Does the implementation of a closed fishing season during the breeding season benefit a species? A per-recruit-based approach using *Cymbula granatina* as an illustration

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1. Abstract

Closed seasons are generally implemented on the presumption that they increase reproductive output of fished populations. This is based on the assumption that the imposition of a closed season during the breeding season allows more individuals to reproduce, as they are not being harvested. We evaluated the validity of imposing closed seasons during the breeding season by creating a simulation model using the limpet *Cymbula granatina* as a test case and compared the following four scenarios:

1) an unharvested population; 2) no closed season imposed; 3) a closed season imposed during the breeding season; and 4) a closed season imposed outside the breeding season, to determine the effects of the latter three situations on the reproductive output and yield. From the outputs of the model, it was determined that closed seasons do not significantly affect the reproductive output of the population and that the timing of closed seasons made no difference to the reproductive output of the population, as the output was the same for populations with closed seasons during the breeding season or outside the breeding season. Survivors, catch in numbers and yield in biomass were affected by the timing of closed seasons, with higher outputs for each obtained when the closed season was closer to the month when individuals become of harvestable size. It was thus concluded that the imposition of a closed season at any time of the year is an effective management measure if imposing the closed season can reduce annual fishing effort, but the imposition of a closed season specifically during the breeding season with a view to increase reproductive output brings no benefits relative to closure at any other time of the year. Moreover, any closure will be ineffective if it does not also bring about a reduction of annual fishing effort. The reasons for advocating closure of a fishery during the breeding season are thus based on false grounds.
2. Introduction

2.1. Background

Due to declines in fish stocks because, in some cases, of ineffective management measurements in the past (Boyer et al. 2001a, Dichmont et al. 2000), there has been a considerable amount of interest in better ways to manage stocks (Cochrane et al. 1997, Holtzhausen et al. 2001) and also to find new resources to exploit (see for example Boyer et al. 2001b, Eekhout et al. 1992). There have been growing concerns over current levels of exploitation of southern African fish stocks, with 70% of our continental shelf fisheries being considered to be fully or overexploited (Boyer et al. 2001b, F.A.O. 1997). Fishing contributes some 1% to South Africa’s Gross Domestic Product (F.A.O. 1997) amounting to about R1.73 billion in 1995, of which R1.34 billion was derived from the commercial fishing sector (Cochrane et al. 1997).

Management measures are generally implemented to restrict fishing effort and catch, and they have had variable degrees of success. Some measures, such as total allowable catch and marine protected areas, are considered relatively successful, depending on the species because they limit the total catch that fishers can remove from the ocean. Others, including closed seasons and bag limits, are regarded as less successful because they do not limit total fishing effort nor do they make fishers more selective towards species harvested (Branch 2001, Cowley et al. 2002, Pradervand & Baird 2002). Some measures are ineffective because fishing effort is set at unrealistic levels mainly due to political pressures. For example, most bag limits for South African linefish are set too high and they are rarely reached, making them ineffective, though they would be successful if set at biologically meaningful levels and implemented affectively.

In the past, many management measures have been implemented based on anecdotes derived from successes and failures elsewhere, or on measures implemented on similar species by other countries. For example, many management measures applied to Namibian fisheries are based on data from South African stocks and species, as few data were collected in Namibia prior to 1990 (Holtzhausen et al. 2001).

One of the above-mentioned management measures is the closed season, which is the focus of this paper. Closed seasons are generally set during the spawning period of the target species and are implemented on the theoretical grounds that they should allow fish to reproduce without interruption during the breeding season. This is based
on the assumption that fish achieve a greater spawning success if they are not harvested during the breeding season (i.e. greater individual output is achieved because spawning is not interrupted by fishing). This rationale is, however, suspect as capture during the breeding season does not necessarily reduce reproductive success any more than would the capture of those individuals before or even after the breeding season, particularly if the overall annual fishing effort remains the same. Few studies have been done to determine the validity of imposing breeding seasons and the focus of this paper is to create a simulation model to test this theory.

The imposition of closed seasons can be a valid option if, by imposing a closed season (at any time of the year), there is a resultant reduction in the total fishing effort and catch. Additionally, if individuals that are not harvested are disturbed during the breeding season due to activities associated with harvesting, the imposition of a closed season during the breeding season could also be considered an effective management procedure.

Proposals have been made for small-scale harvesting of limpets and some modelling has already been done on their population dynamics; and growth and reproductive rates have been measured for various species (see Bosman et al. 1990, Branch 1974a & b, Eekhout et al. 1992). To examine the implications of a closed season, we selected the limpet *Cymbula granatina* as a test case.

2.2. Aims

For this study, a population dynamic model based on variables such as reproductive output, natural and fishing mortality and spawning potential of *C. granatina* was created. This allowed a comparison for reproductive output of four simulated situations: 1) a control population, in which no individuals were harvested; 2) a population that was not fished during the breeding season (i.e. that has a closed season imposed during the breeding season); and 3) a population that had a closed season outside the breeding season; and 4) a population that is fished at the same level of intensity as scenarios 2 & 3 but throughout the year.

For the latter two populations total fishing mortality was assumed to be the same, but concentrated in the fishing season in scenario 2 and spread throughout the year in scenario 3.
C. granatina was chosen as a basis for the model because it is not prone to disturbance, i.e. the removal of individuals does not directly affect the reproductive output of other individuals that are not harvested (G. Branch - pers. comm.).

Also, data such as mortality, growth and reproductive output were readily available for this species because of previous studies (Branch 1974a & b; Bosman et al. 1990, Eekhout et al. 1992).

2.3. Central questions
1) If total annual fishing effort remains unchanged, does the imposition of a closed season during the breeding season have any effect on the reproductive output of a population?

2) Alternatively, if fishing effort can be reduced by a closed season, does it make any difference whether the closed season falls during the breeding season or not?

3. Methods

3.1. General model

A general model was created to simulate a natural, unharvested population of C. granatina. The model is based on data obtained from various sources including Bosman et al. (1990), Branch (1974a & b) and Eekhout et al. (1992) and was used as a control population against which different harvesting scenarios were compared. A von Bertalanffy growth curve (Fig. 1) was fitted to shell length-age data of C. granatina (from Eekhout et al. 1992). The estimated shell length for the von Bertalanffy growth curve was calculated using the equation:

\[ L_t = L_\infty (1 - e^{K(t-t_0)}) \]

Where:
- \( L_t \) is the predicted mean shell length at time \( t \);
- \( L_\infty \) is the maximum length an individual can reach;
- \( K \) is the growth rate parameter;
- \( t_0 \) is the hypothetical time at which the individual had no length; and
- \( t \) is time.

The Microsoft® Excel add-in solver was used to optimise the values for the parameters \( L_\infty, t_0 \) and \( K \) to obtain the best-fit curve to the data by minimising the sum
of the squares of the error between the observed and the predicted shell lengths. The sum of squares was calculated using the equation:

\[ SS = \sum_{n=1}^{\text{max}} (P - D)^2 \]  

(2)

Where: SS is the sum of squares;
       \( P \) is the predicted shell length;
       \( D \) is the collected shell length data; and
       \( n \) is the number of data points

The average somatic weights of individuals at particular sizes were calculated using the equation:

\[ W_i = aL_i^b \]  

(3)

Where: \( W_i \) is the mean weight of individual \( i \);
       \( L_i \) is the length of individual \( i \); and
       \( a = 1.4 \times 10^{-5} \) and \( b = 3.17 \); which are growth constants specific to \( C. \) granatina \)(obtained from Bosman et al. 1990)

Natural mortality of the species was estimated by plotting age against the natural log of survivors (obtained from Branch 1974b) and adding a trendline to the data points, the slope of which represents the instantaneous yearly natural mortality (Fig. 2). This was found to be unrealistically high and was changed to 0.75 per annum and 0.5 per annum for individuals \( \leq \)35mm (juveniles) and \( > \)35mm (adults) respectively (as suggested by Eekhout et al. 1992). These mortalities were converted to instantaneous mortality rates by using the equation:

\[ I = 1 - e^{-A} \]  

(4)

Where: \( I \) is the instantaneous mortality rate; and
       \( A \) is the annual mortality rate
The instantaneous mortality rates were divided by 12 to obtain monthly mortality rates for the respective juvenile and adult populations. These were then substituted into a survivorship equation (6) to obtain survivorship curves for the population (Fig. 3).

Average individual gonad output was calculated by estimating the difference in gonad weight before and after the spawning period (June) based on data from Branch (1974a) for 6g, 9g and 12g individuals and plotting these values against the somatic weight of the individuals to obtain the equation:

\[ y = 0.8x - 0.5 \]  

(5)

Where: \( y \) is the gonad output; and \( x \) is the somatic weight.

The latter equation describes the relationship between gonad output and somatic weight (Fig. 4), where somatic weight is the flesh weight of individuals less the gonad weight.

The gonad output was modelled using an if-then scenario; where the limpet does not spawn if the result of multiplying the maturity index (0 if immature, 1 if mature) by the spawning period (0 if not spawning, 1 if spawning) by the somatic weight is zero. The population reproductive (gonad) output was calculated by multiplying the survivors of each month by the gonad output of those individuals in that month.
The survivors of each month were calculated using the survivorship equation:

$$N_t = N_1 e^{-M}$$ ................................................................. (6)

Where:  
$N_t$ is the survivors at time $t$; 
$N_1$ is the starting population (defined arbitrarily as 1000); and 
$M$ is the natural mortality rate (which differed for individuals $\leq 35$mm and individuals $>35$mm)

The mortalities were fitted into the survivorship equation using an if-then scenario; where the juvenile mortality rate of 75% per annum was used for individuals $\leq 35$mm and the adult mortality rate of 50% per annum was used for individuals $>35$mm.

Due to these differences in mortality rates of adults and juveniles, the mortality function used in equation (6) was edited to:

$$M = (M_j * J) + (M_a * A)$$ ......................................................... (7)

Where:  
$M_j$ is the mortality rate of juveniles; 
$M_a$ is the mortality rate of adults; and 
$A$ and $J$ are functions that describe the maturity of the individuals (if the individuals are less than 36 months old, i.e. juveniles, $J$ would be one and $A$ would be zero, whereas $A$ would be one and $J$ zero if the individuals were 36 months or older, i.e. adults)

By substituting the different mortality rates for juveniles and adults, two slopes were obtained, one for each of the two respective phases (Figs. 3 & 5). This was however not representative of a natural population as the transition between the two groups
should be a continuum and not a sudden change in mortality rate as is obtained by substituting the natural mortality values into equation (4). The natural mortality (survivorship) equation was therefore modified to a dynamic equation:

$$N_{t+1} = N_t e^{-M}$$  \hspace{1cm} (8)

Where: $N_{t+1}$ is the number of survivors during a given month;

$N_t$ is the number of survivors in the previous month; and

$M$ is natural mortality expressed monthly.

This equation was used because it provides a means of unifying the juvenile and adult mortality rates while still simulating the growth and survivorship that exists in a natural population (Fig. 6).

3.2. Survivorship and harvesting

To incorporate fishing mortality, selectivity and the closed season, the equation for predicting the survivors per month (equation 8) was amended to:

$$N_{t+1} = N_t e^{-M-(F*S*V)}$$  \hspace{1cm} (9)

Where: $F$ is mortality due to fishing;

$S$ is the knife-edge selectivity function (i.e. the minimum size limit); and

$V$ is a function that incorporates the presence of a closed season into the survivorship equation.

Figure 5: Population gonad output of the control population showing individual size and number of survivors in a scenario where juvenile and adult mortalities are disjointed at a size of 35mm.

Figure 6: Population gonad output of the control population showing individual size and amended number of survivors in which the survivorship curve is no longer disjointed between juveniles and adults.
The size at first capture (selectivity) was set at 60 mm (after Eekhout et al. 1992) and was calculated for each month using an if-then scenario; where the result would be 0 if the size of the individuals were less than 60mm, i.e. they were juveniles or 1 if it were 60mm or greater, i.e. they were adults.

Closed seasons were incorporated into the equation in a similar way (the outcome of which was 0 if it was a closed month and therefore no harvesting would take place or 1 if it was not). The closed season was set during the reproductive period (June) in scenario (2) as well as to February and October, to assess whether it makes any difference whether the closed season is during the breeding season or falls outside it.

To simulate scenario (3) total annual fishing mortality was kept constant and the closed season was removed and the resulting reproductive output and survivorships were determined.

Five fishing intensities ($F = 0.01, 0.05, 0.1, 0.15$ and $0.2$ mo$^{-1}$) were used to determine the effectiveness of closed seasons at different fishing pressures on a population with a closed season during the breeding season compared to a population with closed seasons that fall outside the breeding season.

To estimate survivorship when the population is fished, the Baranov catch equation was added to the general model to estimate the catch available for harvesting:

$$C_t = \frac{F}{Z} N_t (1 - e^{-(M + F \cdot S \cdot V)})$$

Where:
- $C_t$ is the catch at time $t$;
- $Z$ is the total monthly mortality; and
- $M$ is the natural mortality (divided into juvenile and adult mortalities by equation (7))

Equation 10 multiplied by the mean monthly weight provided an estimate of yield in mass.

### 3.3. Imposing closed seasons

The model was created to assess the effects of closed seasons on the reproductive output of a population. This hypothesis is based on the assumption that, if the total annual mortality were to remain constant, the imposition of a closed season during the breeding season would have a positive effect (i.e. an increase) on the reproductive output of the population, compared to a population in which there is either no closed season, or the closed season occurs at a time other than the reproductive season.
To maintain a constant annual mortality in a population when a closed season was imposed, the fishing mortality is changed as described by the equation:

\[ F_c = F_n \times \frac{12}{N_c} \]  

(11)

Where:  
- \( F_c \) is the monthly fishing mortality with a closed season imposed;  
- \( F_n \) is the monthly mortality when no closed season is imposed; and  
- \( N_c \) is the number of months when harvesting is permitted.

The annual total fishing mortality at \( F = 0.01 \text{ mo}^{-1} \) was kept constant by multiplying the monthly mortality by 12 (representative of the fishing mortality in a population with no closed season) and dividing it by 11 (representative of a population in which a season of one month is closed to fishing). For example, an \( F=0.01 \text{ mo}^{-1} \) for a population with no closed season would have yielded the same total annual fishing mortality as an \( F = 0.0109 \text{ mo}^{-1} \) for fishing concentrated in 11 months with a closed season of one month. The natural mortality was subtracted from this new monthly fishing mortality to obtain a new fishing mortality that was substituted into the original survivorship equation (9) and was repeated for \( F = 0.05, 0.1, 0.15 \) and \( 0.2 \text{ mo}^{-1} \) (equation (11)).

4. Results

4.1. General model

The model describing the population of *C. granatina* was based on estimates from a starting population of 1000 individuals.

From the von Bertalanffy growth curve estimates of shell length and age, the parameters for shell growth \( L_\infty, t_0 \) and \( K \) were calculated to be 85.0 mm, -10.5 months and 0.00135 \text{ mo}^{-1} \) respectively.

The mortality rates obtained from Eekhout *et al.* (1992) were modified and converted to instantaneous monthly mortality rates of 0.0440 \text{ mo}^{-1} and 0.0328 \text{ mo}^{-1} for juveniles and adults respectively by using equation (4) and then changed to a continuous mortality rate that better represented a natural population by modifying equation (6) to incorporate a smooth change in the mortality rate from juveniles to adults (equation 8, Fig. 6).
Individuals were assumed to spawn only during the month of June (Branch 1974a); therefore gonad output was estimated by calculating the change in weight of individuals before and after June. Gonad output per individual was determined from equation (5) and Fig. 4 and summed to obtain the gonad output for the population. As individuals only reproduce in one month of the year (June), a smoothed line was fitted to the data points to express annual output rather than representing output as a series of spikes in June. The population output was compared to the number of survivors and the length of individuals to show the relationship between these three variables over time. The total annual output for the population was 1183 grams. Population gonad (Fig. 6) output followed a different trend from individual output, as most of the reproductive output is contributed by the 60 – 80 month category.

The number of survivors appears to have a role in the reduction in output after 80 months because individual output continues to increase with time (Fig. 7), whereas population output decreases even though somatic weight continues to increase throughout the lives of the individuals (Fig. 8). There was a good correlation between the age and the gonad output of individuals with an R² value of 0.9989, as seen from Fig. 7. There was also a positive relationship between the length of individuals and their individual gonad output i.e. larger individuals have greater gonad output. Females become sexually mature at 36 months and reproduce until the end of their lives.

![Figure 7: The relationship between length and the individual gonad output of different age classes](image1)

![Figure 8: Relationship between the population reproductive output and somatic weight of individuals of an unharvested population as related to the number of survivors](image2)
4.2. Survivorship

Minimum size of catchable limpets was set at 60 mm (75 months), allowing individuals between the ages of 36 months and 75 months to reproduce four times. In an unfished population, reproductive output for the whole population reaches a peak of 281g at 60 months; at which time the individuals become of harvestable size (Fig. 9; age at which individuals become of harvestable size demarcated by an ++-- ).

The available catch at the time at which individuals became of harvestable size was 9.88% of individuals (Fig. 9), whereas the total number of harvestable individuals was 1458.

![Figure 9: Population reproductive output and the number of harvestable individuals at a fishing mortality of zero. ++-- indicates period in which minimum harvestable age falls](image)

4.3. Reproductive Output

Results for reproductive outputs are summarised in Appendix 1.

4.3.1. No closed season

The total reproductive output for the population fished at $F=0.01$ mo$^{-1}$ was 1160 grams, calculated as the sum of monthly reproductive outputs. The population reproductive output shows a slightly faster decline from an unharvested population, although there is still a peak in reproductive output during the third spawning period (Fig. 10).

The population reproductive outputs decline faster at F-values of 0.05 mo$^{-1}$ and 0.1 mo$^{-1}$ than in the unharvested population or in the population fished at $F = 0.01$ mo$^{-1}$.
The reproductive outputs obtained at F-values of 0.05 mo\(^{-1}\) and 0.1 mo\(^{-1}\) were 1089g and 1032g respectively (Fig. 10).

At fishing mortalities of 0.15 and 0.2, the reproductive outputs were 997 and 976 respectively (Fig. 10). The decrease (when compared to an unharvested population and populations fished at lower fishing intensities) as a result of the reduction in number of survivors that breed could be sufficient to result in a population crash.

### 4.3.2 Closed season imposed

A closed season was set during the breeding season (June) by restricting fishing to July through May. To maintain a constant total annual mortality, the fishing intensity (i.e. \(F = 0.01, 0.05, 0.1, 0.15\) or 0.2 mo\(^{-1}\)) was amended by multiplying the monthly fishing intensity by the number of months harvesting takes place without a closed season (i.e. 12) and dividing it by the number of months harvesting takes place with a closed season imposed (i.e. 11). Results for reproductive output were virtually identical to the values obtained when no closed season was imposed (compare Figs. 10 & 11).

For a population with a closed season imposed during the breeding season, the fishing intensity was set at 0.0109 mo\(^{-1}\) for the 11 months of fishing (equivalent to 0.01 mo\(^{-1}\) in a population where no closed season is imposed) and the reproductive output was virtually identical (1183g) to a population in which no closed season was imposed (Fig. 11).

Similar to a population that has no closed season imposed, at fishing mortalities of 0.0545 mo\(^{-1}\) and 0.109 mo\(^{-1}\) (equivalent to 0.05 mo\(^{-1}\) and 0.1 mo\(^{-1}\) respectively) the population reproductive outputs showed faster declines (Fig. 11). At fishing mortalities of 0.164 mo\(^{-1}\) and 0.218 mo\(^{-1}\) (equivalent to 0.15 mo\(^{-1}\) and 0.2 mo\(^{-1}\) respectively) the population reproductive outputs showed rapid declines resulting in reproductive outputs of less than 1 gram per month for age categories above 90 months (Fig. 11).

The effects of a closed season outside the breeding season on reproductive output were measured for two situations in which a closed season was imposed either before (February) or after the breeding season (October). Reproductive outputs at all fishing intensities for the two situations were almost identical to those for a population that had a closed season during the breeding season (Appendix 1).
Reproductive output was virtually identical in populations that have closed seasons imposed compared to populations without closed seasons at all fishing intensities, provided the total annual fishing effort remained unchanged by the act of imposing a closed season (Fig. 12).
4.4. Survivorship, Catch and Yield

Results for survivorship, yield (in mass) and catch outputs are summarised in Appendix 1.

4.4.1. No closed season

Using the Baranov catch equation (10), total catch at a fishing mortality of 0.01 mo\(^{-1}\) was calculated to be 8.12 (Fig. 13), with 1229 individuals being of harvestable size. This catch was estimated for individuals that live for 120 months and reach harvestable size at 75 months, shown by the decline in output of survivors after the 75-month mark has been reached compared to the unharvested population (Fig. 14). The difference was, however, relatively small.

The total annual yield in terms of biomass was calculated by multiplying the catch by the somatic weight of the individuals at that particular age class; which was calculated to be 65.2g and showed a similar trend to catch (Appendix 1). Fishing at this intensity appeared to be sustainable.

At fishing mortalities of 0.05 mo\(^{-1}\) and 0.1 mo\(^{-1}\), the total annual catches were calculated to be 1.19 with 707 individuals being of harvestable size and 0.0356 with 439 individuals being of harvestable size respectively (Figs 13 & 14). The number of individuals that survive at both fishing mortalities decreases due to the increased fishing pressure.

The total annual yields (biomass) at F = 0.05 mo\(^{-1}\) and F = 0.1 mo\(^{-1}\) were calculated to be 8.85g and 0.249g respectively. The annual numerical catches for the respective F-values were 1.19 and 0.0356 and 707 and 439 individuals were of harvestable size in the population respectively.

At fishing mortalities of 0.15 mo\(^{-1}\) and 0.2 mo\(^{-1}\), the total annual numerical catches were calculated to be 9.12 x 10\(^{-4}\) with 311 individuals being of harvestable size and 2.25 x 10\(^{-5}\) with 389 individuals being of harvestable size for the respective fishing intensities (Fig. 14). The total annual yields (biomass) were 0.00617 and 1.49 x 10\(^{-4}\) for populations fished at fishing intensities of 0.15 and 0.2 respectively (Appendix 1).

4.4.2. Closed season imposed

The total catch at a fishing mortality of 0.0109 mo\(^{-1}\) spread over 11 months was calculated to be 7.57 individuals, slightly lower than an unharvested population.
(Fig. 13) with 1224 individuals exceeding harvestable size. The total annual yield was calculated to be 60.4g.

Similar trends were evident at fishing intensities of 0.0545 mo\(^{-1}\), 0.109 mo\(^{-1}\), 0.164 mo\(^{-1}\) and 0.218 mo\(^{-1}\), with slight reductions in numerical catch, yield (biomass) and number of harvestable individuals (Figs. 13 & 14, see Appendix 1). For populations in which the closed season fell outside the breeding season the number of harvestable individuals increased, whereas the total catch and the yield per year decreased in a similar way to a population that had a closed season imposed during the breeding season (Figs. 13 & 14, see Appendix 1).

Figure 13: Reproductive output in grams per year for populations with and without a closed season

Figure 14: Survivorship curves at different annual fishing intensities for populations with and without a closed season showing number of harvestable individuals remaining per year

5. Discussion

5.1. General model

Shell length data obtained from Eekhout et al. 1992 were used as a representation of somatic growth of the population and, using a von Bertalanffy growth equation and the relationship that exists between shell length and somatic weight (described by equation (3)), were converted to an estimate of reproductive output. Population gonad output followed a bell-shaped distribution and the decrease in output after the 60-month mark was a result of the decrease in number of survivors due to natural
mortality (Fig. 6), as individual gonad output continued to increase from the time of maturity to the end of the lives of the individuals (Fig. 7) and was a positively related to the size of individuals (Eekhout et al. 1992).

Natural mortality of the modelled population was determined from survivorship estimates obtained from various sources including Branch (1974b) and Eekhout et al. (1992). Survivorship estimates using data from Branch (1974b) constantly underestimated survivorship (as predicted by Branch 1974b, Fig. 2) and were thus discarded. The central problems with the survivorship curve obtained by plotting the data points and adding a trendline (Fig. 2) were the resultant annual mortality rate of 0.909 yr\(^{-1}\), which was much too high for limpets (G Branch – pers comm.) and the unnaturally abrupt change in mortality rate between juveniles and adults.

Eekhout et al. (1992) studied the dynamics of different limpet populations and found that mortalities were different for juveniles (75% per annum) and adults (50% per annum) of C. granatina and by substituting these mortalities into the respective juvenile and adult phases of the population (Fig. 3), the resultant survivorship curve was disjointed (Fig. 5). As a result, the survivorship equation (6) was changed to equation (8), which united the adult and juvenile growth curves smoothly by estimating instantaneous survivorship (Fig. 6).

The effects of fishing were determined by looking at two scenarios. The first was a scenario that has a starting population of 1000 individuals in which the survivorship and reproductive output of those individuals were followed throughout the lives of those individuals. This scenario was used to determine the yield and catch that were removed from the population per 1000 individuals and was expressed as the catch at any particular mortality. The second scenario was to simulate a snap-shot in time, integrating different age classes and was used to simulate the state of a population in equilibrium if it was sampled at any given time.

Minimum size of harvestable individuals, set at 60mm as suggested by Eekhout et al. (1992), protects the age groups that contribute most to the population and should not be changed.

5.2. Reproductive output

The aim of creating this model was to determine the validity of imposing closed seasons during the breeding season as a putative means of increasing reproductive output. From the outputs of this model it can be determined that, for C. granatina, the imposition of such a closed season for this purpose is invalid. If annual fishing effort...
remained unchanged, reproductive output remained identical whether or not a closed season existed (compare Figs. 10 & 11). As individual limpets are not prone to disturbance by the act of fishing, the removal of individuals does not directly affect the reproductive output of remaining individuals; therefore closed seasons should not affect the reproductive output of the population.

As can be seen from Fig. 10, fishing negatively affected the reproductive output of the population with no closed season, by decreasing the number of individuals of harvestable size that can spawn. This reduction in survivors was especially crucial in the 60-80 month category from which most of the reproductive output was obtained. Therefore, setting a minimum size of capture at 60mm (75 months) was a good management measure as it protects the most crucial age groups. As can be seen from Fig. 10, if fishing mortality rises too high (e.g. $F = 0.15 \text{ mo}^{-1}$ or $F = 0.2 \text{ mo}^{-1}$) the result could be a rapid decline in reproductive output that could potentially remove all individuals of harvestable size.

A closed season was set during the breeding season by prohibiting fishing in June. The effects of imposing a closed season on a population were determined using the same annual mortality rates as when no closed season was imposed (by changing the monthly fishing mortalities per month by spreading the annual effort over 11 months instead of 12). As with the population that has no closed season, fishing intensity still has an effect on the reproductive output of the population (Fig. 11), ranging from 1161g at $F = 0.0109 \text{ mo}^{-1}$ (equivalent to $F = 0.01 \text{ mo}^{-1}$ in a population with no closed season) to 977g at $F = 0.218 \text{ mo}^{-1}$ (equivalent to $F = 0.2 \text{ mo}^{-1}$), which was virtually identical to the reproductive output of a population with no closed season imposed (Appendix 1, Fig. 12).

The reproductive outputs were the same at any given fishing intensity for populations that had closed seasons in June (i.e. during the breeding season) and those with a closed season in February or October (Appendix 1).

5.3. Survivorship, Catch and Yield

The number of individuals above harvestable size remaining in the population when no closed season was imposed ranged from 1229 individuals at $F = 0.01 \text{ mo}^{-1}$ to 238 at $F = 0.2 \text{ mo}^{-1}$, the decrease being a result of increased fishing pressure.

The numerical catch was determined for populations with different fishing mortalities as well as in populations with and without closed seasons, to determine the effects of closed seasons - during or outside the breeding season – on the catch and
the number of individuals that reach harvestable size. When no closed season was imposed, catch at all fishing mortalities was quite low, ranging from between 8.12 individuals at $F = 0.01 \text{ mo}^{-1}$ to as low as $2.255 \times 10^{-5}$ individuals at $F = 0.2 \text{ mo}^{-1}$.

The biomass yield per population was determined at different fishing mortalities, and produced similar results to the catch in numbers. The biomass yield per year of survivors per age class, decreased as a result of higher fishing pressures, ranging from 65.2 g at $F = 0.01 \text{ mo}^{-1}$ to $1.49 \times 10^{-4}$ g at $F = 0.2 \text{ mo}^{-1}$.

When compared to an unharvested population, the number of individuals of harvestable size in fished populations decreased, ranging from 1224 individuals at $F = 0.0109 \text{ mo}^{-1}$ (equivalent to $F = 0.01 \text{ mo}^{-1}$) to 225 individuals at $F = 0.218 \text{ mo}^{-1}$ (equivalent to $F = 0.2 \text{ mo}^{-1}$). Catch and Yield show similar trends to the population in which no closed season was imposed; decreasing as fishing pressure increases.

Slight differences existed in the number of individuals that reach harvestable size, and in the catch and yield, when comparing a population that had a closed season and the one that did not (Fig. 14). This was thought to be as a result of the proximity of the closed season to the month in which individuals first reached a size at which they could be harvested, as catches and yields were higher in populations that had closed seasons close to the month at first capture.

This hypothesis was supported when the model was run with a closed season during February or October and when the month at first capture was changed, which resulted in the same reproductive output but slight differences in the number of individuals that reached harvestable size, and in catch and a yields; some higher than those obtained when no closed season was imposed and others lower (for example see Fig. 13).

6. Conclusions

From the outputs of this model, it can be concluded that closed seasons do not affect the reproductive output of *C. granatina* in any significant way and that it is not valid to impose a closed season during the breeding season with the objective of increasing reproductive output.

If, however, a closed season can be used to decrease annual fishing effort on a population, it then becomes a valid management option, as this would be just as effective as having, for example, a marine protected area or total allowable catch.
The outputs of this model show that, if total annual mortality remains the same in a population that has a closed season when compared to one that does not, the survivorship, catch and yield for the population do not change significantly, though outputs were higher in populations with closed seasons close to the month when individuals become of harvestable size. It can thus be concluded that, if the imposition of a closed season (at any time of the year) reduces annual fishing mortality, it is a valid management option, but if it does not accomplish a reduction in fishing effort it is meaningless.

Closed seasons can therefore be considered good management measures only under two circumstances: 1) if they reduce effort, or 2) if they prevent disturbance of individuals that are not being fished and thereby increase their reproductive success. For species such as limpets and abalone that are unlikely to be disturbed in that way, this second condition falls away.

7. Acknowledgements

I would like to thank my supervisors Dr. Anesh Govender and Prof. George Branch for help with the modelling and on the biological aspects of the limpets used as an illustration for this study, and for their critiques. I would also like to thank the University of Cape Town, the Harry Crossley foundation and the NRF for financial support.
8. References

Bosman AL, S Eekhout and GM Branch, 1990, The exploitation potential of limpets on the coast of Namaqualand, Final report to the Chief Director, Marine Development, Sea Fisheries Research Institute, 76pp


Boyer DC, CH Kirchner, MK McAllister, A Staby and BI Staalesen, 2001b, The Orange Roughy fishery of Namibia: Lessons to be learned about managing a developing fishery, S. Afr. J. mar. Sci. 23: 205-221


## Appendix 1: Summary of outputs of the number of harvestable individuals, reproduction (grams), catch in numbers and yield (biomass), as obtained from a per-recruit model for the limpet *C. granatina*

### Yearly outputs with no closed season imposed

<table>
<thead>
<tr>
<th>Fishing Mortality mo⁻¹</th>
<th>Harvestable individuals</th>
<th>Reproductive output (grams)</th>
<th>Catch (Numbers)</th>
<th>Biomass (grams. population⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>1458</td>
<td>1183</td>
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<td>0</td>
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<td>0.01</td>
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</tr>
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<td>0.000149</td>
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</table>

### Yearly outputs with a closed season imposed during breeding season

<table>
<thead>
<tr>
<th>Fishing Mortality mo⁻¹</th>
<th>Harvestable individuals</th>
<th>Reproductive output (grams)</th>
<th>Catch (Numbers)</th>
<th>Biomass (grams. population⁻¹)</th>
</tr>
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### Yearly outputs with a closed season imposed outside the breeding season (February)

<table>
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<th>Fishing Mortality mo⁻¹</th>
<th>Harvestable individuals</th>
<th>Reproductive output (grams)</th>
<th>Catch (Numbers)</th>
<th>Biomass (grams. population⁻¹)</th>
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</thead>
<tbody>
<tr>
<td>0</td>
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### Yearly outputs with a closed season imposed outside the breeding season (October)

<table>
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<tr>
<th>Fishing Mortality mo⁻¹</th>
<th>Harvestable individuals</th>
<th>Reproductive output (grams)</th>
<th>Catch (Numbers)</th>
<th>Biomass (grams. population⁻¹)</th>
</tr>
</thead>
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