Effect of Maternal Age on Fecundity in white stumpnose, *Rhabdosargus globiceps* (Pisces:Sparidae) and its implications for Fisheries Management.

By

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Submitted 19 February 2007

Submitted in partial fulfilment of the requirements for the degree of Masters of Science in Conservation Biology
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ABSTRACT

A basic assumption of fishery management is spawning stock biomass (SSB) is directly proportional to spawning potential with no demographic influences. To test this assumption, *Rhabdosargus globiceps* were sampled from Langebaan Lagoon, South Africa to assess maternal age and size effects on egg size and number. Egg size range did not differ with age, but the proportion of ripe eggs invested in was non-linearly positively related to age. Old *R. globiceps* females produce more ripe eggs per unit biomass than young females and consequently spawn a disproportionately greater amount of eggs. Age-related egg production was incorporated into a life-time egg production per recruit model and compared with the traditional spawner biomass per recruit model. The SBpR model overestimates the resilience of *R. globiceps* to exploitation. The magnitude of this overestimate was sensitive to the fishing mortality rate. This study suggests that large and old female *R. globiceps* are more important to recruitment than young and small females. Current management strategies require revision to make provision for maternal effects by protecting the age-structure of the population.

Key words: maternal effects, fecundity, egg size, spawner biomass per recruit ratios, egg production per recruit ratios.

INTRODUCTION

Marine fish show a variety of reproductive strategies spanning the entire range from r- to K-selection, but the majority tend towards r-selected life strategies (Heemstra & Heemstra, 2004). r-Selected fish invest energy in millions of tiny eggs which are fertilised externally, usually without parental care (Heemstra & Heemstra, 2004; Walsh *et al.*, 2006). This strategy is a form of hedge-betting against a spatially and temporally heterogeneous environment (Hunter, 1981; Houde, 2002; Berkeley *et al.*, 2004a).
A spawned egg is immediately vulnerable to mortality from a variety of sources, but the fitness of a larva is tested during the period when it is dependent on its endogenous food supply prior to locating an exogenous supply (Berkeley et al., 2004a; Kamler, 2005). Starvation mortality (SM) during this period is high, but is decreased by an abundant supply of yolk and an ability to locate food rapidly (Kamler, 2005). Mortality during all stages from spawning to maturation is estimated at greater than 99.9% (Houde, 2002). SM is thought to be a major contributor, and may cause strong fluctuations among year classes (Lasker, 1975). The ability of larvae to survive this initial SM period is termed the *intrinsic survival potential* (Kamler, 2005).

The size of the spawning stock determines the recruitment strength and determines future potential fisheries yield (harvested biomass). By regulating fishing mortality rates, fishery management aims to maintain a specific biomass of mature fish so that the reproductive output is sufficient to sustain the stock (Berkeley, 2006). Spawning stock biomass (SSB) is the conventional metric for determining spawning potential, based on the assumption that mass is directly proportional to fecundity with no demographic influences (Murawski et al., 2001). Further, the current management paradigm assumes that all eggs have equal intrinsic survival potential and that all fish contribute equally to the replacement of population losses (Berkeley et al., 2004a, Berkeley, 2006). Models based upon these assumptions are used to advise the implementation of catch restrictions.

Recently, a growing body of evidence suggests that these assumptions may underestimate the importance of individual variation in the recruitment process. It has been suggested that genetically effective population sizes ($N_e$) may be orders of magnitude smaller than previously thought. For example, the $N_e$ of the New Zealand Snapper, *Pagrus auratus* (Family: Sparidae), is estimated to be five orders of magnitude lower than the census population, implying that among the millions of individuals, there are only hundreds or thousands of effectively breeding individuals (Hauser et al., 2002). Low $N_e$ was also found in another member of the Sparidae family, the gilthead seabream *Sparus aurata* (Brown et al., 2005).
It is clear that not all individuals in the population are contributing equally to recruitment and maternal age and size effects could be a cause for reproductive bias (Hauser et al., 2002, Birkeland & Dayton, 2005). Firstly, older or larger females may produce exponentially greater number of eggs than younger or smaller females (Birkeland & Dayton, 2005; Kamler, 2005). Secondly, older or larger females may produce fitter eggs and larvae with a greater intrinsic survival potential (Trippel et al., 1997; Berkeley et al., 2004a; Kamler, 2005). Therefore, the phenotype of the mother may influence the fitness of her offspring. Intrinsic survival potential has been related to several attributes from the eggs and larvae and these attributes can be related to maternal effects (Eimum & Fleming, 1999; Kamler, 2005).

For example, there is a positive relationship between female size and egg diameter (Trippel et al., 1997; Berkeley et al., 2004a; Kamler, 2005) which affects larval viability (Marteinsdottir & Steinarsson, 1998). Empirical studies show that egg size positively influences larval size at hatching (Reznick, 1991; Roff, 1992; Eimum & Fleming, 1999, 2000), swimbladder presence at day 10 (Marteinsdottir & Steinarsson, 1998), endogenous oil globule size (Berkeley et al., 2004a), larval growth rate (Marteinsdottir & Steinarsson, 1998; Eimum & Fleming, 2000, Berkeley et al., 2004a), and timing of hatching (Eimum & Fleming, 1999). Older mothers have also demonstrated increased larval hatching success rates (Murawski et al., 2001), food consumption rate and conversion efficiency, vertebrate number and willingness to forage (Walsh et al., 2006). These traits are all linked to intrinsic survival potential (Eimum & Fleming, 2000; Berkeley et al., 2004a; Kamler, 2005) and are evident across a wide range of unrelated taxa, e.g. brown trout Salmo trutta (Eimum & Fleming, 1999, 2000); haddock Melanogrammus aegelfinus (Hislop, 1988), Atlantic cod Gadus morhua (Marteinsdottir & Steinarsson, 1998), blackrock fish Sebastes melanops (Berkeley et al., 2004a) and Atlantic silverside Menidia menidia (Walsh et al., 2006), suggesting a generality in maternal effects across species. However, these attributes act through a reaction norm i.e. the fitter offspring only show their real potential, and importance to recruitment, under stressful conditions (Mousseau & Fox, 1998; Eimum & Fleming, 1999).

The two aims of this study are to (1) quantify maternal age and size effects on fecundity and unfertilised egg diameter in white stumpnose Rhabdosargus globiceps
and (2) to use the results to explore the implications of maternal effects on fishery management by modifying the traditional spawning stock biomass per recruit model to include maternal effects on egg production. *R. globiceps* is a medium sized seabream that is endemic to southern Africa (Griffiths *et al.*, 2002). Over-fishing has caused the collapse of one *R. globiceps* population already (Griffiths *et al.*, 2002).

**MATERIALS AND METHODS**

**Study Area**
*R. globiceps* were sampled from Langebaan Lagoon which is situated on the West Coast of South Africa, and is open to the Atlantic Ocean at Saldhanha Bay (Shannon & Stander, 1977). One of the four discrete populations of *R. globiceps* occur in the Saldanha Bay-Langebaan system. Langebaan Lagoon is part of a marine protected area (MPA) which is partially closed to fishing. Fish were sampled in the exploited and protected area to get a full range of fish sizes.

**Analysis of age, morphometric relationships and reproductive cycle**
*R. globiceps* were caught every month by angling between January 2005 and December 2006. The fish were measured and dissected to yield the following information: total length, fork length, mass, sex, gonad stage (Table 1) and gonad mass. The gonadal somatic index (GSI) was calculated as the ratio of gonad mass to somatic fish mass. Sagittal otoliths were extracted, mounted in resin, sectioned and examined under a dissection microscope. Annual rings were counted and used as an estimate of fish age following the methods described by Griffiths *et al.*, (2002).

**Fish sampled for maternal effects**
To assess maternal effects it was necessary to get a wide range of sizes of females in spawning condition at the same time to minimise differences due to the phase of ovarian cycle. Study on *R. globiceps* on the south coast suggested a protracted spawning season from October to February (Griffiths *et al.*, 2002). In total, 16 female fish of ripe ovarian stage were examined. They were caught between the 17th October and 7th November. Once fish were caught they were put on ice immediately and then analysed as described above.
Ovaries were removed from the fish at the lumen and weighed on an electronic scale with an accuracy of 0.01 g. Stage 5 ovaries were chosen because females in this stage are ripe. Stage 6 fish were almost never seen and it is presumed that either this stage is short-lived or fish do not feed in this stage. Ovaries were immediately frozen at less than -20°C.

**Ovary samples for microscopic analysis**

The gravimetric method of counting was utilised (FAO, 1974). Sub-samples of 0.1 gram were removed from the anterior, middle and posterior regions of a randomly chosen frozen ovary lobe. The sub-samples were weighed on an electronic balance accurate to 1 mg.

Ovary sub-samples were immediately immersed in fresh water inside a closed tube and shaken vigorously to separate unfertilised oocytes (eggs) from ovarian tissue. Larger eggs separated very easily whereas the smaller eggs remained in the ovarian tissue and had to be teased apart. The separated eggs were then shaken into a suspension and divided into a partitioned Petri dish. The total number of eggs in each sub-sample was manually counted with a dissection microscope under x30 magnification. The mean number of eggs per sub-sample was then used to calculate total egg number:

\[
\text{Total}_{\text{Eggs}} = G \sum_{i=1}^{3} \frac{n_i}{g_i}
\]  

(Eq.1)

where \(n_i\) is the number of eggs in sub-sample \(i\), \(G\) is the total weight of the ovaries and \(g_i\) is the weight of sub-sample \(i\).

Only ripe eggs in an ovary are spawned in the current ovarian cycle. The total number of ripe eggs was computed as:

\[
\text{Ripe}_{\text{Eggs}} = (p_{re})(\text{Total}_{\text{Eggs}})
\]  

(Eq.2)
where $p_{re}$ is the proportion of ripe eggs in the sub-sample.

The first 200 eggs randomly encountered in each sub-sample had their diameter measured with a graticule, accurate to 0.026mm, under x40 magnification. Eggs were spherical.

**Statistical methods**

A number of measures were obtained for each fish, and these were used to test relationships between maternal phenotype as the independent variables (length, mass and age), and ovary condition as the dependent variables (egg size, egg number and ovary mass). All regressions were fitted with the least squares procedure (Zar, 1999). For linear and non-linear regressions the sum of squares was used to calculate the correlation coefficient ($r^2$) and the significance of the regression. Natural logarithms were used for all logarithm transformations. Where necessary, t-tests were used to test hypotheses concerning the slope of relationships (Zar, 1999). Fish mass is normally closely proportional to the cube of its length (FAO, 1974) and therefore the slope of relationships of gravimetric measurements against fish mass are normally closely proportional to the cube of the relationship with fish length. All statistics were performed in R (2006) unless otherwise stated.

**Per Recruit Models**

A per recruit model (Butterworth *et al.*, 1989) was used to investigate the influence of maternal effects on the life-time production of fish under different fishing mortality rates. Specifically, a conventional Spawner Biomass per Recruit model (SBpR) was compared to a new model, Egg Production per Recruit (EPPR). The former assumes that reproductive potential is directly proportional to spawner biomass, whereas the latter accounts for maternal effects on egg production.

The SBpR model for iteroparous annual spawning species (Murawski *et al.*, 2001) is:

$$\text{SBpR} = \sum_{t=0}^{\infty} N_t \cdot W_t \cdot m_t$$

(Eq.3)
where \( N_t \) is the number of females alive at age \( t \), \( W_t \) is the mean mass of a female at age \( t \), and \( m_t \) is the proportion of sexually mature females at age \( t \).

The number of fish surviving in year \( t \) is determined by:

\[
N_t = \begin{cases} 
Re^{-M} & \text{if } t \leq t_c \\
N_{t-1}e^{-M} & \text{if } t > t_c 
\end{cases}
\]  \hspace{1cm} (Eq.4)

where \( R \) is the number of fish at age 0 and is set to 1, \( M \) is the instantaneous natural mortality rate per year, \( F \) is the instantaneous fishing mortality rate per year and \( t_c \) is the age at first capture.

The life-time Egg Production per Recruit (EPpR) model is the same as SBpR, except that the biomass term is replaced by an age-related egg production term and is computed by:

\[
EPpR = \sum_{t=0}^{\infty} N_t \cdot E_t \cdot m_t
\]  \hspace{1cm} (Eq.5)

where \( E_t \) = mean number of ripe eggs in a fish at age \( t \).

The effects of fishing mortality on spawner biomass and egg production were expressed as the ratio of SBpR (or EPpR) under different instantaneous fishing mortality rates to the SBpR (or EPpR) in the absence of fishing mortality (\( F = 0 \)). These indices are termed the per Recruit Ratios i.e. SBpR ratio = \( SBpR_{(F+M)}/SBpR_{(M)} \). They indicate the extent to which different fishing mortality rates reduce the average life-time spawning potential of a recruit.

**Parameter values**

Fish length-at-age (\( L_t \)) was calculated by fitting the von Bertalanffy function to age vs. fork length (mm):
\[ L_t = L_\infty [1 - e^{-K(t-t_0)}] \]  
\text{(Eq.6)}

where \( L_\infty \) = theoretical asymptotic length (mm), \( K \) = fish growth rate per year and \( t_0 \) = age at zero length. The function is fitted using an iterative least squares procedure (Microsoft Excel solver routine).

\( M \) was calculated using an empirical relationship (Pauly, 1980):

\[ \ln M = -0.0066 - 0.279 \ln(L_\infty) + 0.6543 \ln(K) + 0.4634 \ln(T) \]  
\text{(Eq.7)}

where, \( T \) = mean water temperature.

\( W_t \) was calculated as a function of \( L_t \) and the parameters were estimated by fitting a ln-ln regression:

\[ W_t = aL_t^{b_0} \]  
\text{(Eq.8)}

\( E_t \) was calculated as a function of \( W_t \) and the parameters were estimated by fitting a ln-ln regression:

\[ E_t = aW_t^{b_0} \]  
\text{(Eq.9)}

\( m_t \) was estimated by fitting a 2 parameter logistic ogive to the fraction of mature fish (gonad stage 3-7) in 10 mm size classes (fork length) against the mid-value of the classes:

\[ pL = 1/(1 + \exp^{-(L-L_{50})/\delta}) \]  
\text{(Eq.10)}

where \( pL \) is the proportion of mature fish at size \( L \), \( L_{50} \) is the length-at-50\% maturity and \( \delta \) is the width of the ogive. Then the \( pL \) was used in conjunction with the von Bertalanffy growth function (Eq.6) to estimate \( m_t \).
The effect of varying F was modelled over a range of values from 0.1 y\(^{-1}\) to 1.0 y\(^{-1}\). Because of the large variability around the Pauly (1980) relationship, a sensitivity analysis was carried out by halving and doubling the M estimate (Eq.7).

**RESULTS**

**Sample description**
A total of 910 fish were measured and dissected for general morphometric analysis and description of the ovarian cycle for the period of January 2005 to December 2006. Otoliths from 840 fish were read successfully. Sizes ranged from 130 mm to 472 mm fork length and ages ranged from 1 to 14. Of these fish 16 were selected for microscopic ovarian measurements. The sizes of these fish ranged from 248 mm to 454 mm fork length and ranged from ages 2 to 13 (Table. 2).

The gonadal somatic index confirmed a protracted breeding season from October to February in the West Coast population (Fig. 1). Peaks were evident during October, December and February. The October peak is the most important and consistent, whereas the latter two were variable and did not correspond to a male peak (December) or involved less fish (February).

The logarithm of ovary mass of stage 5 females was linearly correlated with the logarithm of fork length and the logarithm of fish mass (Table. 3). With respect to fork length the slope of the relationship \(b_0\) exceeded 3.0 and with respect to mass the slope exceeded 1.0 (t-test: \(P < 0.05\)) (Table. 4), indicating hyper-allometric growth of ovaries.

**Maternal effects**
All sizes of fish produced the same range of egg sizes but in different proportions. The distributions changed from an asymmetrical bimodal distribution in young fish to a symmetrical bimodal distribution in older fish as the second peak became progressively stronger with fish size (Fig. 2). The same pattern held true for length
and mass. The median was chosen above the mean as a description of central
tendency because the median is robust to non-normal distributions, including bimodal
distributions presented in Fig. 2 (Zar, 1999). The modal size of egg present in the
ovary matrix was universally 0.13 mm which was an immature egg size. The largest
egg found was 0.98 mm and the smallest was 0.078 mm.

Median egg diameter had non-linear relationships against fork length, mass and age.
Quadratic relationships describe fork length, and mass (Fig. 3a) and (Table. 3) and
indicated an optimal fecundity around 391 mm fork length and 1411 g. Age explained
72% of the variation in median egg diameter when fitted with a von Bertalanffy
function (Fig. 3b).

**Spawning Fecundity**

A bimodal distribution of egg sizes in a stage 5 female fish suggests that the eggs in
the second peak are ripe (Bennett & Griffiths, 1986) signifying that the second peak
represents the batch of eggs that is about to be spawned (Fig. 2). The size of 0.5 mm
diameter represents the minimum diameter of a ripe egg that would be spawned in the
current sampling season across all fish sizes. In confirmation of this observation, eggs
of 0.5 mm and larger separated easily from the ovarian tissue indicating ripeness and
readiness to spawn. By contrast smaller eggs did not separate easily from the ovarian
tissue. Santer (*Cheimerius nufar*) of the family Sparidae also have an identical size
range of eggs as *R. globiceps*; their eggs are histologically ripe at 0.447 mm (Coetzee,
1978).

A significant linear relationship was revealed between the logarithm of ripe eggs and
the logarithm of fish mass (Fig. 4a; Table 3). A two-tailed t-test on the ln-ln
regression parameters found the relationship against fish mass to be significantly
different from a linear relationship ($b_0>1.0; \ P < 0.05$) (Table 4) showing that biomass
is not directly proportional to spawning potential. The relationship between ripe eggs
against fork length was significant (Table 3) but was not significantly different from
an isometric relationship ($b_0 = 3.0; \ P < 0.1$) (Table 4). Age explained 90% of the
variation in the number of ripe eggs when fitted with a von Bertalanffy function (Fig.
4b).
The highest spawning fecundity, 3,600,000 eggs, was present in the heaviest but second oldest fish. The lowest spawning fecundity, 590,000 eggs, was found in the third lightest fish but second youngest fish. There was no significant relationship between the number of ripe eggs per gram vs. fork length, mass or age (Table. 3).

**Per recruit model Parameters**

Parameter values used in the per recruit models are given in Table 5 and their estimations are described below.

The fitted von Bertalanffy function estimated the maximum fork length of *R. globiceps* as 456 mm and a growth rate of 0.22 y\(^{-1}\).

By the method described by Pauly (1980), the natural mortality rate of *R. globiceps* is estimated to be 0.246 per year when the mean water temperature in Langebaan Lagoon is 16 \(^\circ\)C.

The mass of a fish increases in an isometric fashion with fork length and is significantly described by a power relationship (Table. 3). The value of the regression slope was not significantly different from 3.0 (Table. 4).

The length-at-25%-maturity for female *R. globiceps* was 180 mm, length-at-50%-maturity was 223mm and length-at-100%-maturity was 280mm. The \(m_t\) values for ages 1, 2, 3 and 4 were 0.25, 0.50, 0.75 and 1.0 respectively (Table 5).

\(E_t\) values were based on the regression against mass rather than age because age was less reliably determined. Otolith readings are often imprecise due to the variation in birth date, and may be biased as well.

**Per recruit models**

The rate of loss of life-time egg production with increasing fishing mortality is greater than that predicted by SSB (Fig. 5). The absolute values do not differ greatly but the scale of the discrepancy becomes larger under high fishing mortality (at \(F = 0.1\) y\(^{-1}\), discrepancy was 4.8% whereas at \(F = 1.0\) y\(^{-1}\) the discrepancy was 31%) (Fig. 6).
These discrepancies were dependent on the values of M. Lower M values exacerbate discrepancies (Fig. 6).

Two biological reference points for F on an exploited population are referred to in fishery management: overexploited (40% of the unfished reproductive potential) and collapsed (25% of the unfished reproductive potential). The stock is considered overexploited when $F = 0.18 \text{ y}^{-1}$ and $F = 0.20 \text{ y}^{-1}$ for egg production and spawning biomass respectively (Table 6).

**DISCUSSION**

**Ovarian cycle**

*Rhabdosargus globiceps* is an r-strategist and batch spawner, spawning two to three times in the season between October and February. Ovaries that were examined came from fish caught in October, the main spawning month.

**Maternal effects**

The study demonstrated a strong correlation between maternal phenotype (age, mass and length) and ovary condition (egg size, egg number and ovary mass). Variation in the median egg size was not a reflection of differences in absolute egg size but a reflection of the changes in the proportion of ripe to immature eggs. Studies on other species infer an effect of egg and larval quality from egg size (Marteinsdottir & Steinarsson, 1998; Einum & Fleming, 1999, 2000), but *R. globiceps* females seem to invest more heavily in ripe egg quantity with age, rather than egg size, confirming their r-strategy.

A quadratic relationship was fitted to median egg diameter with mass and fork length, and the optimum mass and length for a reproductive female to produce the maximum number of ripe eggs was 1411 g and 391 mm respectively. The apparent decline in median egg diameter with large size is equivocal, as no such evidence was apparent in
the regression against age. It has been evident in three species of fresh water fish but is not present in other species studied. It was suggested that few of these species reach an age old enough to present these effects (Kamler, 2005). Greater sample size should resolve this discrepancy.

It can be predicted from the egg size frequency distributions that older female *R. globiceps* begin investing in the next batch earlier than young females. The next batch spawned by young females, after the October spawning peak, should contain even fewer eggs or may miss the second spawning thereby, explaining the greater variation and reduced GSI later in the season. The number of batches spawned by Atlantic cod *G. morhua* (Kjesbu *et al.*, 1996) and hake *Merluccius Merluccius* and *M. hubbsi* (Murua *et al.*, 1998; Macchi *et al.*, 2004 respectively) has been positively related to female age and size. Consequently the breeding season can be shorter for younger cod and hake females (Birkeland & Dayton, 2005).

**Spawning fecundity**

Spawning biomass is not directly proportional to spawning potential for *R. globiceps* nor a variety of other species such as cod *G. morhua* (Buzeta & Waiwood, 1982 as cited by Murawski *et al.*, 2001) and Icelandic summer-spawning herring *Clupea harengus* (Óskarsson & Taggart, 2006). Older *R. globiceps* females produce more ripe eggs per unit biomass than younger fish and consequently spawn a disproportionately greater amount of eggs. It takes more than 20 years for the age vs. egg production relationship to asymptote. The catch size limit for *R. globiceps* is 250 mm total length which corresponds to two years of age, from which it can be inferred that the proportion of females that attain maximum fecundity is vulnerable to depletion. The per recruit models suggest that traditional SSB metrics overestimate the spawning potential of the exploited *R. globiceps* stock. The discrepancy between the two models is not dramatic but increases in a logistic fashion with fishing mortality rate.

Fishing mortality rates on South African seabreams are typically estimated to be over 0.5 y⁻¹ but range from 0.2 y⁻¹ to over 1.0 y⁻¹ (Mann, 2000). In this range, SBpR models can overestimate spawning potential by between 9% to 31% respectively. The
EPpR model only includes one parameter for maternal effects on egg production because egg quality and intrinsic survival ability cannot be inferred for *R. globiceps* from ovarian egg size data without information on either nutritional content of eggs or their survivorship. Further maternal effects have been documented in another seabream, the black bream *Acanthopagrus butcheri*. Maternal age had a significant effect on larval growth rates of this species (Doupé & Lymbery, 2005).

Egg quality and larval survival data have been documented and modelled in other species. For example, in Atlantic cod *G. morhua*, the magnitude of the discrepancy between spawning biomass and age-related egg production models were similar to those found in *R. globiceps*. However, the discrepancy was larger when egg production was replaced with age-related larval viability (number of larvae surviving at day 10 with swimbladders for age t), suggesting that larval viability is more important to recruitment than egg production alone (Murawski *et al.*, 2001). The age at which improved reproductive capacity begins is also important to the magnitude of the discrepancies (O’Farrell *et al.*, 2006).

Continued size selective fishing of *R. globiceps* will indirectly select against positive reproductive traits because they are linked to size and age phenotype of mothers. Under current fishing pressure, which selects for large old fish, a survival advantage is created for small, slow growing fish. Thus there is directional selection towards slower growth and smaller size (Walsh *et al.*, 2006). Such a change in age structure would select for lower fecundity and possibly a shorter spawning season in *R. globiceps*. This effect has been termed the age truncation effect which causes a population to be vulnerable to collapse and variability in abundance through a reduced hedge-betting ability (Hsieh *et al.*, 2006).

**Management implications**

Under the current estimates of F = 0.5, *R. globiceps* can be classified as vulnerable to collapse regardless of which model is used. But to work towards sustainable management of *R. globiceps*, maternal age effects on egg production will need to be incorporated to more accurately assess the effects of fishing pressure on stocks and to
reduce the overestimation of stock resilience. Managing for age and size structure will improve the resilience of the stock (Murawski et al., 2001; Berkeley et al., 2004b; Hsieh et al., 2006). This can be achieved by increasing size limits but this is impractical as catch and release often damages fish and size limits are not effectively policed. No-take marine protected areas (MPA) are the most feasible strategy for maintaining age structure (Berkeley et al., 2004b). They create a refuge where proportions of a stock can be entirely protected from fishing pressure.

**Conclusions**

*R. globiceps* is an r-strategist, investing more energy into egg quantity rather than egg size. The presence of a maternal age reproductive bias towards older and larger females causes traditional spawning biomass models to overestimate the resilience of the populations because large females release more eggs than is predicted by their mass and current fishing pressure selects against large and old fish. A clear relationship has been found between *R. globiceps* ripe egg production and female size, mass and age. Further work should focus on maternal effects on the nutritional quality of eggs, the size of fertilised eggs, and survival rates in larvae. Maternal effects should also be assessed later in the spawning season (December and February). These studies may show that additional factors are required to further moderate the estimated resilience of r-strategists to intense fishing.

**ACKNOWLEDGEMENTS**

I owe the greatest gratitude to my supervisor at Marine and Coastal Management (MCM), Dr. Colin Attwood, for his support and enthusiasm throughout the entire time of the study and for granting access to morphological and ovarian data on *R. globiceps* caught between January 2005 and September 2006. Thank you to Lucinda Fairhurst for aging all of my fish. Also thank you to my supervisor at Dr. John Field at the University of Cape Town for his encouragement.
References


Table 1: Macroscopic gonad maturity stage criteria for *R. globiceps*

<table>
<thead>
<tr>
<th>Stage</th>
<th>Ovary</th>
<th>Testes</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Juvenile: Ovary appears as thin translucent/pinkish flaccid sacks</td>
<td>Testes are thin and threadlike</td>
</tr>
<tr>
<td>2</td>
<td>Immature resting: Translucent orange tubes, no eggs visible with naked eyes</td>
<td>Narrow and flat but larger than those in stage 1, beige in colour</td>
</tr>
<tr>
<td>3</td>
<td>Active: Eggs visible to naked eye as tiny granules in gelatinous orange matrix, little increase in diameter of ovary</td>
<td>Wider and triangular in cross section, no sperm in main duct</td>
</tr>
<tr>
<td>4</td>
<td>Developing: Gonad larger and orange/yellow in colour, eggs clearly discernable</td>
<td>Testes wider and deeper, pinky beige in colour, sperm present in main duct</td>
</tr>
<tr>
<td>5</td>
<td>Ripe: Ovaries are large in diameter, may be a few hydrated eggs, yellow eggs take up all the space</td>
<td>Testes creamy/white with sperm present in main duct and in tissue, gonad soft, breaking when lightly pinched</td>
</tr>
<tr>
<td>6</td>
<td>Ripe running: Large with substantial proportion of hydrated eggs, which may or may not fill the lumen</td>
<td>Free flowing sperm extruded from fish when the abdomen is lightly squeezed, testes very delicate and breaks easily when handled, sperm present in main duct and in tissue</td>
</tr>
<tr>
<td>7</td>
<td>Spent: Ovary reduced in size, similar to stage 2 flaccid, few yoked eggs remaining</td>
<td>Testes small and bloodshot, white in colour</td>
</tr>
</tbody>
</table>

Table 2: Morphometrics of *R. globiceps* maternal samples

<table>
<thead>
<tr>
<th>Fish</th>
<th>Mass (g)</th>
<th>Total Length (mm)</th>
<th>Fork Length (mm)</th>
<th>Age</th>
<th>Ovary Weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>343</td>
<td>278</td>
<td>248</td>
<td>2</td>
<td>14.6</td>
</tr>
<tr>
<td>2</td>
<td>329</td>
<td>280</td>
<td>250</td>
<td>3</td>
<td>17.7</td>
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<td>3</td>
<td>437</td>
<td>304</td>
<td>274</td>
<td>3</td>
<td>30.2</td>
</tr>
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<td>4</td>
<td>395</td>
<td>295</td>
<td>267</td>
<td>3</td>
<td>15.6</td>
</tr>
<tr>
<td>5</td>
<td>484</td>
<td>314</td>
<td>283</td>
<td>3</td>
<td>22.6</td>
</tr>
<tr>
<td>6</td>
<td>509</td>
<td>314</td>
<td>282</td>
<td>3</td>
<td>24.6</td>
</tr>
<tr>
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<td>408</td>
<td>300</td>
<td>279</td>
<td>3</td>
<td>19.7</td>
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<tr>
<td>8</td>
<td>526</td>
<td>330</td>
<td>290</td>
<td>4</td>
<td>23.5</td>
</tr>
<tr>
<td>9</td>
<td>561</td>
<td>332</td>
<td>309</td>
<td>4</td>
<td>27.8</td>
</tr>
<tr>
<td>10</td>
<td>809</td>
<td>388</td>
<td>345</td>
<td>4</td>
<td>40.1</td>
</tr>
<tr>
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<td>742</td>
<td>366</td>
<td>330</td>
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<tr>
<td>12</td>
<td>861</td>
<td>375</td>
<td>339</td>
<td>5</td>
<td>49.3</td>
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<tr>
<td>13</td>
<td>1271</td>
<td>427</td>
<td>383</td>
<td>6</td>
<td>65.0</td>
</tr>
<tr>
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<td>1618</td>
<td>482</td>
<td>439</td>
<td>9</td>
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<tr>
<td>15</td>
<td>2011</td>
<td>506</td>
<td>454</td>
<td>12</td>
<td>126.0</td>
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<tr>
<td>16</td>
<td>1651</td>
<td>488</td>
<td>434</td>
<td>13</td>
<td>82.0</td>
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</table>
Table 3. Results of linear and non-linear regressions of maternal effects in *R. globiceps*

<table>
<thead>
<tr>
<th>Dependent</th>
<th>Independent</th>
<th>Regression</th>
<th>a</th>
<th>b₀</th>
<th>b₁</th>
<th>n</th>
<th>r²</th>
<th>adjusted r²</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ovary Mass (g)</td>
<td>FL (mm)</td>
<td>Ln(y)= b₀Ln(x)+log(a)</td>
<td>-17.10</td>
<td>3.58</td>
<td></td>
<td>116</td>
<td>0.68</td>
<td>0.67</td>
<td>&lt; 2.2x10⁻¹⁶</td>
</tr>
<tr>
<td></td>
<td>Mass (g)</td>
<td>Ln(y)= b₀Ln(x)+log(a)</td>
<td>-4.46</td>
<td>1.22</td>
<td></td>
<td>115</td>
<td>0.68</td>
<td>0.67</td>
<td>&lt; 2.2x10⁻¹⁶</td>
</tr>
<tr>
<td>Median Egg Diameter</td>
<td>FL (mm)</td>
<td>y=ax²+b₀x+b₁</td>
<td>-1.31x10⁻⁵</td>
<td>1.03x10⁻²</td>
<td>-1.63</td>
<td>16</td>
<td>0.89</td>
<td>0.87</td>
<td>6.83x10⁻¹⁷</td>
</tr>
<tr>
<td>(mm³)</td>
<td>Mass (g)</td>
<td>y=ax²+b₀x+b₁</td>
<td>-2.48x10⁻⁷</td>
<td>6.65x10⁻⁴</td>
<td>-4.52x10⁻²</td>
<td>16</td>
<td>0.82</td>
<td>0.79</td>
<td>1.52x10⁻⁵</td>
</tr>
<tr>
<td>Ripe Eggs</td>
<td>FL (mm)</td>
<td>Ln(y)= b₀Ln(x)+log(a)</td>
<td>-8.37</td>
<td>3.70</td>
<td></td>
<td>16</td>
<td>0.88</td>
<td>0.87</td>
<td>9.22x10⁻⁶</td>
</tr>
<tr>
<td></td>
<td>Mass (g)</td>
<td>Ln(y)= b₀Ln(x)+log(a)</td>
<td>4.72</td>
<td>1.26</td>
<td></td>
<td>16</td>
<td>0.89</td>
<td>0.88</td>
<td>4.84x10⁻⁹</td>
</tr>
<tr>
<td>Ripe Eggs per gram</td>
<td>FL (mm)</td>
<td>y=ax+b₀</td>
<td>8.74</td>
<td>9382</td>
<td></td>
<td>16</td>
<td>0.03</td>
<td>-0.04</td>
<td>0.55</td>
</tr>
<tr>
<td></td>
<td>Age (years)</td>
<td>y=ax+b₀</td>
<td>171.20</td>
<td>11531</td>
<td></td>
<td>16</td>
<td>0.02</td>
<td>-0.05</td>
<td>0.56</td>
</tr>
<tr>
<td></td>
<td>Mass (g)</td>
<td>y=ax+b₀</td>
<td>8.92x10⁻⁵</td>
<td>1.15x10⁻⁶</td>
<td>16</td>
<td>0.02</td>
<td>-0.05</td>
<td>0.63</td>
<td></td>
</tr>
<tr>
<td>Fish Mass (g)</td>
<td>FL (mm)</td>
<td>Ln(y)= b₀Ln(x)+log(a)</td>
<td>1.50x10⁻²</td>
<td>3.01</td>
<td></td>
<td>898</td>
<td>0.98</td>
<td>0.98</td>
<td>&lt; 2.2x10⁻¹⁰</td>
</tr>
</tbody>
</table>

Table 4: Two tailed t-test results for testing linear relationships of ln-ln transformed regressions in *R. globiceps*

<table>
<thead>
<tr>
<th>Dependent</th>
<th>Independent</th>
<th>Slope</th>
<th>SE</th>
<th>Hypothesized slope</th>
<th>t-value</th>
<th>t0.05(2), (n-2)</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ovary Mass (g)</td>
<td>FL (mm)</td>
<td>3.58</td>
<td>0.23</td>
<td>3.0</td>
<td>2.48</td>
<td>1.98</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td></td>
<td>Mass (g)</td>
<td>1.22</td>
<td>0.08</td>
<td>1.0</td>
<td>2.74</td>
<td>1.98</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Ripe Eggs</td>
<td>FL (mm)</td>
<td>3.70</td>
<td>0.37</td>
<td>3.0</td>
<td>1.88</td>
<td>2.15</td>
<td>&gt;0.1</td>
</tr>
<tr>
<td></td>
<td>Mass (g)</td>
<td>1.26</td>
<td>0.12</td>
<td>1.0</td>
<td>2.16</td>
<td>2.15</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Fish Mass (g)</td>
<td>FL (mm)</td>
<td>3.01</td>
<td>0.02</td>
<td>3.0</td>
<td>0.78</td>
<td>1.96</td>
<td>&gt;0.20</td>
</tr>
</tbody>
</table>

SE= standard error
Table 5. Parameter estimates used in *R. globiceps* life-time contribution per recruit models

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Equation/value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length-at-Age (mm)</td>
<td>$L_t = 456 \left(1-e^{-0.22(t-1.3)}\right)$</td>
</tr>
<tr>
<td>Weight-at-Length (g)</td>
<td>$W_t = 0.2 \times 10^{-4} L_t^{3.01}$</td>
</tr>
<tr>
<td>Natural Mortality Rate ($y^{-1}$)</td>
<td>$0.246 = e^{-0.0066-0.279 \ln(456)+0.6543 \ln(0.22)+0.4634 \ln(16)}$</td>
</tr>
<tr>
<td>Proportion Mature-at-Age</td>
<td>$m_1 = 0.25$, $m_2 = 0.5$, $m_3 = 0.75$, $m_4$ and older = 1.0</td>
</tr>
<tr>
<td>Ripe Egg Number</td>
<td>$E_t = 113 W_t^{1.258}$</td>
</tr>
</tbody>
</table>

Table 6. Biological reference points for spawning biomass, egg production and instantaneous fishing mortality rate ($F$) for *R. globiceps*

<table>
<thead>
<tr>
<th>Reference Point</th>
<th>Spawning Stock Biomass</th>
<th>Ripe Egg Production</th>
</tr>
</thead>
<tbody>
<tr>
<td>25% of the unfished level</td>
<td>$F = 0.36 \ y^{-1}$</td>
<td>$F = 0.31 \ y^{-1}$</td>
</tr>
<tr>
<td>40% of the unfished level</td>
<td>$F = 0.20 \ y^{-1}$</td>
<td>$F = 0.18 \ y^{-1}$</td>
</tr>
<tr>
<td>$F = 0.1 \ y^{-1}$</td>
<td>59% of pristine</td>
<td>56% of pristine</td>
</tr>
</tbody>
</table>
Fig. 1: Gonal Somatic Index changes over time for male and female *R. globiceps* with standard error bars.
Fig. 2: Egg diameter frequency histograms for *R. globiceps* from stage 5 ovaries.
Fig. 3: Median egg diameter versus: (a) fork length (mm) of $R.\ globiceps$ fitted with a quadratic regression ($\text{adjusted } r^2 = 0.79; P = 1.5\times10^{-5}$), and (b) fish age fitted with a von Bertalanffy function ($r^2 = 0.72$).

Fig. 4: $R.\ globiceps$ ripe egg numbers: (a) Logarithm of fish mass (g) against logarithm of ripe eggs fitted with a linear regression ($\text{adjusted } r^2 = 0.88; P = 4.835\times10^{-8};$ t-test for non-linear relationship, $P < 0.05$); (b) Fish age (years) against ripe eggs fitted with a von Bertalanffy function ($r^2 = 0.90$).
Fig. 5: Spawner biomass per recruit ratios and Egg Production per recruit ratios in relation to the instantaneous fishing mortality rates. Natural mortality rate = 0.246.

Fig. 6: Sensitivity analysis of the natural mortality rate (M) expressed as the percentage difference between SBpR ratios and EPPpR ratios.