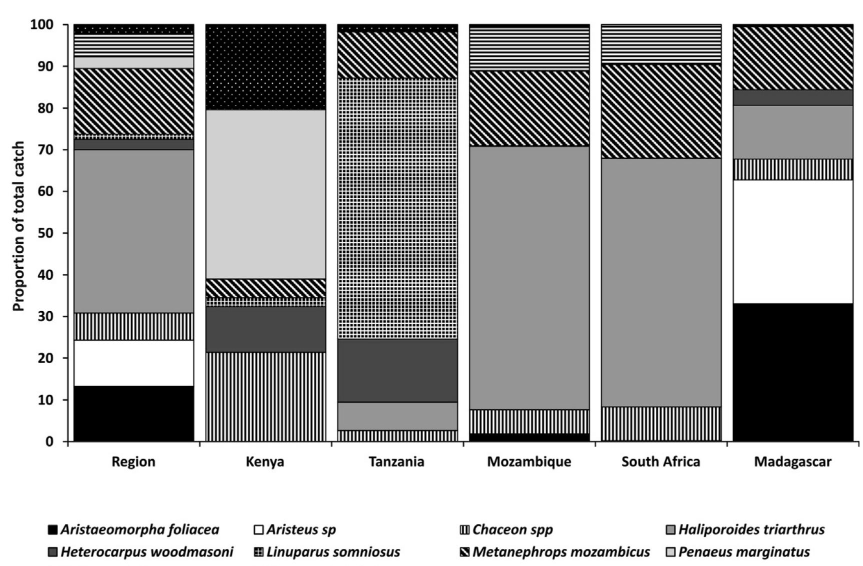

Fig. 5. Proportion of the selected crustaceans that were caught by country and for the region.

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

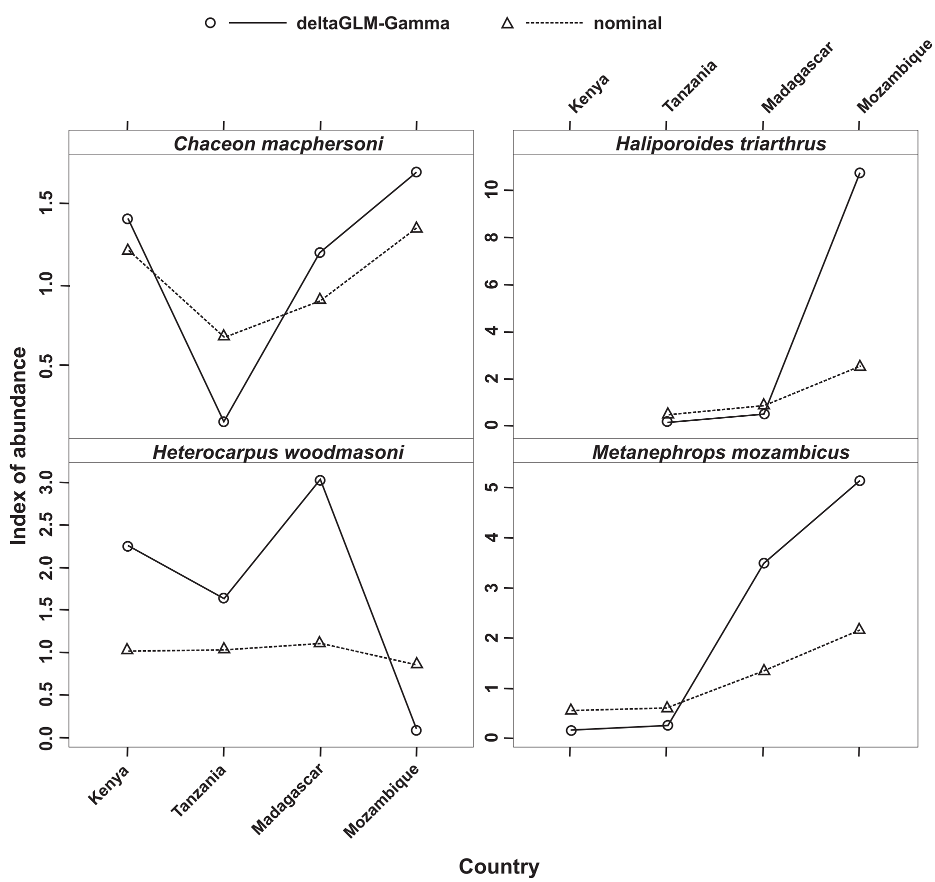

Fig. 6. Standardized CPUE indices for *Chaceon macphersoni*, *Haliporoides triarthrus*, *Heterocarpus woodmasoni* and *Metanephrops mozambicus* by country, based on the final delta models.

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.

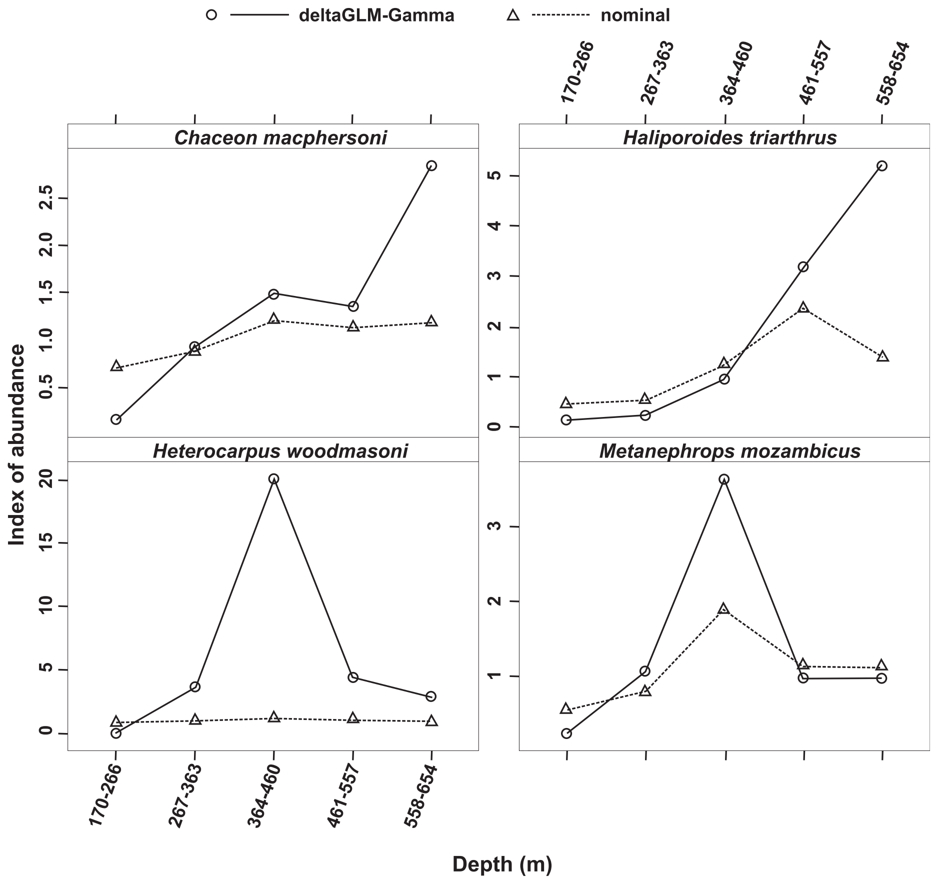

Fig. 7. Standardized CPUE indices for *Chaceon macphersoni*, *Haliporoides triarthrus*, *Heterocarpus woodmasoni* and *Metanephrops mozambicus* by depth interval, based on the final delta models.

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

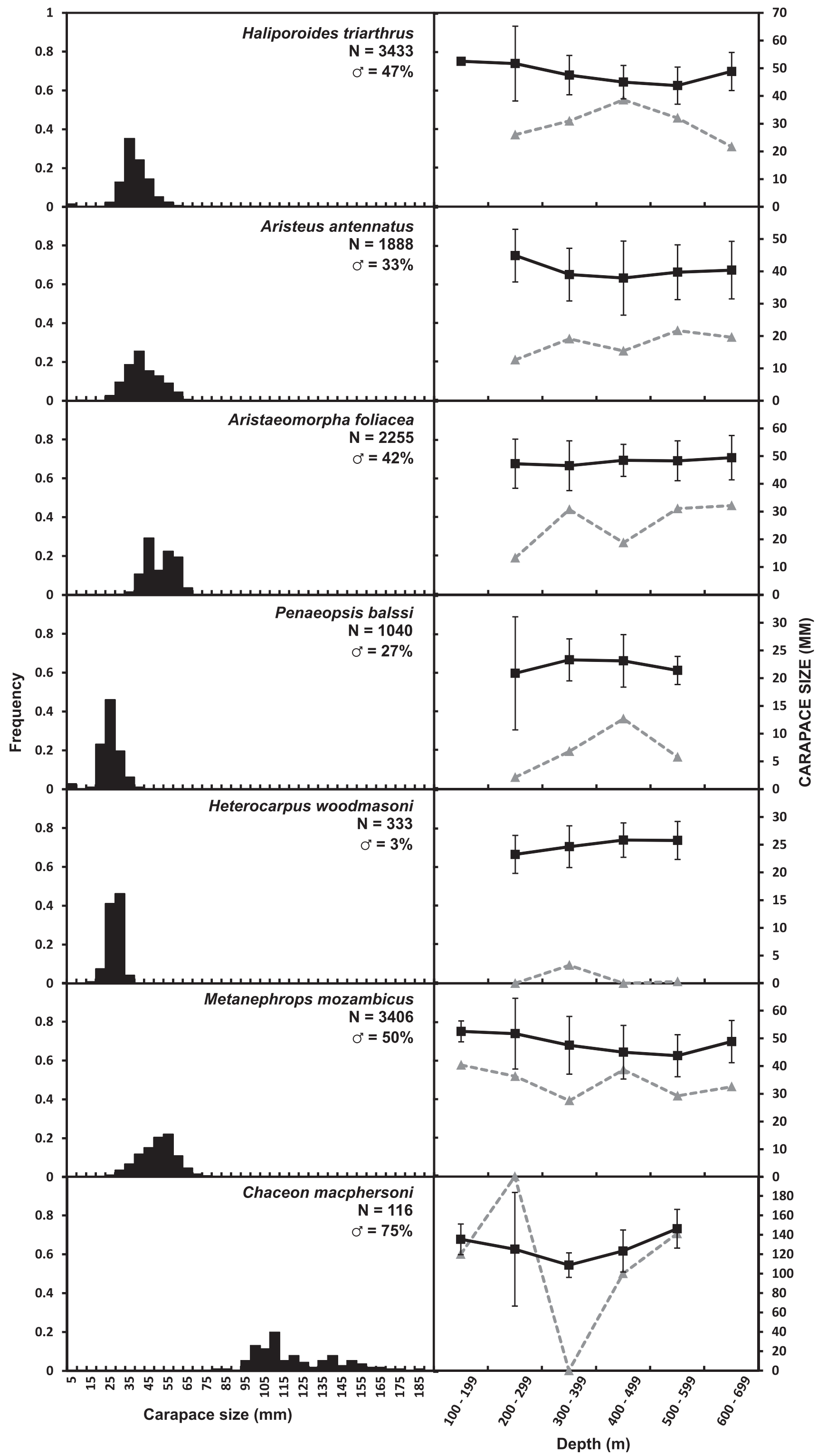

Fig. 8. Size distribution frequencies (left column) and mean size and proportion of males per depth category of the selected crustaceans.

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

We thank the South West Indian Ocean Fisheries Project (SWIOFP) and the Western Indian Ocean Marine Science Association (MASMA Programme) for funding the surveys and data analyses. Teresa Athayde, Desmond Hayes and James Robey are thanked for organizing survey logistics, assistance with sampling at sea, and data handling. Technical and scientific staff from SWIOFP countries spent many days at sea to collect data. The South African Association for Marine Biological Research (SAAMBR) provided logistical support, and organized a workshop for data analyses.

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 saumâtres). 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.