REPRODUCTIVE BEHAVIOR, SPAWNING SUCCESS AND MATE CHOICE OF THE LUMPFISH CYCLOPTERUS LUMPUS L., IN NEWFOUNDLAND

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REPRODUCTIVE BEHAVIOR, SPAWNING SUCCESS AND MATE CHOICE OF THE LUMPFISH *Cyclopterus lumpus* L., IN NEWFOUNDLAND

BY

© DENIS CHARLES GOULET, B.Sc. (Honors)

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ABSTRACT

A field study in Broad Cove, Newfoundland, was conducted to describe the reproductive behavior, mate selection and spawning success of the lumpfish *Cyclopterus lumpus*.

Prior to courtship male lumpfish exhibited a characteristic nuptial coloration consisting of a greyish-black body and orange-red ventral surface and fins. After an extended courtship involving nest site cleaning, caressing and quivering, females released gametes. Following fertilization, males engaged in molding behavior manipulating the eggs into the nest site producing funnel-like depressions in the egg mass.

Males remained with the eggs throughout the incubation period exhibiting parental behaviors essential for egg development and hatching. Parental care behaviors of males were independent of male size. Pectoral fanning and puffing were the predominant parental care behaviors exhibited throughout the incubation period. Puffing behavior appeared to increase as the eggs neared hatching. During hatching emergent larvae were swept from the nest site by male fanning and puffing behaviors.

Qualities of the male and characteristics of the nest site were tested as criteria for mate choice, and their effect on male spawning success was evaluated. The number of eggs guarded was not correlated with male length. Nest site location variables; depth, distance offshore and distance to the nearest male were not related to spawning success. Nest topography and nest site concealment were also not significant criteria for female choice.

The hatching success of an egg mass was not predictable on the basis of the size of the guarding male. Guarding males, regardless of size, were unable to defend their eggs from predation by cunners, *Tautogolabrus adspersus*. Hatching success of eggs was also independent of nest characteristics. Most egg masses hatched regardless of the characteristics of the nest site. Female lumpfish, therefore, may increase the probability that some of their eggs will hatch by spawning with a number of males.

ACKNOWLEDGEMENTS

A field study such as this often required the invaluable assistance and support of numerous individuals. Dr. John M. Green is given special recognition for his significant contribution as the supervisor of this work.. His support and advice were invaluable to this thesis. Thanks John.

A number of divers; Suzan Dionne, Guy Martel, Carolyn Gravel, Kent Gilkinson and Don Chafe, must be given credit for spending many long hours in cold water assisting with the data collection.

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A very special thanks goes out to my friends who supported me and did some of the initial reviewing of this manuscript. Jack Lawson has etched a permanent spot in this thesis through his professionally done figures. Mary-Lynn Dickson's assistance with the figures and typing were invaluable. Her encouragement and support, especially during the latter phases of the thesis shall never be forgotten.

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Chapter 1
INTRODUCTION

Theories of sexual selection are based primarily on the assumptions that there is competition within one sex for members of the opposite sex, and that there is differential choice by members of one sex for members of the opposite sex (Darwin 1871). Darwin (1871) observed that males generally tend to be active in courtship and eager to mate, whereas females are passive. Bateman (1948) attributed this sexual asymmetry to the different costs involved in gamete production. Male gametes are energetically inexpensive and can be produced in large quantities. Thus, male reproductive success is limited only by the number of copulations achieved. Males are therefore, expected to be indiscriminate and compete for access to females. Female gamete production, on the other hand, is costly and fewer gametes are produced relative to males. As a result, females are expected to be more selective than males in choosing a mate.

Trivers (1972) described sexual selection in terms of differential parental investment in offspring. He defined parental investment as any contribution made by a parent that increases the probability of survival of an offspring at the expense of investing in further reproduction. The sex whose parental expenditure is greater will become a limiting resource for the opposite sex. Individuals of the sex expending less energy on offspring will compete, either directly (intrasexual selection) or indirectly (intersexual selection), for members of the sex investing more (Trivers 1972).

Females in many animal species, invest more than males in their offspring and should be more selective than males in mating (Fisher 1958; Williams 1966; Trivers 1972). Criteria used by females in mate choice are dependent on the amount of male parental investment (Trivers 1972). For species in which the extent of male investment is strictly genetic (i.e. gametes only), female mate choice is based on either characteristics that increase the number or quality of all offspring or by epigamic characteristics that increase the mating success of male offspring (Fisher 1958; Weatherhead and Robertson 1979).

Females often mate with males that demonstrate vigorous courtship displays (Bastock 1967; Las 1980; Schmale 1981) as sperm supply and the willingness to transfer it are often correlated with courtship intensity (Trivers 1972; Halliday 1976, 1978, 1983).

Females selecting older males as mates may acquire better genes for their offspring. Older males have demonstrated the ability of their genotype to survive longer and through variable environmental conditions (Trivers 1972; Howard 1978a). Larger (Hanson and Smith 1967; Davies and Halliday 1978; McCauley and Wade 1978; Wilbur et al. 1978; Borgia 1981; Downhower and Brown 1980; Berven 1981; Gatz 1981; Noonan 1983) and dominant males (Whitney and Krebs 1975; Cox and LeBoeuf 1977; Payne and Payne 1977; Crankshaw 1979; Borgia 1980; Cole 1982) are often preferred by females, as these traits demonstrate superior competitive and survival abilities.

When males contribute significant parental investment by possessing resources essential to females, qualities of the resource or the male that affect resource accrual, are factors that can influence female choice (Emlen and Oring 1977). Resources that influence female choice include food (Verner and Willson 1966; Thornhill 1976, 1979, 1980); nest sites (Campanella and Wolf 1974; Kodric-Brown 1977; Howard 1978b; Itzkowitz 1978; Jones 1981) and territories that offer food and protection for females and their offspring (Holm 1973; Weatherhead and Robertson 1977; Pleszczynska 1978; Searcy 1979; Lennington 1980).

Male quality can influence female mate choice when it directly affects the survival of the offspring. In species where male parental care is important, the extent of paternal care will be an important criteria in mate choice (Trivers 1972; Halliday 1978, 1983; Krebs and Davies 1981).

In teleosts, male parental care is common (Breder and Rosen 1966; Ridley 1978; Blumer 1979, 1982). A number of hypotheses have been presented to explain the patterns of male parental care observed in vertebrates (Trivers 1972; Alexander 1974; Williams 1975; Dawkins and Carlisle 1976; Gross and Shine 1981). In addition to sexual selection and female choice, factors such as increased assurance of paternity, multiple mating and the low cost of piscine paternal behavior are cited as major benefits in the evolution and maintenance of male parental care in fish (Blumer 1979; Perrone and Zaret 1979).

Investigations of male parental care patterns in fish have revealed that female choice does occur (e.g. Brown 1981; Noonan 1983; Schmale 1981; Grant and Colgan 1983). Male or spawning site characteristics, or a combination of both are commonly cited as factors that influence female choice. Female mottled sculpins (*Cottus bairdi*) choose mates on the basis of male size (Downhower and Brown 1980; Brown 1981; Brown and Downhower 1982). Sargent (1982) found that the degree of nest concealment within a male's territory was the primary determinant in female choice in the stickleback, *Gasterosteus aculeatus*.

Male parental care is a characteristic of the reproductive behavior of the lumpfish, *Cyclopterus lumpus* (Fulton 1907; Cox 1920; Cox and Anderson 1922; Zhitenev 1970; Mochek 1973; Shears 1980). Both sexes move into inshore areas in the spring where males establish nest sites in which females deposit eggs. Females leave the eggs immediately after oviposition for the males to fertilize and guard. Paternal care consists of aeration of the eggs as well as their defense from predators (Fulton 1907; Zhitenev 1970; Mochek 1973; Shears 1980). Males remain at the nest site until all the eggs have hatched and then they move offshore to deeper water.

Previous field studies in Newfoundland indicated that there is differential spawning and hatching success amongst males and wide variation in the amount of parental care exhibited by males (Shears 1980). If we assume that the number of eggs acquired is a function of the males' traits, female lumpfish may be exhibiting mate choice in an effort to gain desirable traits and maximize offspring survival. Female choice, in this study, was examined by comparing the spawning success of males against various measurable male qualities. Alternately, females might base choice of mates on characteristics of the nest site rather than the male himself. Male nest site characteristics were investigated as alternate potential criteria by which females could select mates.

The courtship and spawning behavior of the lumpfish (*Cyclopterus lumpus*) is poorly known and has only been reported from laboratory observations (Fulton 1907; Cowan 1929; Mochek 1970). The first part of the thesis presents a qualitative in situ description of the courtship and spawning behavior of lumpfish. Quantitative analyses of the effect of male and nest site attributes on spawning success follow to determine if female lumpfish are exhibiting mate choice.

Chapter 2
METHODS AND MATERIALS

2.1. Study Area and Nest Site Location

Field data were collected during June and July 1982, and during May, June and July of 1983 and 1984 at Broad Cove, Conception Bay, Newfoundland (47° 37' N, 52° 53' W). Broad Cove is a semiprotected bay with a bottom topography consisting primarily of bedrock with scattered outcroppings of boulders throughout the intertidal and subtidal zone. The latter provide sufficient substrate for lumpfish nest sites. At depths greater than six meters the bottom is primarily sand, with little or no boulder outcroppings, and is unsuitable for lumpfish spawning.

The entire cove, to a maximum depth of six meters, was surveyed by skin divers to locate and monitor lumpfish nest sites (Figure 2-1). Spawning sites were marked with numbered, submersible markers to facilitate relocation and individual identification. A nest site consisted of the immediate area (1.0 m^2) occupied by a male guarding eggs. A total of 21, 42 and 103 nests were present in Broad Cove in 1982, 1983 and 1984, respectively (Figure 2-2). Nests were examined on nine days from June 3 to July 18, 1982, on 59 days from May 6 to July 27, 1983 and on 62 days from May 6 to July 20, 1984. During these surveys the presence or absence of the males and eggs, and the condition and developmental state of the spawn were noted.

Figure 2-1. The survey area within Broad Cove, Conception Bay, Newfoundland. "FH" denotes the field house used during the study. The dashed line depicts the outer perimeter of the surveyed area.

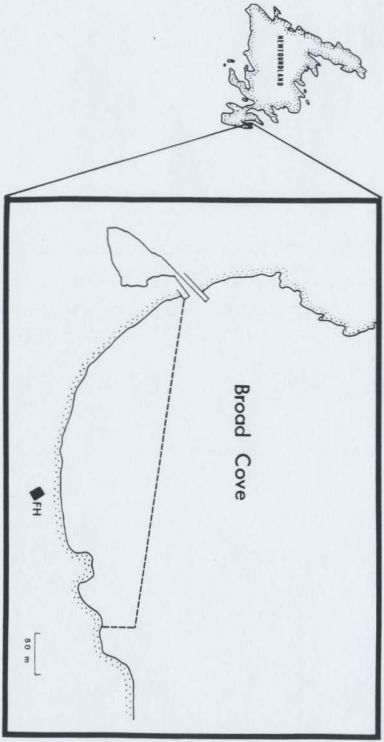
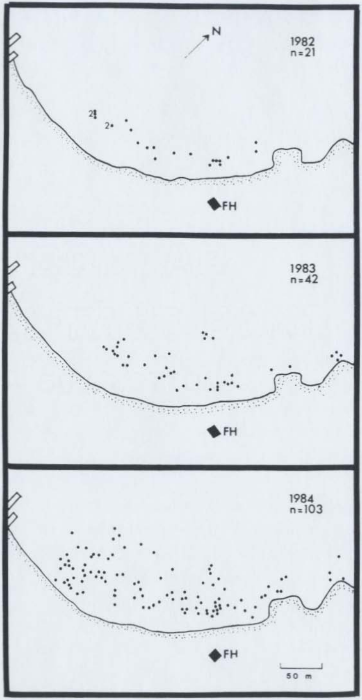

NEWFOUNDLAND
Broad Cove
FH
50 m

Figure 2-2. Location of lumpfish males with egg masses for each year of the study. Numbers beside dots indicate the number of males with nests less than one meter apart.


N
1982
n=21
2
2
FH
1983
n=42
FH
1984
n=103
FH
50 m

2.2. Tagging and Measurement of Male Lumpfish

In June 1982, twenty-one male lumpfish were individually captured, placed in a cloth mesh bag and taken ashore to be measured, weighed and tagged. Total lengths to the nearest ± 0.1 cm, were recorded. Wet weights (± 0.1 kg) were determined using a Pennsylvania weight scale. Numbered Floy FD 67 "spaghetti" tags were inserted into the dorsal hump of each fish. Additionally, four males collected 300 meters north of Broad Cove were measured and tagged in the same manner. Each male was returned to its nest site.

Using SCUBA, total lengths (± 1.0 cm) of 41 and 98 males were measured at their nest sites in 1983 and 1984 respectively. To avoid any disturbance effect on behavioral observations, males in 1983 were not tagged. Males were tagged in 1984 using the same procedure as in 1982.

2.3. Egg Mass Sampling

In 1982, 23 egg masses were collected (19 from Broad Cove and four 300 meters north of Broad Cove). In 1984, 20 egg masses were collected at a site about 500 meters south of Broad Cove. Eggs were collected with fine mesh handheld dipnets by SCUBA divers. At the surface, egg masses were placed in individual plastic bags, labelled and preserved in 4% formalin. Final preservation of the eggs involved decanting the formalin solution off the eggs and replacing it with 70% ethanol in glass mason jars.

The number of eggs in each mass, which was used as a measure of male spawning success, was gravimetrically estimated. Each mass was removed from the ethanol, allowed to surface dry for 5 minutes, and placed on a Mettler PC 4400 scale. To estimate the number of eggs in each mass, the resulting weight was multiplied by a conversion factor previously derived by weighing three samples of 500 eggs each and calculating a sample mean weight ($\overline{x}$=3.30 g, S.D.=0.11). The gravimetric method was better than a volumetric technique because of its greater accuracy and easier application to large egg masses.

Egg mass surface area was used as a measure of male spawning success in 1983 and 1984. Surface area was determined with a mesh screen delineated by 2

X 2 cm squares. A diver approached and captured the male at its nest site, while a second diver placed the grid over the egg mass surface and counted the number of squares covering the eggs. The male was then returned to its nest. This procedure was used because it permitted the collection of <u>in situ</u> post-spawning behavior and hatching success data on males located within Broad Cove.

2.4. Nest Site Measurements

Quantitative measures of 170 nest sites included; their distance offshore, depth, and distance to the nearest nest. Using an underwater measuring line, marked in feet, offshore distances, nest depths and inter-male distances were measured. All distance measurements were recorded to the nearest foot and later converted to metric units for data analysis.

Distance offshore was measured from the high tide level at the nearest shore point to the nest site. Depths were measured from nest site to the water surface at high tide. Distances between males were measured along a straight line from the center of a nest site to the center of its nearest neighbor's nest.

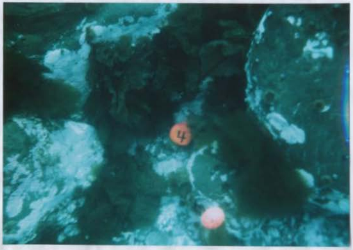
The degree of cover and topography of each nest site were categorized visually. Degree of cover refers to the amount of concealment the nest site provided the egg mass. Egg masses were identified as exposed, moderately sheltered and sheltered (Figure 2-3). In an exposed nest site less than 25% of the egg mass was hidden from view. Moderately sheltered nest sites covered 25% - 75% of the eggs. Nest sites which concealed greater than 75% of the eggs were considered sheltered.

Nest site topography described an area of one meter around each nest. Nest sites were categorized as bedrock, boulder or boulder/vegetation (Figure 2-3). Bedrock type nests included sites situated on the ocean floor and ledges. Nests located between, under or beside boulder(s) were classified as boulder type. Boulder/vegetation nest sites were similar to boulder type with the addition of vegetation such as *Agarium cribrosum* and *Desmarestia sp.*, as important features of the topography.

Figure 2-3. Photographs of the three categories of nest site topography. (A) Bedrock type nest with an exposed egg mass. (B) Boulder type nest with exposed eggs. (C) Boulder/vegetation type nest site with sheltered eggs. The egg mass was situated in the crevice formed by the boulder, whose entrance was covered by the vegetation.

A

B



C

2.5. Behavioral Observations

Descriptions of 16 courtships and two spawnings were made in 1983 and 1984 by observers floating on the water surface and remaining as motionless as possible. Male courtship behaviors, female responses and spawning were recorded on Polypaper TM Plastic paper. The durations of specific behaviors were timed with a Remex Sport Diver underwater watch. Males and females found in close proximity were observed for a minimum of 15 minutes, depending upon the level of courtship behavior. Pairs judged to be near gamete release were observed for extended periods.

In 1983, male parental care was observed in 12 randomly-selected males from the original 42 found in the cove. A total of 336 fifteen minute observation sessions were completed. Behavioral observations were conducted between 0900 and 1100 hrs from May 27 to June 30, 1983. Each day the order of nests observed was randomly determined. If a male was not present at its nest site the observer remained at the nest site for 15 minutes before switching to the next subject. The cumulative duration of the following six parental behaviors were recorded during each session:

1. Pectoral Fanning - Males orientate parallel to or in front of the egg mass while moving their pectoral fins at variable speeds. Pectoral fanning is achieved by either a paddling motion with both fins fully expanded and moving synchronously or a sculling motion. The two pectoral fins can be moved either in unison or in opposition.

2. Dorsal Fanning - Side to side movements of the second dorsal fin while the male is either parallel to or facing away from the eggs.

3. Caudal Fanning - Lateral movement of the caudal fin creating water currents over the egg mass. The male is either beside or facing away from the eggs.

4. Puffing - Facing the egg mass, males blow water onto the egg mass surface by rhythmically expanding and contracting the opercula.

5. Predator Removal - Removal of invertebrates such as sea urchins (*Strongylocentrotus droebachiensis*), and periwinkles (*Littorina sp.*) from the surface of the eggs. These are grasped in the mouth and wrenched from the surface by rapid pectoral fin paddling accompanied by rapid body jerking.

6. Predator Displacement - Males attack or chase either conspecific or heterospecific nest intruders. Predator displacement behavior ranges from short lunges to prolonged chases with the male subsequently returning to his nest.

2.6. Statistical Analyses

Analyses of data were conducted using various programs provided by SPSS (Nie et al. 1975) and SPSS-X (SPSS Inc. 1983).

Regressions were used to test for relationships between male characteristics and nest location parameters with spawning success. The relationship between nest topography and degree of cover with spawning success was tested using an analysis of variance (ANOVA). A two-way analysis of variance using a regression approach for unequal cell frequencies (Neter and Wasserman 1974) was initially conducted to test for interaction effects. All interactions were found to be non-significant at P=0.05, permitting the use of one-way ANOVA. Students' t and Chi-square tests were used to test the effect of male and nest site characteristics on hatching success.

Trends in behavior over the incubation period were tested using a robust, non-parametric test known as "Page's L" (Page 1963; Sokal and Rohlf 1981). When a large number of ties exist in the ranked data, as was the case with pectoral fanning and puffing, reliability of the Page's L test decreases. This is countered by increasing the level of acceptance. A level of acceptance of P<0.001 was chosen in testing for trends in the mean duration of all parental care behaviors over the spawning season. Factors that may have contributed to the variation in parental behaviors were investigated using a multiple regression approach.

Chapter 3
RESULTS

3.1. Reproductive Behavior

3.1.1. Courtship and Spawning

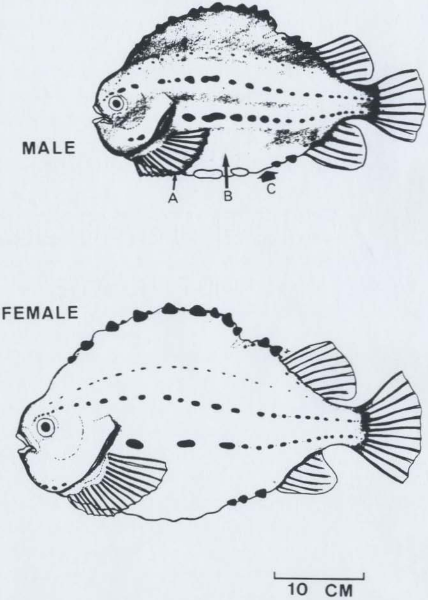
During field surveys conducted in 1983 and 1984 courtship and spawning acts were observed. From these observations a general pattern of courtship and spawning behavior can be outlined.

A change in coloration was characteristic of courting males. The entire body darkened to a deep grayish-black. A small, metallic-silver patch along the flank, posterior to the pectoral fin margin and below the second row of body tubercles, became highly visible (Figure 3-1). The ventral surface, pectoral fins, sucking disc, anal, caudal and dorsal fins became bright orange-red. Males displayed this coloration in the presence of a female. Some males appeared in nuptial hues 2-3 days before a female arrived and one male was observed displaying for 5 days before spawning. Approximately 20 minutes after spawning, the courtship coloration faded, returning to the normal olive green coloration.

When a female arrived at a male's site, the male became visibly 'excited' and attentive. Males initiated courtship which could last for several hours. Throughout the courtship period males typically engaged in nest site cleaning, caressing of the female and body quivering as part of their courtship repertoire.

During nest site cleaning, the male orientated directly towards the potential oviposition site. Distance from the nest surface to the snout was variable, with the male occasionally pushing his snout and head into the nest. This position was maintained by side to side movements of the caudal fin and asynchronous movements of the pectoral fins. Cleaning was accomplished by fanning and puffing directed towards the egg laying site.

Figure 3-1. Illustration depicting the sexual dimorphism between male and female lumpfish during spawning. Females are always larger and light greenish-blue in color. Males display courtship coloration with a dark body, orange-red dorsal, caudal, anal and pectoral fins (A) and vental surface (C), and a metallic silver patch (B).


MALE
A
B
C
FEMALE
10 CM

The nest site appeared to be simply a crevice or depression in the substrate. Crevices could include rock interstices, and cracks in boulders or bedrock. Depressions in bedrock or vertical rock faces also seemed to meet the requirements. Of all nest sites sampled, none was ever found on a flat, smooth surface of a boulder or bedrock.

The male lightly caressed the female with his pectoral fins prior to spawning (Figure 3-2). While asynchronously moving the pectoral fins, a male hovered beside or above the female. Once in this position, the male periodically moved along the length of the female brushing her flank, back and head. Caressing generally lasted less than 10 seconds but occasionally occured for longer periods.

Caressing behavior was frequently followed by quivering. During quivering, the male rested the gular area on the dorsal surface of the female, and rapidly vibrated his entire body; during which time all other fin movements ceased (Figure 3-3). Quivering was short in duration, lasting only 2-3 seconds, but was often done 2-4 times in succession. In one case, the male actually attached himself to the female with his ventral sucker during quivering.

Females, on the other hand, remained relatively passive throughout the courtship period. The only behavior in which the female actively participated in was nest site cleaning. Females and males alternately, or simultaneously, cleaned the intended egg deposition area.

As a female prepared to spawn, the body wall around the cloaca became distended. Prior to egg release, the female approached the nest site and turned onto her side, at the same time pushing the cloacal protuberance close to the nest surface. From this position, she released a mass of bright pink eggs, turned upright and swam away.

Immediately after the female had vacated the nest, the male darted in, positioned his cloacal area above the eggs and released milt onto the eggs. The entire spawning act (i.e. gamete release) lasted approximately 5-10 seconds.

On three separate occasions a second male was located approximately 1 meter from a courting pair. In all cases, the second male was smaller and had normal olive green, camouflaged coloration. Throughout the courtship period, the small males remained motionless.

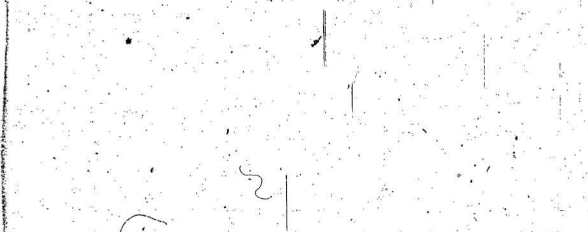
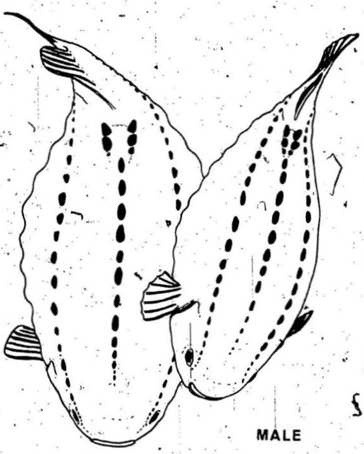
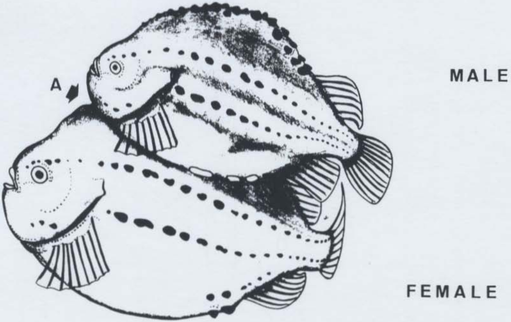


Figure 3-2. Male lumpfish caressing a female with his pectoral fin.



MALE
FEMALE

Figure 3-3. A courting male quivering against a female. Notice the male's gular area making contact on the dorsal surface of the female (A).


A
MALE
FEMALE

In 1983 a sneak spawning was observed. As soon as the female laid her eggs, the small male moved towards the nest site. The larger male moved rapidly towards the intruder and confronted him. Using his snout, the large male butted the small male three times, but was unsuccessful at displacing him. The sneaker released his milt first, followed immediately by the resident male, then swam off. The larger resident male began to mold (see below) the eggs and assumed guardianship of them.

After fertilizing the eggs the male orientated at a right angle to the egg mass and with his snout pushed the eggs into the crevice of the nest site (Figure 3-4). The main thrust for this molding behavior came from hard and rapid side to side movements of the dorsal and caudal fins. The male moved about the egg mass pushing and prodding in a number of areas. The result was a characteristic pattern of funnel-like depressions found on all lumpfish egg masses (Fulton 1907; Cox 1920; Zhitenev 1970; Mochek 1973).

Initially males were very intense and engaged in this behavior without distraction. Ten to 15 minutes later the intensity of this molding behavior decreased with males taking periodic breaks between bouts. After 20-30 minutes, the male stationed himself beside the egg mass.

3.1.2. Parental Care

During the incubation period, male lumpfish remained with the eggs providing parental care. Male guardianship can be divided into two categories; aeration and predator control. Aeration of the eggs was accomplished by pectoral, dorsal, and caudal fanning and puffing. Table 3-1 summarizes the percent of time each of the observed guarding males was engaged in the various parental behaviors during the incubation period. For all males pectoral fanning and puffing predominanted as the major paternal behaviors. In most cases, with the exception of fish numbers 9 and 13, caudal and dorsal fanning occupied less than 10% of the total time.

Predator control consisted primarily of the removal of invertebrates from the eggs and nest defence from heterospecific predators. In all 12 fish observed,

Figure 3-4. A male lumpfish molding newly spawned eggs into the nest.

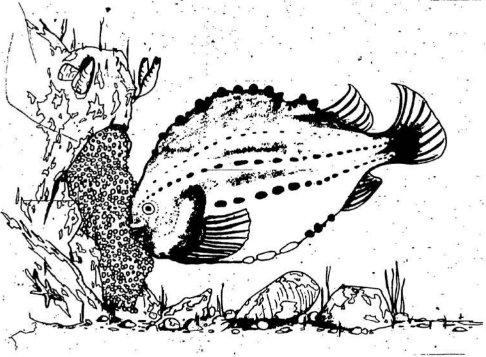


Table 3-1: The percentage of time each male was involved in each of the parental care behaviors throughout the observation periods in 1983.

Fish #	N	Pectoral Fanning	Dorsal Fanning	Caudal Fanning	Puffing	Predator Removal	Predator Displacement
3	28	53.30	3.81	0.0	19.63	0.71	0.04
5	28	67.65	2.86	2.14	13.35	0.03	0.10
7	26	69.62	4.49	1.15	13.94	0.0	0.0
8	24	41.66	0.0	0.0	5.68	0.0	0.0
9	26	69.53	12.82	7.69	24.14	0.06	0.17
10	27	59.27	7.28	1.11	15.21	0.0	0.04
11	26	43.34	2.56	0.0	16.13	0.0	0.02
12	26	2.29	0.0	0.0	7.18	0.12	0.08
13	27	69.40	24.32	17.16	14.03	0.0	0.06
15	26	49.36	3.87	2.59	9.07	0.53	0.24
16	28	20.85	5.02	1.07	10.27	0.15	0.03
18	28	17.30	1.19	0.0	7.30	0.06	0.0

N=the number of 15 minute observation periods predator removal and displacement occurred infrequently and occupied less than 1% of the total time alloted towards parental care (Table 3-1).

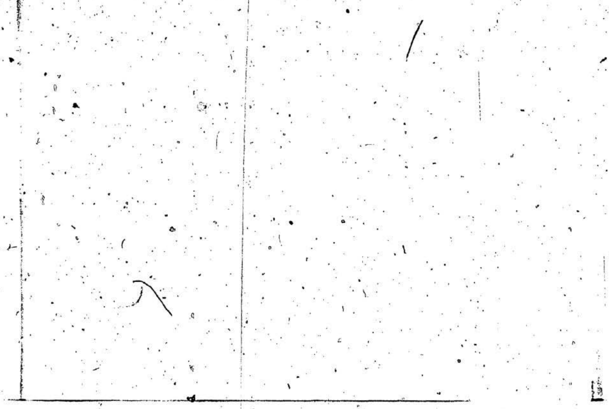
Figures 3-5 and 3-6 illustrate the mean duration of pectoral fanning and puffing for each observation day throughout the incubation period. The mean duration of pectoral fanning remained fairly constant throughout the incubation period (Page's L: $L=6{,}530$, $K=28$, $r=1$, $P>0.001$) whereas the mean duration of puffing showed a significant increase as the number of days after spawning increased ($L=7{,}407$, $K=28$, $r=1$, $P<0.001$).

Sea state significantly affected the amount of pectoral fanning and puffing. During calm sea conditions guarding males fanned and puffed more than during rough sea conditions (ANOVA: $F_{(2,317)}=13.513$, $P<0.001$; $F_{(2,317)}=16.829$, $P<0.001$). In a multiple regression the variation in behavior among the observed males, observation day number and sea state were entered sequentially. This analysis however only explained a small portion of the variation in the daily means of pectoral fanning and puffing (Figures 3-5 and 3-6).

The regression accounted for 42.5% of the variation for pectoral fanning ($F_{(14,250)}=13.223$, $P<0.05$). Variation attributed to the twelve guarding males accounted for 38.5% whereas observation day number and sea state explained only a small proportion of the variation (0.3% and 3.7%, respectively). An explanation for the observed decrease in fanning on days 1, 2, 3, 16 and 17 was not apparent.

For puffing the model explained 49.0% of the observed variation ($F_{(14,250)}=17.401$, $P<0.05$). The majority of the explained variation was attributed to the observation day number (38.5%). The males and sea conditions accounted for only 6.5% and 4.0%, respectively. Therefore, the observed increase in puffing may be related to the approach of hatching (Figure 3-6).

Figure 3-5. Means of pectoral fanning behavior for all twelve fish on each observation day throughout the incubation period from May 10 to June 30, 1983.



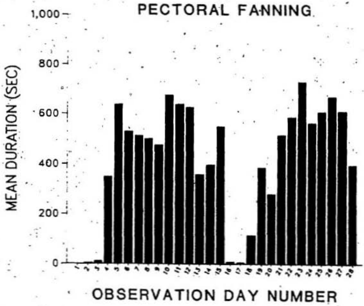
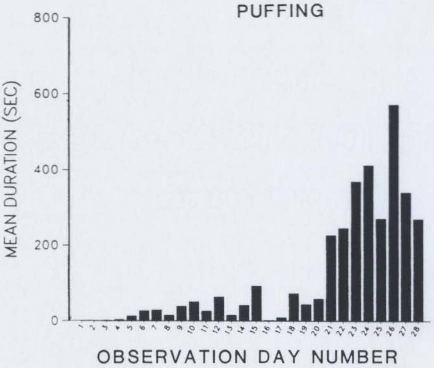

PECTORAL FANNING
MEAN DURATION (SEC)
1,000
800
600
400
200
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
OBSERVATION DAY NUMBER

Figure 3-6. Means of puffing behavior for all twelve fish on each observation day throughout the incubation period from May 10 to June 30, 1983.


PUFFING
MEAN DURATION (SEC)
800
600
400
200
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
OBSERVATION DAY NUMBER

3.1.3. Hatching

Male lumpfish in 1983 and 1984 were checked daily until completion of hatching. Incubation periods ranged from 29 to 53 and 25 to 51 days (with $\overline{x}$=42.5 and 38.5 days) for 1983 and 1984, respectively (Table 3-2). These values were consistent with previous studies in Newfoundland (Collins 1976) and other parts of the world (Fulton 1907; Cox and Anderson 1922; Mochek 1973).

During hatching males faced the eggs, puffing and fanning water towards the egg mass. In addition, males were often observed to remove pieces of empty egg membranes. This is accomplished by clasping the debris with the mouth and twisting the body or simply withdrawing from the eggs.

As the larvae emerged from the egg mass, they were swept from the nest site by the male's vigorous puffing and fanning. Once out of the nest site, water movement resulting from tidal currents and wave action helped disperse the young. Larval lumpfish were never observed clinging to the guarding male or forming "candles" as reported in previous studies (Zhitenev 1970; Mochek 1973).

Hatching was generally completed the same day it began (57% in 1983; 84% in 1984). In one instance in 1983 hatching extended over nine days. Extended hatching periods were most commonly associated with male lumpfish that possessed multiple egg batches. For example in 1984, nine of thirteen (64.7%) prolonged hatchings were males guarding more than one egg mass. Guarding males usually left the area of the nest within one day of the completion of hatching; in 111 observed hatchings, only three males remained at the nest site for longer than one day.

3.2. Spawning Success

Male spawning success was determined in 1982 by counting the number of eggs guarded and in 1983 and 1984 by measuring egg mass surface area (EMSA). Egg masses could be the result of single or multiple spawnings, but counting the number of egg masses a male acquired was not a reliable measure of his spawning success. An egg mass composed of two spawnings may actually have fewer eggs than one resulting from a single spawning. Egg mass surface area (EMSA) was

Table 3-2: Yearly comparisons of the male, egg mass and nest site variables measured. Number of observations is in parenthesis (n). Values are means ± standard deviations.

	1982	1983	1984
Total Length (cm)	30.0 ± 3.6 (23)	30.0 ± 3.8 (41)	30.1 ± 3.7 (98)
Weight (kg)	1.0 ± 0.3 (19)	--	--
Number of Eggs	69000 ± 39000 (23)	160000 ± 82000^{+} (38)	107000 ± 57000^{+} (99)
Egg Mass Surface Area (cm^2)	--	323 ± 162 (38)	219 ± 113* (99)
Depth (m)	2.5 ± 0.8 (20)	3.0 ± 1.0 (42)	3.2 ± 1.0 (103)
Distance Offshore (m)	34.1 ± 12.9 (20)	38.1 ± 22.1* (42)	45.1 ± 23.8* (103)
Distance to Nearest Male (m)	8.4 ± 8.8 (20)	13.5 ± 12.1* (41)	7.6 ± 4.5* (103)
Mean Incubation Period (Days)	--	42.5 ± 6.4 (14)	39.0 ± 7.5 (22)
Hatching Success (%)	--	73.2 (30)	78.6 (81)

*=significantly different from the previous year (t-test).

$^{+}$=estimated from the regression on page 36.

found to be a reliable predictor of the number of eggs (r^2=0.94, n=20) (Figure 3-7) and therefore used to estimate the number of eggs guarded. All sampled egg masses, regardless of male size, were completely fertilized and viable.

The average number of eggs guarded per male was lowest in 1982 and highest in 1983 (Table 3-2). Spawning success of males in 1984 showed a significant decline from the previous year (t=4.27, df=135, P<0.001).

3.2.1. Male Characteristics

Length and body weight were the only male characteristics that could be tested against spawning success. Courtship encounters were not quantified due to the unpredictable nature of their occurrence.

Male Size

Weights of 19 males collected in 1982 ranged from 0.5 kg to 1.6 kg with a mean weight of 1.0 kg (Table 3-2). A length-weight regression yielded a linear relationship described by the equation Wt = 0.08(TL) - 1.37 (r^2=0.74, $F_{(1,17)}$=49.25, P<0.05). The number of eggs guarded by a male was unrelated to its weight (r=0.02, n=17, P>0.40). In 1983 and 1984 weights were not collected because handling during weight determination caused desertion of nest sites. Secondly, the length-weight relationship revealed that either variable can be used to test male characteristics on spawning success.

The mean lengths of breeding males in Broad Cove, were virtually identical from 1982 to 1984 (Table 3-2). Regressions between the total length of males and their spawning success were not significant at the P=0.05 level (Table 3-3).

3.2.2. Nest Site Characteristics

Nest site characteristics encompassed three factors, nest location, nest topography and the degree of cover the nest site provided. Nest location was comprised of three variables; depth, distance offshore and the distance to the nearest male. The influence of each measure of nest characteristics on male spawning success was determined.

Figure 3-7. Regression line and 95% confidence intervals for the relationship between egg mass surface area and number of eggs in an egg mass.

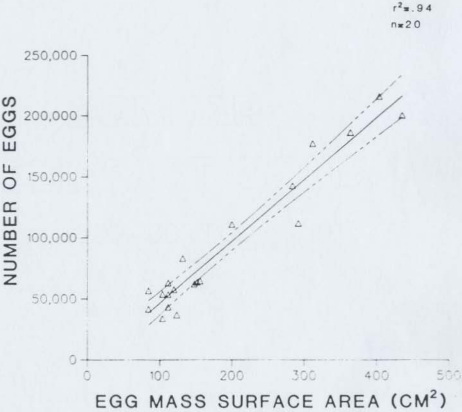

r^2=.94
n=20
250,000
200,000
150,000
100,000
50,000
0
NUMBER OF EGGS
0
100
200
300
400
500
EGG MASS SURFACE AREA (CM^2)

Table 3-3: Regression coefficients (r^2) for the relationship between total length (TL) or weight (Wt) of male and spawning success.

Year	TL		Wt	
	r^2	n	r^2	n
1982	0.029	(21)	0.0003	(17)
1983	0.028	(38)	--	
1984	0.033	(98)	--	

Nest Location

The mean depth of a nest did not significantly differ between years (1982-1983, t=-1.870, df=64, P>.05; 1983-1984, t=-1.138, df=143, P>.05) (Table 3-2). Lumpfish males established themselves further offshore in each year (1982-1983, t=-3.338, df=60, P<0.05; 1983-1984, t=-7.982, df=143, P<0.05). The distance between males in 1983 increased significantly from 1982 (t=-5.568, df=59, P<0.05) but decreased in 1984 (Table 3-2). The yearly changes in distance offshore and inter-male distance were probably a function of the increased number of breeding males within the survey area. Depth of the nest, distance offshore and distance to the nearest male were not related with spawning success (P>0.05) (Table 3-4).

Nest site topography

Nest sites were most commonly associated with boulders (Figure 3-8). Boulder-type topography surrounded 62.5%, 73.2% and 43.7% of all nests in 1982, 1983 and 1984 respectively. In 1982 and 1983 the least frequently occupied topography type was bedrock. Bedrock, however, was the second most frequent topography type in 1984 (32.0%, n=33).

Nest site topography was found to be a significant factor in male spawning success only in 1983 (ANOVA: $F_{(1,33)}=6.174$, P<0.05). Males whose nests were associated with boulder/vegetation were found to have larger egg masses than those with nests among boulders alone. In 1982 and 1984 the topography of the nest had no effect on the size of the egg mass a male guarded (Table 3-5).

Degree of Cover

Figure 3-9 illustrates the percentage of nests found in each cover type for each year of the study. Nest sites providing a moderate degree of cover were utilized by 62.5%, 48.8% and 37.8% of the males in 1982, 1983 and 1984,

Table 3-4: Regression coefficients (r^2) for the relationship between nest site location characteristics with spawning success.

Year	Depth (m)		Distance Offshore (m)		Distance to the Nearest Male (m)	
	r^2	n	r^2	n	r^2	n
1982	0.061	(22)	0.040	(18)	0.015	(18)
1983	0.083	(38)	0.009	(38)	0.071	(37)
1984	0.001	(99)	0.008	(99)	0.002	(99)

Figure 3-8. The percentage of egg masses in bedrock (BR), boulder (Bol) and boulder/vegetation (Bol/Veg) nest site topography types.

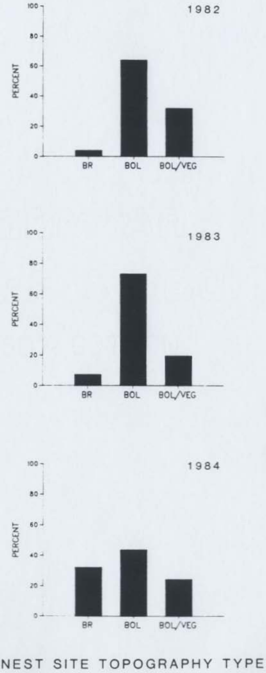
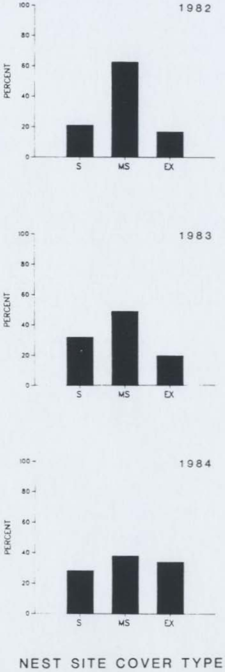

1982
PERCENT
100
80
60
40
20
0
BR
BOL
BOL/VEG
1983
PERCENT
100
80
60
40
20
0
BR
BOL
BOL/VEG
1984
PERCENT
100
80
60
40
20
0
BR
BOL
BOL/VEG
NEST SITE TOPOGRAPHY TYPE

Table 3-5: The relationships between nest site characteristics and spawning success.

Year	Topography		Degree of Cover	
	F	d.f.	F	d.f.
1982	0.377	(1,20)	0.163	(2,20)
1983	6.174*	(1,33)	2.731	(2,35)
1984	3.037	(2,96)	9.423**	(2,96)

*=significant at 0.05 level.
**=significant at 0.001 level.

Figure 3-9. The percentage of egg masses in sheltered (S), moderately sheltered (MS) and exposed (**EX**) nest site cover types.


1982
1983
1984
PERCENT
100
80
60
40
20
0
S
MS
EX
NEST SITE COVER TYPE

respectively. In 1984, exposed nests were the second most frequent representing 35 of 103 nests (34.0%), whereas only 4 of 24 (16.7%) and 8 of 41 (19.5%) nests lacked cover in 1982 and 1983.

A two-way analysis of variance revealed no significant interaction between nest site topography and degree of cover (1982, $F_{(2,16)}=0.991$, $P>0.30$; 1983, $F_{(2,29)}=1.205$; $P>0.30$; 1984, $F_{(4,90)}=1.485$, $P>0.20$). The effect of nest cover on spawning success was therefore analysed independently using a one-way analysis of variance.

The effect of nest site cover on the spawning success of males is illustrated in Table 3-5. In 1982 and 1983 the degree of cover of the nest site did not affect the number of eggs deposited. In 1984, however, there was a positive relationship between the amount of nest site cover and the number of eggs deposited ($F_{(2,96)}=9.423$, $P<0.001$). Egg mass sizes in sheltered nests were significantly larger than those in either moderate or exposed sites ($P>0.05$). In moderately sheltered and totally exposed nest sites, egg mass surface areas did not differ significantly.

3.3. Hatching Success

Hatching success of each egg mass was recorded for all lumpfish in 1983 and 1984. The criterion for successful hatching was whether or not the entire egg mass hatched. The hatching success of egg masses in 1983 and 1984 was 73.2% and 78.6% respectively.

Failure to hatch resulted from either abandonment or desertion. Abandoned eggs occurred when the guarding male was forced to leave the nest by heterospecific predators. Deserted egg masses resulted when for no apparent reason males permanently left their nest during incubation. In both cases the ultimate destruction of the eggs was from predation. In 1983 and 1984, 16.7% and 13.6% of the total number of unsuccessful egg masses were abandoned. Deserted nests accounted for 9.5% and 3.9% of the failed egg masses for 1983 and 1984.

3.3.1. Male Characteristics

Male Size

In both 1983 and 1984 there was no significant difference in the mean size of successful and unsuccessful males (Table 3-6).

The hatching success of the eggs guarded by the 12 males selected for behavioral observations in 1983, was 100%. Egg masses attended by males that exhibited little paternal behavior hatched as successfully as those eggs guarded by males displaying substantial parental care (Table 3-1). For example, fish number 12 exhibited little parental care towards it's eggs, yet the eggs hatched as successfully as the other males which had invested more time in parental care. Results from the behavior observations revealed that paternal care was unrelated to the size of the guarding male or the size of the egg mass being guarded (Table 3-7). Parental care was necessary for successful hatching, but was independent of male size.

3.3.2. Nest Site Characteristics

Nest Location

Nest location variables were for the most part unimportant in the hatching success of egg masses (Table 3-6). Depth of the nest did not affect hatching success, as the mean depth of failed nest sites did not significantly differ from successful sites (1983, $t=0.11$, $df=14$, $P>0.05$; 1984, $t=0.62$, $df=101$, $P>0.05$). In 1983, hatched egg masses were those that were located farther offshore ($t=-2.34$, $df=40$, $P<0.05$). Such was not the case in 1984. Inter-male distance had no effect on hatching success in either year (Table 3-6). Egg masses of males in close proximity to one another, were therefore just as likely to hatch as egg masses of males further apart.

Table 3-6: The effects of male size (TL) and nest site location variables on hatching success.

Year	Male Length (cm)		Nest Depth (m)		Distance Offshore (m)		Distance to the Nearest Male (m)	
	t	n	t	n	t	n	t	n
1983	0.49	(41)	0.11	(42)	-2.34*	(42)	-0.18	(41)
1984	-0.25	(98)	0.62	(103)	-1.02	(103)	-0.27	(103)

*=significant at 0.05 level

Table 3-7: The correlation (r) of male size (TL) or egg mass surface area (EMSA) with parental care behaviors.

	Pectoral Fanning	Dorsal Fanning	Caudal Fanning	Puffing	Predator Removal	Predator Displacement
TL (cm)	-0.15	-0.009	-0.03	-0.04	0.01	-0.04
EMSA (cm^2)	-0.04	0.05	-0.01	0.01	-0.04	-0.08

Nest Site Topography

Figure 3-10 illustrates the proportion of successfully and unsuccessfully hatched egg masses associated with each type of nest site topography. In 1983 all egg masses laid in the boulder/vegetation topography hatched. The hatching success of egg masses in bedrock and boulder topography were identical (66.7%). In 1984, however, nests in boulder topography had the highest hatching success (88.9%), followed closely by nests in bedrock topography (78.8%), while nests in boulder/vegetation topography had only a 60.0% hatching success. In both years, most nests were in boulder topography and only 48.8% and 38.8% respectively, of the egg masses hatched.

In 1983 the hatching success of egg masses in the various topographical types was not significantly different from the expected value (Table 3-8). In the following year, however, hatching success was greater than expected ($\chi^2=7.99$. d.f.$=2$, $P<0.05$), in the various nest site topography types.

Degree of Cover

The percentage of hatched and failed egg masses in relation to the degree of nest concealment is depicted in Figure 3-11. In 1983, moderately sheltered egg masses had the highest rate of success, followed closely by sheltered nests (80.0% and 76.9% respectively). Egg masses laid in exposed sites had a 50.0% chance of hatching. Nests in exposed cover types had a much higher rate of success in 1984 (Figure 3-11). Hatching success in moderately sheltered and sheltered nest site cover types were 79.5% and 72.4%. The number of hatched egg masses associated with the various cover types was not significantly different from the expected values in both 1983 and 1984 (Table 3-8).

Figure 3-10. The percentage of successful and unsuccessful egg masses in bedrock (BR), boulder (Bol) and boulder/vegetation (Bol/Veg) nest site topography types.

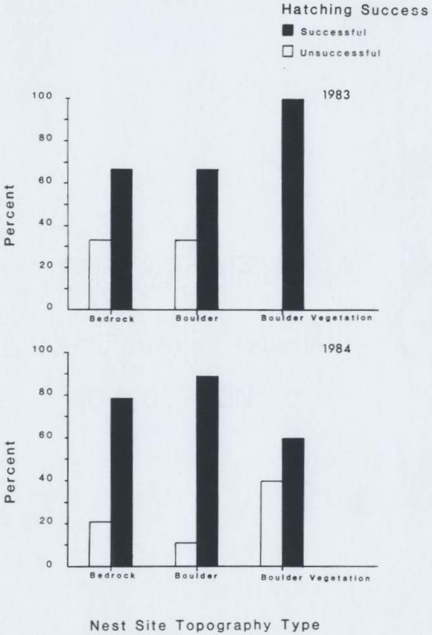
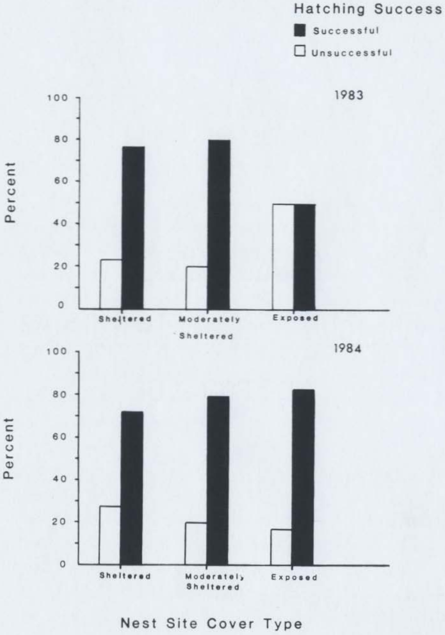

Hatching Success
■ Successful
☐ Unsuccessful
1983
Percent
100
80
60
40
20
0
Bedrock
Boulder
Boulder Vegetation
1984
Percent
100
80
60
40
20
0
Bedrock
Boulder
Boulder Vegetation
Nest Site Topography Type

Table 3-8: Chi-squared values for the relationship between hatching success and nest site characteristics.

Year	Topography		Degree of Cover	
	χ^2	n	χ^2	n
1983	3.64	(41)	2.76	(41)
1984	7.99*	(103)	1.06	(103)

*=significant at 0.05 level

Figure 3-11. The percentage of successful and unsuccessful egg masses in sheltered (S), moderately sheltered (MS) and exposed (EX) nest site cover types.


Hatching Success
■ Successful
☐ Unsuccessful
1983
Percent
100
80
60
40
20
0
Sheltered
Moderately Sheltered
Exposed
1984
Percent
100
80
60
40
20
0
Sheltered
Moderately Sheltered
Exposed
Nest Site Cover Type

Chapter 4
DISCUSSION

4.1. Paternal Behavior

Male parental behavior consists predominantly of pectoral fanning and puffing; dorsal and caudal fanning should not be considered important components of the lumpfish's parental behavior. These behaviors may be more related to movements concerned with postural adjustments and maintaining stability at the nest site. For example, fish numbers 9 and 13 exhibited the majority of dorsal and caudal fanning during rough sea conditions, which suggests that the bouts of fanning were probably associated with maintaining stability.

Fanning behavior during the incubation period is essential for normal development and hatching of the eggs in many species of inshore fish that exhibit parental care (Sevenster 1951, 1961; van Iersel 1953; Morris 1955, 1958; Qasim 1956; Mathisen 1979). In the three-spine stickleback (*Gasterosteus aculeatus*) fanning behavior peaked a few days before hatching (van Iersel 1953). The amount of fanning was correlated with the oxygen deficit at the nest (van Iersel 1953; Morris 1958). The river bullhead (*Cottus gobio*) on the other hand, exhibited a high level of pectoral fanning throughout the parental phase (Morris 1955).

It is possible that changes in the oxygen uptake and ammonia production of the egg mass have an important influence on the pattern and rate of pectoral fanning and puffing in lumpfish. Ammonia production is highest just after spawning but, in general quite low throughout incubation (Davenport et al. 1983). After fertilization males are engaged in the molding behavior during which time the pectoral fins are constantly moving. This behavior may therefore provide sufficient water circulation for waste removal. A high level of pectoral fanning throughout the incubation period should then be sufficient for removal of of embryonic excretory products.

Oxygen uptake by egg masses increases to the onset of hatching (Davenport, 1983). Pectoral fanning alone may be insufficient to provide adequate oxygenated water to the deeper regions of the developing egg mass. Puffing may force aerated water into the deeper recesses of the egg mass, providing the oxygen required for normal development and emergence. The increased time expended in puffing as development proceedes thus possibly reflects the increased oxygen demand of the developing eggs (Figure 3-6).

The sea urchin, *Strongylocentrotus droebachiensis*, is the most common invertebrate predator of lumpfish eggs. Deserted eggs became covered with urchins within 2-4 days and eventually were consumed. Control of invertebrate predators is normally necessary and predator removal occurs throughout the incubation period. Generally, resident males prevented the eggs from being overrun by urchins. In four cases however, males tolerated the presence of urchins on their eggs. Damage appeared to be minimal in these situations, as successful hatching occurred. At the time of hatching the males removed the urchins facilitating emergence of the larvae. Why these fish tolerated the urchins and why the eggs were not destroyed when urchins were not removed is not known.

Motile predators such as heterospecific fish, generally avoided guarding male lumpfish. Potential predators such as sculpins (*Myoxocephalus scorpius* and *M. octodecemspinosus*) and flounder (*Pseudopleuronectes americanus*) were never observed to attack male lumpfish or their egg masses. Ocean pouts (*Macrozoarces americanus*) and cunners (*Tautogolabrus adspersus*) were the major causes of unsuccessful hatching of tended nests. Confrontations involving a single cunner never resulted in the guarding male lumpfish being displaced. Single conflicts however, often turned into group encounters as other cunners were attracted to the nest site. By swarming the resident male, the defensive behaviors of the male were rendered ineffective in preventing destruction of the egg mass. Initially guarding males attempted to chase the predators, but eventually gave up, leaving their eggs to be eaten. Feeding frenzies consisted of 20 to 40 cunners which were capable of consuming the entire egg mass in less than 20 minutes.

4.2. Female Choice and Reproductive Success

Female choice can be influenced by qualities of the male or the oviposition site. Male attributes influencing female choice could be either phenotypic expressions which might ultimately affect offspring fitness or characteristics that provide proximate gains to the female in terms of offspring survival (Howard 1978a). Male size and age are indicators of survival ability, while male courtship behavior and appearance are indicators of reproductive ability (Fisher 1958). Nest site quality may demonstrate a male's ability to provide suitable resources for offspring survival.

In mottled sculpins (*Cottus bairdi*), large males have increased reproductive success as females preferentially mate with them (Downhower and Brown 1980). Larger males have been shown to be better guardians (Downhower and Yost 1977; Brown 1981). Brown (1981) demonstrated that parental care abilities of male mottled sculpins were size-dependent; large male sculpins provided better defence against predatory intrusions. In *C. lumpus*, male size was not found to be a significant predictor of spawning success. It appears that in terms of fertilization all reproductively mature males have the same potential spawning success regardless of size. Smaller males were often found guarding large egg masses, while some large males guarded smaller than average egg masses.

Paternal care abilities of lumpfish do not appear to be size-dependent. Large males were no more successful at thwarting attacks by groups of cunners than were small males and small males were as capable of providing sufficient aeration for their egg masses as large males. The absolute amount of aeration seems to be unimportant; as long as guarding males provide a minimum of water circulation throughout the egg mass, development progresses normally. One male for example, exhibited little parental care towards his egg mass, yet the eggs hatched normally. Since there are no size-dependent differences in parental care abilities of males, male size would not seem to be an important criteria for mate choice by females.

A function of courtship is to communicate the readiness and willingness of an animal to reproduce (Bastock 1967). The appearance and activities of a male during courtship may be used by females as cues to evaluate potential mates. In both the guppy, *Poecilia reticulata*, and the goby, *Coryphopterus nicholsi*, courtship intensity affects male reproductive success (Farr 1980; Cole 1982). Females were attracted to the males that courted most vigorously. In *C. nicholsi* dominant males courted more vigorously than subordinate males. By selecting dominant males, females were more likely to acquire superior genes for their offspring.

The absence of quantitative data on courtship behavior made it impossible to investigate the effect of male courtship ability on reproductive success. Observations, however, did reveal that not all male courtship attempts resulted in successful egg deposition. Courtship behaviors, such as caressing and quivering may be criteria that females use to assess males as potential mates.

A relationship between courtship intensity and male territoriality or dominance status appears unlikely. Male lumpfish did not appear to compete for nest sites. Male-male interactions rarely occurred, suggesting that dominance hierarchies or territories were not established. In 10 cases where the inter-male distance was less than two meters, aggressive interactions commonly associated with dominance or territoriality were not observed. Each male tended its eggs, ignoring its neighbor completely. Successful spawning by males, therefore appears to be achieved by simply surpassing some minimum threshold level of stimulation of the female.

The choice of a nest site in a heterogenous environment should be non-random because some nest sites may be especially defensible, preferred by females for spawning or conducive to higher hatching success (Williams 1975). The quality of the nest site has been shown to have a significant effect on reproductive success in birds (Verner and Willson 1966; Plezczynska 1978; Garson 1980). In some fish species, nest site variables are also important criteria for female choice (Kodric-Brown 1977; Itzkowitz 1978; Sargent and Gebler 1980; Sargent 1982). For example in the pupfish (*Cyprinodon sp.*) females demonstrated a preference for spawning on rock substrate. The reproductive success of males with breeding territories on rock substrate was three times higher than those males breeding on sand substrate (Kodric-Brown 1977). In sticklebacks (*Gasterosteus aculeatus*) males with concealed nests spawned more often than males spawning in open nests (Sargent and Gebler 1980).

Location of the nest site did not appear to influence spawning success (Table 3-4). Female lumpfish apparently had no preference for the water depth in which they spawn. Males closer inshore had similar spawning success when compared with males further offshore, despite the significant changes in mean distance offshore of males over successive sample years. Inter-male distances also had no effect on male reproductive success.

It appears that in lumpfish, nest site concealment does not consistantly provide any advantage in acquiring eggs to the resident male. In two out of the three years of the study, the number of eggs guarded by males with exposed nest sites generally did not differ from those males whose nests concealed the eggs. In 1984, when males with sheltered nest had the largest egg mass sizes, the number of eggs laid in moderately sheltered and exposed nests were not significantly different from each other. Males with exposed nest sites spawned as successfully as males with moderately concealed nests. The topographical features of the nest site affected the number of eggs the resident males received only in 1983. In all other years, males that spawned on bedrock substrate, guarded on average the same number of eggs as males spawning on boulder or boulder/vegetation substrate.

These inconsistant patterns of nest site characteristics affecting male spawning success suggest that female lumpfish do not appear to be choosing their mates according to features of the nest site. The minimum requirement for a nest site appears to be a crevice or depression in the substrate. Any male fulfilling this minimum requirement can acquire spawnings.

4.3. Male Hatching Success

Not all mated male's egg survive to hatching. For no apparent reason some male lumpfish desert their eggs, while others are forced to abandon the eggs. In both cases the ultimate destruction of the egg mass is from predation.

During spawning, predation is negligible as at this time water temperatures are below 5 °C and cunners *Tautogolabrus adspersus* are in torpor (Green and Farwell 1971). As the water temperature increases, ocean pouts (*Macrozoarces americanus*), sculpins (*Myoxocephalus scorpius* and *M. octodecemspinosus*) and flounder (*Pseudopleuronectes americanus*) become more active and cunners emerge from torpor. Emergent, cunners actively feed to replenish depleted energy reserves. In Broad Cove, cunners are ubiquitous and no nest site is exempt from potential predation. Predator displacement ability of male lumpfish was not related to size. Group attacks by cunners were always successful regardless of the size of the guarding male. Therefore any male was a potential victim of cunner predation. Female lumpfish appear to have no prior information regarding predation pressure at each nest site or the probability of the male deserting the eggs.

In sticklebacks, a disproportionately high number of males nest among rocks, in crevices and in dense vegetation (Black and Wootton 1970; Moodie 1972; Kynard 1978). Nests in concealment had more fry than nests in open areas. Furthermore, males with concealed nests suffered less intraspecific egg predation than males with their nest in the open (Sargent and Gebler 1980). Additional benefits of concealed nests include; (1) decreased stolen fertilizations (i.e. sneak fertilizations) (2) decreased interspecific egg predation, and (3) increased allotment of time and energy to parental care (Sargent and Gebler 1980). In the lumpfish, nest site concealment did not appear to affect significantly hatching success; the majority of egg masses in all types of cover hatched. This is further reflected by the high overall hatching success for each year (73.2% in 1983, 78.6% in 1984).

In resource defence polygyny, males provide resources that are essential for females (Emlen and Oring 1977). Female mate choice can be influenced by the defended resources (territory quality, nest quality), but also by the quality of the defending male. Males possessing 'superior' resources or traits generally have higher reproductive success. Male lumpfish qualities and/or nest site traits did not appear to significantly influence female choice or subsequent reproductive success. The mating system of *C. lumpus* can be best classified as promiscuous, with both males and females obtaining multiple matings (Emlen and Oring 1977). Females move inshore and appear to mate indiscriminately with males regardless of their size, nest site characteristics or the number of previous spawnings, before moving on to mate elsewhere. The apparent inability of female lumpfish to assess prior to spawning a male's probability for deserting eggs or the likelihood of his eggs being preyed upon; coupled with the fact that all males appear to be equally capable of providing parental care, contribute to the success of such a strategy of multiple mating. Females therefore increase the probability that at least some of their eggs will be reared successfully.

4.4. Density Effects

The density of a breeding population can have effects on female mate choice and male reproductive success. For example if resources are limited, high densities can reduce the availability of optimal nest sites. In such a situation some males would be forced into sub-optimal habitat. Males in these areas may be less attractive to females and subsequently acquire fewer matings (Verner 1964; Verner and Wilson 1966; Kodric-Brown 1977; Borgia 1980).

In each year of the study the number of mated males located within Broad Cove more than doubled (Figure 2-2). A significant factor contributing to this observed increase was closure of the lumpfish fishery in Conception Bay since 1982. The fishery was size selective for females, but numerous males were caught as by-catch (Warren 1980; Sturge 1980). Closure of the fishery therefore permitted unimpeded inshore migration of lumpfish.

The changes in the distance offshore and distance between males was probably a function of the increased male density. As density increased, the mean distance offshore of nest sites increased. Distance offshore however, had no effect on spawning success. Males further offshore had similar spawning success as those males located inshore (Table 3-4).

Inter-male distance might be expected to decrease as the number of individuals occupying the study area increases. Such a pattern was not observed in 1983, as the mean distance to the nearest male increased considerably (Table 3-2). Males were more dispersed throughout the study area; further along the coast line and offshore. The following year, at an even higher male density, inter-male distances were much shorter. The proximity of males to one another, over the range measured, did not have any effect on a male's ability to attract females and mate successfully.

As male density increased a large proportion of the males spawned in exposed nest sites (Figure 3-9). Such a pattern might be expected if sheltered and moderately sheltered sites were the preferred nest types and limited in number. As more males move inshore, fewer sheltered nests would be available and more males would have to settle for more exposed sites. Males spawning in these areas would be expected to acquire fewer eggs. At low densities males in exposed nest sites did not appear to have significantly lower spawning success than those in sheltered or moderately sheltered nest sites (Table 3-5). At high densities males that spawned in sheltered sites had larger eggs masses while males with moderately sheltered and exposed nests had similar spawning success. Therefore given a large enough sample of males to choose from, female lumpfish may select males with sheltered nest sites, but do not differentiate between moderately sheltered and exposed nest sites.

The most important effect of increasing male density appears to be the reduction in the quantity of eggs acquired (Table 3-2). The average spawning success of males was highest in 1983 but, then declined significantly in the following year. With the closure of the roe fishery, it is reasonable to assume that the number of breeding females could increase. Under these conditions average spawning success per male could increase as there is a greater probability of acquiring additional matings. Such a pattern however, was not observed in 1984. If the proportion of females were approximately equal or declined, females could spawn more frequently but release fewer eggs at each spawning. Therefore at high male densities the amount of spawn a male received may decrease.

4.5. Summary

1. Male courtship behavior was characterized by a change in coloration, nest site cleaning, caressing and quivering. Females remained relatively passive throughout courtship, occasionally participating in nest site cleaning.

2. Immediately following gamete release, males engaged in molding behavior, producing the characteristic pattern of funnel-like depressions in the egg mass.

3. Puffing behavior was observed to increase as the number of days post-spawning increased. The cause of this observed increase is not fully understood, but might be a function of metabolic demands of the developing eggs.

4. During hatching, emergent larvae were swept from the nest site by the males puffing and fanning behavior.

5. Parental care was essential for hatching, but independent of male size.

6. Male reproduction success, as determined by the number of eggs guarded was not correlated with male size.

7. Nest site characteristics were found to occasionally affect male

spawning or hatching success. Generally however, nest site topography and the degree of cover of the nest did not appear to be important criteria for mate choice.

8. The major cause of unsuccessful hatching was predation by cunners (*Tautogolabrus adspersus*). Attacks by cunners were unpredictable and always resulted in the guarding male abandoning the eggs.

9. Female lumpfish do not appear to be choosing males based on the male or nest site characteristics measured. Spawning appears to be random with females spawning with more than one male. Such a strategy seems to ensure survival of at least some offspring in the face of unpredictable predation.

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