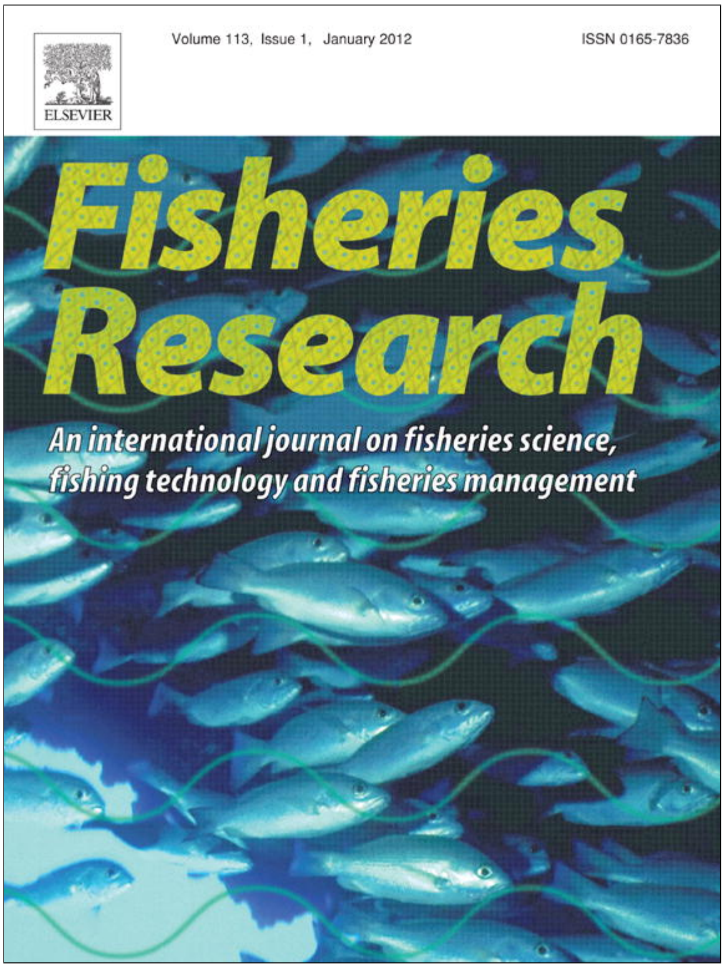
Volume 113, Issue 1, January 2012
ISSN 0165-7836
ELSEVIER
Fisheries Research
An international journal on fisheries science, fishing technology and fisheries management

Fisheries Research 125–126 (2012) 190–197

Contents lists available at SciVerse ScienceDirect

Fisheries Research

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

The reproductive cycle of *Octopus cyanea* in southwest Madagascar and implications for fisheries management

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ARTICLE INFO

Article history:
Received 25 August 2011
Received in revised form 21 February 2012
Accepted 22 February 2012

Keywords:
Octopus cyanea
Fisheries management
Reproductive cycle
Recruitment
Depth-refuge
Southwest Madagascar

ABSTRACT

The *Octopus cyanea* fishery is the most economically important fishery in southwest Madagascar. Growing concerns over the sustainability of exploitation have promoted a number of conservation efforts to improve management of the fishery. We analyse one year of catch data to identify seasonal variations in sexual maturity and key reproductive periods of the species, using microscopic analysis of gonad tissues to validate field assessments of maturity. Data show seasonal variability in maturity and size at first maturity for both sexes, as well as temporal changes in the sex ratio of the species. Maturity occurred at a minimum mean weight of 2246 g for females and 643 g for males. A clear relationship between gonad weight and total weight in male octopus indicates that total weight can be used as a proxy for sexual maturity in males. Conversely, females show high variability in weight at first maturity and no clear relationship between total weight and maturity stage. Fully sexually mature females were very rare, constituting less than 1% of the total sample. We hypothesise that the artisanal fishery may not be currently exploiting mature female individuals because females retreat to deeper waters prior to reproduction, thus remaining beyond the reach of the fishery. An abundance of juvenile individuals in the catch from June, and again from October to November, indicates recruitment peaks at these two times. In recent years, management of this species in southwest Madagascar has focused on short-term closures to fishing within specific tidal reef flat areas. Identification of the key phases of the reproductive cycle of *O. cyanea* in southwest Madagascar may provide managers with biological evidence to support seasonal closures designed to protect key life stages of the species.

1. Introduction

The reef octopus *Octopus cyanea* is thought to be the most common octopus species on reefs worldwide and is the dominant octopus in many coral reef habitats in the Indian Ocean region (Van Heukelem, 1983; Roper and Hochberg, 1988). However despite its abundance, research into the biology of the species has been limited to a few key studies (Guard and Mgaya, 2002; Van Heukelem, 1973, 1983; Caverivière, 2006). The species is of considerable commercial value to artisanal fisheries in coastal East Africa and Western Indian Ocean island states, where catches are generally sold through a network of collectors to reach national and international export markets (L'Haridon, 2006), and there are few alternatives to marine resource extraction, as the arid climate prevents any form of large-scale agriculture.

Exploitation of octopus stocks has increased rapidly since 2003 as a result of expanding commercialisation of Madagascar's octopus fishery, responsible for 60–70% of the value of marine resources purchased by collection and export companies in southwest Madagascar (L'Haridon, 2006). In recent years local communities have expressed concerns about the over-exploitation of octopus stocks and associated direct reef damage, both of which threaten the traditional livelihoods of the local *Vezo* communities that inhabit the southwest coast of Madagascar (Langley, 2006; Epps, 2007; Astuti, 1995). Fishing pressure is depth-limited by the nature of the gleaning and spear fishing techniques and octopus are generally only exploited on reef flats in shallow intertidal and subtidal zones.

Effectively managing the fishery requires a thorough understanding of *O. cyanea* reproductive biology so that management measures can be targeted at key periods in the life cycle to enhance effectiveness. In particular, temporary closures of individual fishing sites have been trialled in southwest Madagascar since 2004 and are timed to coincide with theoretical recruitment and spawning peaks. To date, the timings of these closures have largely been based on anecdotal reports from fishers and scientific theories. Quantitative data to support the timing of these closures will greatly contribute to continued management of the fishery.

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doi:10.1016/j.fishres.2012.02.025

O. cyanea are dioeceous and females lay between 150,000 and 700,000 eggs in a single clutch (Caverivière, 2006; Van Heukelem, 1973). Mature female individuals often migrate from shallow reef flats into deeper subtidal areas for spawning (Oosthuizen and Smale, 2003; Smale and Buchan, 1981; Whitaker et al., 1991). Upon hatching, planktonic larvae move into the water column for one to two months, and dispersal is thought to be wide ranging with larvae travelling up to several hundred kilometres in ocean currents (Murphy et al., 2002; Casu et al., 2002). Thus it is likely that spawning females contribute to the maintenance and replenishment of stocks at a regional level, not simply in the vicinity of the spawning locality. Prior studies of the reproductive cycle of *O. cyanea* in the Indian Ocean are limited. Reproduction of *O. cyanea* has been documented to occur throughout the year in both Tanzania and Madagascar with reproductive peaks in June and December (Guard and Mgaya, 2002; Caverivière, 2006) suggesting this species utilises an intermittent spawning strategy occurring over an extended period of time as described by Rocha et al. (2001).

This study presents data from 12 months of monitoring patterns of sexual maturity and recruitment of *O. cyanea* from fishery landings in southwest Madagascar to provide insight into the reproductive patterns of the species in this region, with a view to advising managers on recommending timings for temporary fishery closures.

2. Materials and methods

2.1. Study area

The study area is located in the Mozambique Channel on the southwest coast of Madagascar, approximately 200 km north of the regional city of Toliara (Fig. 1). Octopus catch data originates from fishers in villages along approximate 30 km of coastline – from Ampasilava in the south to Andragnombala in the north (Fig. 1). Within this region, octopus fishers predominantly target the reef flat along the nearshore fringing reefs, the shallow lagoonal reef flats and the offshore barrier reefs. Fishers sell their catches to one of a number of buyers representing seafood collection companies.

2.2. Sampling methods

Sampling was conducted from February 2005 to February 2006 in the village of Andavadoaka. Data were collected every day that octopuses were landed in the village, and fishers surveyed were selected through haphazard, convenience sampling by community data collectors when they arrived at the landing collection point. It was not possible to sample all octopuses caught by all fishers. Within 2 h of landing the following information was recorded for each sampled octopus: octopus weight (including gonads), weight and length of extracted gonads, octopus sex, and in-field visual assessment of gonad maturity. For a randomly selected subset of individuals, total octopus length and dorsal mantle length were recorded for one day per spring tide.

Octopus weight was measured using a spring balance graduated in 50 g intervals to a maximum of 4 kg, and gonad weight was measured using an electronic scale accurate to 1 g. Sex was determined by identification of the heterocotylus and spermatophoric groove on the third right arm of males (Mangold, 1983b). Gonad length, total octopus length and dorsal mantle length were measured using a 1 mm graduated tape measure. Gonad maturity was assessed through observation of the maximum size and colour of the gonads for both sexes, the presence of a white border at the beginning of the oviduct glands in females, and the appearance of spermatophores in males (Table 1). Gonads were extracted prior

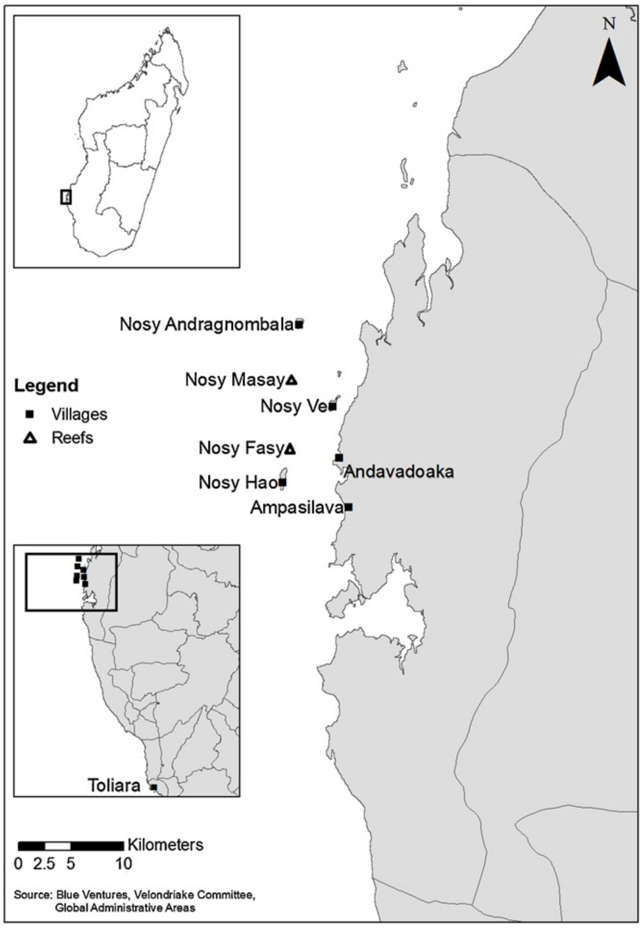

Fig. 1. Regional map and local area map showing study location, villages and reef areas.

to recording of measurements and fishers, who sell individuals per unit wet weight of catch, were given a small fee to compensate for the reduction in total weight.

For the randomly selected subset, gonad samples were prepared for secondary laboratory assessment using Bouin solution, and treated with 70% alcohol solution to remove residual stain. Samples were viewed using a microscope at 100× magnification, to determine number, arrangement and diameter of spermatophores for males, and the maximum diameter and length of oocytes for

Table 1
Maturity indices for male and female *Octopus cyanea*.

Maturity stage		Identification	
		Gonad mass	Gonad appearance
Males			
I	Immature	<2 g	<8 spermatophores in Needhams' complex
II	Pre-maturation	2–5 g	Spermatophores are disordered and number 8–208
III	Mature	>5–47 g	Spermatophores arranged in parallel and number 18–687
Females			
I	Immature	<3 g	Ovary white
II	Incipient maturity	3–7 g	Ovary white/pale yellow
III	Mature	8–80 g	Ovary pale yellow/yellow
IV	Fully Mature	>80 g	Ovary yellow/dark yellow
V	Post Laying	4–16 g	Distended empty ovary

After Mangold (1983a), Khallahi (2001) and Guard and Mgaya (2002).

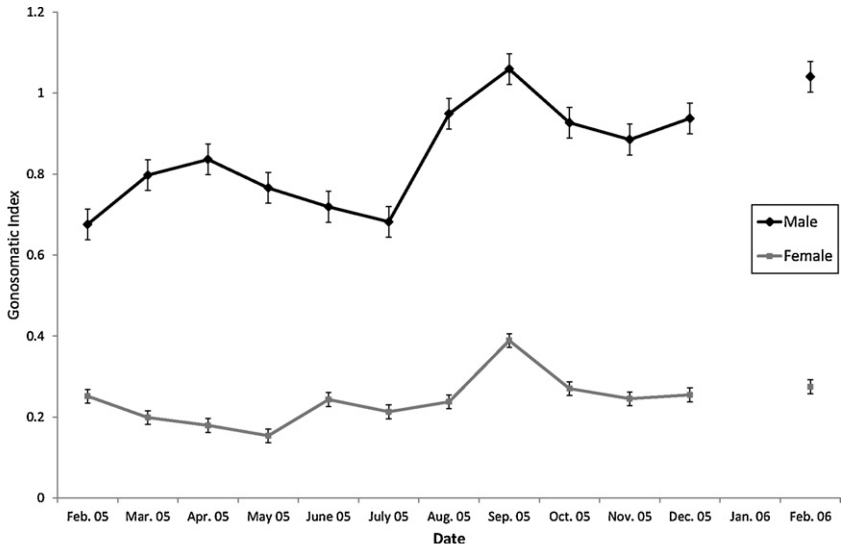

Fig. 2. Monthly gonosomatic index for field sampled *O. cyanea*. Error bars represent standard error around the monthly mean.

females, using an ocular micrometre. These measurements were used to determine gonad maturity stage based on the characteristics described in Table 1.

No data were available for January 2006 due to the regional closure of the octopus fishery from 15th December to 1st February, thus the results from February 2006 may not reflect the expected seasonal fluctuations in octopus if fishing pressure had been maintained during that period. Data for February 2005 were removed for these analyses, because a low sample size reduced the statistical power of these data.

Data were collected from a total of 3253 octopuses (1578 female, 1675 male) over the study period, gathered from catches derived from 738 fishers and 28 fishing sites. Total octopus and dorsal mantle length were measured for a sub-sample of 812 (532 male, 280 female) and a further 131 (68 female, 63 male) octopuses were randomly selected for laboratory analysis. All field-sampled octopuses were re-assigned a maturity stage based on the laboratory confirmation drawn from the subsample.

2.3. Data analyses and calculation of sex ratio, biometric and life-history parameters

Sex ratios were calculated for each month and tested for significant fluctuations from the expected 50:50 ratio using Pearson's Chi Squared test.

Regression analyses were carried out on the random subset of the individuals selected for laboratory analysis to investigate biometric relationships between a variety of weight and length measurements, and to determine whether total weight or length may be used as a proxy for gonadal development. Linear regressions were run to compare total length (from head to the end of the longest arm) with dorsal mantle length, and total weight with gonad weight. Power regressions were run to compare total weight with total length and dorsal mantle length.

The mean weight at first sexual maturity was determined by using a generalised linear model for binary data (binomial likelihood with a logit link function) to plot individual octopus weight and percentage of the catch at maturity stage III (as observed through gonosomatic observation). The mean weight is that at which 50% of individuals sampled are mature according to this logistic fit.

Recruitment was calculated by recording the number of individual octopus caught per month weighing less than 200 g. Octopus of 100 g is generally considered to be newly recruited (Van Heukelem, 1983), but individuals this small were rarely captured using the fishing techniques employed in this region. Therefore for the purposes of this analysis octopus caught weighing less than 200 g were considered to be newly recruited, since the size difference between 100 and 200 g is represented by approximately 2 weeks of growth (Caverivière, 2006). Thus, the proportion of the monthly catch that was smaller than 200 g was considered a proxy for octopus recruitment to the reef.

In order to assess the sexual maturity of individuals in relation to gonad development, gonosomatic index (GSI) was calculated using the formula $GSI = Mo/(Mt - Mo) \times 100$, where Mo is the weight of the ovary and Mt is the total wet weight of the individual (Guard and Mgaya, 2002). Monthly variations in calculated gonosomatic indices were tested using a *t*-test and Kruskal–Wallis non parametric analysis.

Weight frequency distributions were plotted to show distribution of octopus weight by sex and differences in the mean were tested using Welch's *t*-test.

3. Results

Secondary laboratory assessments showed that in-field assessment of maturity was between 72–100% accurate for females and 48–100% for males, depending on maturity stage. Overall differences between in-field and laboratory maturity estimates were significant ($t = 1.69$, $df = 117$, $p = <0.05$). In-field assessment of maturity stages for both male and female individuals in stage I was 100% accurate (Table 2). For females accuracy remained high across two

Table 2
Comparison of the accuracy of assessment of maturity stage in field and in the laboratory.

Maturity stage	% correct in field (*n*)	% over estimated in field (*n*)	% under estimated in field (*n*)
Males			
I	100 (9)	0	n/a
II	48 (10)	52 (11)	0
III	88 (29)	n/a	0
Females			
I	100 (24)	0	n/a
II	84 (16)	16 (3)	0
III	72 (18)	n/a	8 (5)

n/a = not applicable.

Table 3
Biometric relationships for male and female *Octopus cyanea* (total length (TL), dorsal mantle length (DML), total weight (TW), gonad weight (GW)).

$f(x)M$	r^2	p	n	Equation
Male				
TL(DML)	0.78	0.000	523	$y = 7.2824x - 1.1975$ (linear)
TW(TL)	0.83	0.000	523	$y = 0.057x^{2.2052}$ (power)
TW(DML)	0.87	0.000	523	$y = 1.858x^{2.5745}$ (power)
TW(GW)	0.87	0.000	1675	$y = 78.275x + 185.01$ (linear)
Female				
TL(DML)	0.82	0.000	380	$y = 7.2756x - 0.6324$ (linear)
TW(TL)	0.87	0.000	380	$y = 0.0379x^{2.3004}$ (power)
TW(DML)	0.89	0.000	380	$y = 1.602x^{2.6364}$ (power)
TW(GW)	0.15	0.000	1578	$y = 14.422x + 770.52$ (linear)

further maturity stages. It was not possible to classify females as higher than stage III in the field. The maturity stage of males was frequently overestimated in in-field measurements, with males commonly classed as stage II when laboratory studies showed they were in fact stage I. It was not possible to underestimate stage I, or overestimate stage III individuals as these represent the lowest and highest stages which can be identified in the field, so these values are recorded as not applicable (n/a) (Table 2).

We found strong correlations between total length (TL), dorsal mantle length (DML) and total weight (TM) for both females and males (Table 3). Similarly, gonad weight (GM) in males was also strongly correlated to total weight ($r^2 = 0.87$). The relationship between total weight and gonad weight was very much weaker for females ($r^2 = 0.15$).

The gonosomatic index (GSI) generally showed very little variation throughout the study period for females (range = 0.23, variance = 0.004) with the exception of a distinct peak in September (Fig. 2). This peak was very slightly significant when compared with grouped samples from all other months ($t = 1.79$, $p = 0.04$). In contrast, the GSI for males varied more throughout the year (range = 0.38, variance = 0.017) and between month variation was statistically significant ($X^2 = 93.57$, df = 9, $p = <0.001$). A highly significant difference in male GSI was found between the first 5 months of the study (March–July) and the second 5 months (August–December) ($t = 9.62$, $p = <0.001$).

Sex ratio was not constant throughout the study period (Fig. 3, range = 25.85; variance = 55.70), and overall more males were recorded although this was not significant (51.5% male, 48.5% female; $X^2 = 3.43$, df = 1, $p = 0.1$). However, significant skews towards dominance by male individuals occurred in both March ($X^2 = 10.85$, df = 1, $p = <0.001$) and June ($X^2 = 8.57$, df = 1, $p = <0.005$).

Weight frequency analyses of male and female octopuses showed similar distributions (Fig. 4). The mean weight was fairly similar for both sexes, 805 g for males and 823 g for females, and the difference between the means was not significant ($t = 0.78$, df = 3212, $p = 0.4$). Octopuses were generally small with 95% of all octopuses ($n = 3095$) weighing less than 2 kg and 75% ($n = 2448$) less than 1 kg.

We observed large variation in the range of maturity found at a given size. The smallest stage III individuals observed weighed 400 g (male) and 450 g (female) and the largest weighed 6400 g and 5500 g respectively (Table 4). Average weight at first maturity is expressed as the weight at which 50% (M50) of sampled individuals were mature (stage III). Results of these field assessments of maturity suggest average weight at first maturity was 550 g for males and 2200 g for females (Fig. 5).

Maturity stage of males varied throughout the year with apparent peaks in May, August–September and February, although these were not significant (Fig. 6). No immature individuals were recorded in February 2006 following the opening of the national closure. The highest abundance of mature females (stages III and IV) was found between September and January (Fig. 7). Fully mature females (stage IV) were present during all months except April–May, but both fully mature and post-laying individuals were caught infrequently, representing only 0.95% of all females sampled.

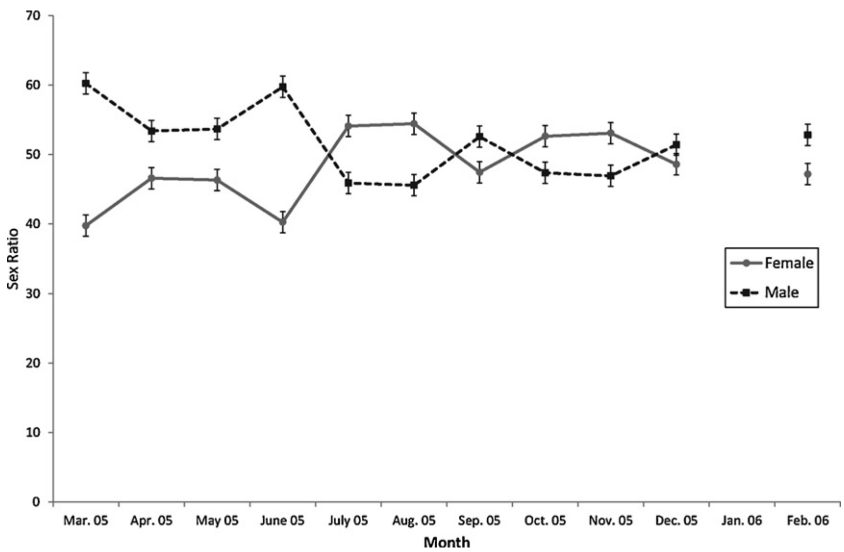

Fig. 3. Monthly sex ratio for sampled *O. Cyanea*. Error bars represent standard error around the monthly mean.

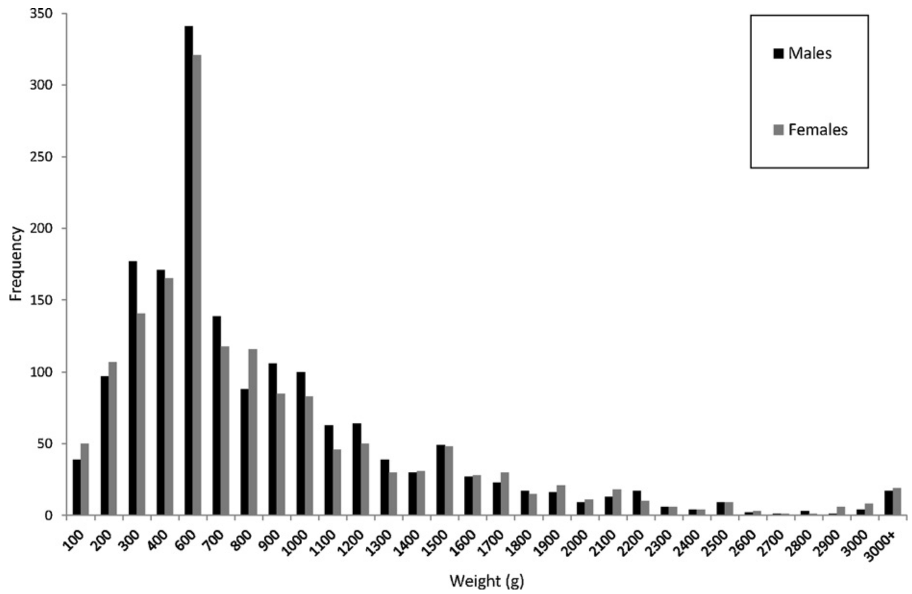

Fig. 4. Weight distributions for male and female octopuses sampled.

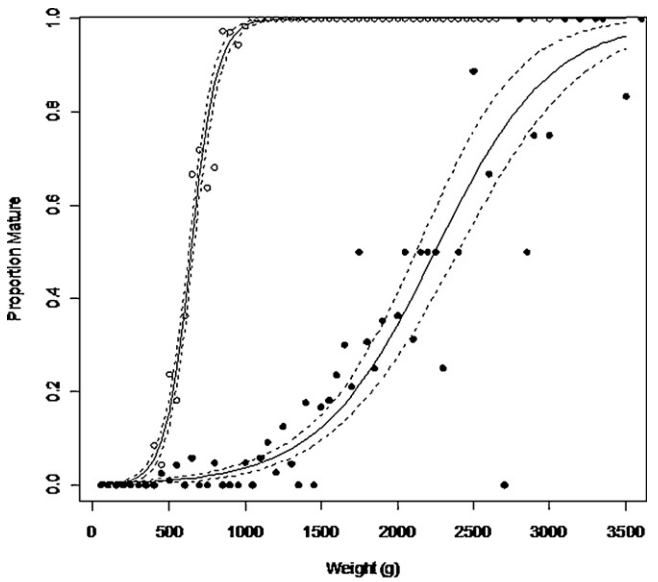

Fig. 5. Size of first maturity of stage III males and females (with a logistic curve to generate 50% data). Filled dots represent female distribution, open dots represent male distribution, horizontal dotted line represents 50% maturity, dashed lines either side of male and female curves represent variance. Vertical arrows represent weight at which 50% of individuals (M50) were at stage III maturity.

The results showed two significant peaks in recruitment, when a greater number of individuals weighing less than 200 g were caught (females: $t = 3.06$, $p = <0.005$; males: $t = 3.56$, $p = <0.005$) (Fig. 8).

4. Discussion

Although results showed a high error rate in field maturity assessments for male octopus, the majority of errors occurred in the classification of 'immature' and 'pre-mature'. Therefore this error is unlikely to greatly influence conclusions drawn regarding any seasonal variation in the relative abundance of 'mature' males (i.e. stage III) since field assessment of 'mature' octopuses was predominantly correct. This was supported by the high significance of all the biometric relationships for males, which further indicated that male maturity can be effectively estimated in the field through measuring weight.

Field assessment of female maturity was more accurate than males in general apart from the fact that stage IV and V individuals cannot be identified. The very weak correlation between total individual and gonad weight for females indicated that female sexual maturity cannot be reliably inferred from individual weight, and suggests that gonad sampling for microscopic analysis is the only certain way to accurately assess all stages of maturity in female individuals. This finding is consistent with other studies (Mangold, 1983a; Domain et al., 2000).

Table 4
Weight (g) of smallest and largest octopus from each maturity stage.

Sex	Stage I: immature	Stage II: incipient maturity	Stage III: mature	Stage IV: fully mature	Stage V: post laying
Female ($n = 1578$)					
Smallest	50	400	450	1800	1750
Largest	1350	3500	5500	5500	2800
Mean	1232	462	2053	3154	2350
n	490	976	97	12	3
Male ($n = 1675$)					
Smallest	50	300	400	n/a	n/a
Mean	400	1000	6400	n/a	n/a
Largest	499	232	1199	n/a	n/a
n	513	311	851	n/a	n/a

n/a = not applicable as males are only categorised into three stages.

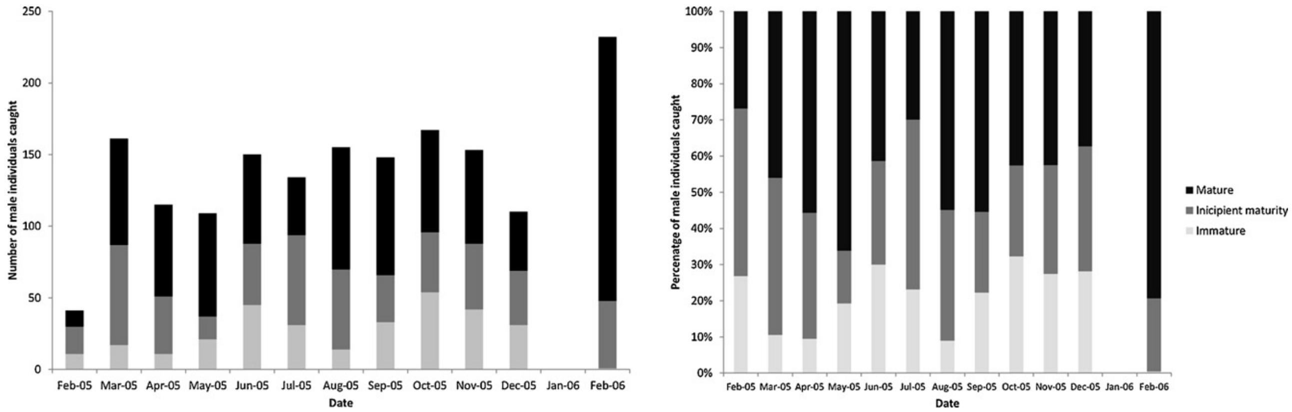

Fig. 6. Number and percentage change in sequential stages of maturity (assessed in the field) of male octopuses during the 12 months of sampling (total $n = 1677$). No individuals are recorded for January 2006 due to the fishery closure during this time.

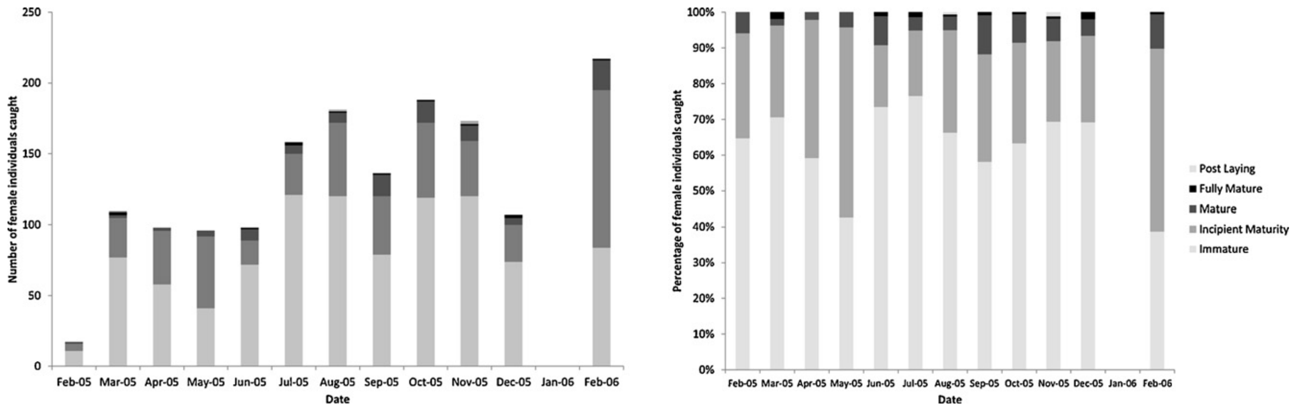

Fig. 7. Number and percentage of individuals at different stages of maturity (based on field observations, verified through laboratory subset) of female octopuses during the 12 months of sampling (total $n = 1581$).

We found that 50% maturity of male and female octopuses occurred at 643 g and 2246 g respectively. This is similar to findings for *O. vulgaris* in Spain (903 g and 1788 g; Otero et al., 2007) but much higher than previous research on *O. cyanea* in Tanzania (320 g and 600 g; Guard and Mgaya, 2002), indicating that the vast majority of female octopuses caught in Andavadoaka's artisanal fishery are likely to be immature. Just 8% ($n = 130$) of female individuals were heavier than 2246 g whereas 67% ($n = 1123$) of males caught were heavier than the 643 g average size at first maturity.

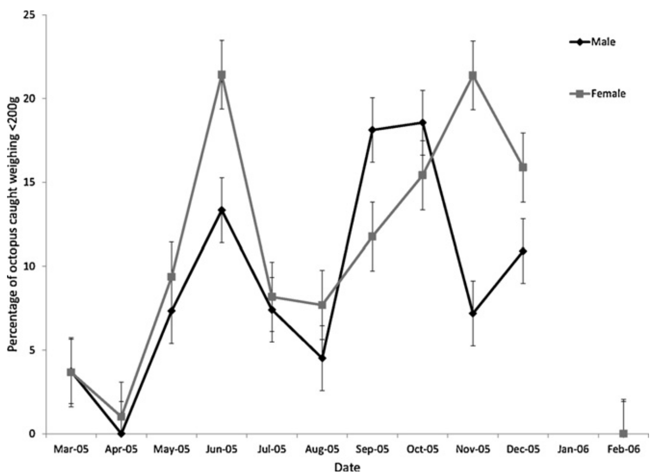

Fig. 8. Monthly variation in *O. cyanea* recruitment index (percentage of total catch <200 g, ±5% error around the monthly mean).

Maturity variance varied greatly between the male and female weight frequency distributions. Males were consistently mature by 643 g whereas the weight at maturity for females was much more variable indicating that total weight cannot be used as a proxy for maturity in female octopuses.

Stage III females were present throughout the study period, indicating that spawning may be occurring throughout the year. *O. cyanea* are known to be simultaneous terminal spawners (Van Heukelem, 1983) but we conclude that the timing of this spawning does not appear to correlate to a specific time of year as supported by previous reproductive studies for this species (Caverivière, 2006; Guard and Mgaya, 2002) but is likely related to a combination of environmental and biological factors including climate and habitat availability as shown in studies related to other octopus species (Leporati et al., 2007; Katsanevakis and Verriopoulos, 2004). However, minor peaks in the number of female stage III individuals caught during the year in June, September and October, and in stage IV individuals in both December and March may correspond to periods of increased reproductive effort and spawning. The small number of mature females observed in this study (only 8% of the 1581 females were stage III or above ($n = 128$), and just over 1% were stage IV or above ($n = 16$)) precludes any firm conclusions over possible seasonality of female spawning.

The apparent higher GSI in the second half of the year suggests that male octopus may be more sexually active between August and December, however extended research is required to assess whether this trend is repeated in subsequent years. Sex ratio remained relatively constant throughout the year with some expected variation around 50%. There was a consistent peak in male sex ratio between March and June, which coincided with the period of statistically significant reduced GSI for males, suggesting that during this period the fishery was dominated by juvenile males.

Assuming that seasonal spawning patterns drive the two observed recruitment peaks, the timing of the peaks may be used to calculate periods of maximum spawning. Peak spawning periods are documented for *O. vulgaris* in May and December in Greece (Katsanevakis and Verriopoulos, 2006), in April and May and between September and November in the Canary Islands (Hernandez-Garcia et al., 1998), in April and May in Spain (Otero et al., 2007) and in South Africa in July and December (Oosthuizen and Smale, 2003). A delay of between five and six months between peak spawning and recruiting periods would be expected, depending on growth rate caused by temperature and prey availability during the pelagic larval phase (Caverivière, 2006; Van Heukelem, 1973, 1983). The June recruitment period would therefore correlate with a January–February spawning event, and the September–October recruitment peak to spawning peaks between April and June. However, other forces such as seasonal patterns in mortality (natural death of octopus and larvae) or dispersal (natural currents) may also be driving the observed recruitment peaks (Boyle, 1990).

4.1. Implication of biological results to fisheries management

Our findings support previous studies showing that spawning occurs throughout the year in *O. cyanea* in southwest Madagascar (Caverivière, 2006) and show that intertidal fishing grounds are rarely home to large mature females. The scarcity of fully mature females in the sampled catch, despite consistently high levels of fishing effort throughout the year, is likely to be due to the depth-limited nature of the fishery in southwest Madagascar. Fishers are only able to exploit octopus residing on the shallow reef flats exposed at low tide, as well as shallow reef edges up to depths of approximately 5 m. One plausible cause of the on going recruitment of individuals to the fishery is that the fished individuals, caught only in shallow water habitats, have recruited from a brood stock of subtidal octopus protected from fishing by exploiting deeper habitats beyond the reach of fishers. This 'depth refuge' phenomenon is reported in a number of other octopus species (Oosthuizen and Smale, 2003; Sanchez and Obarti, 1993; Whitaker et al., 1991) and brooding female octopus are observed at depths of up to 85 m (Mangold and Boletzky, 1973).

This observation also raises caution over the introduction of deeper water fishing gears for the exploitation of *O. cyanea* in the region. Traps or pots are commonly employed to catch octopus in many other octopus fisheries (Jouffre et al., 2002), and this gear is often favoured over the use of spear fishing, as it allows fishers to target octopus in different habitats, and spend less time searching for individuals. The lack of damage inflicted on the mantle during landing from a trap fishery (as opposed to speared octopus) also results in a catch with a potentially higher export value making it an increasingly attractive method for local fishers. Although not currently practiced in Madagascar, the introduction of trap fishing techniques enabling fishers to exploit deeper waters could have ecologically detrimental impacts on the population, negatively impacting the species' apparent resilience to the current high level of shallow-water fishing effort. Any future development of deep water fishing techniques should be managed carefully to prevent over-exploitation of mature females prior to spawning as well as maintaining numbers of smaller individuals that will subsequently reach full maturity. Sampling of individuals from these deeper habitats is needed to confirm or refute this hypothesis.

Temporary closure periods were successfully trialled in southwest Madagascar in 2006 and recent findings show that they have positive fisheries and economic impacts (Benbow and Harris, 2011). Positive results are observed from octopus closures in other countries (Navarte et al., 2006; Fernandez-Rueda and Garcıa-Florez, 2007; Leite et al., 2009), and results from a study of the artisanal octopus fishery in Tanzania show that a traditional fishing regime which includes the rotation of fishing sites leads to enhanced biological effects on octopus size (Guard and Mgaya, 2002).

Given the short time frame of socially acceptable closure periods, it is important to consider the life cycle of the target species to gain maximum fisheries benefits from the closure. The identification of potential peaks in recruitment has important management implications for the fishery. In particular, identification of clear recruitment peaks indicates that the short term closure of a reef flat for a period of only a few months could significantly increase the average size of octopus caught at that particular site once a closed area is reopened, as well as increasing the catch per unit effort (Basson et al., 1996; Perry et al., 1999; Navarte et al., 2006; Leite et al., 2009). The slight recruitment peak observed in this study suggests that the most effective period to close reserves in order to produce a significant increase in the average octopus weight would be between June and August, opening in September, or September and October and opening in November.

Acknowledgements

The authors thank Copefrito SA, Murex International and the fishers of Andavadoaka for their cooperation during the data collection stages of this study. We thank James Anderson, Alasdair Harris, Frances Humber, Kirsten Oleson and Tom Oliver for constructive comments on previous drafts of this manuscript; and Paul Medley for help with the preparation of the generalised linear model used to generate Fig. 5. Thanks also go to Man Wai Rabenevanana, Edouard Mara, Guy Christian Ralijaona, Richard Rasolofonirina and Thierry Lavitra for their help in developing this study, which was funded by Blue Ventures Conservation.

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