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Smooth fan lobster *Ibacus novemdentatus* in the southwestern Indian Ocean: an overlooked fisheries resource?

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Bottom-trawl data collected by the RV *Dr Fridtjof Nansen* off Mozambique (in 1990, 2007 and 2018) and off eastern South Africa (in 2018) were analysed to investigate the distribution, abundance and size composition of the smooth fan lobster *Ibacus novemdentatus* as a potential fisheries resource. The lobsters occurred shallower (depth 53–297 m) than traditional deep-water trawl grounds, were concentrated in 'hotspots' at the seaward edges of sand/mud banks at the Thukela Bank, Delagoa Bight and Sofala Bank, and exhibited segregated juvenile and adult populations. Three other high-value lobster species and several marketable teleost species occurred in trawl nets where *I. novemdentatus* was present. Further exploration by trawling should be considered to better define hotspots of adults of this species and to investigate the contribution that *I. novemdentatus* could make to mixed-species commercial catches.

Keywords: crustaceans, deep-water trawls, EAF-Nansen Programme, fisheries development, mixed-species catches, survey data

Introduction

Deep-water crustacean trawl fisheries in Mozambique and eastern South Africa rely on mixed catches of prawns, langoustines, lobsters and deep-sea crabs for profit. Bottom-trawling effort is focused on the depth range 200–600 m, where the commercially most-valuable species mix occurs (Groeneveld and Melville-Smith 1995). Consequently, the crustacean and fish resources at this depth have received considerable research attention (Fennessy and Groeneveld 1997; Everett et al. 2015a, 2015b). Less is known about crustaceans occurring in the rarely trawled 50–200 m depth interval, although spiny lobsters (family Palinuridae) and slipper and fan lobsters (family Scyllaridae) have been reported at these shallower depths (Ivanov and Krylov 1980; Cockcroft et al. 1995). Several studies have addressed the fisheries potential of spiny lobsters and slipper lobsters of the southwestern (SW) Indian Ocean (Cockcroft et al. 1995; Groeneveld et al. 2012), though very little is known about some slipper lobsters, including their potential as a fisheries resource.

Fan lobsters of genus *Ibacus* Leach, 1815 (family Scyllaridae, subfamily Ibacinae) have a relatively small maximum body length of ~23 cm, are dorsoventrally flattened with a characteristic fan-shaped carapace, and live on soft sedimentary substrates into which they dig (Faulkes 2006). The genus comprises eight known species that are restricted to the Indo-West Pacific region, mainly in Southeast Asia and Australia (Holthuis 1991; Brown and Holthuis 1998; Webber and Booth 2007). They are caught as a bycatch of bottom-trawl fisheries, and sold fresh on seafood markets in Korea, Japan, Taiwan and Australia, where a number of species are called 'bugs' (Haddy et al. 2007; MacDiarmid et al. 2013).

The smooth fan lobster *Ibacus novemdentatus* Gibbes, 1850 is the only ibacinid known from the SW Indian Ocean (Holthuis 1991). Ivanov and Krylov (1980, p 287) found them to be "very common in the catches taken on the shelf and in the upper part of the continental slope from Kenya to southern Mozambique and on the Mascarene Ridge banks." In this region, *I. novemdentatus* have been reported from depths between 37 and 400 m (Holthuis 1991), but were most common in research trawls made between 150 and 200 m depth (Ivanov and Krylov 1980).

The Norwegian research vessel *Dr Fridtjof Nansen* (hereafter abbreviated to '*Nansen*') has undertaken >40 surveys in the western Indian Ocean since 1975, with most of them including bottom trawling, to assess the distribution, species composition and abundance of demersal taxa (Bianchi et al. 2017; Everett 2017; Fennessy et al. 2017). Not all of the accumulated data have yet been analysed. Bottom-trawl surveys undertaken in eastern South Africa and off Mozambique in 2018 found fan lobsters to be abundant in patches (JCG and LDZ, pers. obs.). We hypothesised that the contribution of fan lobsters to mixed-species catches of existing deep-water trawl fisheries can be increased by expanding the targeted depth range. The depth distribution, size composition and relative abundance of fan lobsters were investigated, based on new and historical data collected by the *Nansen*. Co-occurring species captured in the same

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trawls and considered commercially valuable, especially other lobster species, were assessed as part of a potential mixed-species catch.

Materials and methods

Data acquisition

The bottom-trawl surveys undertaken by the *Nansen* in the western Indian Ocean, the trawl gear used, and the survey strategy have been described in detail (Saetersdal et al. 1999; Axelsen and Johnsen 2015; Everett 2017; Fennessy et al. 2017). We extracted data on the bottom-trawl stations sampled and catches by species from the vessel's 'Nansis' database (Strømme 1992; Bianchi et al. 2017), for surveys undertaken in Mozambique in 1990, 2007 and 2018 (survey reference numbers 1990402, 1990406, 2007409 and 2018402), and in eastern South Africa in 2018 (2018401). These were the only years for which comparable data were available. Station data comprised the GPS location, depth (m), duration (h), and velocity (nautical miles h^{-1}) of the trawl, and catch weights. The catch composition per trawl was determined according to a standard procedure during all surveys undertaken by the vessel, by sorting the catch by type, identifying species using standard reference guides, and weighing and counting of specimens (Fennessy et al. 2017). Large trawl catches were subsampled and results raised by a factor equal to the ratio between total catch weight and sample weight. For this study, we selected data from all bottom trawls in which fan lobsters were present.

Biological sampling of fan lobsters was undertaken on board during the 2018 surveys (2018401 and 2018402). The carapace length (CL, ±1 mm) of the first 100 specimens collected per trawl was measured from the rostral tip to the posterior carapace edge; sex was determined macroscopically from the pleopod shape and location of genital openings; and the presence/absence of external eggs on female lobsters was recorded. Individual specimens were weighed (W, ±1 g).

Three voucher specimens and tissue samples (1 leg per lobster) were collected for species verification during survey 2018401. Genomic DNA was isolated using a Qiagen DNeasy Blood and Tissue Kit, following the manufacturer's protocol. The cytochrome oxidase subunit I (COI) was amplified using standard universal primers (Folmer et al. 1994). Polymerase chain reactions (PCRs) were carried out in 25-µl reaction volumes, containing 12.5 µl of OneTaq Quick-Load 2X Mastermix (New England BioLabs Inc.), 0.2 µM of each 10 µM primer, 2 µl of 8–20 ng genomic DNA, and 9.5 µl of PCR-grade H_2O. The thermal cycling program started with an initial denaturation at 95 °C for 10 min, followed by 35 cycles of 95 °C for 30 s, annealing temperature of 50 °C for 30 s, and 72 °C for 45 s. The final extension step was carried out at 72 °C for 10 min. The PCR reactions were run with a negative and a positive control. After sequencing at the Central Analytical Facilities of Stellenbosch University (South Africa), chromatograms were inspected manually using FinchTV 1.4.0 (www.geospiza.com), and specimen metadata and COI sequences were deposited on the Barcode of Life Data Systems web platform (BOLD; www.boldsystems.org), and compared with reference sequences.

Replicate metal cylinders were attached to the trawl gear to collect sediment samples during bottom trawling. Sediments were first appraised visually for colour, odour, and bioclastic and nannofossil properties, and were then analysed for grain-size distribution (taken as representative of the trawled habitat). Wet-sieving methods were employed for the sand fraction (>63 µm), with the sand types categorised according to the nomenclature of Wentworth (1922).

Data analysis

Swept area (*a*) was estimated as $a = (V \times t) \times E$, where V = velocity of the trawl over the ground when trawling (converted from nautical miles h^{-1} to km h^{-1}), t = time spent trawling (hours), and E = effective net width, which was kept constant at 18.5 m during all bottom-trawl surveys on the *Nansen* (Fennessy et al. 2017). Relative densities (kg km^{-2}) at each trawl site were obtained by dividing the catch weight by the swept area, and overall densities were estimated by depth stratum (50–199 m or 200–299 m depths), survey year (1990, 2007, 2018), and country (a proxy for area).

Biological data (i.e. CL and W) were used to construct a nonlinear length–weight relationship, using a least-squares algorithm in Excel. The statistical software package R 2.14.0 (R Development Core Team 2011) was used to analyse the length-composition data. A Shapiro–Wilk test of normality could not detect significant departures from normality in the data, and a two-way ANOVA, followed by a Tukey test, was used to investigate the effects of sex (three levels: male, female, undetermined), trawl site (five trawls, where sample sizes were adequate), and their interaction, on size variability of *I. novemdentatus*.

Results

Species identity was confirmed as *Ibacus novemdentatus* based on a comparison of DNA barcodes generated in this study (GenBank accession numbers: MK624965–MK624967) with reference barcodes on BOLD. The new DNA sequences showed a 99.3% match to a reference barcode originating from *I. novemdentatus* caught in Mozambique (BOLD:AAW9449), and a 96.7% match to another specimen originating from South Korea (BOLD:ACH9536).

Ibacus novemdentatus was present in 26 of 108 bottom trawls (24% of trawls) undertaken at between 53 and 297 m depth off eastern South Africa and Mozambique (Figure 1). The total weight of all species of marine fauna in trawls where *I. novemdentatus* was present amounted to 3 910 kg, in which some 83 families could be identified. The bulk of the catch comprised the Ariommatidae (driftfishes), Sparidae (seabreams), Loliginidae (pencil squids) and Carangidae (jacks and scads) (Figure 2). Some 199 kg (6%) of the total catch weight comprised Scyllaridae (slipper and fan lobsters) and Palinuridae (spiny lobsters).

Four lobster species were abundant in the trawl catches, with *I. novemdentatus* dominating by weight and numbers, followed by the deep-water Natal spiny lobster *Palinurus delagoae*, Cape slipper lobster *Scyllarides elisabethae* and banded whip lobster *Puerulus angulatus* (Figure 3). The average individual body weight of *I. novemdentatus* (0.16 kg [SD 0.15], n = 26 trawls) was much lower than that of *P. angulatus* (0.29 kg [SD 0.13],

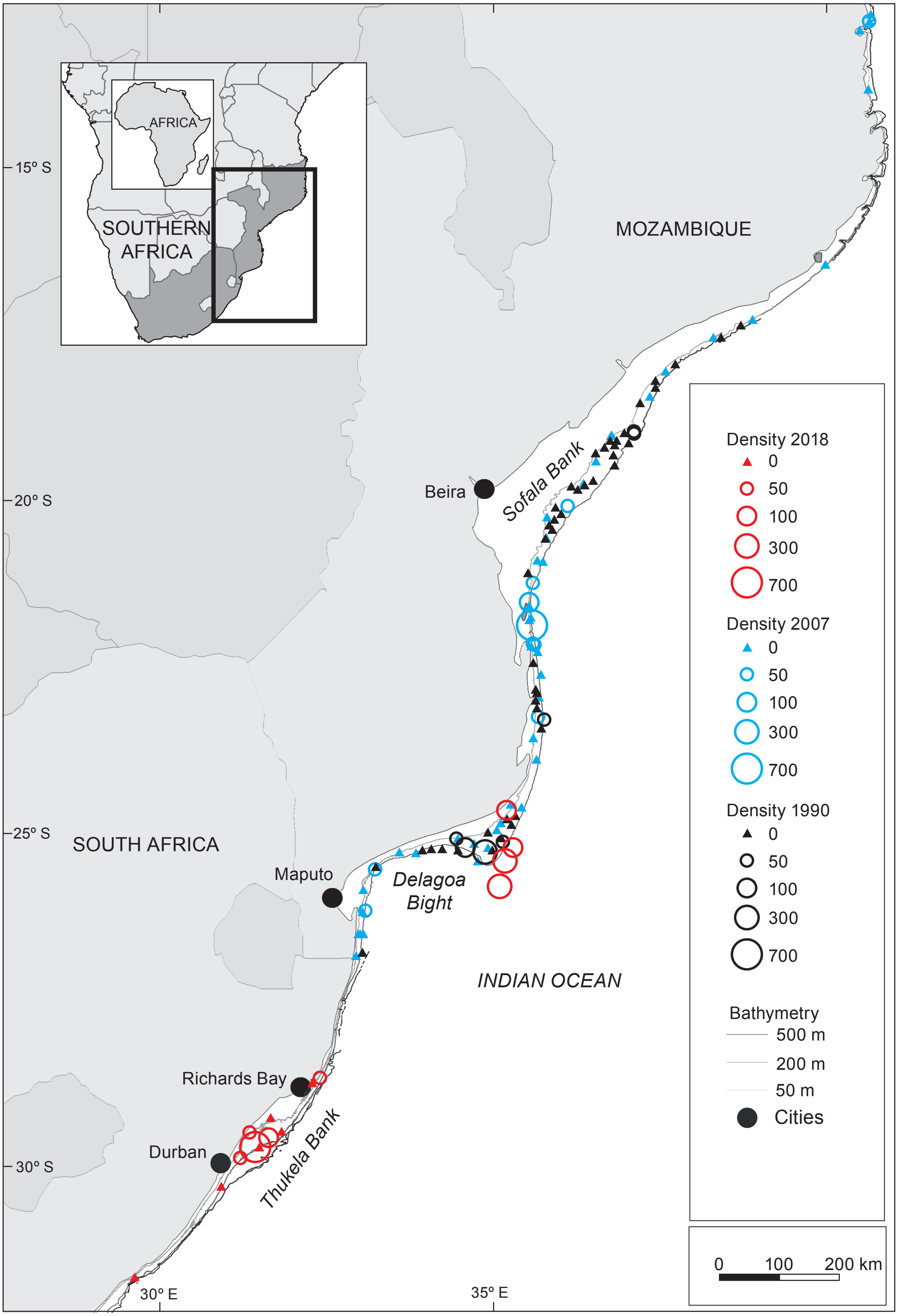

Figure 1: Map of all bottom trawls made between 50 and 300 m depth by the RV *Dr Fridtjof Nansen* in surveys undertaken in 1990, 2007 and 2018. The relative densities (kg km^{-2}) of *Ibacus novemdentatus*, based on trawl catches, indicates geographical hotspots on the outer Thukela Bank, in the northern Delagoa Bight, and on the southern Sofala Bank

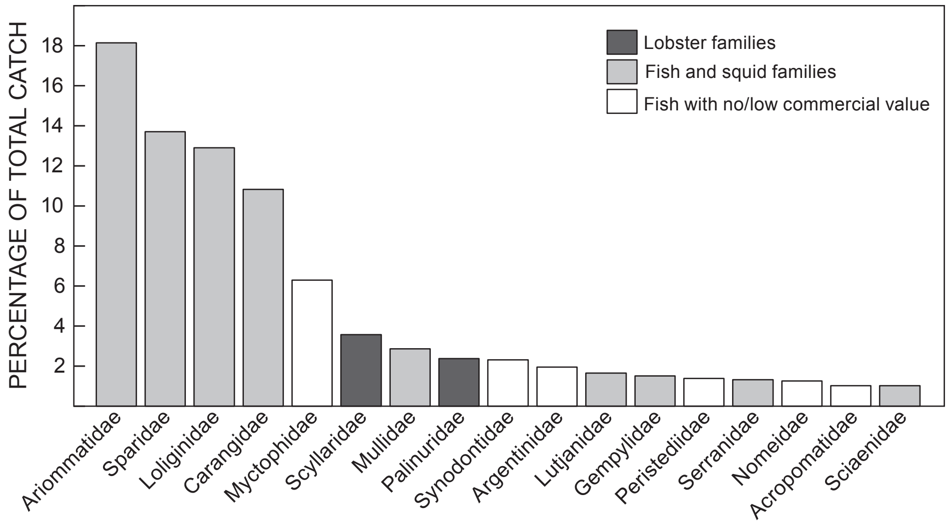

Figure 2: Relative catch composition of all marine fauna by weight, for all trawls in which *Ibacus novemdentatus* were present. Lobster families are shown in dark grey; squid and fish families with potential market value are shown in light grey; white bars denote fishes with no market value. Taxa that contributed <1% to the total catch weight are not shown

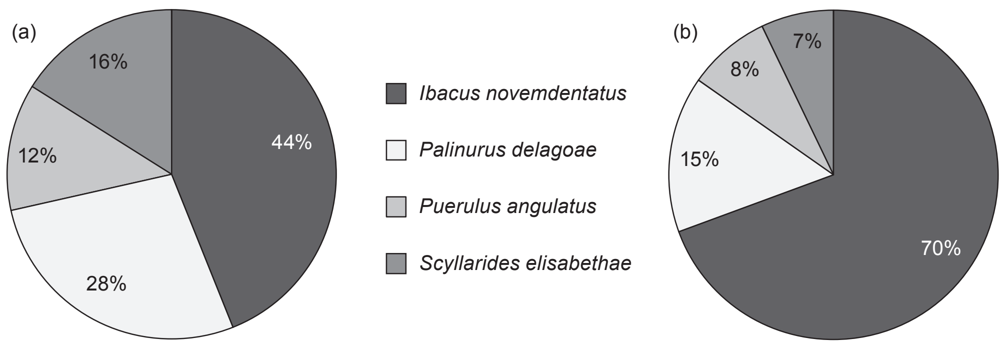

Figure 3: Catch composition (%) of lobster species captured in all trawls made by the RV *Dr Fridtjof Nansen* off eastern South Africa and Mozambique in which *Ibacus novemdentatus* were present, based on (a) weight (total catch = 199 kg) and (b) numbers (total catch = 1 099 ind.)

n = 3), *S. elisabethae* (0.49 kg [SD 0.18], n = 15) and *P. delagoae* (0.53 kg [SD 0.31], n = 4).

Catches of *I. novemdentatus* per trawl were highly variable (1–272 lobsters trawl^{-1}), and the derived relative densities per trawl site likewise ranged from 1–621 kg km^{-2} (Table 1). Three hotspots with high densities were identified, at the Thukela Bank (maximum density estimates of 87 and 481 kg km^{-2} per individual trawl), at the northern Delagoa Bight (91, 168 and 272 kg km^{-2} per trawl), and at the southern Sofala Bank (62 and 621 kg km^{-2} per trawl) (Figure 1). Densities in areas between the hotspots were substantially lower. Substrates at the Thukela Bank sites comprised very fine to fine sand with mud, but no silt or clay. Some bioclastic material occurred, but detritus was absent. Based on sieving analysis, the first sediment sample, collected from 140 m depth, consisted of 57% mud and 43% sand, and the second, from 185 m depth, of 85% sand, 14% mud and 1% gravel.

By sampling year, mean densities of *I. novemdentatus* were lowest in 1990 and highest in 2018; by depth, the densities were greater in the 50–200 m stratum than in the 201–300 m stratum (Table 1). Within-stratum variability was very high and the sample numbers too small to attempt further statistical analysis (Table 1). By area, using country as a proxy, the lobster densities were higher in the north (Mozambique) than the south (South Africa), based on 2018 data only.

Of 411 *I. novemdentatus* sampled on board the vessel, 210 were males, 161 were females (a sex ratio of 1:0.77), and 40 small specimens were not sexed. The CL of specimens ranged from 25 to 75 mm (mean 56 mm [SD 10]), and individual body weight ranged from 12 to 205 g (mean 93 g [SD 41]). The nonlinear CL and W regression fitted the pooled data well (R^2 = 0.97; Figure 4), and the exponent (2.82) was close to 3.0, indicating isometric growth (Froese 2006). Sex-based CL and W regressions also showed isometric growth in both males ($W = 0.0017 \times CL^{2.6884}$, R^2 = 0.95) and females ($W = 0.0011 \text{ x } CL^{2.8066}$ R^2 = 0.96). Sex significantly affected CL (ANOVA, $F_{2,\ 400}$ = 410.1, p < 0.001), and a Tukey HSD test revealed that males (mean 60 mm [SD 7]) were significantly larger than females

Table 1: Relative densities of *Ibacus novemdentatus* in bottom-trawl surveys by the RV *Dr Fridtjof Nansen* off eastern South Africa and Mozambique, by year, depth interval and region

Category	*n* (trawls)	Relative density (kg km^{-2})	
		Range	Mean (SD)
1990	7	1.1–145.9	38.1 (51.3)
2007	10	2.7–621.3	80.2 (191.1)
2018	9	5.0–481.4	132.2 (156.9)
50–200 m	15	2.7–481.4	92.8 (132.0)
201–300 m	11	1.1–621.3	78.8 (182.2)
Mozambique (2018)	4	63.9–272.8	148.9 (93.3)
South Africa (2018)	5	5.0–481.4	118.9 (205.5)

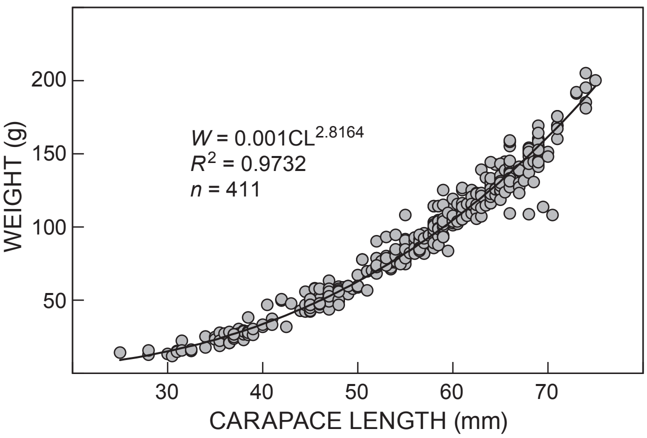

Figure 4: Length–weight regression on data for *Ibacus novemdentatus* (sexes pooled) sampled on board the RV *Dr Fridtjof Nansen* during 2018

(mean 56 mm [SD 9]; $p < 0.001$), on average. The CL of 10 egg-bearing females ranged from 60 to 74 mm.

Length composition of *I. novemdentatus* differed markedly between trawl stations (ANOVA, $F_{4, 400} = 137.6$, $p < 0.001$; Figure 5). Lobsters caught at two stations on the Thukela Bank were relatively large, and of a statistically similar mean CL (Tukey test, $p = 0.93$). Lobsters caught at the three Delagoa Bight stations were smaller than those on the Thukela Bank, and differed significantly from each other and from the Thukela Bank samples in pair-wise Tukey test comparisons ($p < 0.05$ in all cases). The interaction between sex and site was marginally significant in the ANOVA ($F_{4, 400} = 3.0$, $p = 0.02$), suggesting only a minor influence.

Discussion

Catches of *Ibacus novemdentatus* in survey trawls were sporadic and restricted to depths between 53 and 297 m, and the numbers captured per trawl were highly variable. Three geographical hotspots with high densities were identified on deep-shelf/upper-slope habitats: on the Thukela Bank, in the northern Delagoa Bight, and on the southern Sofala Bank (Figure 1). The hotspots were

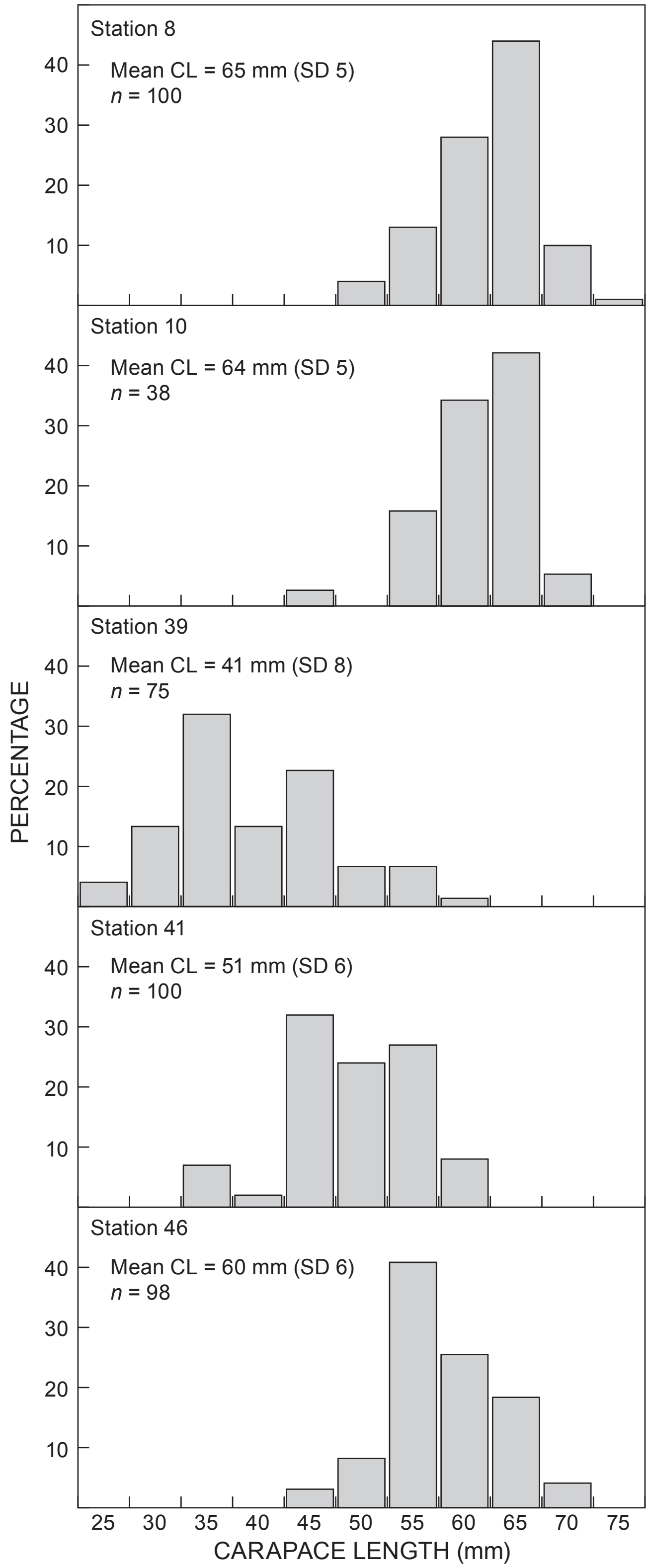

Figure 5: Length composition of *Ibacus novemdentatus* sampled at two trawl sites on the Thukela Bank (Stations 8 and 10) and at three sites in the Delagoa Bight (Stations 39, 41 and 46) during 2018. CL = carapace length

all located along the seaward edges of large sand/mud banks formed by terrigenous sediments deposited in nearshore areas by runoff from major rivers. Apart from the hotspots, *I. novemdentatus* was scarce in trawls along the coast, caught sometimes singly or in small numbers. The identification of geographical hotspots of *I. novemdentatus* is novel and partially explains the high observed variability in catches and density estimates.

Several species of *Ibacus* in Australia inhabit relatively soft sandy or muddy substrates (Haddy et al. 2007), where they display a distinct digging behaviour, and spend much of the time under sand (Faulkes 2006). When presented with a choice of substrates, *I. peronii* from southern Australia preferred digging into sand, rather than shell grit, but showed no preference for different types of sand (Faulkes 2006). In the present study, *I. novemdentatus* captured on the Thukela Bank was most abundant on substrates of very fine to fine sand with mud, suggesting that hotspots might coincide with these soft-sediment habitats, into which the lobsters can dig. All three observed hotspots were furthermore associated with offshore sand/mud banks, where biological productivity is enhanced by riverine inputs of sediments, nutrients and organic matter (De Lecea et al. 2013, 2016).

The catchability (or availability) of *I. novemdentatus* by the survey trawl net could not be determined, but based on the species' flat body shape and digging behaviour, the catchability coefficient is most likely low (Haddy et al. 2007). Rubber bobbins fixed to the *Nansen*'s trawl net create a ground clearance during trawling, through which small bottom-dwelling or burrowing organisms can escape capture. In a comparative study in the Benguela Current region, nets towed by commercial trawlers had better bottom-contact than those used by the *Nansen*, increasing the catchability of bottom-dwellers (Axelsen and Johnsen 2015). Based on this, we expect commercial trawl nets to be more efficient, and to have higher catch rates of *I. novemdentatus*, than the survey nets used by the *Nansen* in the present study.

Catchability differs according to species, based on spatial distribution patterns relative to the net's tow path, behaviour when confronted by an approaching net, and the selectivity properties of the net (Walsh 1996). In the absence of species–specific catchability coefficients, direct abundance comparisons among species, based on trawl data, is meaningless. Even so, when using a standardised trawling regime, a constant relative catchability, by species and over time, is not an implausible assumption (Walsh 1996). The finding that *I. novemdentatus* was proportionally more abundant than *Palinurus delagoae*, *Scyllarides elisabethae* and *Puerulus angulatus* in the sampled depth range, in spite of an apparent low catchability coefficient inferred from its body shape and digging behaviour, suggests that *I. novemdentatus* might be relatively more abundant than the data suggest.

Despite using a Gisund Super trawl as a standard net in all surveys carried out by the *Nansen*, and maintaining the effective horizontal net opening at ~18.5 m, gradual technological advances over the study period are likely to have increased the efficiency of the trawling gear over time (Axelsen and Johnsen 2015). Likewise, the replacement of the original *Nansen* (active 1975–1993) with a larger, more powerful modernised version in 1994, and again in 2017, must also have resulted in abrupt vessel-associated increments in trawl efficiency (Saetersdal et al. 1999; Axelsen and Johnsen 2015; Everett 2017; Fennessy et al. 2017). Improvements in the accuracy of sampling and data interpretation have been facilitated by progressively more-sophisticated navigation technology, echosounding, bottom-mapping and *in situ* gear performance (Axelsen and Johnsen 2015). The apparent increase in relative densities of *I. novemdentatus* between 1990 and 2018 (Table 1), therefore, is considered to be artefactual, and a result of improved trawl efficiency rather than higher lobster densities.

Size- or sex-structured populations are common in lobsters and imply some form of migratory behaviour (Groeneveld and Branch 2002). The clear size-progression of *I. novemdentatus* seen at three neighbouring sites on the edge of the Delagoa Bight (Figure 5) strongly suggests that juveniles of the species undertake migrations to habitats suitable for adults. Similarly, the absence of small specimens at two sampled sites on the Thukela Bank suggests that juveniles must be elsewhere. In combination, the data support a hypothesis of segregated life-history stages, connected by benthic migrations. Populations of *Ibacus chacei*, *I. peronii*, *I. alticrenatus* and *I. brucei* in Australia display various levels of population structure (Haddy et al. 2007), including long-distance counter-current migrations by *I. chacei* to release larvae upstream of settlement areas (Stewart and Kennelly 1998). A similar mechanism could explain the observed size structure in *I. novemdentatus*, considering that they inhabit the shelf edge/upper slope in an area strongly influenced by the northern Agulhas Current (Lutjeharms 2006) and Mozambique Channel eddies (Quartly and Srokosz 2004), and have a drifting larval phase of >40 days (Wakabayashi et al. 2012). At least two deep-water spiny lobster species in the Agulhas Current region have evolved similar long-distance counter-current migrations, to release larvae upstream of settlement areas (Groeneveld 2002; Groeneveld and Branch 2002).

Ibacus novemdentatus was found in a shallower depth interval (53–297 m) than traditional trawl grounds for mixed crustaceans (200–600 m; Groeneveld and Mellville-Smith 1995), and trawling at a shallower depth is expected to change the mix of species that will be caught. Our study showed that at least four high-value lobster species can be caught in the shallower depth interval, and that several teleosts with commercial value will also form part of the catch. High-value species traditionally caught by the deep-water trawl fishery, such as the prawns *Haliporoides triarthrus*, *Aristaeomorpha foliacea* and *Aristeus* spp., the langoustine *Metanephrops mozambicus*, and the deep-sea crab *Chaceon macphersoni* were, however, scarce in the shallower depth interval (Groeneveld and Melville-Smith 1995). Nevertheless, further exploration by commercial trawlers to better define hotspots of adult *I. novemdentatus* and investigate the contribution that this species can make to mixed-species catches, should be considered.

Fan lobsters are largely unknown to local seafood consumers in South Africa and Mozambique. In Australia, where *Ibacus* is also a bycatch of prawn-trawl fisheries, increased consumer awareness, expanding markets and price increases have resulted in fishers specifically targeting fan lobsters (Haddy et al. 2005). At the Sydney Fish Market (www.sydneyfishmarket.com.au), the so-called 'bugs' are medium-high priced, and more expensive in areas where they are caught, as they are familiar and popular. They are sold live or fresh, or as frozen whole lobster, tails or meat. Wholesale market prices are higher for larger than for smaller specimens, irrespective of processing method (Haddy et al. 2007). In southern Africa, markets for fan lobsters could grow, but only when the resource becomes available at seafood outlets and thereafter becomes familiar to consumers. Alternatively, fan lobsters caught by trawlers could be exported to seafood markets in Australia or Japan, where there are established markets for them.

In conclusion, *I. novemdentatus* might be overlooked as a fisheries resource because it occurs shallower than the traditional deep-water trawl grounds for crustaceans in the SW Indian Ocean. Adults concentrate in hotspots along the seaward edges of offshore sand/mud banks, where they can be caught in considerable numbers by trawling. Three other high-value lobster species and several marketable teleost species occurred in research trawl nets where *I. novemdentatus* was present, suggesting a potential for expanding the mixed-species deep-water trawl fishery to shallower depths.

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References

Axelsen BE, Johnsen E. 2015. An evaluation of the bottom trawl surveys in the Benguela Current Large Marine Ecosystem. *Fisheries Oceanography* 24: 74–87.

Bianchi G, Koranteng K, Strømme T. 2017. Historical overview of the Nansen Programme. In: Groeneveld JC, Koranteng KA (eds), *The RV Dr Fridtjof Nansen in the Western Indian Ocean: voyages of marine research and capacity development.* Rome: Food and Agriculture Organization of the United Nations. pp 9–22.

Brown DE, Holthuis LB. 1998. The Australian species of the genus *Ibacus* (Crustacea: Decapoda: Scyllaridae), with the description of a new species and addition of new records. *Zoölogische Mededeelingen* 72: 113–141.

Cockcroft AC, Groeneveld JC, Cruywagen GC. 1995. The influence of depth, latitude and width of the continental slope on the size distribution and availability of spiny lobster *Palinurus delagoae* off the east coast of South Africa. *South African Journal of Marine Science* 16: 149–160.

De Lecea AM, Fennessy ST, Smit AJ. 2013. Processes controlling the benthic food web of a mesotrophic bight (KwaZulu-Natal, South Africa) revealed by stable isotope analysis. *Marine Ecology Progress Series* 484: 97–114.

De Lecea AM, Smit AJ, Fennessy ST. 2016. Riverine dominance of a nearshore marine demersal food web: evidence from stable isotope and C/N ratio analysis. *African Journal of Marine Science* 38(Supplement): S181–S192.

Everett B. 2017. Study area, vessels and surveys. In: Groeneveld JC, Koranteng KA (eds), *The RV Dr Fridtjof Nansen in the Western Indian Ocean: voyages of marine research and capacity development.* Rome: Food and Agriculture Organization of the United Nations. pp 22–35.

Everett BI, Groeneveld JC, Fennessy ST, Dias N, Filipe O, Zacarias L et al. 2015a. Composition and abundance of deep-water crustaceans in the southwest Indian Ocean: enough to support trawl fisheries? *Ocean and Coastal Management* 111: 50–61.

Everett BI, Groeneveld JC, Fennessy ST, Porter S, Munga CN, Dias N et al. 2015b. Demersal trawl surveys show ecological gradients in southwest Indian Ocean slope fauna. *Western Indian Ocean Journal of Marine Science* 14: 73–92.

Faulkes Z. 2006. Digging mechanisms and substrate preferences of shovel-nosed lobsters, *Ibacus peronii* (Decapoda: Scyllaridae). *Journal of Crustacean Biology* 26: 69–72.

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.

Fennessy ST, Krakstad JO, Groeneveld JC, Bianchi G, Everett B. 2017. Demersal resources based on bottom trawl and other sampling methods. In: Groeneveld JC, Koranteng KA (eds), *The RV Dr Fridtjof Nansen in the Western Indian Ocean: voyages of marine research and capacity development.* Rome: Food and Agriculture Organization of the United Nations. pp 101–124.

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R. 1994. DNA primers for amplification of mitochondrial cytochrome C oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294–299.

Froese R. 2006. Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. *Journal of Applied Ichthyology* 22: 241–253.

Groeneveld JC. 2002. Long-distance migration of the rock lobster *Palinurus delagoae* off South Africa and Moçambique. *African Journal of Marine Science* 24: 395–400.

Groeneveld JC, Branch GM. 2002. Long-distance migration of South African deep-water rock lobster *Palinurus gilchristi*. *Marine Ecology Progress Series* 232: 225–238.

Groeneveld JC, 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 African Journal of Marine Science* 15: 123–136.

Groeneveld JC, Kirkman SP, Boucher M, Yemane D. 2012. From biomass mining to sustainable fishing – using abundance and size to define a spatial management framework for deep-water lobster. *African Journal of Marine Science* 34: 547–557.

Haddy JA, Roy DP, Courtney AJ. 2005. Aspects of the reproductive biology and growth of Balmain bugs (*Ibacus* spp.) (Scyllaridae). *Journal of Crustacean Biology* 25: 263–273.

Haddy JA, Stewart J, Graham SKJ. 2007. Fishery and biology of commercially exploited Australian fan lobsters (*Ibacus* spp.). In: Lavalli KL, Spanier E (eds), *The biology and fisheries of slipper lobsters. Crustacean Issues* No. 17. Boca Raton, Florida: CRC Press, Taylor and Francis Group. pp 359–375.

Holthuis LB. 1991. FAO species catalogue. Volume 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. Rome: Food and Agriculture Organization of the United Nations.

Ivanov BG, Krylov VV. 1980. Length–weight relationship in some common prawns and lobsters (Macrura, Natantia and Reptantia) from the western Indian Ocean. *Crustaceana* 38: 279–289.

Lutjeharms JRE. 2006. *The Agulhas Current.* Berlin: Springer-Verlag.

MacDiarmid A, Cockcroft A, Butler M. 2013. *Ibacus novemdentatus*. The IUCN Red List of Threatened Species 2013: e.T170023A6710751.

Quartly GD, Srokosz MA. 2004. Eddies in the southern Mozambique Channel. *Deep-Sea Research II: Topical Studies in Oceanography* 51: 69–83.

R Core Team. 2013. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Sætersdal G, Bianchi G, Strømme T, Venema S. 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. Rome: Food and Agriculture Organization of the United Nations.

Stewart J, Kennelly SJ. 1998. Contrasting movements of two exploited scyllarid lobsters of the genus *Ibacus* off the east coast of Australia. *Fisheries Research* 36: 127–132.

Strømme T. 1992. Software for fishery survey data logging and analysis. User manual. *FAO Computerized Information Series (Fisheries)*. Report No. 4. Rome: Food and Agriculture Organization of the United Nations.

Wakabayashi K, Sato R, Ishii H, Akiba T, Nogata Y, Tanaka Y. 2012. Culture of phyllosomas of *Ibacus novemdentatus* (Decapoda: Scyllaridae) in a closed recirculating system using jellyfish as food. *Aquaculture (Amsterdam, Netherlands)* 330–333: 162–166.

Walsh SJ. 1996. Efficiency of bottom sampling trawls in deriving survey abundance indices. *NAFO Scientific Council Studies* 28: 9–24.

Webber WR, Booth JD. 2007. Taxonomy and evolution. In: Lavalli KL, Spanier E (eds), *The biology and fisheries of slipper lobsters. Crustacean Issues* No. 17. Boca Raton, Florida: CRC Press, Taylor and Francis Group. pp 25–52.

Wentworth CK. 1922. A scale of grade and class terms for clastic sediments. *The Journal of Geology* 30: 377–392.

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