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THE UNIVERSITY OF ALBERTA

MATE CHOICE AND SPAWNING PERIODICITY IN THE REDLIP BLENNY (PISCES: BLENNIIDAE)

BY

ISABELLE MARIE COTE

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND

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ABSTRACT

The redlip blenny (*Ophioblennius atlanticus*) is a small, benthic herbivorous fish commonly found on shallow-water Caribbean reefs. Males and females hold permanent territories and reproduce year round, for two weeks every month. Females travel to males' territories to spawn and males guard the eggs until hatching. Both polygyny and polyandry were observed.

The monthly reproductive success (RS) of 44 males was measured from January to August 1986 on the North Bellairs Reef on the west coast of Barbados. There was significant variation between males in the number of egg batches obtained and hatched during each reproductive period. The influence of male, nest and territory characteristics on male RS was assessed. Male size explained 43% of the variance in male RS with large males obtaining more egg batches than small males. The size of the largest nest entrance also significantly influenced male RS. Males with nests having a large entrance area were more successful than other males. None of the territory characteristics measured affected male RS. Because male-male interactions were extremely rare, and females initiated the reproductive process by travelling to male's territories, most of the variance in male RS was attributed to female choice.

Females approached and spawned with large males more often than with small males. In addition, females deposited larger egg batches when spawning with large males than with small males. The reasons underlying female choice for large males were examined. Large males lost significantly fewer egg batches than small males. Large males did not achieve higher hatching success by possessing less vulnerable nests, or by being more aggressive. Instead, large males guarding eggs left their nests significantly less often than small males.

The presence of male mate choice was also observed. Males accepted large females into their nests and actively rejected smaller females. Since the size of egg batches deposited was positively correlated with female size, males maximised their reproductive success per ejaculate by mating with large females.

The effects of mate choice by both sexes were discussed in the context of sexual selection. In addition, the spawning periodicity observed in the redlip blenny was explained as a male strategy to maximise reproductive success while constrained by the costs of egg guarding.

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Many people helped me, in various ways, bring this thesis to completion. I would like to thank my supervisor, Dr. Ralph Nursall, who gave me free range to design this study as I saw fit but who always gave knowledgeable advice. The members of my supervisory committee, Drs. Jan Murie, Susan Hannon, and Bev Mitchell, were [illegible] available and willing to offer comment on my work. Special thanks to Dr. Jan Muri[illegible]s co-supervisor during the final phase of this study.

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Jamais je n'aurais pu commencer ou terminer cette thèse sans l'aide de mes parents, Rodolphe et Marguerite Côté, qui m'ont sans cesse offert leur support et encouragement malgré les quatre mille kilomètres qui nous séparent depuis bientôt trois ans. Leur confiance en moi m'a permis d'accomplir tout ce que j'ai fait jusqu'à présent et est ma garantie de succès pour l'avenir.

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CHAPTER I - INTRODUCTION

Mate choice may be defined as any pattern of behaviour shown by members of one sex that leads to their being more likely to mate with certain members of the opposite sex than with others (Halliday 1983). The benefits an animal may derive from choosing a particular mate range from immediate gains such as courtship feeding to the possible long-term advantage of mating with an individual of high genetic quality (Weatherhead and Robertson 1979, but see Kirkpatrick 1985). The relative gametic investment contributed by each parent into offspring will determine which sex should exhibit mate choice (Trivers 1972). Parental investment by either sex will tend to result in the lower-investing sex competing to mate with the higher-investing sex. The sex investing more is predicted to be choosy about its mating partners. When care by both parents is comparable, both males and females are expected to exhibit some degree of choice.

While mate choice may be exercised by either or both sexes, research has concentrated on organisms in which females are the choosier sex (See Bateson 1983 for review). Females should choose mates in a way that maximises their reproductive success and the fitness of their offspring. They should choose based on: 1) male phenotype when males contribute only gametes (e.g. Whitney and Krebs 1975; Weatherhead and Robertson 1979); 2) male resource quality (e.g. Gwynne 1982; Thornhill 1973) or territory quality (e.g. Campanella and Wolf 1974; Howard 1978; Jones 1981) when males contribute materially to reproduction such as in providing nuptial gifts or oviposition/nesting sites; and 3) male quality when males contribute behaviourally such as in egg defense or offspring feeding (Downhower and Brown 1980). Female mate choice based on one or more of these characteristics has been well documented in mammals (Geist 1971; Cox and LeBoeuf 1977), birds (Nisbet 1973; Cooke and

Davies 1983), insects (Thornhill 1976), and amphibians (Howard 1978).

Female choice in fish has also been well documented. Large differences in mating success among territorial egg-guarding males are usually attributed to female choice based on some aspect of the quality of the male or its territory. Male reproductive success in fish has been correlated with male size (Downhower and Brown 1980; Brown 1981; Loiselle 1982; Noonan 1983; Keenleyside et al. 1985; McKaye 1986), levels of male aggression (Schmale 1981; Jones 1981), frequency of courtship (Schmale 1981; Jones 1981; Cole 1982), intensity of breeding coloration (Kodric-Brown 1983), previous reproductive experience of the male (Ridley and Rechten 1981; Marconato and Bisazza 1986), characteristics of nest site (Perrone 1978; Sargent 1982), and position and topography of the territory (Jones 1981; Kodric-Brown 1983; Thompson 1986). These studies are useful in that they identify characteristics potentially important to females. However, male-male competition for acquisition of breeding territories is usually intense in many species and may confound the effects of female choice. In addition, although variables that correlate with male reproductive success are often cited as criteria of female choice, there is often no evidence that females are actively choosing, and that there are direct reproductive consequences to choosing mates according to those critera.

Although females generally make a greater gametic investment in reproduction than males, and are expected to be more discriminating in their choice of potential mates (Trivers 1972), males may also sometimes gain by mating discriminately. If females vary in quality, e.g. in fecundity or in ability to provide parental care, and if males are limited in the number of females with which they can successfully mate (Dewsbury 1982; Nakatsuru and Kramer 1982), then selection should favour males choosing females that will yield them the highest reproductive return per unit investment. Until recently, male mate choice had been largely overlooked. Male choice based on female size has now been shown in organisms in which female fecundity varies with body size, such as insects (Gwynne 1981; Johnson 1982; Thornhill and Alcock 1983), amphibians (Berven 1982; Verrel 1982), and fishes (Downhower and Brown 1980; Loiselle 1982; Rowland 1982; Sargent et al. 1986). Since paternal care is the most common form of parental care in fish (Keenleyside 1979), the likelihood of male choosiness is increased, suggesting that male choice could be a more widespread phenomenon among egg-guarding teleosts than is documented at present.

The main objective of this study was to investigate simultaneously male and female mate choice in the redlip blenny, *Ophioblennius atlanticus*. The redlip blenny is a small benthic herbivorous fish commonly found on shallow-water Caribbean reefs (Randall 1968). Males and females defend permanent territories against all intruders, especially neighbouring conspecifics (Nursall 1977). Spawning takes place year round, in the first three hours of daylight in the week around full moon (Marraro and Nursall 1983). During the reproductive period, males prepare nests in holes or depressions on their territories. Just following sunrise, females leave their territories and travel to those of males. A male may either accept a female into his nest or chase her away. After a female has deposited a batch of eggs in a male's nest, she returns to her territory. Males guard the eggs until they hatch, some 106 to 112 hours after spawning (Labelle and Nursall 1985). Males are polygynous, tending the eggs of many females each month (Labelle 1982) and qualitative evidence suggests that females may spawn with more than one male during each reproductive period (Marraro and Nursall 1983). The suggestion that the species is polyandrous was examined in the present study and information on the spawning periodicity of the species was gathered. I looked at variation in male reproductive success and presented evidence of male and female choice in the redlip blenny. I investigated some factors influencing female mate choice (e.g. male attributes and/or territory/nest characteristics) and male choice. Finally, I discussed the potential reasons underlying mate choice by both sexes, and how discriminate spawning by both sexes acts as a constraint on male and female reproductive strategies in the redlip blenny.

CHAPTER II - METHODS

STUDY SITE

The field study was conducted on a shallow fringing reef north of Bellairs Research Institute on the west coast of Barbados, West Indies (59°37'W, 13°04'N; Figure 1). The reef was approximately 150 m wide and 100 m long. The 60m^2 study site was situated in the middle of the reef at the seaward end of a spur, surrounded on three sides by sand and continuous with the main reef on the eastern side. Depth on the site varied from 1 m at its eastern edge to 3 m at its western edge.

Blennies were not marked because of the difficulty in capturing them alive. However, individual adults were easily recognisable by the location of their territory on the site, and in some instances, by physical characteristics or behaviour.

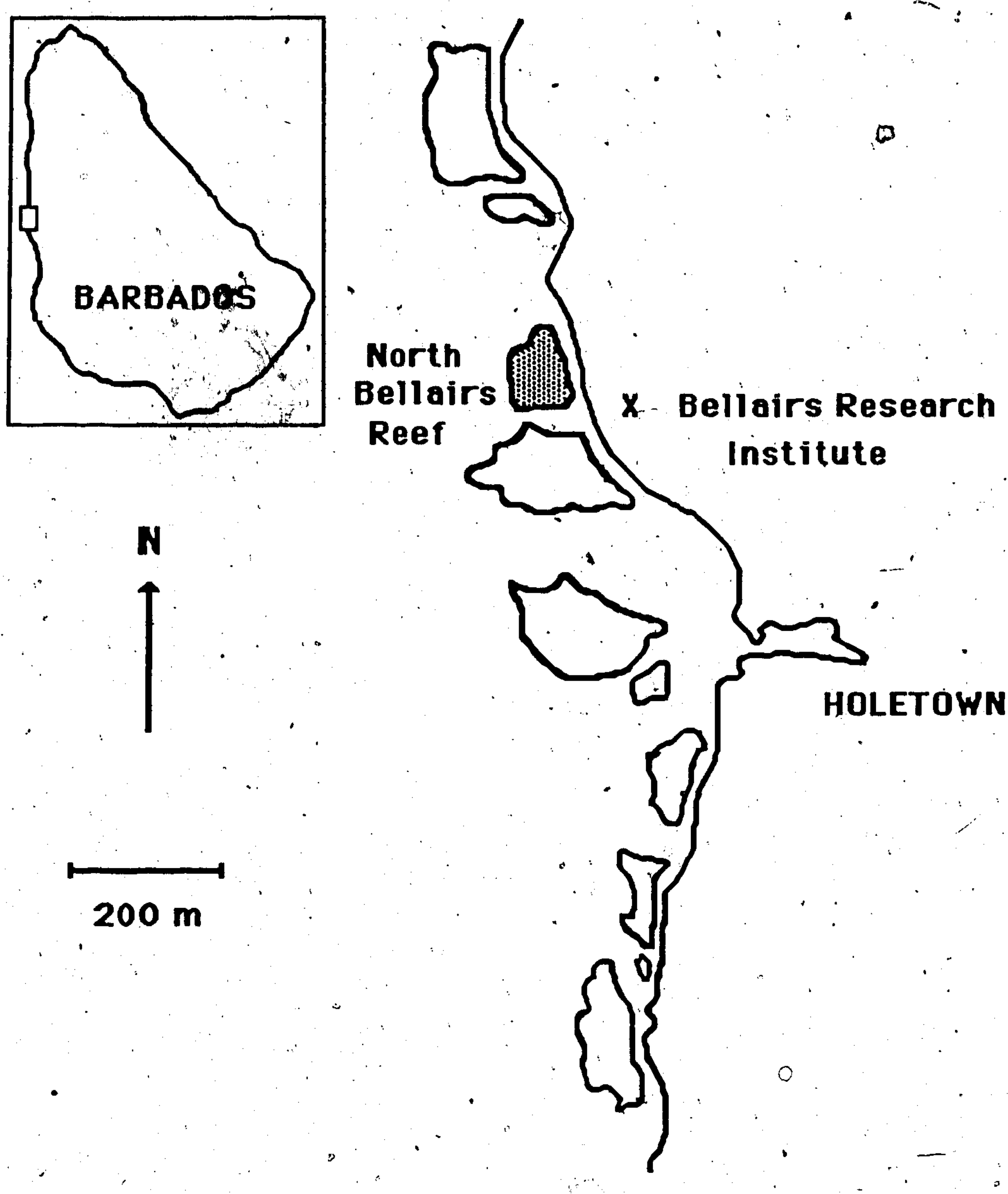
SIZE AND SEX

The size of blennies was estimated by measuring the distance between natural markings on the substrate against which the fish rested. The sex of blennies was determined using behavioural observations, which was possible only for sexually mature fish during the reproductive period. Two criteria were used to identify sex: 1) males typically returned to the same location on their territories following a disturbance, while females resettled at any location within their territories, and 2) during morning observation, males stayed within their territories, while females visited other territories. To check the accuracy of field observations, 25 blennies were poisonned using rotenone and brought into the laboratory to be measured and their sex determined by the shape of the urogenital papilla (Marraro 1978). All blennies had been appropriately sexed and their size estimated to within 2.5 mm in the field.

TERRITORY CHARACTERISTICS

Territories were delineated by observing resident blennies patrolling their territory periodically and interacting with neighbours at

FIGURE 1 - Position of North Bellairs Reef on the west coast of Barbados.


BARBADOS
North Bellairs Reef
X Bellairs Research Institute
HOLETOWN
N
200 m

territorial boundaries (as in Nursall 1977). Territorial limits were marked with colored nuts and territories were measured to obtain a planar area. Five rugosity measurements were taken for each territory by laying a fine chain five times on the substrate across different parts of the territory so as to conform to surface irregularities. The straight line distance between the ends of the chain above the coral surface as well as the length of the chain lying on the substrate were measured. The average for the 5 straight line/rugose distance ratios was used as a rugosity index of a territory. Rugosity indices varied between slightly more than 1.00 for nearly flat territories to 1.90 for territories with high relief.

The number of male and female blennies residing in a 2m radius of each territory was recorded. The position of each territory on the study site was recorded as the distance in metres from the closest seaward edge of the reef.

NEST CHARACTERISTICS

Nest entrances were measured to the nearest mm using calipers. The size of the largest entrances and the number of entrances for each male's nest were recorded. Nest depth, length and width were estimated by inserting a ruler, pencil or a piece of pliable wire inside the nest. The entrance area and volume of each nest were then calculated. The number of wall surfaces (including ceiling and floor) cleared by the male to receive eggs was recorded. This permitted calculation of the inner surface area available for egg attachment.

AGGRESSION, FEEDING AND PATERNAL CARE

From January 26 to April 26 1986, 18 males on the study site and adjacent spurs were each observed for 10 minutes between 1400 and 1600 hours. These were divided into 2 groups which were observed on alternate days. For each male, total length, number of neighbours, territory size and nest dimensions were recorded. Aggressive interactions against con- and heterospecifics were recorded during each 10-minute period. The identities of participants in each interaction were recorded. The number of bites taken on the substrate and the time spent in and out of the nest by the focal male were also recorded.

REPRODUCTIVE SUCCESS

From January to July 1986, spawning activity by redlip blennies was monitored from 10 days before full moon (FM-10) until 4 days after full moon (FM+4). Observation periods typically began 10 minutes before sunrise and lasted 2 to 3 hours. A session was terminated when no spawning had been observed for at least 30 minutes. All observations were made using a mask and snorkel and were recorded underwater on a plastic slate. A total of 200 hours was spent observing reproductive behaviour in the morning.

The size of the study site and the distribution of blennies on the site precluded simultaneous observation of the entire study population. As a result, observations were focussed on males and their nests, and 4 to 5 groups of neighbouring males and females were observed sequentially. The time spent observing each group was recorded and later incorporated in the behavioural data to avoid bias resulting from unequal observation time for each group.

Approaches were recorded when a female travelled to and waited at a male's territorial boundary. Males could then chase or court approaching females. Visits were recorded when an approaching female entered a nest. Visits sometimes resulted into spawning. Spawning occurred when a female deposited a batch of eggs in a male's nest. Spawning could be confirmed upon checking a nest after a female's visits. However, this caused considerable disturbance to normal spawning activity. The occurrence of spawning was therefore determined by female movement inside the nest. In open nests, spawning females could be seen rubbing their abdomen against the nest wall. In more closed nests, a back and forth motion of the female's head through one of the nest entrances indicated spawning. Observation of females and subsequent verification of the nests validated this method. In addition, spawning never occurred during visits of less than 4 minutes.

The identities of blennies involved in approaches, visits and spawning were recorded. Most approaching females were identified by following them back to their territories. The identities of participants in any aggressive interaction toward con- or heterospecifics were also recorded.

In August 1986, emphasis was put on finding females spawning in the nests of known males. After females had spawned, they were followed back to their territories for identification and size measurement. The length and width of egg batches deposited by the identified females were measured to the nearest mm with calipers.

Nests on the study site were checked every afternoon for the presence of eggs. Eggs were easily seen by shining an underwater light into the nest. In more closed nests, a dental mirror and a flashlight were used to see eggs on ceilings and otherwise inaccessible walls. The number, position and age of egg batches were recorded. The age of egg batches was accurately determined using Labelle's (1982) description of colour change during egg development - from light orange when laid to silver when ready to hatch after 106-112 hours. To increase sample size, 18 additional males were found on spurs adjacent to the main site. Their nests were also checked every day for the presence of eggs during and between reproductive periods.

ANALYSIS

To determine whether spawning in *O. atlanticus* followed a lunar cycle, egg batches were grouped according to the portion of the lunar cycle during which they were spawned. A X^2 test of equal frequencies was then carried out to determine differences between spawning frequencies in the four phases of the lunar month. In addition, the mean number of egg batches spawned inside the peak reproductive period (PRP) was compared to the mean number of egg batches spawned outside the PRP by means of a two-tailed unpaired t-test with a level of significance of 0.05. Consistency of monthly reproductive success (RS) for males staying on the site more than one month was analysed using a Spearman rank correlation.

Relationships between male size and nest and territory characteristics were analysed by means of linear regression. Prior to analysis, all data were checked for normality and equality of variance.

A square root transformation was performed on the size of the largest nest entrance to normalise the data.

The influence of male, territory, and nest characteristics on reproductive success, mating success and hatching failure were also analysed using linear regression, unless the relationships were significantly better fitted by non-linear regression. When two correlated variables showed a significant effect on reproductive success, residuals of the significant regression between reproductive success and one of the variables were obtained and used as corrected values in the regression with the second variable. This removed the effect of the first variable and allowed examination of the independent influence of the second variable on reproductive success (Atchley et al. 1976; Gibson and Bradbury 1985).

CHAPTER III - SPAWNING PERIODICITY AND REPRODUCTIVE CHARACTERISTICS OF THE STUDY POPULATION.

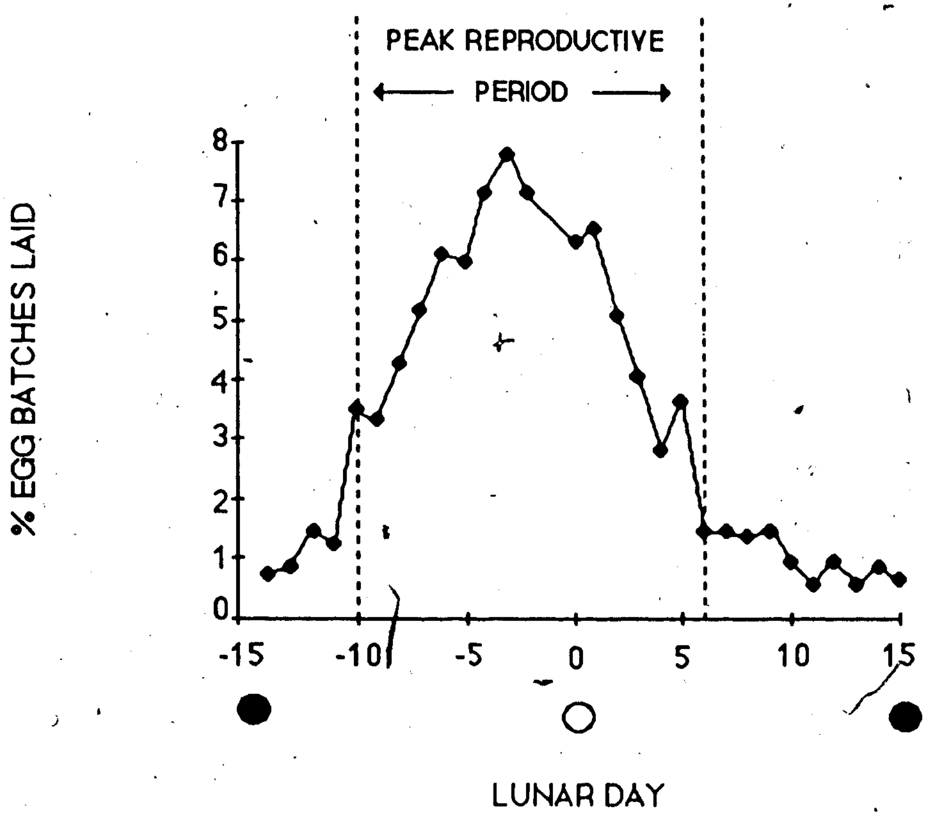
Redlip blennies at Barbados have been the subject of two previous studies of population dynamics and reproductive behaviour (Marraro 1978; Labelle 1982). For comparative purposes, the following chapter presents reproductive characteristics of the subset of the North Bellairs blenny population which was the focus of the present study. Although spawning in the redlip blenny has been described as occurring year round and being centered around full moon, additional information on the reproductive periodicity of *O. atlanticus* is provided.

RESULTS

Monthly population density varied greatly on the site, from 0.79 to 5.38 blennies/m^2, as a result of a massive juvenile recruitment in May 1986. The adult population density varied from 0.36 to 1.31 adults/m^2, when juveniles were recruited into the breeding population in August 1986. The average size (TL) of males on the study site was 84.66 ± 0.99 mm (n=44). The average size of females was 82.75 ± 1.10 mm (n=48). There was no significant difference in the sizes of adult males and females (t=1.283, p>0.25). The adult sex ratio (1 male:1.09 females) did not differ significantly from unity (X^2= 0.17, p>0.25).

A total of 968 egg batches were laid in the nests of the 44 males observed between January and July 1986. Spawning activity increased sharply 10 days before full moon (FM-10), peaked at FM-3, rapidly decreased by FM+6, and remained low thereafter (Figure 2). The numbers of egg batches observed in each quarter of the lunar cycle were significantly different from an equal distribution (X^2 = 330.3, p<0.001). Significantly more batches were laid during the FM-10 /FM+6 interval than at other times of the month (t=9.779, p<0.0005). The period between FM-10 and FM+6 was therefore

FIGURE 2 - Distribution of spawning activity of redlip blennies as a function of lunar day, obtained from 6 reproductive periods (February - July 1986). Closed circles represent new moon and open circles, full moon.


PEAK REPRODUCTIVE
PERIOD
% EGG BATCHES LAID
8
7
6
5
4
3
2
1
0
-15
-10
-5
0
5
10
15
LUNAR DAY

defined as the peak reproductive period (PRP). In all months, tides were ebbing at dusk, when hatching is believed to occur, during the PRP's (Figure 3).

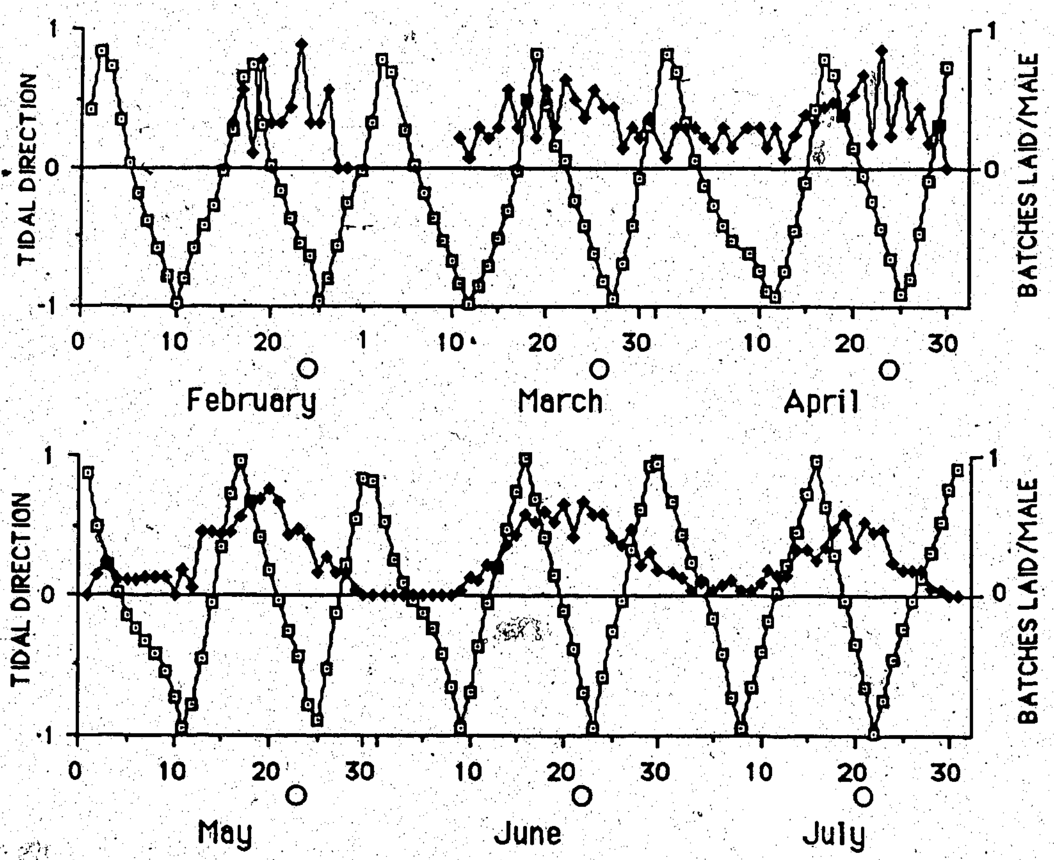
Individual spawning patterns showed that all males spawned during all months of their presence on the study site. Data on the spawning pattern of individual females are less complete but also suggest monthly spawning by all females.

Approaches, visits and spawning were most frequent during the first hour of daylight. Fourty four percent (526/1194) of all approaches led to visits, and 26 % (137/526) of visits observed resulted in spawning. While paternity of egg batches was readily determined, the sequential rather than concurrent observation of groups of blennies on the site made it impossible to witness all spawning events and determine maternity of all batches. Maternity was ascertained on average for 59% of batches deposited on the study site each month.

Thirty one of 44 (70%) individual males obtaining more than one egg batch spawned with 2 or more different females during each peak reproductive period. Quantitative estimates of polyandry are conservative since observations focussed on males rather than on females, and maternity of all egg batches was not ascertained. However, at least 24 of 47 (51%) individual females observed spawned with more than one male in at least one reproductive period. Of these, 83% (20/24) spawned with the same male more than once in at least one reproductive period.

Spawning lasted between 4 and 52 minutes. Males were aggressive to all intruders, including other approaching females, when females were spawning in their nests. Interactions between males were rarely seen. Small males were seen intruding on large males' territories twice in over 200 hours of observation in the morning. Large males were never seen intruding on the territories of males of smaller or similar sizes. Similarly, interactions between females approaching the same male were absent.

FIGURE 3 - Tidal direction (open squares) prevailing daily at dusk (2000 hrs) from January to July 1986. Positive values (0 to 1) indicate flowing tide, and negative values (0 to -1) indicate ebbing tides. Raw tidal data was obtained from Barbados Port Authorities. Daily spawning activity is also shown (closed diamonds) as a function of time. Open circles represent full moon.

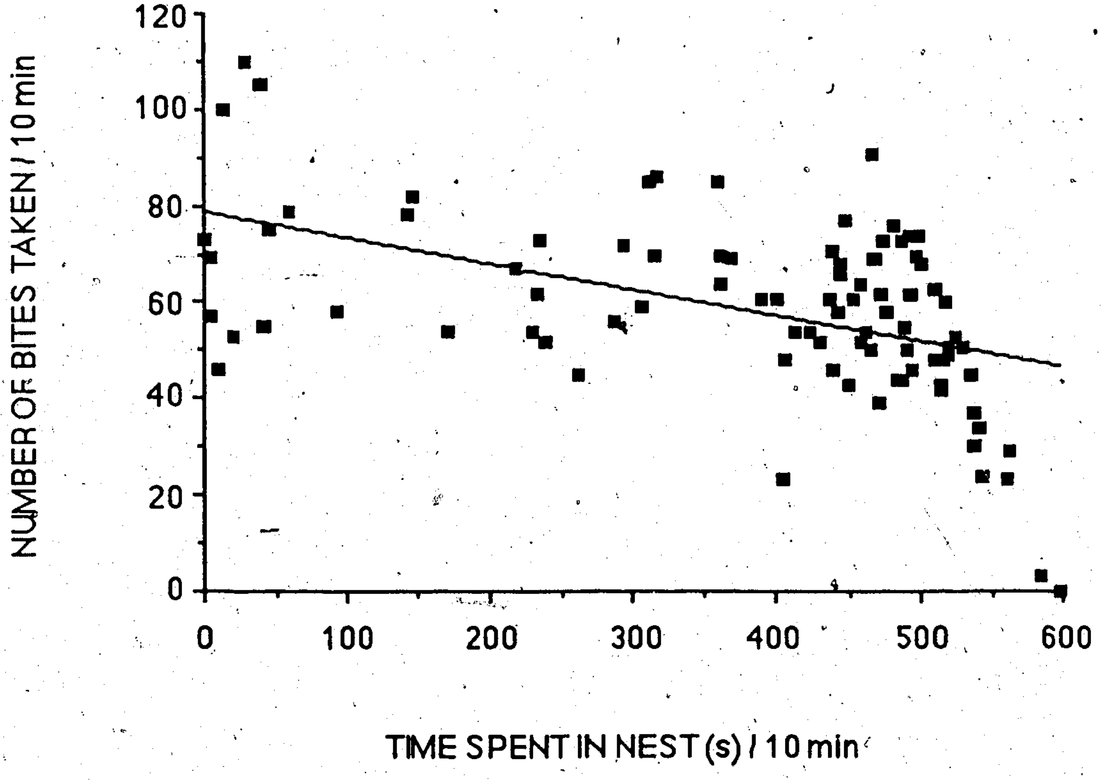

TIDAL DIRECTION
BATCHES LAID/MALE
1
0
-1
1
0
0
10
20
1
10
20
30
10
20
30
February
March
April
TIDAL DIRECTION
BATCHES LAID/MALE
1
0
-1
1
0
0
10
20
30
10
20
30
10
20
30
May
June
July

Spawning activity was also observed outside the peak reproductive periods (Figure 2). Eight individual males extended their reproductive activity between two consecutive PRPs. There was a tendency for the average size of these males (88.25 ± 2.24 mm) to be greater than the average size of males in the study population (84.99 ± 0.99 mm) (t=1.431, 0.05<p<0.1). Moreover, these males had a significantly higher reproductive success (0.69 ± 0.07 batches hatched / guarding day) in the PRP preceding the extended spawning period than the average RS for all other males in the population (0.39 ± 0.03 batches / guarding day) (t=-3.73, p<0.0005).

The ranks of reproductive success of the eight individual males in the PRP following the extended bout of spawning did not correlate with ranks of RS in the PRP preceding it (Spearman rank correlation; r_S=0.09, p>0.5, n=7). This may be attributed to low sample size (see Chapter IV). Three of 7 males had higher RS, 3 had lower RS, and one male had the same RS before and after extended reproduction. These proportions are not significantly different from those found for males that did not reproduce between PRPs (X^2= 1.48, p>0.1). Therefore, extended spawning does not seem to influence short-term reproductive success.

The onset of egg guarding was marked by a change in the behaviour of males with eggs in their nests. The time males spent inside the nest increased significantly when males obtained egg batches (t= 30.31, p<0.0005, n=188). A concurrent decrease in feeding rate was observed. The number of bites taken on the substrate was significantly negatively correlated to the time spent in the nest (Figure 4, r=0.65, p<0.01, p=90), indicating a potential feeding cost to egg guarding. Males guarding eggs were not more aggressive than males without eggs in their nest (t=0.213, p.0.4, n=70). Aggression was measured as the number of aggressive acts given to intruders per 10 min in the afternoon.

FIGURE 4 - Number of bites taken on the substrate as a function of the time spent in the nest by male redlip blennies per 10 minutes. ($y = -0.257x+78.908$)


NUMBER OF BITES TAKEN / 10 min
120
100
80
60
40
20
0
0
100
200
300
400
500
600
TIME SPENT IN NEST (s) / 10 min

DISCUSSION

The population of redlip blennies observed during this study did not show reproductive characteristics different from populations studied previously (Marraro 1978; Labelle 1982). The absence of sexual dimorphism and unity of sex ratio observed during the present study had already been reported for this species (Marraro and Nursall 1983). Although polygyny had been observed and polyandry was suspected in the redlip blenny (Marraro 1978; Labelle 1982), quantitative evidence of polygyny and polyandry have been obtained for the first time. Over 70% of males obtaining more than one egg batch spawned with more than one female. As well, at least 51% of females spawning more than once spawned with at least two different males. The apparently high proportion of females returning to spawn with the same male twice during a reproductive period (83%) is probably biased since females may also have spawned with unobserved males outside the study site or with males that were observed infrequently.

Individual spawning periodicity in *O. atlanticus* was also documented for the first time. All males and females appeared to be reproductively active at each peak reproductive period.

Reproduction in the redlip blenny is closely tied with the lunar cycle (Marraro and Nursall 1983; present study). In this study, a distinct peak in reproduction occurred three days before full moon. Peak hatching was inferred to occur one day after full moon, based on a 4-day incubation period of *O. atlanticus* eggs (Labelle and Nursall 1985). However, the reproductive period was not as discrete was previously described (Marraro and Nursall 1983). A few males (8) were reproductively active for over 60 days, or two full lunar cycles.

Monthly lunar spawning cycles have been reported in many marine organisms (e.g. Luckhurst and Luckhurst 1977; Johannes 1978). Various hypotheses have been proposed to account for the presence of lunar spawning activity in reef fishes (Allen 1972; Johannes 1978; Lobel 1978; Pressley 1980). The hypothesis obtaining most support to date is that lunar spawning cycles minimise larval and egg predation by facilitating their transport offshore away from reef-associated planktivores (Johannes 1978). It is also believed that moonlight might help phototactic larvae avoid benthic predators (Allen 1972; Moyer 1975).

These hypotheses are not mutually exclusive, and both may contribute to an explanation of spawning periodicity in the redlip blenny. Hatching is believed to occur at dusk in *O. atlanticus* (Labelle and Nursall 1985). Tides were ebbing at dusk in the period of peak hatching every month of this study, thus sweeping larvae off the reef. A second period of ebbing tides at dusk consistently occurred around new moon. On the basis of the first hypothesis alone, one could not explain the absence of a second peak of reproduction around new moon. However, larvae of *O. atlanticus* are positively phototactic upon hatching (Labelle and Nursall 1985), and will be attracted to high surface illumination. Peak hatching in redlip blennies thus should occur only at ebbing tides and at maximum moonlight intensity if larval survival is to be maximised.

Reproductive synchrony cued on tides or intensity of moonlight is usually seen as a mechanism used to increase either larval survival or the likelihood that gametes will be fertilised. However, reproductive synchrony, at least in demersal egg-guarding species, may also be used as a reproductive strategy by males constrained by egg-guarding costs. Continuous availability of ripe females is suggested by the long reproductive period of some males. This, associated with a marked spawning peak, suggests that males control the timing of reproduction.

The feeding cost associated with paternal care may limit the number of days a male can spend guarding. If this is so, all male blennies should therefore concentrate their spawning activity in the most optimal period for larval survival, i.e. around full moon. Although nothing prevents males from 'cheating' and spawning outside the peak reproductive period, because of the feeding cost associated with egg guarding, it seems that only large males can 'cheat' and sustain a low feeding rate for extended periods of time. Although there is no evidence that extended reproduction affects deleteriously short-term reproductive success, long-term effects cannot be ruled out. In addition, since spawning outside the reproductive period could have a major effect on larval survival, the apparent increase in reproductive success, measured in number of batches hatched, resulting from extended spawning may not be matched by an equal increase in the number of larvae surviving and recruiting onto the reef, which is the ultimate measure of reproductive success.

CHAPTER IV - MALE REPRODUCTIVE SUCCESS AND FEMALE MATE CHOICE

1

Variance in male reproductive success usually reflects the intensity of sexual selection on males (Wade and Arnold 1980). This variance may be the result of male-male competition, female choice, or both. The objectives of this chapter were: 1) to measure the variance in reproductive success of male redlip blennies; 2) to identify some correlates of male reproductive success; 3) to determine the relative importance of male competition and female choice; and 4) to examine the potential advantages to females of choosing males according to the correlates identified.

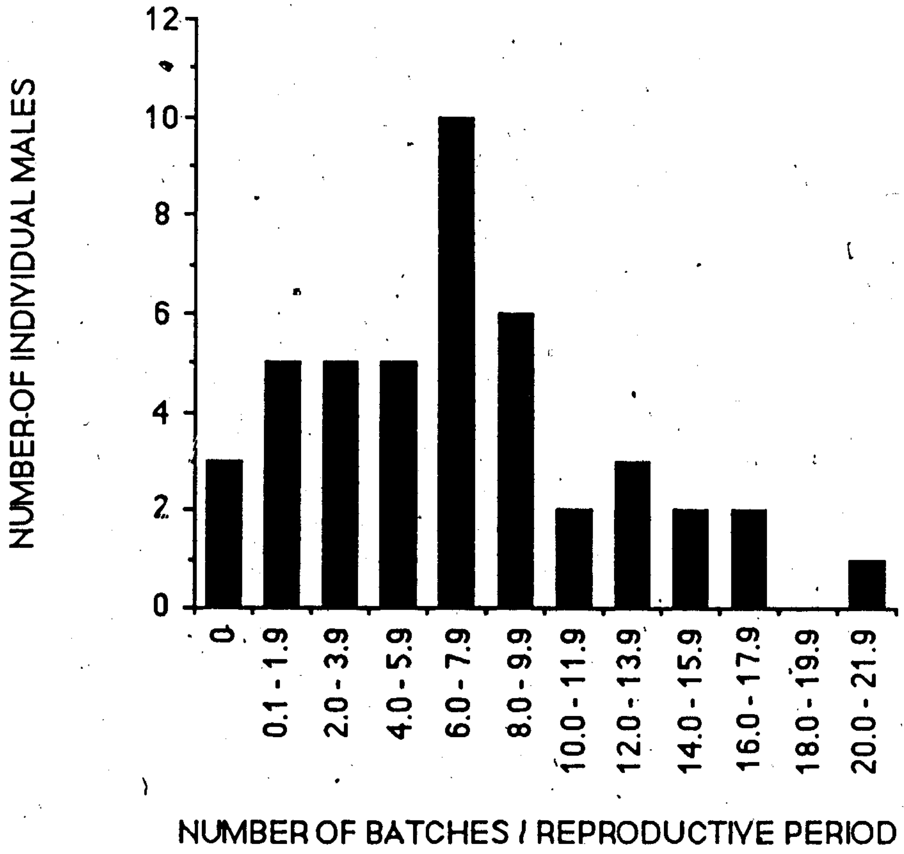
RESULTS

Variance in male reproductive success

To account for egg batches lost before hatching, male reproductive success (RS) was expressed as the total number of egg batches guarded and successfull hatched per reproductive period. Male RS varied between 0 and 21 egg batches per reproductive period (Figure 5) with a mean of 6.9 batches per reproductive period.

Males stayed on the study site for 3 months, on average, before disappearing as a result of predation. The variable length of residency of individual males made comparison of reproductive success between more than two consecutive months difficult. When few males (<15) were present in two or more consecutive months, there was no significant correlation between the ranks of individual males' reproductive success (Spearman rank correlation; $r_S<0.50$ for 3 pairs of consecutive months). However, for June-July, the trend in reproductive success among males was consistent with males with high- and low-success maintaining their relative rank between months ($r_S=0.63$, $p<0.001$, $n=23$)

FIGURE 5 - Distribution of reproductive success of 44 male redlip blennies.


NUMBER OF INDIVIDUAL MALES
12
10
8
6
4
2
0
0
0.1 - 1.9
2.0 - 3.9
4.0 - 5.9
6.0 - 7.9
8.0 - 9.9
10.0 - 11.9
12.0 - 13.9
14.0 - 15.9
16.0 - 17.9
18.0 - 19.9
20.0 - 21.9
NUMBER OF BATCHES / REPRODUCTIVE PERIOD

Correlates of reproductive success

Reproductive success, expressed as the number of batches hatched per guarding day, was separated into two components: mating success (MS), or the number of batches obtained per guarding day, and hatching failure (HF), i.e. the number of batches lost before hatching. The relationship between eleven characteristics of male, nest and territory quality (Table I) and male reproductive success and its two components were examined (Table II).

Male size and three of four nest characteristics were significantly related to male mating success (Table II). However, nest volume and surface area were also significantly correlated to male size (Table III). The effect of male size on mating success was removed by using the residuals of the mating success vs. male size regression. These residuals were then regressed onto volume and surface area. Once the effect of male size was removed, the influence of nest volume and surface area on male mating success became non-significant (volume: r=0.22, p>0.10, n=31; surface area: r=0.31, p>0.10, n=34). The size of the largest nest entrance was not correlated to male size (Table III); thus its effect on MS was independent of male size.

There was a trend for owners of nests with many entrances to obtain more egg batches than other males but this trend was not significant (Table II, 0.1>p>0.05). None of the territory characteristics had a significant effect on mating success.

The second component of reproductive success, hatching failure, was significantly influenced by male size (Table II). Large males lost fewer batches than small males (Figure 6, r= -0.42, p<0.01, n=41). Hatching failure was also significantly correlated with aggression in the afternoon (Table II). Males showing high levels of aggression lost significantly more batches. In addition, there was a tendency for the size of the largest nest entrance to correlate positively with the number of batches lost (Table II). Territory characteristics did not affect hatching failure.

TABLE 1 -Characteristics of male, nest and territory quality measured in the field and included in analysis of mating success, hatching failure and reproductive success.

MALE QUALITY	NEST QUALITY	TERRITORY QUALITY
Male size	Volume	Area
Male aggression	Surface area	Rugosity
	Number of entrances	Number of female neighbours
	Largest entrance area	Number of male neighbours
		Position

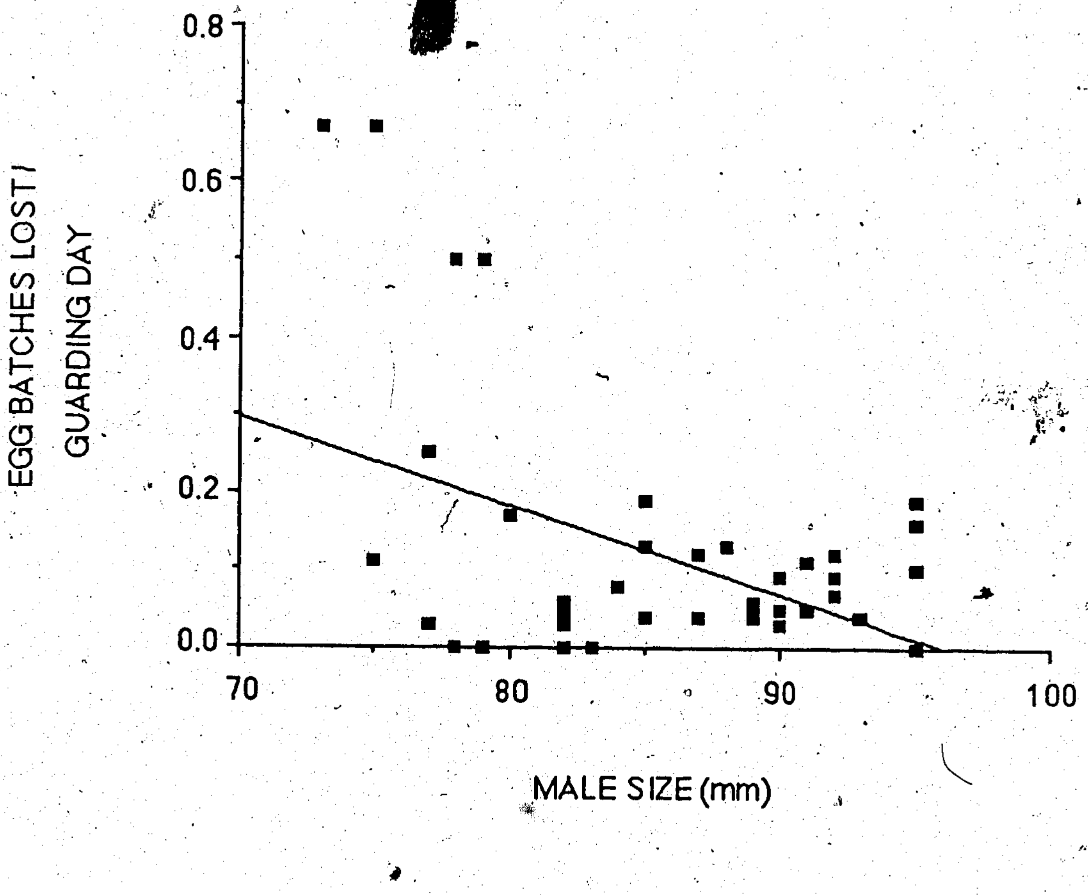
TABLE II -Effects of characteristics of male, nest and territory quality on male mating success, hatching failure and reproductive success. Pearson correlation coefficients and levels of significance are given. Square-root of largest nest entrance area was used in the analysis to normalise the data. Sample sizes are given in ( ). ** = $p<0.005$, * = $p<0.05$, º = $0.1>p>0.05$

VARIABLE	MATING SUCCESS	HATCHING FAILURE	REPRODUCTIVE SUCCESS
MALE QUALITY			
Male size	0.38 (41)*	-0.42 (41)*	0.65 (41)**
Aggression (AM)	0.35 (22)	-0.28 (22)	0.35 (22)
Aggression (PM)	----	0.57 (14)*	0.56 (14)*
NEST QUALITY			
Largest entrance	0.47 (34)**	0.29 (34)º	0.47 (34)*
# entrances	0.28 (37)º	-0.10 (37)	0.28 (37)º
Volume	0.49 (34)*	0.12 (34)	0.49 (34)**
Surface area	0.52 (31)**	-0.18 (31)	0.52 (31)**
TERRITORY QUALITY			
Area	0.12 (26)	0.04 (26)	-0.06 (26)
Rugosity	0.10 (26)	0.17 (26)	-0.05 (26)
Female neighbors	0.23 (37)	0.08 (37)	0.13 (37)
Male neighbors	0.19 (39)	-0.07 (39)	0.23 (39)
Position	0.10 (40)	0.10 (40)	0.004 (40)

TABLE III - Pearson correlation coefficients betwen male size and nest characteristics. Square-root of largest nest entrance area was used in analysis to normalise the data. Sample sizes are given in ( ). Probability levels: ** = $p<0.005$, *=$p<0.05$, º = $0.1>p>0.05$

VARIABLE	LARGEST ENTRANCE	NUMBER OF ENTRANCES	VOLUME	SURFACE AREA
Male size	-0.07 (37)	0.10 (37)	0.34 (37)*	0.53 (32)**
Largest entrance		-0.31 (37)º	0.40 (37)*	0.19 (32)
# of entrances			0.34 (37)*	0.18 (32)
Volume				0.60 (32)**

FIGURE 6 - Number of egg batches lost per guarding day as a function of male size, for 41 individual males. ($y = -0.011x + 1.091$)


0.8
0.6
0.4
0.2
0.0
EGG BATCHES LOST /
GUARDING DAY
70
80
90
100
MALE SIZE (mm)

Through its effects on both mating success and hatching failure, male size was the variable that explained the largest amount of variance in male reproductive success (Table II). Once the effect of male size on reproductive success was removed, nest volume and surface area did not explain a significant amount of variance in male RS (volume: $r=0.08$, $p>0.25$, $n=34$; surface area: $r=0.23$, $p>0.25$, $n=31$). The size of the largest nest entrance was also significantly correlated with male RS (Table II). Reproductive success increased as the size of the largest nest entrance increased. None of the territory characteristics measured affected reproductive success significantly (Table II).

Female mate choice or male competition?

Interactions between males were rarely observed during morning observations (Chapter III), and only occurred in the context of interactions with neighbours in the afternoon. It is therefore unlikely that direct male competition, in the form of overt aggression or interference, is a major source of variance in male mating success.

However, there was evidence to suggest that females were actively choosing their mates. The pattern of approaches of males by females was significantly different from random ($X^2 = 17.16$, $p<0.001$) and showed that females approached preferentially males that were larger than themselves (Figure 7). The largest females were the largest blennies in the population, thus could not approach males larger than themselves. They were therefore excluded from the analysis.

Large males were also approached by females more often than small males (Figure 8, $r= 0.62$, $p<0.005$, $n=23$). To control for the longer reproductive period of larger males (see below), the analysis was repeated using only data obtained on days when all males on the site were reproductively active. The rate of approaches by females was still correlated with male size ($r=0.45$, $p<0.05$, $n=20$), indicating that when all males were available, females preferentially approached large males. However, the number of visits by females to males' nests / 30 minutes was not correlated with male size ($r=0.24$, $p>0.10$, $n=25$). Rates of female visits may have been influenced by courtship intensity,

FIGURE 7 - Size of males approached as a function of female size. The line (slope = 1) represents theoretical choice by females for males of equal size.

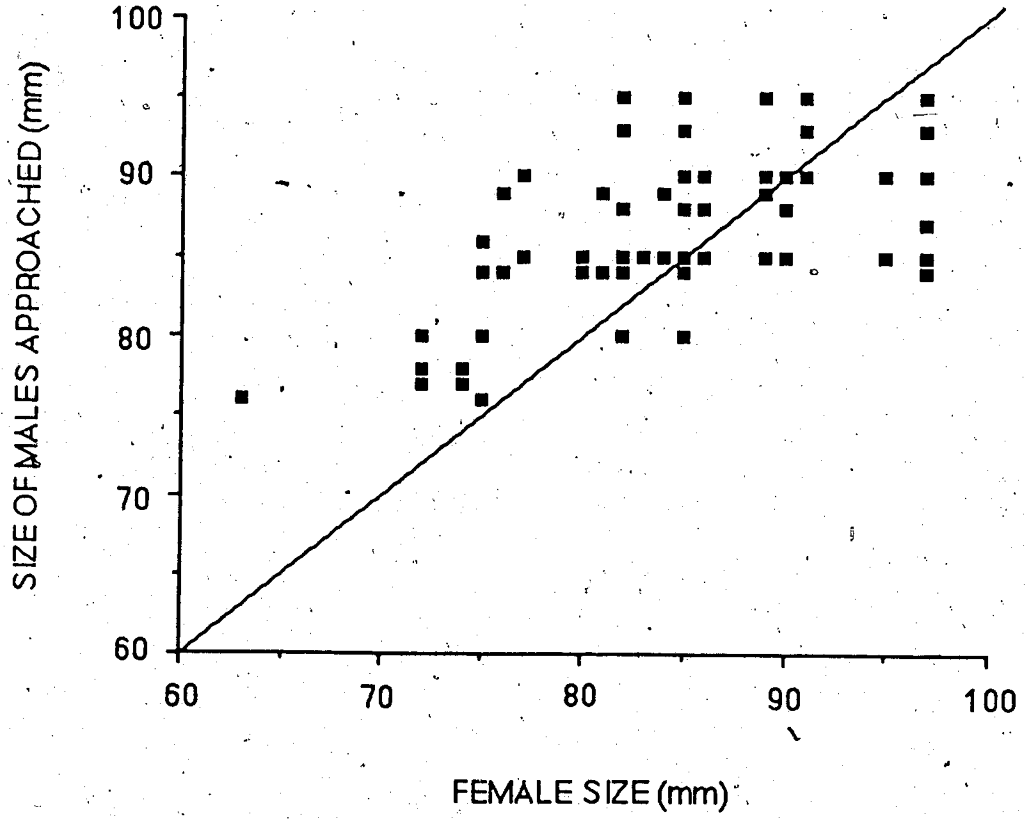
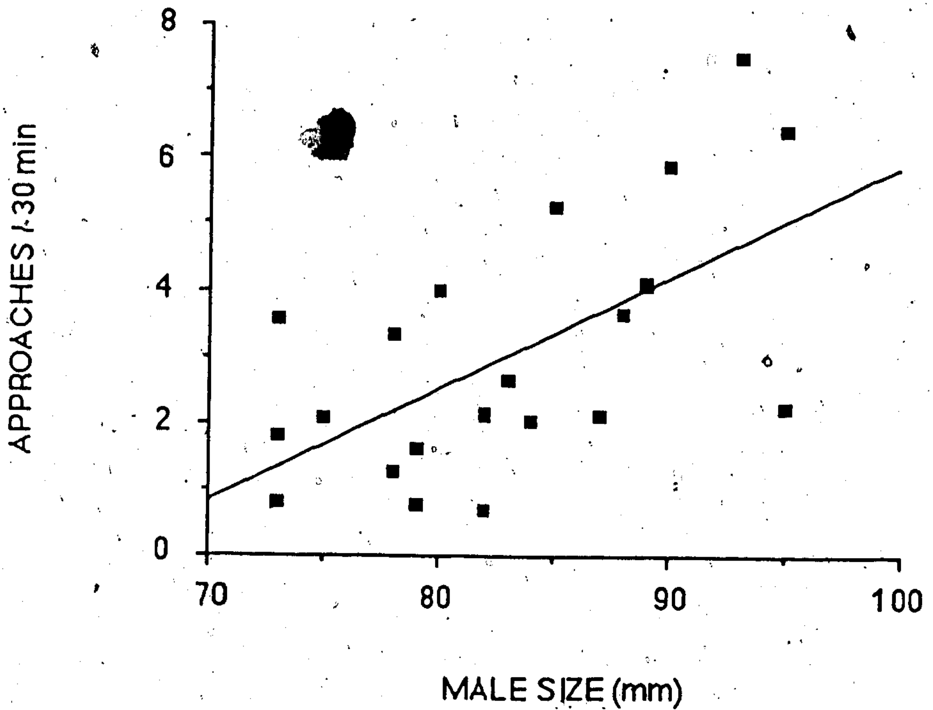

100
90
80
70
60
SIZE OF MALES APPROACHED (mm)
60
70
80
90
100
FEMALE SIZE (mm)

FIGURE 8 - Number of approaches by females per 30 minutes as a function of male size, for 23 individual maes. ($y = 0.168x - 10.946$)


8
6
4
2
0
70
80
90
100
APPROACHES / 30 min
MALE SIZE (mm)

which was not quantified in this study. The outcome of visits (i.e. spawning or no spawning) was influenced by male size. Large males obtained significantly more egg batches per guarding day than small males (Figure 9, $r=0.38$, $p<0.025$, $n=41$). This suggests that females prefer to spawn with large males.

Female size and egg batch size were significantly correlated (Figure 10, $r=0.72$, $p<0.001$, $n=41$). The residuals of each point on Figure 10 were significantly correlated with male size ($r=0.33$, $p<0.05$, $n=41$), indicating that once the effect of female size was removed, male size explained a small but significant proportion of the variance in egg batch size. Thus, females may be able to vary the number of eggs they release according to the size of the males with which they spawn, and will release more eggs when spawning with a large male than with a small male. The size of egg batches released was not correlated with nest surface area ($r=0.24$, $p>0.1$, $n=34$), nor with the number of batches already present in the nest ($r=0.16$, $p>0.25$, $n=37$).

Rates of approaches and visits by females were not correlated with the size of the largest nest entrance (approaches: $r=0.09$, $p>0.25$, $n=20$; visits: $r=0.25$, $P>0.25$, $n=21$). However, males with largest nest entrances obtained more batches than other males (Table II).

Why choose particular males?

Large males lost fewer egg batches than small males (Figure 7, Table II). Males having nests with large entrances tended to lose more eggs than males having smaller nest entrances.

The last egg batch deposited in any nest at the end of a reproductive period had a greater probability of disappearing before hatching than batches laid earlier during the reproductive period (hatching success of last batches: 44/99 or 44%; hatching success of all other batches: 782/869 or 90%; $X^2=227.98$, $p<0.001$). There was no relationship between the hatching probability of last batches and male size ($r=0.15$, $p>0.25$, $n=41$).

Male aggression against intruders in the morning was significantly correlated with male size ($r=0.49$, $p<0.05$, $n=25$). Aggressive acts were directed almost exclusively against approaching females. Morning aggression rate was also correlated with rate of female approaches to

FIGURE 9 - Number of egg batches obtained by males per guarding day as a function of male size, for 44 individual males. (y= 0.795x - 54.219)

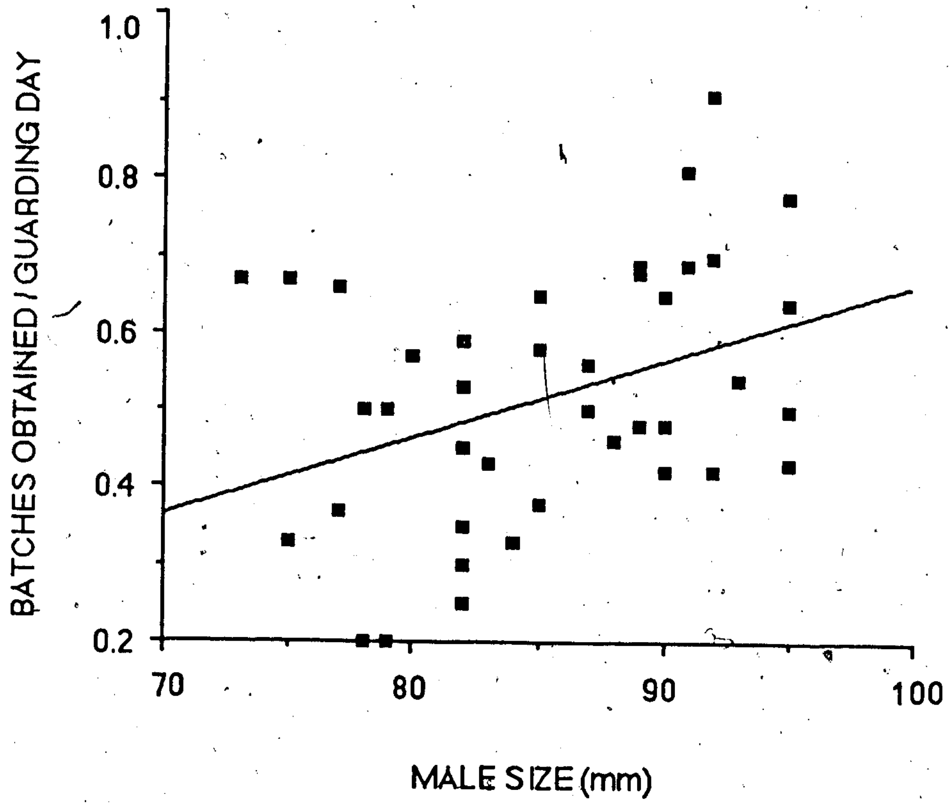
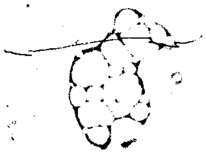
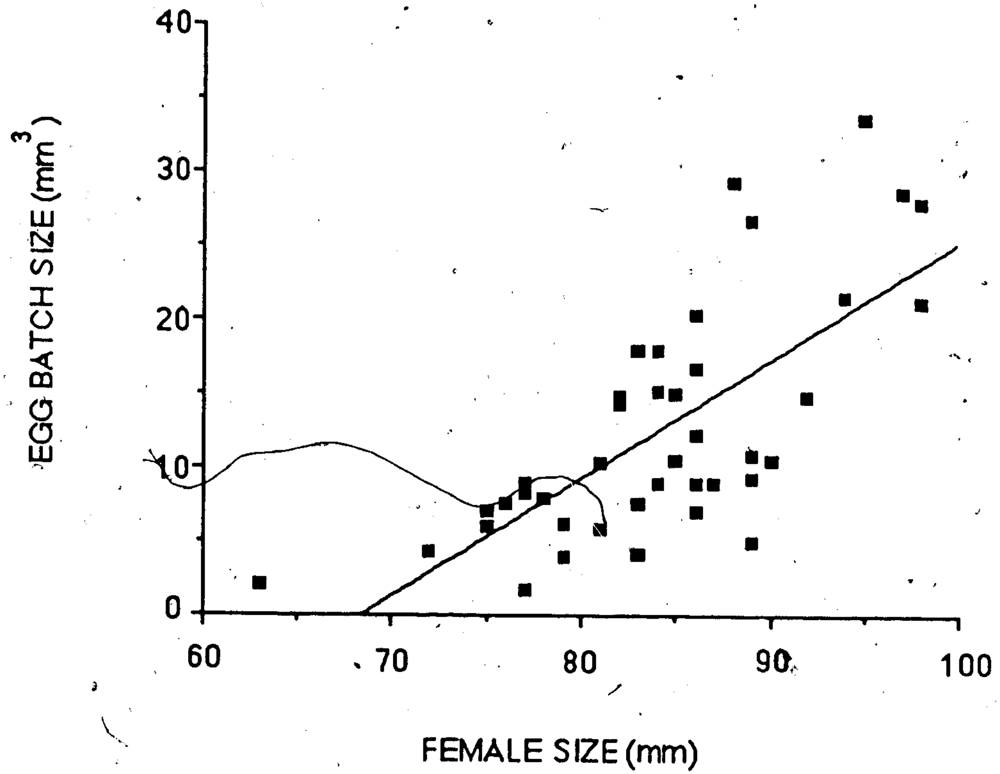

1.0
0.8
0.6
0.4
0.2
BATCHES OBTAINED / GUARDING DAY
70
80
90
100
MALE SIZE (mm)

FIGURE 10 - Size of egg batches as a function of female size. (y = 0.795x - 54.219)




40
30
20
10
0
EGG BATCH SIZE (mm^3)
60
70
80
90
100
FEMALE SIZE (mm)

males' territory (Figure 11, r=0.70, p<0.005, n=23). Once the effect of approach rate was removed, there was no significant relationship between aggression and male size (r=0.06, p>0.25, n=23). High aggression rates by large males in the morning may thus simply result from high intrusion rates, and hence not be related to more intense egg defense by large males.

There was no relationship between aggression rate and male size in the afternoon (r=0.20, p>0.25, n=14). High aggression rate appears to be deleterious to efficient egg guarding. Aggression rate was significantly correlated with the number of egg batches lost (Table II). In addition, the total number of aggressive acts per observation period was significantly correlated with the size of the largest nest entrance (Figure 12, r=0.68, p<0.01, n=17), and owners of nests with large nest entrances tended to lose more batches than males having nests with smaller entrances (Table II). Since aggression rate reflects the rate of intrusion on males' territories, nests with large entrances may have been more attractive to predators.

The time spent in the nest by guarding males was correlated with male size (Figure 13, r=0.54, p<0.01, n=22). The time spent in the nest by males was not related to the number of egg batches present in the nest (One-way ANOVA, F=1.193, p>0.25, DF=178).

The length of the guarding period, expressed as number of guarding days per reproductive period, was significantly related to male size (Figure 14, r=0.59, p<0.0001, n=44). Large males obtained their first egg batch earlier (r=0.49, p<0.01, n=37), and stopped guarding later than small males (r=0.49, p<0.01, n=37).

FIGURE 11 - Number of aggressive acts given by males in the morning as a function of number of approaches by females to males' territories. ($y = 0.225x - 0.021$)

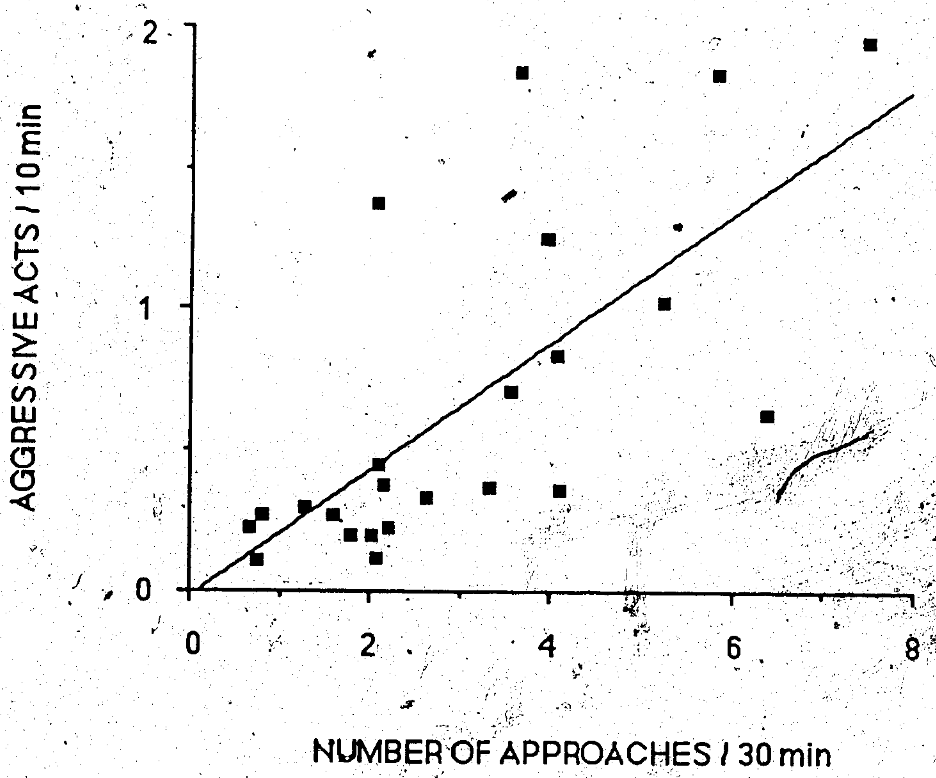

AGGRESSIVE ACTS / 10 min
2
1
0
0
2
4
6
8
NUMBER OF APPROACHES / 30 min

FIGURE 12 - Average number of aggressive acts given per 10 minutes in the afternoon as a function of the square-root of the size of the largest nest entrance, for 17 individual males.
($y = 0.198x - 0.193$)

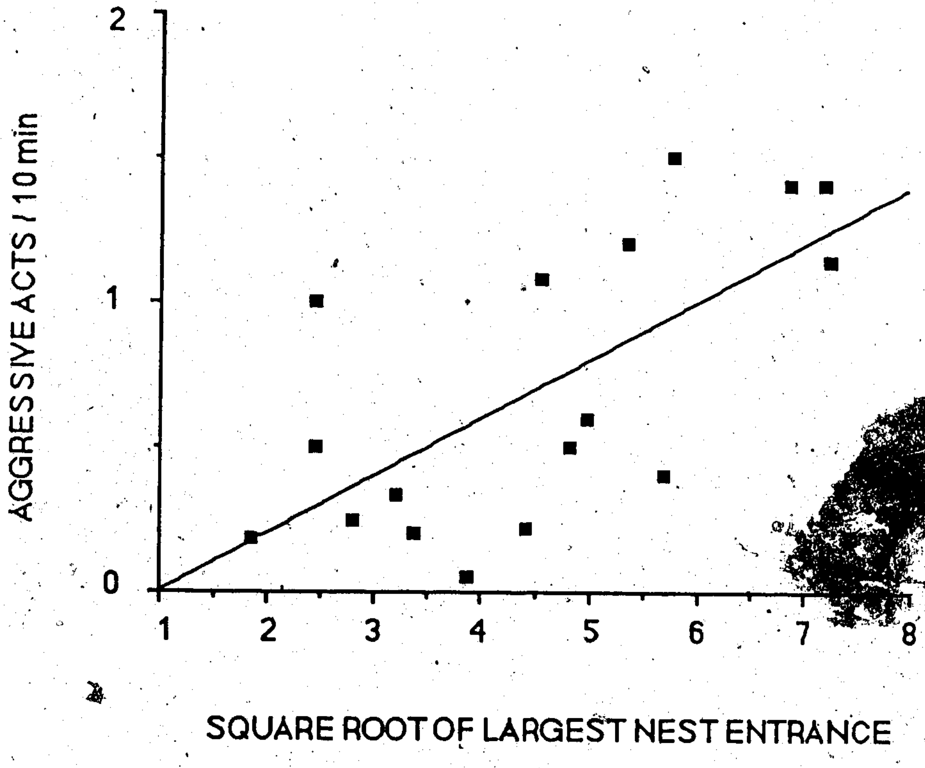

AGGRESSIVE ACTS / 10 min
2
1
0
1
2
3
4
5
6
7
8
SQUARE ROOT OF LARGEST NEST ENTRANCE

FIGURE 13 - Time spent in the nest by males per 10 minutes [illegible] a function of male size, for 22 individual males. (y = 7.278x - 188.407)

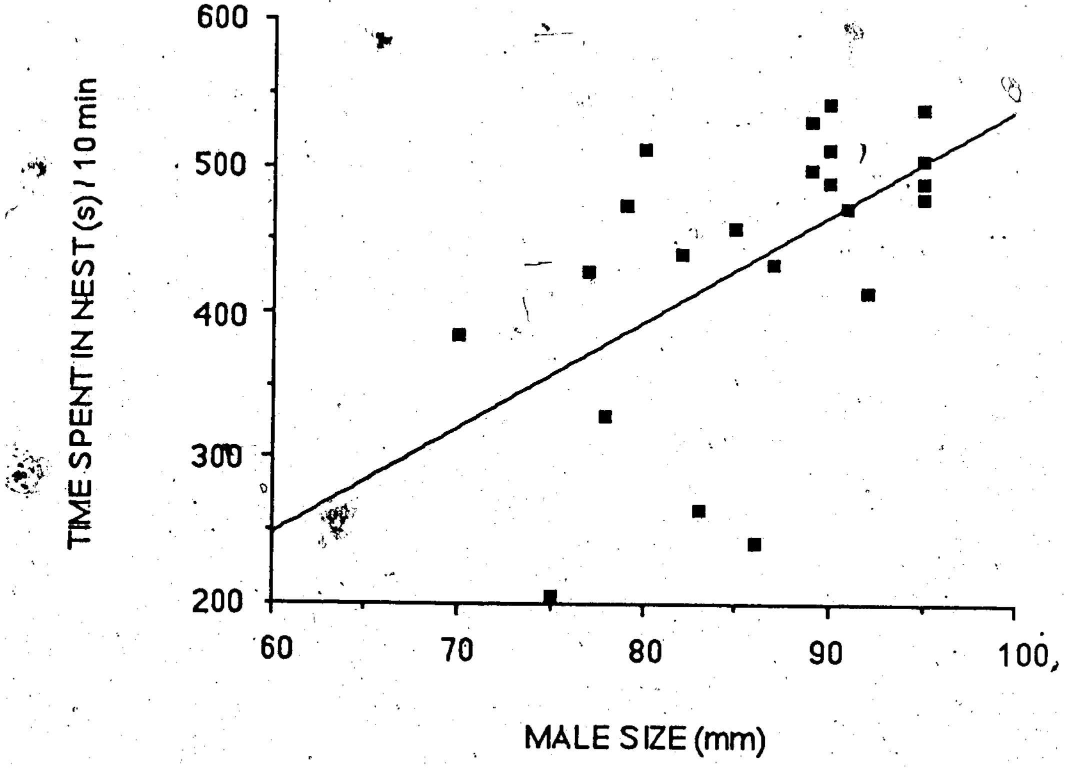
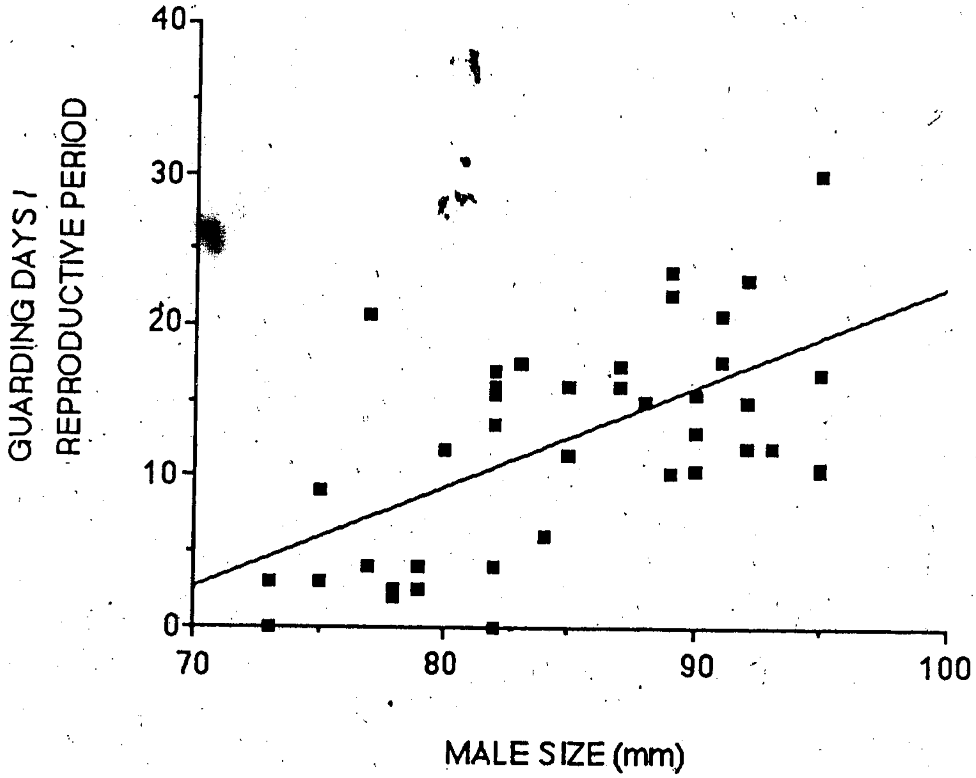

600
500
400
300
200
TIME SPENT IN NEST (s) / 10 min
60
70
80
90
100
MALE SIZE (mm)

FIGURE 14 - Number of guarding days per reproductive period as a function of male size, for 44 individual males. ($y = 0.667x - 44.055$)


GUARDING DAYS /
REPRODUCTIVE PERIOD
40
30
20
10
0
70
80
90
100
MALE SIZE (mm)

DISCUSSION

Male reproductive success: Variance and Correlates

Reproductive success of individual male redlip blennies was variable. Although the differences in reproductive success could be consistent between two consecutive months, it was impossible to determine whether these short-term differences reflect variance in lifetime reproductive success.

Reproductive success was separated into two components: mating success and hatching failure, to determine if different factors governed the ability to obtain and to hatch egg batches. Mating success of individual males was related to male size and to one nest characteristic. Size-dependent mating success has been reported in other egg-guarding teleosts. In damselfish (Schmale 1981), mottled triplefin (Thompson 1986), stickleback (Sargent and Gebler 1980), mottled sculpin (Downhower and Brown 1980), and in various cichlids (Perrone 1978; Noonan 1983; Keenleyside et al. 1985), large males obtained more egg batches than did small males. Since size is often correlated with age in teleosts (e.g. Grant and Colgan 1983), age may have also been a factor influencing male reproductive success. However, age could not be determined during this study.

Territoriality is often associated with male parental care, and the effects of territory quality have been considered in numerous studies. However, results conflict as to the importance of territory quality to male reproductive success (Jones 1981; Kodric Brown 1983; Thompson 1986). The characteristics of territories measured in this study: territory area, rugosity, number of male and female neighbours, and the position of territories on the reef, did not have a significant effect on male RS. The effect of territory position could still be important to reproductive success when measured in terms of larval survival since the distance of the territory to the closest seaward edge may affect the probability of larvae being successfully swept off the reef, away from planktivorous predators (Johannes 1978). However, the lack of importance of territory characteristics on reproductive success is supported by the fact that territory shifts by male blennies were not observed (Nursall 1977;

pers.obs.); thus males did not seek to improve the quality or position of their territory.

Despite the obvious importance of nests to demersal egg-guarding species, few researchers have attempted to quantify nest suitability. Nest depth in the water column in the cichlid, *Cichlasoma maculicauda* (Perrone 1978) and concealment of artificial nests in sticklebacks, *Gasterosteus aculeatus* (Sargent 1982) have been found to influence male RS. However, nest dimensions have never been quantified before, nor has their effect on reproductive success been evaluated. This study provides evidence that at least one nest characteristic, the size of the largest nest entrance, was correlated with male mating success. Males having nests with a large nest entrance area obtained more egg batches than other males. The size of the nest entrance may influence water circulation inside the nest may and could be critical in insuring proper oxygenation of the eggs.

In the damselfish, *Eupomacentrus partitus* (Schmale 1981) and the protogynous wrasse, *Pseudolabrus celidotus* (Jones 1981), display rate by males significantly affected reproductive success. Display rate was not quantified during this study, but qualitative observations suggested that intensity of courtship varied among males, and could have influenced male mating success.

The second component of reproductive success, hatching failure, was also affected by male size and by the size of the largest nest entrance. Since increasing male size resulted in both increased number of batches obtained and reduced number of batches lost, male size was the variable which accounted for the largest amount of variance in male reproductive success. Alternately, the size of the largest nest entrance had opposite effects on each component of male reproductive success. Large entrances resulted in higher mating success but also increased number of batches lost. Males may therefore face a tradeoff when selecting a nest. However, since the overall effect of increasing size of the largest nest entrance is an increase in reproductive success, the effect of nest entrance on mating success may override its effect on hatching failure.

Male competition or female choice?

Although small males are physiologically able to spawn, they usually obtained fewer batches than larger males. In other species, that is often because aggressive dominance of larger males results in large males controlling better territories/oviposition sites (Kodric Brown 1983; Thompson 1986). In such situations, apparent female choice for larger males may be confounded by the ability of large males to obtain high quality territories. That may not be the case for redlip blennies, which grow on the territories where they settled as juveniles (Nursall 1977). There is no 'floating' population of adults waiting for space to become available on the reef and competition for territories is absent among adult fishes. In addition, this study has shown that territory characteristics did not influence reproductive success. Reproductive interference by large males is also unlikely since male-male interactions were rare during reproductive hours, and only occurred in the context of interactions between neighbours at other times of the day. Intrasexual selection is thus apparently absent in the form of male competition for high quality territories or as intermale competition for access to females. The variation observed in reproductive success is therefore probably determined largely by female choice.

The initial choice of mates is done by females which leave their territories to visit those of males. Females approached males larger than themselves more often than smaller males, indicating a preference by females for large males. In addition, large males obtained more egg batches than small males. Further evidence for female choice was the tendency for females to deposit larger egg batches with large males.

Why choose particular males?

Female mate choice for large males in territorial egg-guarding teleosts has been well documented (Perrone 1978; Downhower and Brown 1980; Schmale 1981; Grant and Colgan 1983; Noonan 1983; Keenleyside et al. 1985; Thompson 1986). However, the reasons for choosing large mates have been investigated only in two freshwater species. Downhower and Brown (1980) suggested that female mottled sculpins prefer large males because their egg batches have a higher probability of hatching. They identified three mechanisms by which large males could improve the survival of egg batches: large males abandon their nest less frequently than small males; egg losses to cannibalism or predation occur less often when a large male guards a nest; or large males remain with the fry for longer periods after hatching. Similarly, Grant and Colgan (1983) found that older male johnny darters were more aggressive than small males, had a higher hatching success, and were chosen by females more often.

Female blennies may prefer large males because they lose fewer egg batches than small males. Large males can achieve lower hatching failure either by possessing good nests or by being good egg guardians. A good nest may be defined as one in which egg survival is high. The size of the largest nest entrance was the only variable measured which affected the number of batches lost to predation. For a given male size, owners of nests with large entrances tended to lose more eggs than those with smaller entrances. Therefore, a good nest, in terms of egg survival, is one with a small entrance. All large males, however, did not possess such nests. Therefore, large males did not lose fewer eggs because they possess 'better' nests, considering the variables measured in this study.

Large males may be better egg guardians, either through aggression towards potential predators, or passively, by remaining close to the eggs/nest. Large male blennies were more aggressive than small males during morning observations. Aggressive acts were directed mainly towards approaching females. However, large males also had more females approaching and intruding on their territories than small males. Once the effect of approaches was removed, there was no relationship between male size and aggression. High rates of aggression by large males in the morning may therefore reflect higher intrusion rates on large males' territories rather than more active nest defense. In the afternoon, larger males were not more aggressive than small males. Note that the intensity of aggression was not quantified and may have differed between males. However, males whose nests had large entrance areas were more aggressive than other males. The pattern of batch loss suggested that nests with large entrance area tended to be more vulnerable to predation. High rates of aggression by owners of these nests may therefore reflect the higher attractiveness of these nests to egg predators. Males were more aggressive to intruders when guarding than small males in mottled sculpins (Brown 1981), in johnny darters (Grant and Colgan 1983), and in damselfish (Schmale 1981). However, in those studies, no attempts were made to measure rates of intrusion on males' territories or nest vulnerability.

If aggression rates reflect ability for egg guarding, large male blennies were not better guarders than small males. In fact, high levels of aggression by males resulted in higher hatching failure, indicating that egg defense is probably not achieved by this means in *O. atlanticus* . However, large males did spend more time in their nests than small males. This form of passive egg guarding may be an efficient method to prevent predators from entering the nest.

Finally, female blennies may also prefer to spawn with large males because those males are less likely to abandon their nests. Males may abandon their nests because of the cost associated with egg guarding (Chapter III). In redlip blennies, the last batch deposited in a male's nest had a high probability of disappearing. Females should therefore avoid being the last to deposit an egg batch in a male' s nest. Since large males end their reproductive season significantly later than small males, females may decrease the probability of depositing a last batch by choosing to spawn with large males.

CHAPTER V - MALE MATE CHOICE

Although most of the variance in male reproductive success was ascribed to female mate choice (Chapter IV), this may not be the only force shaping the mating system of *O. atlanticus* . Rejection of some females by males has been observed in an earlier study of the redlip blenny (Marraro 1978), suggesting that male mate choice may also be present.

RESULTS

The sizes of males and females in spawning pairs were significantly correlated (Figure 15, $r=0.75$, $p<0.001$, $n=37$). This could result from mate choice by either or both sexes. However, there was evidence that males actively choose their mates. Sufficient data on rates of rejection by males of approaching females were available for only 9 males since not all approaching females were identified, and since only rejections occurring when males did not already have a female visiting their nest were considered. The average size of females accepted in a nest after an approach was greater than the average size of females chased following an approach (Figure 16). The difference between each pair of means was significant for all males ($p<0.05$), except for the largest male, indicating that males were selective and allowed large females to visit their nests more readily than small females.

The rate of female approaches to males' territories per 30 minutes of observation was significantly correlated with male size (Figure 8). Although egg batch size was significantly correlated with female size (Figure 10), spawning time, or the time required by a female to deposit an egg batch in a male's nest, was not correlated with female size ($r=0.06$, $p>0.25$, $n=57$).

FIGURE 15 - Average size of females as a fun[illegible] of male size in spawning pairs. Standard erro[illegible]out the means are given. (y = 0.80x + 14.87)

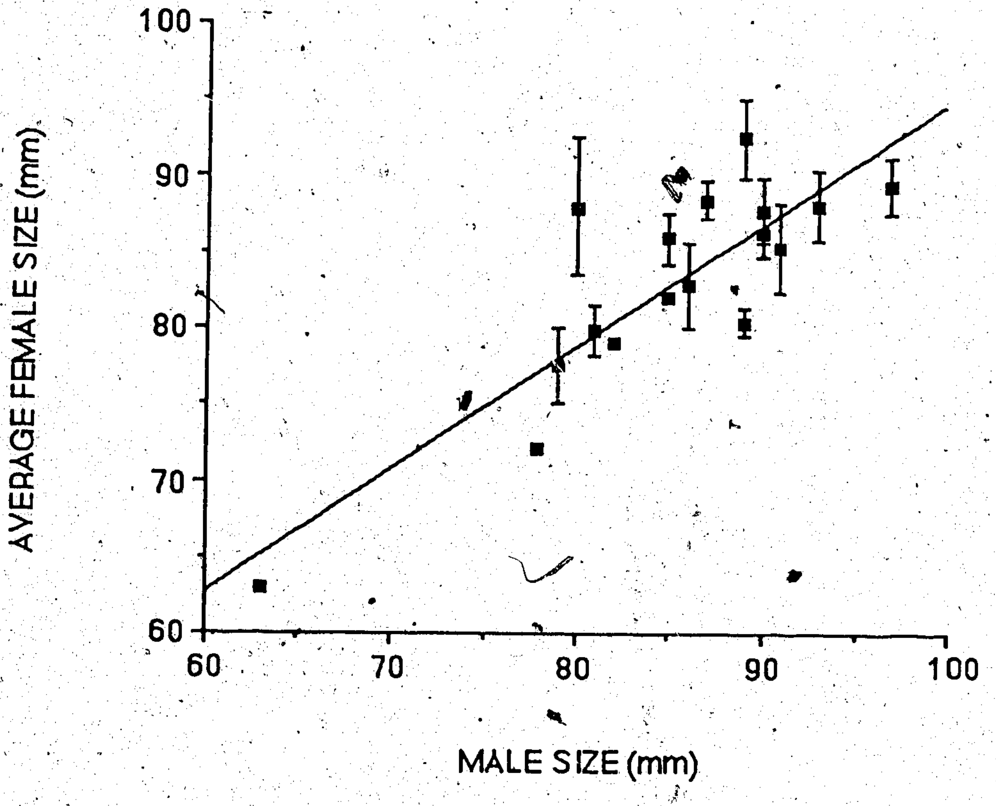
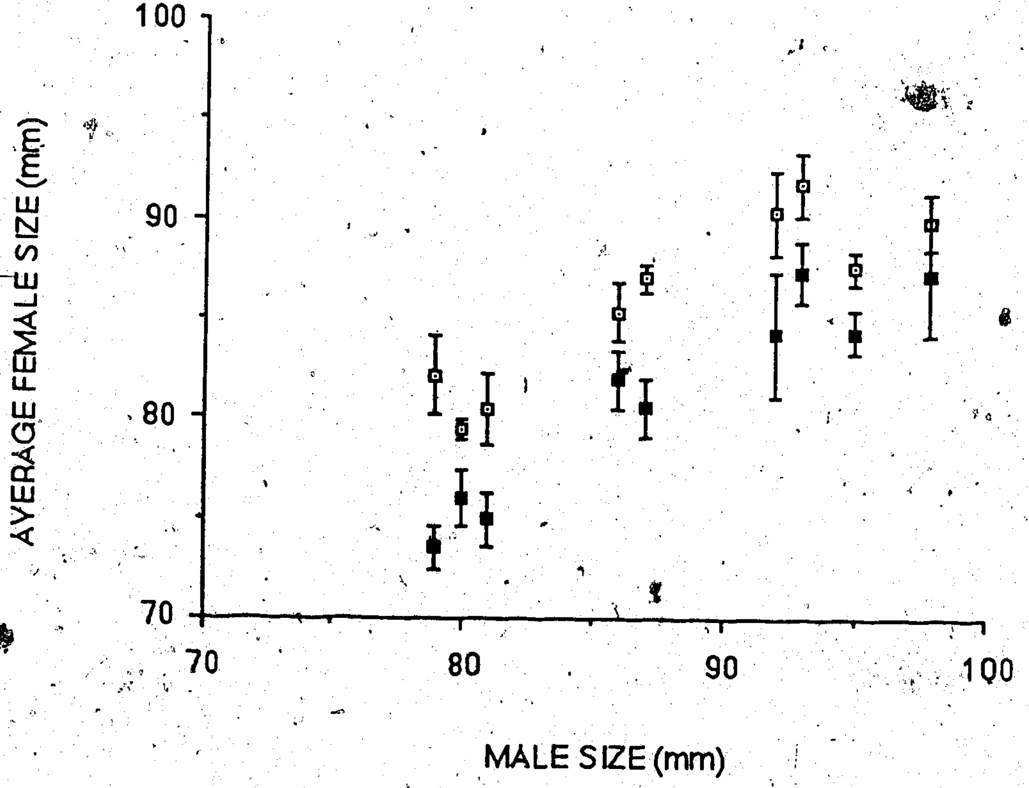

100
90
80
70
60
60
70
80
90
100
AVERAGE FEMALE SIZE (mm)
MALE SIZE (mm)

FIGURE 16 - Average size of females approaching males as a function of male size, for 9 individual males. Open squares represent females accepted into the nest. Closed squares represent females rejected. Standard errors about the means are given.


100
90
80
70
70
80
90
100
AVERAGE FEMALE SIZE (mm)
MALE SIZE (mm)

DISCUSSION

In redlip blennies, the sizes of males and females in spawning pairs were significantly correlated. In the absence of intrasexual competition, that can only result from mate choice by both sexes. Recent laboratory experiments suggest that mate choice by males may occur in fishes. Male sticklebacks (*Gasterosteus aculeatus*) preferentially courted the larger female and the larger female dummy when presented with pairs of females or dummies of unequal sizes (Rowland 1982; Sargent et al. 1986). Similarly, male pupfishes (*Cyprinodon macularius*) courted and spawned more often with larger females in a free-choice situation (Loiselle 1982). In the coho salmon (*Oncorhynchus kisutch*), a species with female parental care, males distributed themselves among females in direct proportion to female quality, devalued by male competition (Sargent et al. 1986). In the latter two cases, male parental care is not extensive, but in all cases, female quality varies significantly.

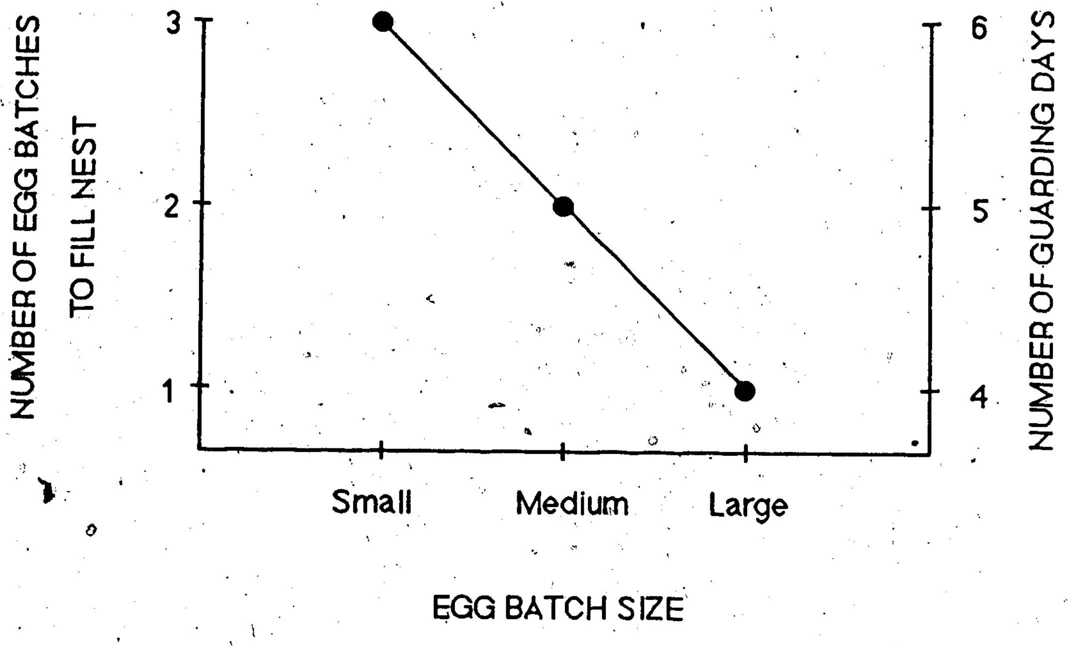
The results of this study indicate that male redlip blennies also preferred to spawn with large females and actively rejected smaller females. Fecundity increases with body size in female blennies (Labelle 1982), following the pattern described for female teleosts (Bagenal 1967). This affects the size of single egg batches deposited by females, which increases with increasing female body size, providing high variance in female quality which males may use to discriminate among mating partners.

Dewsbury (1982) suggested that males may gain by trying to mate with high quality females if they are limited in the number of females with which they can successfully mate. One type of limitation to the number of matings a male can achieve is sperm depletion, which has been documented in the lemon tetra, *Hyphessobrycon pulchripinnis* (Nakatsuru and Kramer 1982). In that species, males produce multiple ejaculates every day, a rare occurrence in redlip blennies. Male blennies observed in this study seldom obtained more than one egg batch per day. However, in *Blennius basiliscus* , a Mediterranean relative of *O. atlanticus* , males must maintain a sperm suspension inside their nests to insure fertilisation of eggs before they attach to the nest walls (Heymer 1985). That process could also occur in redlip blennies, possibly limiting the time a male can remain reproductively active or the number of females with which a male can mate.

Spawning and guarding costs may also explain why males should spawn with large females. If reproductive return obtained by males after a mating investment is defined as the number of eggs obtained per mating devalued by the number of mating opportunities lost while spawning, the time spent spawning could be a significant factor influencing male choice. Time invested per female was an important criterion of male mate choice in the amphipod, *Gammarus lawrencianus* (Hunte et al 1985). Since spawning time and female size were not correlated in blennies, large female will deposit more eggs per unit time than small females. Within size classes, males will lose a similar number of mating opportunities when accepting a female into their nests to spawn. However, large males are approached by potential mates more often than small males, so may have more mating opportunities to lose than small males. This cost to larger males relative to small males may be offset by the fact that females tend to lay larger egg batches in large males' nests.

Male blennies incur at least one significant cost when guarding. There is a feeding cost associated with egg guarding (Chapter III), which could be translated into costs to growth and future reproductive success. Male blennies should therefore attempt to maximise their reproductive success while minimising the time spent guarding and, hence, the cost of guarding. This goal could be achieved by mating with large females to obtain as many eggs as possible on the same day so as to decrease the time spent guarding (Figure 17). Since male redlip blennies rarely obtain more than one egg batch per day, the number of eggs obtained per day may be increased by increasing the size of egg batches obtained through preferential mating with large females. The variation in egg batch size (Chapter IV) appears to be sufficient for the model to be realistic.

FIGURE 17 - Model of the effect of egg batch size (or female size) on the number of batches necessary to fill a hypothetical nest and on the number of guarding days necessary to hatch all batches in the nest.


NUMBER OF EGG BATCHES TO FILL NEST
3
2
1
6
5
4
NUMBER OF GUARDING DAYS
Small
Medium
Large
EGG BATCH SIZE

CHAPTER IV - GENERAL DISCUSSION

In most systems, the process of sexual selection is a mixed one in which both intra- and intersexual selection operate and the effects of each are difficult to separate (Maynard Smith 1978). The presence of variance in reproductive success in one sex usually suggests that sexual selection is acting on that sex. In this study, all male blennies did not do equally well, large males obtaining and hatching more egg batches than smaller males. Although reproductive success of females was not measured during this study, variance in reproductive success may also be expected on the basis of the size-related fecundity observed in female redlip blennies (Marraro 1978; Labelle 1982). Although size appears to be a major determinant of reproductive success for both males and females, it is unlikely that individuals of a same sex will achieve a similar lifetime reproductive success, given the variable lengths of residency, hence of lifetimes, of blennies observed on the study site, and possible variation in growth rates within size classes.

Differences in reproductive success among males may arise as a result of contests between males (Trivers 1976; Howard 1978; Sargent and Gebler 1982). In redlip blennies, male-male interactions during periods of reproductive activity were rare. This does not exclude the possibility that competition between males may assume a more subtle form, such as increased courtship displays by males when a female approaches a neighbouring male. However, the influence of male interactions probably accounts for little of the variance in male reproductive success.

The relegation of male interactions to a minor influence on mating success is often taken as evidence that female choice has a major effect on the mating distribution (Gibson and Bradbury 1986). Because female blennies initiate the reproductive process, they appear to have considerable control over the allocation of matings. Empirical evidence of female choice was obtained. Females approached, spawned, and deposited larger egg batches with large males more often than with small males, thus exercising mate choice.

Direct competition between females for access to males was not observed and is not believed to have influenced female reproductive success significantly. However, males were observed exercising mate choice by rejecting females smaller than the females they accepted into their nests. Intersexual selection may therefore be the major source of variance in both male and female reproductive success.

To act as a selective force, mate choice must influence the reproductive success of the individual choosing. Reproductive success of male redlip blennies may be divided into two components: 1) the number and size of batches obtained; and 2) the hatching probability of each batch of eggs. The second component is a direct function of male size. Female reproductive success may, in turn, be separated into two similar components: 1) the number of eggs produced (which includes number and size of batches produced); and 2) the hatching probability of each egg produced. The first component of female fitness is a direct function of female size.

Male choice may influence the number of batches obtained, and will definitely influence the size of batches obtained, since males prefer to spawn with larger females, and large females produce larger egg batches. Similarly, female choice will enhance female reproductive success since females prefer to spawn with large males which lose fewer egg batches than small males. Choosing mating partners will therefore affect directly an individual's reproductive success, but full benefits will be realised only if both males and females mate with the largest possible members of the opposite sex.

However, there are factors which may restrict the range of choice in mating partners available to males or females. Time and distance have been identified as constraints on female choice in the mottled sculpin *Cottus bairdi* (Brown and Downhower 1983). To delay spawning when searching for the 'ideal' male may be costly if egg batches laid later have a lower probability of hatching (Downhower and Brown 1980). Similarly, in redlip blennies, the last batch laid in a male's nest had a higher probability of disappearing before hatching than batches laid earlier in that nest. Distance and the risks involved in travelling to males' territories may also limit the number of males a female can sample. Errors in discrimination resulting from these constraints may be less costly for female blennies than for mottled sculpins since blennies, unlike sculpins, produce multiple batches (Labelle 1982), and can thus divide their monthly reproductive output among various males.

Another constraint that reduces the number of potential mating partners for females is male choice. Mate choice by males will be similarly constrained by female choice, since males are attached to their nest site and must wait for females to approach their territory. Mate choice by both sexes will in effect restrict the range of sizes from which an individual may choose mating partners.

The effects of 'mutual' mate choice on reproductive success will not be constant over all size classes but will result in a disproportionate increase of the reproductive success of large blennies relative to smaller fishes. Indeed, the effect of female choice on male reproductive success will be size-dependent, since large males obtain more and larger egg batches. The effect of male choice on female reproductive success will also be size-biased in favor of large females since large males lose fewer batches than small males.

Mate choice by both sexes is expected when parental investment into offspring is high for both parents (Trivers 1972). Female blennies produce 'expensive' eggs and travel to male's territories at risk while males guard the eggs at some feeding cost. Although modern sexual selection theory predicted that when care by both parents was comparable, both males and female would be expected to exhibit some degree of choice, empirical evidence was lacking to show that mate choice by both sexes is present within one sex.

Intersexual selection may be the major force shaping a mating system only if variance among members of one sex exists in some trait that will affect the reproductive success of the other sex. That trait can then form the basis of mate choice. In redlip blennies, size is a variable trait which ultimately translates into choice for high fecundity by males and for high hatching probability by females. A common preference by both sexes for a trait such as large size will result in the size assortative mating pattern observed in this study. It will also favor large sizes for both males and female, perhaps explaining the absence of size dimorphism in redlip blennies.

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