

ABUNDANCE AND BIOLOGY OF THE LANGOUSTINE *METANEPHROPS MOZAMBICUS* (NEPHROPIDAE) ON DEEP-WATER TRAWL GROUNDS IN EASTERN SOUTH AFRICA

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ABSTRACT

Abundance trends, population structure, and biology of the langoustine *Metanephrops mozambicus* (Macpherson, 1990) were investigated, based on commercial logbook information (1988-2010; 49 990 trawls) and biological samples collected off eastern South Africa. A generalized linear model (GLM) framework was used to model variation in catch rates, carapace length (CL), sex ratio, and maturation size. Standardized catch rates were inversely related to fishing effort, gradually increasing between 2002 and 2010, when fishing effort was lower. Catch rates were greatest in trawls made at 300 to 599 m depth and between June and December. Langoustines ranged in size from 17.5 to 72.6 mm CL, and the mean CL decreased with increasing depth. Males predominated in November, but equal numbers of males and females were observed in other months. The smallest egg-bearing female had a CL of 33.5 mm, and L_{50} was estimated at 49.4 mm, based on the incidence of external eggs. Females with freshly spawned eggs were most abundant in August, and the incidence of egg-bearing remained high until March, where after it declined. Eggs about to hatch occurred mainly in May. Growth parameter estimates (L_{∞} and K) were 65.5 mm and 0.7 year^{-1} for sexes combined, based on modal progression and the standard von Bertalanffy growth function, and longevity was estimated to be 3-4 years. Combining analyses of fisheries data with biological samples yielded insights into spatio-temporal population trends, as well as the correlation of reproduction and moulting in *M. mozambicus*.

KEY WORDS: catch rates, growth, maturity, *Metanephrops mozambicus*, population structure

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INTRODUCTION

Metanephrops Jenkins, 1972 is the most diverse clawed lobster genus (Nephropidae), comprising 18 extant and 3 fossil species (Tshudy et al., 2007; Chan, 2010). Known in the vernacular as langoustine, lobster, lobsterette, or scampi, *Metanephrops* bears a strong morphological resemblance to *Nephrops* Leach, 1814, to which its members were previously assigned (Jenkins, 1972). The genus can, however, be distinguished by the possession of a branchial carina (absent in *Nephrops*) and more prominent supraorbital and antennal ridges. *Metanephrops* occurs between 35°N and 50°S, mostly in the Central and West Indo-Pacific, although a few species occur in the western Atlantic. They are most common along the outer continental shelf edge and upper slope areas at depths ranging from 50 to 994 m, but mostly > 150 m (Holthuis, 1991; Tshudy, 2003). Most of the known species become large enough to be considered of present or potential commercial interest and some are caught by bottom trawl fisheries (Holthuis, 1991; Bell et al., 2013).

Landings of *Metanephrops* in FAO fishing areas are relatively modest, and are dominated by catches of *M. chalcongeri* (Balss, 1914) from the Southwest Pacific (Bell et al., 2013). A targeted trawl fishery for this species in New Zealand developed during the late 1980s, and landings have

been maintained at around 700-1000 tonnes per year. Landings of other species of *Metanephrops* as targeted catches or by-catches of fisheries in Australia (*M. australiensis* (Bruce, 1966), *M. boschmai* (Holthuis, 1964), *M. velutinus* Chan and Yu, 1991 (Holthuis, 1991; Bell et al., 2013)), the Central West Pacific (*M. thomsoni* (Bate, 1888) (Choi et al., 2008)), western Indian Ocean (*M. mozambicus* (Macpherson, 1990) (Groeneveld and Melville-Smith, 1995)) and the western Atlantic (*M. binghami* (Boone, 1927) Paramo and Saint-Paul, 2012) are far less, and often go unreported.

The African lobster (or langoustine) *M. mozambicus* occurs off eastern Africa, between Kenya and South Africa, and in western Madagascar (Holthuis, 1991). It inhabits soft muddy substrata at depths of 200 to 750 m (Berry, 1969; Holthuis, 1991). Prior to 1990, langoustine catches from eastern South Africa and Mozambique were attributed to *Nephrops* (or *Metanephrops*) *andamanicus* Wood-Mason, 1892, a morphologically similar species that occurs northwards from Kenya, in the Andaman Sea, South China Sea and Indonesia (Chan and Yu, 1991; Holthuis, 1991). It remains unclear whether specimens from Tanzania are *M. andamanicus* or *M. mozambicus*, or whether both species occur there (Chan and Yu, 1991).

An estimated 100-300 tonnes per year of *M. mozambicus* are caught by deep-water trawling in the southwest In-

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dian Ocean region, mostly from eastern South Africa and Mozambique (Groeneveld and Melville-Smith, 1995; Bell et al., 2013). The deep-water trawl fishery targets a mixture of high-value crustaceans, but landings mostly consist of knife prawn *Haliporoides triarthrus* Stebbing, 1914 and *M. mozambicus* (approximately 17% of total crustacean landings; Fennessy and Groeneveld, 1997). Experimental trawling in eastern South Africa started as early as the 1920s (Gilchrist, 1922), but formal recording of catch and effort statistics did not commence until 1988, when a standardized logbook system was instituted. Since 1988, up to eight permits per year have been available for fishing on the deep-water trawl grounds, although only three to five vessels have been active since 2004. The literature on the deep-water crustacean trawl fishery in eastern South Africa has focussed on the species composition of catches (Fennessy and Groeneveld, 1997), variations in time and space of target crustaceans (Groeneveld and Melville-Smith, 1995), and biological investigations of *H. triarthrus* (Berry et al., 1975; de Freitas, 1985; Robey et al., 2013), *M. mozambicus* (Berry, 1969), eastern deep-water lobster *Palinurus delagoae* Barnard, 1926 (Berry, 1973; Groeneveld, 2000), and deep-water geryonid crab *Chaceon macphersoni* (Manning and Holthuis, 1988) (Groeneveld et al., 2013).

Berry (1969) described the biology and life history of *M. mozambicus* from monthly trawl samples undertaken in eastern South Africa. More females than males were present in catches in most months, and the smallest females with eggs had a carapace length (CL) of 42 mm (maturation size $L_{50} = 48$ mm; maximum CL = 72 mm). Spawning activity peaked in August, and hatching occurred nine to ten months later, with a peak in May. The majority of sexually mature females moulted in May to July, prior to spawning in August, whereas mature males moulted mainly in December to March, with lower levels of moulting throughout the year. Females carried 600–1400 eggs, and larvae hatched in an advanced state of development (Berry, 1969). Larvae presumably settle within a few hours or days of hatching, as in *M. challengerii* (Wear, 1976) and *M. japonicus* (Tapparone-Canefri, 1873) (Okamoto, 2008), thus limiting dispersal potential. *M. mozambicus* presumably lives in burrows, like the other species of *Metanephrops* (Bell et al., 2013), although emergence behaviour and diel activity patterns have not yet been inferred, as in *M. challengerii* (Tuck, 2010), *M. australiensis* (Ward and Davis, 1987) and *M. binghami* (Paramo and Saint-Paul, 2012).

The aims of this study were to investigate trends in the abundance, biology and population structure of *M. mozambicus* off eastern South Africa, based on logbook data collected from deep-water trawlers between 1988 and 2010, and on biological samples. The population demographic structure (size, sex ratio), and reproductive biology (size at maturity and breeding season) were investigated for the first time since Berry (1969), and length-based analyses were used to estimate growth parameters. Our findings were compared with Berry (1969) for *M. mozambicus*, and with biological information available for other *Metanephrops*, particularly the exploited populations.

MATERIALS AND METHODS

Study Area

The deep-water trawl grounds in eastern South Africa (KwaZulu-Natal Province; KZN) are located along the eastern edge of the Natal Bight (approx. 29 to 31°S), and comprise approximately 1750 km² between 100 and 600 m depth (Fig. 1). The substratum varies from mud to hardened accretions of sediment, foraminifera and spicules (Berry, 1969). The powerful Agulhas Current flows in a south-westerly direction along the shelf-edge of the Natal Bight at speeds up to 3 knots, and shear edge disturbances in this area sometimes result in local eddies near 30°E (see Lutjeharms, 2006 for a review). The average bottom temperature on the trawl grounds ranges between 9 and 12°C (Berry, 1969) or between 8 and 10°C (L. Guastella, c/o University of Cape Town, South Africa; e-mail: lisagus@telkomsa.net).

Field Sampling and Logbook Data

Samples of *M. mozambicus* were collected during six quarterly sampling trips on-board a commercial trawler during normal fishing operations between December 2010 and March 2012. A nylon bottom trawl net with 50 mm stretched mesh was used, and the sampled trawls were mainly located in the southern part of the trawl grounds (approx. 29.5 to 30°S) between 400 and 500 m depth (Fig. 1). Random samples were obtained by shovelling 10 to 20 kg of the mixed trawl catch into a crate, and then sampling all *M. mozambicus* from the crate.

Females were identified by the oviduct opening on the third pereopod and males by the vas deferens opening on the fifth pereopod (Farmer, 1975). Carapace length (CL \pm 0.1 mm) was measured between the inner eye socket edge and the posterior carapace margin, and shell condition recorded as hard or soft. Females with external eggs were assumed to be sexually mature and the eggs were staged following a macroscopic key after Berry (1969): 1) freshly spawned (bright royal blue; no embryo development); 2) early development (dark blue-purplish; embryo visible as thin tissue); 3) well-formed (dark purple to pink; appendages just visible); 4) about to hatch (red; fully formed larvae with eyes visible). Size-graded packs (large, medium and small *M. mozambicus*; 2 kg of each) were purchased directly from the vessel during months in which sampling at sea did not take place. From these, individuals were weighed (\pm 1 g) and measured in the laboratory for length and weight analyses.

The skippers of commercial trawlers recorded information on langoustine catches (packed weight per trawl, kg) and fishing effort (hours trawled) in logbooks between 1988 and 2010. Fishing effort information included the time, duration, depth, and position of each trawl. A total of 27 individual trawlers have participated in the fishery since 1988, several of them for short periods only. Trawlers mostly used single otter trawls deployed from the stern, and trawl sizes ranged from 25 to 60 m footrope lengths, with stretched mesh size from 70 mm in the wings to 38 mm in the cod-end, although in 2000, a minimum stretched mesh size of 50 mm was introduced. Trawl speeds were 2–3 knots, and trawling took place on a 24-hour basis with a duration of 4.2 ± 1.2 hours per trawl (mean \pm S.D.). The logbook data were cleaned by removing anomalous records in which trawl localities, depth, date or catch composition were clearly incorrect and/or mismatched. Catch and fishing effort records of 49 990 trawls remained, from which langoustine abundance could be estimated.

Logbook Data Analysis

Variability in *M. mozambicus* abundance (kg \cdot h⁻¹ trawled) by year, month, depth, vessel and latitude (Table 1) was explored using generalized linear models (GLM) in the statistical software package R, version 2.14.0 (R Development Core Team, 2011). The data contained many records with zero *M. mozambicus* catches, and therefore the delta method (Lo et al., 1992; Maunder and Punt, 2004) was selected for the analysis. The delta method involves fitting 2 submodels to the data. In the first submodel, the probability of a non-zero catch is modelled, based on presence/absence information, and assuming a binomial error distribution. In the second submodel, only the positive catch is modelled, assuming a log-normal, Poisson, negative-binomial or gamma error distribution. The gamma model was selected, because preliminary tests showed that the relationship between the logarithms of the mean and variance of non-zero catch rates was close to 2 (data highly dispersed) (McCullagh and Nelder, 1989; Stefánsson, 1996). Final models were selected based on a stepwise approach, involving modeling combinations of error structures, link functions and explanatory variables. The most parsimonious models were selected based on Akaike's Information Criterion (AIC) (Akaike,

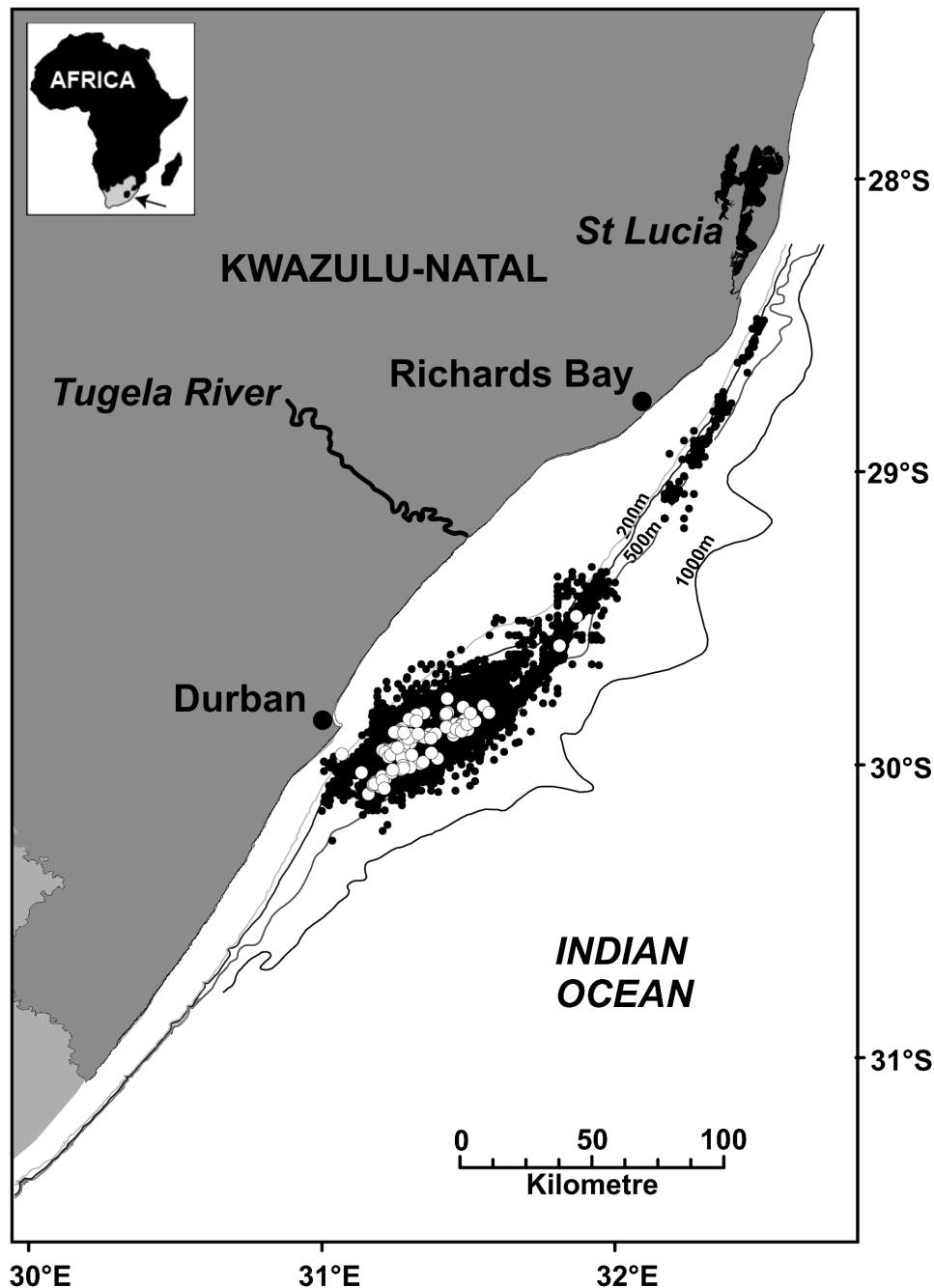


Fig. 1. Deep-water trawl grounds for crustaceans along the coast of the KwaZulu-Natal province of South Africa. Black dots indicate all commercial trawls made between 1988 and 2010, and white dots indicate the trawls sampled by the observer during the present study.

1974) and visual assessment of residual plots (Table 2). Abundance indices were computed as the product of the probability of catch (binomial model) and non-zero catch (gamma model), obtained from model coefficients. The most frequently recorded observations of each variable were used as the reference points (i.e. 1988, July, 300 m depth and vessel 6).

Size Structure, Sex Ratios and Female Maturity

Size data (CL, continuous, interval-scale) were normally distributed, and after running trials, a Gaussian error distribution with a log link function was selected to model variability relative to year, month, depth and sex (Table 2). The AIC and visual assessments were used in a hierarchical way to select the most parsimonious model, in which non-significant variables in the analysis of deviance were omitted. A binomial error distribution with

a logit link function was used to model sex ratio (probability of capturing a male) relative to year, month, depth and size (Table 2). The coefficients (α and β) of a logistic equation to estimate size at maturity of female langoustines was estimated from a GLM with binomial error structure and logit link function (Table 2). The proportion of females with external eggs (presumed to be mature) at each size was calculated as the inverse logit. The sizes at 25, 50 and 75% probability of maturation, defining the mean size (L_{50}) and maturation range ($L_{25} - L_{75}$), were calculated on simulation with the inverse logit and the estimated parameters.

Growth Models

Male and female length frequencies did not differ significantly within months tested (Pearson's χ^2 test of independence, $P > 0.05$) and sexes

Table 1. Candidate factors hypothesized to affect the abundance, size structure, maturation size and sex ratio of langoustine *M. mozambicus* caught in deep-water bottom trawls off eastern South Africa.

Explanatory variable	Type	Description
Year	Categorical	1988-2010
Month	Categorical	January-December
Depth	Categorical	Divided into depth strata 100-199 m 200-299 m 300-399 m 400-499 m 500-599 m 600-699 m ≥700 m
Latitude	Categorical	Trawl localities divided by latitude North of 29.15°S South of 29.15°S
Vessel	Categorical	27 Vessels operated between 1988 and 2010
Size	Continuous	17.5-72.6 mm CL
Sex	Categorical	Male and female

were therefore combined for growth analyses. Monthly length frequency distributions were plotted and modes (interpreted as cohorts or age classes) identified visually. The means, standard deviations and proportions of modes were calculated using the Solver optimization tool in MS Excel, and software developed in MS Excel similar to MIX (Macdonald and Pitcher, 1979; Macdonald and Green, 1988). Constraints used when fitting modes were that: length observations within a mode were normally distributed; mean length increments of a cohort decreased with size (or time); and standard deviations remained constant.

May was assumed to be the birth month, based on the peak hatching period of the eggs (Berry, 1969). Using this reference point, the von Bertalanffy growth function (VB) was applied to mean size at age, as follows:

$$L_t = L_\infty \left(1 - e^{-K(t-t_0)}\right)$$

where L_t (mm) is the length at time t , L_∞ (mm) is the mean asymptotic length, K (year^{-1}) is the growth coefficient and t_0 (year) is the theoretical age at the start of growth. The model was fit to the combined data of the two best represented cohorts, using non-linear least squares optimization, and assuming a normal error. The standard deviation of each mode or age group was used to weight (1/SD) the regression.

RESULTS

Trends in Fishing Effort and Catch Rates

The number of trawl hours decreased from 16 641 in 1989 to 4551 in 1994, when some vessels did not fish, and stabilized at a low level between 2004 (6563 hours) and 2010 (8186 hours) (Fig. 2). Trawling occurred year round, but less frequently in autumn and winter (April to June) than in spring (September to November), and most trawling occurred between 400 and 499 m depth (mean \pm S.D. = 400.3 \pm 81.3 m). Langoustines were present in 80% of trawls and on average, 51.5 \pm 15.2 t (mean \pm S.D.) were landed per year. Most langoustines were caught in October and between 400 and 499 m depth (Fig. 2).

Year, month, depth and vessel were all significant explanatory variables in the final presence/absence (binomial) submodel of catch rates, with the probability of capturing a langoustine increasing from 1989 to 2007, decreasing from July to December and being lowest at 100 to 299 m depth (Table 2). In the conditional gamma model for positive oc-

currences, the effects of year, month, depth and vessel were all significant as well. The final delta model, i.e., the product of the probability of capture (binomial submodel) and catch rate of trawls with non-zero langoustine catches (gamma submodel), resulted in trends very similar to those of the gamma submodel; standardized catch rates increased between 1989 and 1994, declined between 1995 and 2003, and thereafter gradually increased to the highest level on record in 2010 (Fig. 3). By month, catch rates were lower between January and April than during the rest of the year. By depth, the highest catch rates were observed between 300 and 599 m. The increase in catch rates at depths \geq 700 m is almost certainly artificial, as these reported trawl depths are unlikely to be valid (K. Sorenson, experienced skipper from Spray Fishing, personal communication).

A negative correlation was observed between standardized catch rates and yearly fishing effort (Fig. 4). Lower than average fishing effort was reported in 1994 to 1996, when some vessels did not fish, and in 2004 to 2010 when only three vessels fished regularly. These periods correlated with increased catch rates, suggesting an increase in langoustine abundance during periods of reduced fishing pressure. Conversely, increased fishing effort in 2001 to 2003 corresponded with a decline in catch rates over the same period.

Size Structure and Reproductive Biology

A total of 1963 langoustines was sampled from 95 trawls, ranging in CL from 17.5 to 72.6 mm. Size distributions of all langoustines combined showed 2 modes for males (38 and 54 mm CL) and for females (40 and 50 mm CL) (Fig. 5). In the size model, the effects of month and depth were significant (Table 2). By month, the mean CL was smaller in March (autumn) and November (spring) than in other months, although the size difference was <4.1 mm (Fig. 6). Despite a relatively narrow depth range sampled (325-500 m), the mean CL decreased consistently with increasing depth, from 49.2 to 39.9 mm.

Table 2. Final generalized linear models (GLM) selected to describe variation in the catch rate, size, sex ratio and female maturity of *M. mozambicus* captured off eastern South Africa. The most appropriate error structures and link-functions are shown for each model, and the Akaike Information Criterion (AIC) was used to compare model fits. The coefficients (\pm SE) of the model parameters are provided. Estimates marked with # were not significantly different ($P = 0.05$) from the intercept.

	Catch rate		Catch rate		Size		Sex ratio		Maturity	
Error	Binomial		Gamma		Gaussian		Binomial		Binomial	
Link	Logit		Log		Log		Logit		Logit	
n	49 990		49 990		2033		2033		992	
AIC	42 840		226 487		14 848		2792.8		758.06	
Explained deviance	26 593		345 248		4 009 764		25.5		641.14	
Df	66		834		11		6		12	
Chisq (P)	0		0		0		0.0003		<0.00001	
Explanatory variable	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
1988	-4.276	0.153	2.056	0.088						
1989	-4.680	0.147	1.681	0.085						
1990	-4.545	0.149	1.756	0.086						
1991	-4.181	0.150	1.907	0.085						
1992	-3.724	0.150	1.852	0.085						
1993	-4.045	0.146	2.305	0.084						
1994	-3.973	0.153	2.414	0.088						
1995	-3.508	0.156	2.248	0.087						
1996	-3.646	0.151	2.081	0.085						
1997	-3.328	0.152	2.107	0.084						
1998	-3.506	0.152	1.934	0.085						
1999	-3.254	0.155	1.900	0.085						
2000	-2.603	0.162	2.061	0.084						
2001	-2.669	0.152	1.854	0.083						
2002	-2.758	0.152	1.686	0.083						
2003	-2.879	0.152	1.599	0.084						
2004	-2.569	0.161	1.866	0.085						
2005	-2.998	0.162	1.875	0.085						
2006	-3.075	0.162	1.859	0.086						
2007	-0.404	0.145	2.049	0.078						
2008	-0.832	0.153	2.019	0.082						
2009	-0.280	0.144	2.211	0.079						
2010	-0.227 #	0.143	2.262	0.080						
Jan	0.000	0.000	0.000	0.000						
Feb	0.091	0.053	0.007 #	0.024	3.983	0.032	0.469 #	0.121	-11.757	1.187
Mar	0.070 #	0.056	0.029 #	0.025	3.981	0.031	0.485 #	0.094	-11.437	1.130
Apr	-0.118	0.057	0.034 #	0.026						
May	0.343	0.061	0.157	0.025	3.948	0.033	0.461 #	0.109	-11.858	1.113
Jun	0.655	0.065	0.275	0.026						
Jul	0.869	0.065	0.320	0.025						
Aug	0.556	0.061	0.287	0.025	3.895	0.030	0.514 #	0.126	-13.591	1.252
Sep	0.608	0.058	0.197	0.024						
Oct	0.372	0.056	0.292	0.024						
Nov	0.621	0.058	0.128	0.024	3.949	0.025	0.623	0.110	-11.810	1.168
Dec	0.409	0.062	0.146	0.025	3.910	0.030	0.518 #	0.105	-11.124	1.170
100-199 m	0.000	0.000	0.000	0.000		Est	SE	Est	SE	
200-299 m	2.374	0.123	-0.191	0.075	325-349 m	0.000	0.000	0.000	0.000	
300-399 m	4.872	0.137	0.142	0.080	375-399 m	-0.079	0.034	-1.581	0.806	
400-499 m	4.730	0.134	-0.204	0.079	400-424 m	-0.110	0.030	-1.272	0.744	
500-599 m	3.985	0.180	0.179	0.102	425-449 m	-0.149	0.029	-1.147 #	0.721	
600-699 m	4.010	0.922	-0.874	0.490	450-474 m	-0.178	0.030	-1.884	0.763	
≥ 700 m	4.021	0.205	-0.154 #	0.101	≥ 475 m	-0.209	0.052	-1.891	1.028	
Size									0.258	0.018
Vessel 1-27: Coefficients ranged from -2.022 ± 0.225 to 10.009 ± 62.497 for the binomial model, and from -0.512 ± 0.192 to 0.901 ± 0.189 for the gamma model of trawl catch rate.										

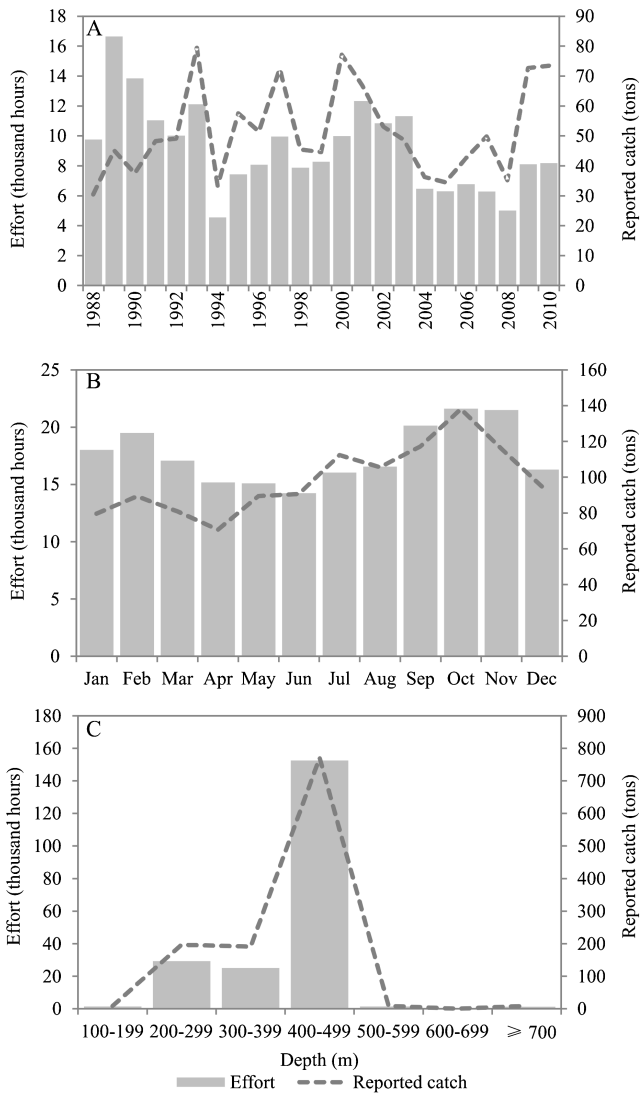


Fig. 2. Nominal fishing effort (hours trawled) and reported catch (tons) of *M. mozambicus* from the deep-water trawl fishery off eastern South Africa, obtained from logbooks between 1988 and 2010 and shown by a) year b) month and c) depth stratum for the entire period.

The sex ratio was marginally skewed towards males (1:0.89) and month was the only significant variable in the final model (Table 2). The model predicted sexual parity in most months, except November, when males were predominant (Fig. 7). Size, month and depth were significant in the final model of female maturity (Table 2). Based on the presence of external eggs (ovigerous method), females achieved maturity in the standard range of 45.1–53.6 mm CL ($L_{50} = 49.4$ mm) (Fig. 8). The smallest observed female with eggs measured 33.5 mm CL. By month, December had the highest (52%) and August the lowest (21%) probability of capturing an ovigerous female (Fig. 7). When restricting the range to females > 49.3 mm CL (i.e. mature females only), the probability of egg-bearing increased to 80% in December and decreased to 27% in August. By depth, the probability was 97% between 325 and 350 m, but declined to 62% at depths > 450 m, where smaller females occur.

Most egg-bearing females carried stage 1 eggs in August (73%), suggesting a recent mating event (Fig. 9). By

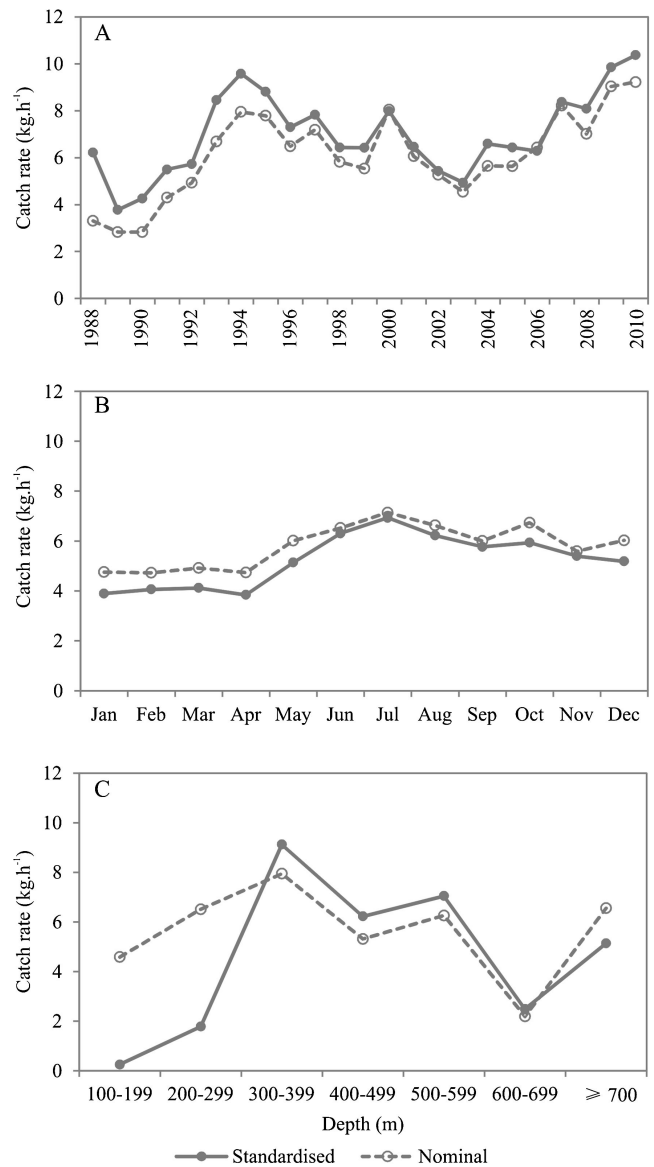


Fig. 3. Nominal and standardized catch rates (based on final delta model) for *M. mozambicus* captured in deep-water trawls off eastern South Africa by a) year, b) month and c) depth stratum. For the standardized trends, reference variables 1988, August and 400 m were chosen, because these were the most common in the dataset.

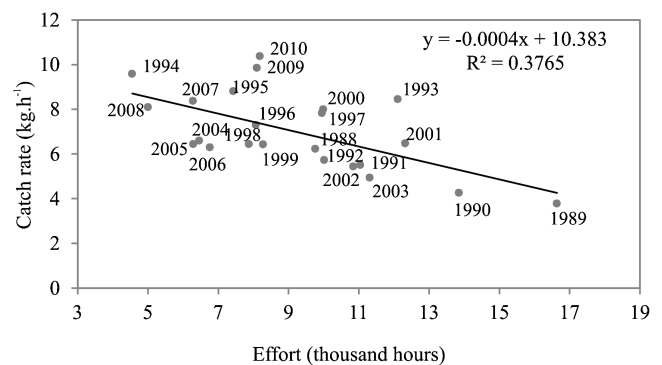


Fig. 4. Relationship between standardized catch rate and total nominal fishing effort per year (1988 to 2010) for the deep-water trawl fishery off eastern South Africa.

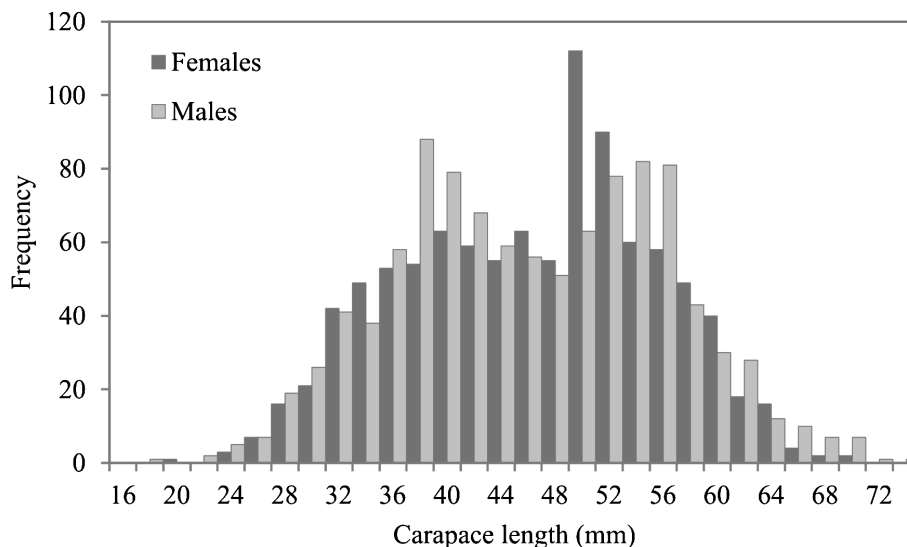


Fig. 5. Length frequency of male ($n = 1041$) and female ($n = 922$) *M. mozambicus* sampled on board a commercial deep-water trawler between 2010 and 2012.

November, the proportion of females with egg clutches dominated by stage 2 eggs had progressed to 75%, and females with eggs in stages 3 and 4 gradually became

noticeable in samples after December. Nearly all of the egg clutches observed in May (71%) were in Stages 3 and 4, suggesting that hatching takes place during this period. It should be mentioned, however, that some females with eggs in stage 1 were observed throughout the year. No clear

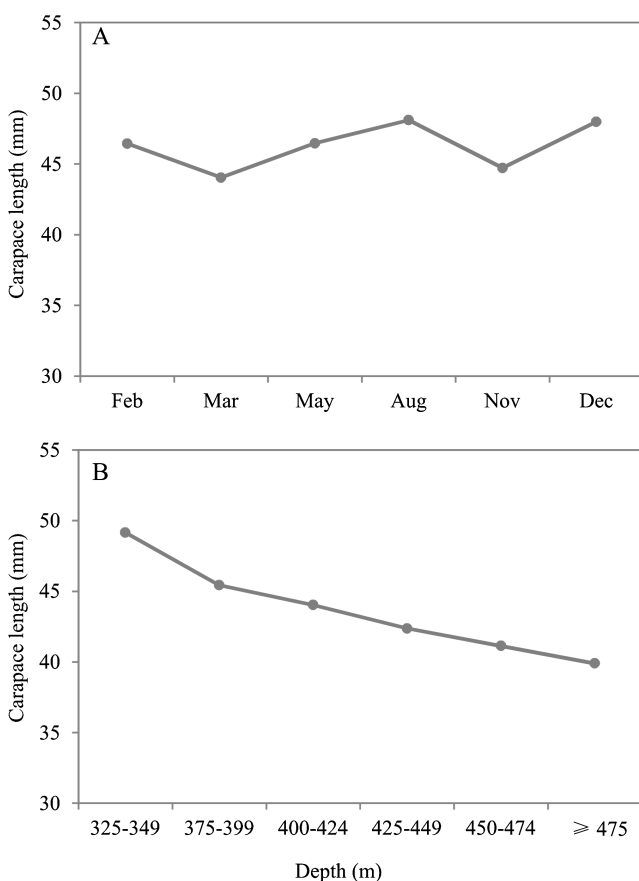


Fig. 6. GLM-standardized carapace length estimates of *M. mozambicus* sampled from deep-water trawl catches off eastern South Africa by a) month and b) depth. Reference values were March and 400 m depth, because these were the most common values.

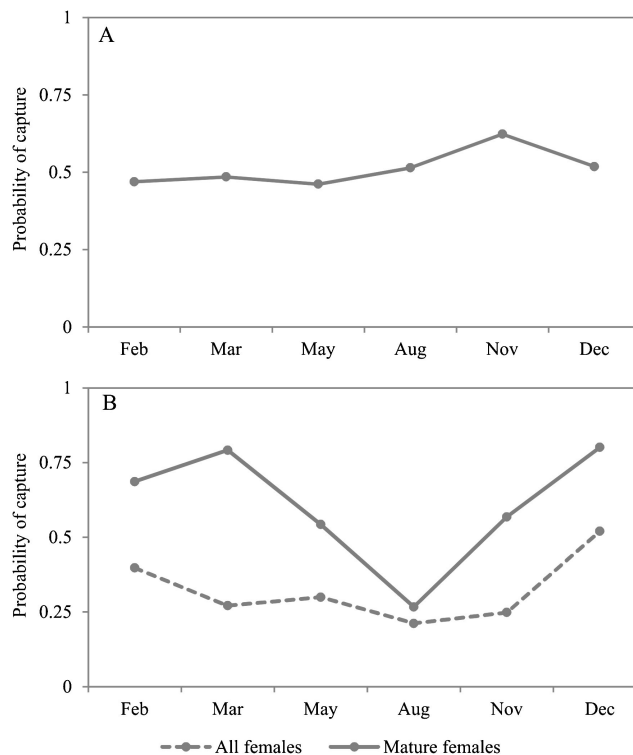


Fig. 7. A, Monthly probability of capturing a male, relative to a female *M. mozambicus* in trawl nets off eastern South Africa, based on the final sex ratio model; B, of capturing a female *M. mozambicus* with eggs, relative to one without eggs, in each month. The dotted line shows the probability of encountering an egg-bearing (berried) female based on all females sampled, whereas the solid line is based on a dataset restricted to females larger than the L_{50} (i.e. >49.4 mm CL).

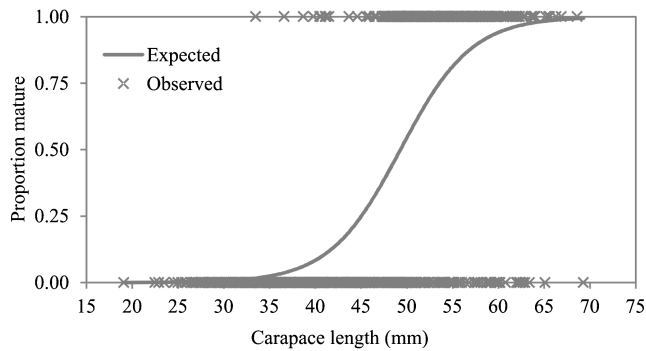


Fig. 8. Size at maturity ogive for female *M. mozambicus* off eastern South Africa.

moulting season could be identified from shell condition, and it was often difficult to distinguish between soft-shelled individuals (recently moulted) and those damaged by the trawl gear.

Conversions of Carapace Length to Whole Weight

All CL (mm) to WW (g) regressions were significant ($P < 0.0001$) and the high r^2 values indicated that the models fitted the data well. A broad CL range of 24.0–68.1 mm was available for male langoustines ($WW = 0.0003 \times L^{3.224}$, $n = 254$, $r^2 = 0.96$), whereas the female sample comprised langoustines of 31.0–66.9 mm ($WW = 0.0004 \times L^{3.115}$, $n = 329$, $r^2 = 0.93$). No significant difference was found between sexes ($P = 0.08$), and a sexes-combined equation was therefore determined (Fig. 10).

Growth

The identification of modes (or cohorts) of large and small langoustines was difficult because too few individuals of these sizes were caught. However, in the intermediate size classes, distinct modes could be identified in each month, and their progression followed over time (Fig. 11). Monthly samples were unimodal, except in March, when two prominent peaks were identified. Subsequent examination showed that these two peaks were for males and females, respectively, and consequently they were combined into a single mode based on the mean CL. In other months no clear distinction in modes by sex was observed. A total of 5 modes were identified, starting at 22 mm CL and increas-

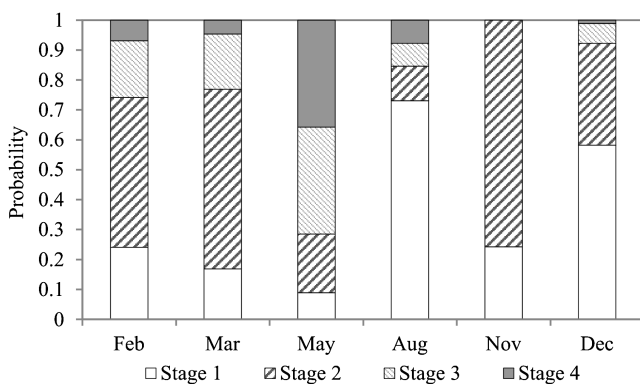


Fig. 9. The proportions of egg-bearing *M. mozambicus* females by egg-stage in field samples collected during 6 trips on a commercial trawler off eastern South Africa.

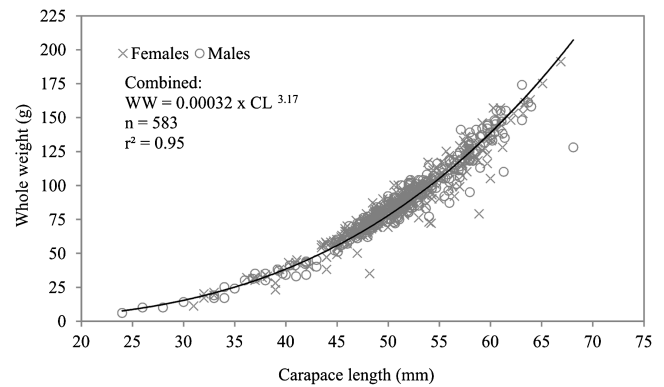


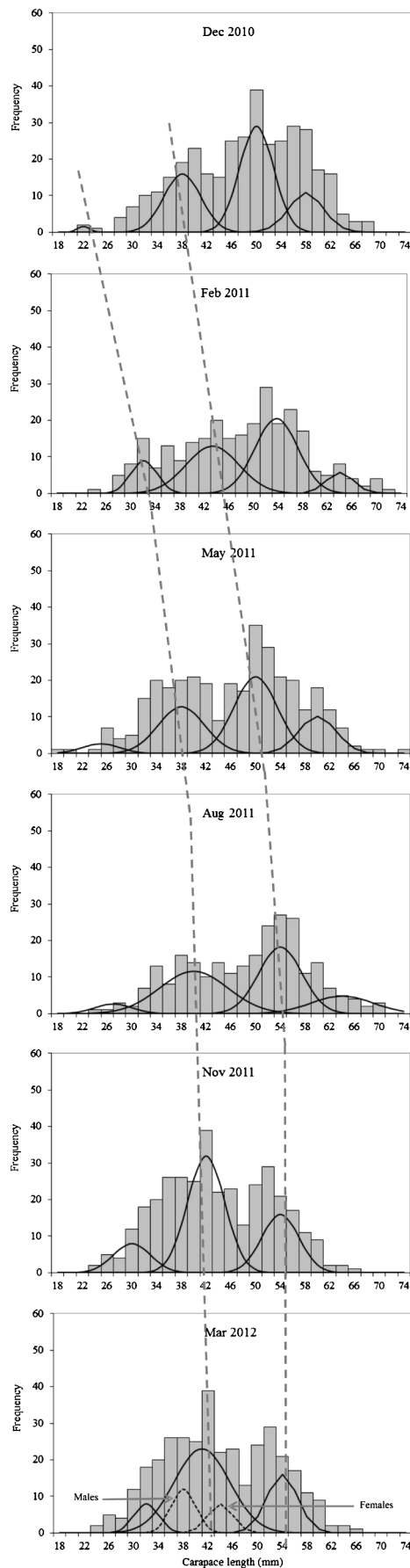
Fig. 10. Relationship between carapace length and whole weight of *M. mozambicus* males and females, respectively.

ing to 64 mm before dissipating. Two modes were used to fit the von Bertalanffy growth model (VB) as they best represented the data and could easily be distinguished from the others. The estimates of L_{∞} and K (\pm S.E.) obtained in the weighted non-linear fit of the VB growth model were relatively precise and invariable between cohorts ($L_{\infty} = 65.5 \pm 4.4$ mm CL; $K = 0.7 \pm 0.1$ year $^{-1}$; Fig. 12). Season-averaged growth curves suggested a life span of approximately 3–4 years, which could explain the dissipation of the largest sizes in the modal progression analysis.

DISCUSSION

Metanephrops mozambicus were most abundant at depths of 300 to 599 m, from June to December and between 1993–1995 and 2009–2010. These findings were based on commercial trawl catch rates and on the assumption that catch was proportional to fishing effort. The latter assumption is not always true, however, because natural fluctuations (population abundance, distribution, structure and behaviour) and changes in fishing strategy (time, location and depth of fishing activities, gear-effects, targeting practices) can affect the relationship between catch and effort. Nevertheless, the GLM framework used in this study is appropriate for partitioning variability in catch rates of fisheries data (Maunder and Punt, 2004). Given the large volume of data available, we are confident that the analyses and interpretations presented realistically capture the abundance patterns of langoustines on the trawl grounds.

Individual fishing vessels were incorporated into the models to correct for differences in fishing power. However, the vessel effect could not be separated into components which may individually, or over different time scales, have increased the efficiency of trawling. Advances in trawl net design, electronic navigational systems, increasing skipper experience and improved targeting practices over time (1988–2010) may all have contributed to more efficient trawling, thus biasing catch rates (see Robins et al., 1998; Lynch and Garvey, 2005). This may in part explain the gradual increases in catch rates in the early 1990s and after 2002. Data on technological improvements and skipper experience were largely unavailable for the present study, and additional modelling would be required to fully assess their impact on abundance estimates.



The negative correlation between fishing effort and catch rate furthermore suggests that abundance of langoustines on fishing grounds increase when fishing effort is reduced over time, or that effort saturation (defined here as competition for space by fishing trawlers on a fishing ground of limited size) have been reduced by vessels moving out of the area (see Groeneveld et al., 2003). The latter hypothesis supposes that too many trawlers on the fishing ground at any one time would lead to repetitive fishing of the same trawl lanes, despite decreasing catches, because of competition for space. We could, however, not isolate and compare the effects of technological advances versus reduced fishing effort on the increase in catch rates after 2002, and suggest that a combination of factors may have given rise to the fluctuations in the inter-annual abundance trend.

Both nominal and standardized catch rates indicated that *M. mozambicus* were more abundant at 300 to 399 m and 500 to 599 m depths and less abundant at the intermediate 400-499 m depth. Groeneveld and Melville-Smith (1995) found a similar distribution pattern and Berry (1969) suggested that abundance peaked at 350-400 m, based on research trawls preceding commercial trawling. Most commercial trawling takes place between 400 and 499 m (see Fig. 2), where a mix of deep-water prawns and langoustines occur (Groeneveld and Melville-Smith, 1995). The lower langoustine abundance between 400 and 499 m depth, compared to shallower and deeper strata, may be caused by a local depletion of langoustines at this depth, or by high sediment disturbance caused by frequent trawling. These factors are thought to influence the catchability of *Nephrops norvegicus* Linnaeus, 1758 in the northwestern Mediterranean Sea (Maynou and Sardà, 2001). The local depletion hypothesis presumes that langoustines undertake few benthic movements and that immigration into recently fished areas occurs at a slow rate. Tagging of *M. challengerii* produced low returns over small spatial scales, consistent with limited adult movements (Cryer and Stotter, 1999; Tuck et al., 2009). A combination of fishing strategy, disturbance and limited movements might therefore explain the observed abundance pattern between 300 and 599 m depth in *M. mozambicus*.

Seasonal patterns in catch rates and sex ratios in populations of *Metanephrops* have previously been related to patterns of moulting (Bell et al., 2013). As in *N. norvegicus*, *M. mozambicus* may remain sheltered in their burrows while moulting, thus reducing their availability to trawling gear. In the present study, lower catch rates between January and April, compared to the second half of the year, suggest that most moulting took place then. Berry (1969) found that mature male *M. mozambicus* moulted in December to February, while immature males moulted throughout the year, but with a major peak in March (Table 3). Immature females also moulted predominantly in March, with several smaller peaks in other months. Mature females moulted in May to July, al-

Fig. 11. Monthly modal peaks of *M. mozambicus* from deep-water trawl catches off eastern South Africa. Dotted lines intersect the monthly cohort means used to fit the von Bertalanffy growth function (VB) and solid lines indicate the standard deviation and proportion of each cohort by month, over the 6 months sampled. March had two peaks caused by a variation in the size-frequencies of males and females (separately); the mean of these two peaks was used in the VB growth function.

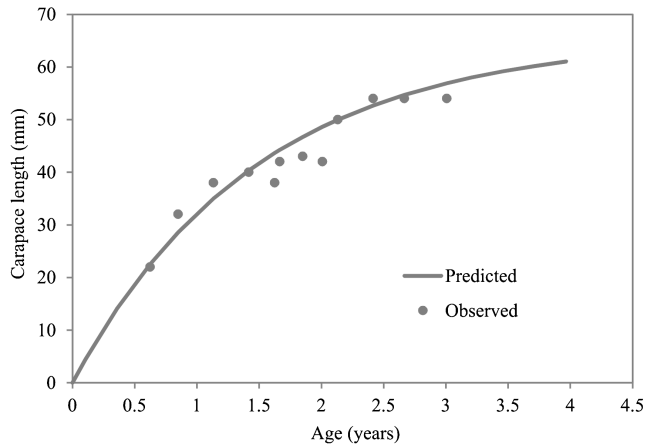


Fig. 12. The von Bertalanffy growth curve for *M. mozambicus* (sexes combined) sampled from deep-water trawl catches off eastern South Africa.

though the percentage of moulting remained low. The lower catch rates during the first four months of the year therefore coincides broadly with the moulting season of *M. mozambicus* as described by Berry (1969), especially for all males and immature females.

Catch rates of *N. norvegicus* are affected by biological rhythms, with emergence patterns strongly linked to diel cycles and environmental drivers (Aguzzi et al., 2003; Aguzzi and Sardà, 2008; Aguzzi and Bahamon, 2009), and these patterns may bias abundance estimates (Sardà and Aguzzi, 2012). Diel activity rhythms have also been shown for some *Metanephrops*: *M. australiensis* catchability peaked near dusk and dawn, and female catch rates were more variable than males (Ward and Davis, 1987); *M. binghami* were active during the night, but burrowed during daylight hours (Paramo and Saint Paul, 2012); but no pattern could be discerned in *M. andamanicus* (Ward and Davis, 1987). We did not include day/night variations in catch rates in the GLM in the present study, because individual trawls were of long duration (4.2 ± 1.2 h), and often included day and night in a single tow. Assuming that trawlers operated in a similar way throughout the study period, it is unlikely that the omission of a day/night variable in the GLM would have affected standardized catch rates by depth, month or year. Nevertheless, the effect of emergence patterns on *M. mozambicus* abundance estimates is presently being investigated in another study.

The percentage of egg-bearing females in samples declined after March, reaching its lowest ebb in August. This downwards trend corresponded with the May to July moulting

season for mature females proposed by Berry (1969). Egg-bearing increased after August, reaching a peak in December. Berry (1969) found that few females bore eggs in July, but that the incidence of egg-bearing increased thereafter and remained at above 85% of mature females between October and March. Egg-stage frequencies further confirmed the August to March breeding period; most eggs were in stage 1 in August, and in stages 3 and 4, about to hatch, in May. Whereas our results of the synchronization between moulting and egg-bearing of females are similar to those proposed by Berry (1969), the egg-bearing probabilities were much lower. This was presumably an artefact of analysis methods – we used all sampled females, whereas Berry (1969) restricted the analysis to females $> L_{50}$ (48 mm CL). Restricting our analysis to females $> L_{50}$ (i.e., >49.3 mm) resulted in comparable egg-bearing incidence of up to 80% in December.

The moulting season could not be substantiated by sex ratios of catches, which remained close to parity, except in November, when more males were caught. Perhaps males moved around and fed more actively shortly before the onset of moulting in December and were therefore more available to trawl nets. This pattern has previously been shown for crabs and spiny lobsters (Lipcius and Herrnkind, 1982; O'Halloran and O'Dor, 1988). Alternatively, the skewed sex ratio in November may be as a result of ovigerous females hiding in burrows during the peak reproductive season, although this behaviour does not seem to be as common in *Metanephrops*, as in *N. norvegicus*. Interestingly, Berry (1969) found more females than males in catches during most months, except October, giving some support to our finding of higher male availability during November.

Small *M. mozambicus* were under-represented in catches, suggesting a lower catchability than for larger individuals. Berry (1969) observed a similar trend, suggesting that few small individuals were captured in trawls, because they moulted more frequently than larger individuals, therefore remaining in their burrows for longer periods. The size of *M. mozambicus* caught in our study ranged from 17 to 73 mm CL, similar to the 16 to 72 mm reported by Berry (1969). The largest size class therefore remains present in the population, despite regular trawl fishing over the intervening 4 decades. The size of *M. mozambicus* appears to be somewhat larger than other species of *Metanephrops*, such as *M. binghami* in the Caribbean Sea (15–57 mm; Paramo and Saint-Paul, 2011), *M. thomsoni* in the East China Sea (12–42 mm; Choi et al., 2008), and *M. challengerii* in New Zealand waters (Tuck and Dunn, 2012; Tuck, 2013).

Table 3. Seasonal correlation and synchrony of moulting and reproduction in *M. mozambicus*, considering maturity status and sex of specimens. The lowercase x-symbols indicate the months over which the activity was recorded by Berry (1969), with # indicating aspects that could be confirmed by the present study. Peak activity in capital X-symbols.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Mature male moult	x#	x#	x#									x
Mature female moult					x#	x#	x#					
Mating					x	x	x					
Spawning		#	#		x	x	x	X#	x	x	#	#
Hatching			x#	x	X#	x	x					

They are also larger than *N. norvegicus* caught in southern Portugal (18–59 mm CL; Fonseca et al., 2007) and northwest Mediterranean waters (12–58 mm; Maynou et al., 1998), but smaller than those from central and northern Portugal (up to 94.9 mm CL; Ayza et al., 2011). The smaller maximum size in some of these species may be because larger size classes have been fished down (Bell et al., 2013).

The L_{50} of female *M. mozambicus* was estimated as 49.4 mm CL, compared to 48 mm found by Berry (1969). Both studies relied on the presence of external eggs (ovigerous method) and this indicator often results in an overestimate of L_{50} (Redant, 1994). Using the same method, the L_{50} of *M. challengerii* in New Zealand ranged between 37.0 and 43.2 mm, depending on the geographical area sampled (Tuck and Dunn, 2012; Tuck, 2013). Estimates based on ovary staging were smaller in *M. challengerii* (29.7 mm; Tuck and Dunn, 2012) and in *M. binghami* (30.5 mm; Paramo and Saint-Paul, 2008). *N. norvegicus* in the northeast Atlantic and Mediterranean matured over a broad size range of 21.2 to 50.7 mm, depending on area sampled and method used (Bell et al., 2013). Growth rates and the onset of maturity in crustaceans are strongly influenced by the environment, and maturity is generally age rather than size dependent (Wahle and Fogarty, 2006). Variation in individual growth rates of *M. mozambicus*, combined with the ovigerous estimation method used, may therefore explain the difference between the L_{50} (49.4 mm) and the smallest egg-bearing female recorded (33.5 mm).

Our study showed multiple cohorts (modes) in the sampled population, similar to size frequency distributions shown for other *Metanephrops* (Cryer et al., 2005; Choi et al., 2008; Paramo and Saint-Paul, 2011). In the absence of direct information on absolute age (generally unavailable for crustaceans; Wahle and Fogarty, 2006), the progression of cohorts over time was used to fit a continuous von Bertalanffy growth model, without seasonal effects. Although often used to approximate crustacean growth, it does not recreate a discontinuous (step-wise) growth pattern, as in moult process models. These models explicitly model individual growth increments and intermoult duration (or moult probability) (Wahle and Fogarty, 2006). These variables can only be obtained from in situ tagging and aquarium experiments, and were not available for the present study. Our estimates of L_{∞} (65.5 mm) and K (0.7 year^{-1}), based on length-frequency analysis, suggest a life span of 3–4 years. These estimates remain broad approximations, but they are nevertheless useful for stock assessments. Estimates of longevity, L_{∞} and K can vary widely within a species, depending on geographical sampling area. For example, L_{∞} in *N. norvegicus* may range from 45.5 to 94.9 mm, and K from 0.16 to 0.41 year^{-1} (Bell et al., 2013). It is therefore not unlikely that our estimates for *M. mozambicus* will vary over time and space.

To conclude, our study is the first to address abundance trends and biology of *M. mozambicus* in eastern South Africa and the first published account for this species from the western Indian Ocean region since Berry (1969). By combining long term data from commercial logbooks and biological samples, it was possible to recreate spatio-temporal abundance trends, and confirm reproductive and moulting

seasons and synchrony (see Berry, 1969). Comparisons with *Metanephrops* fished in other parts of the world, and with *N. norvegicus*, showed broadly similar life history, growth rates, and population structure.

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