

ALTERNATIVE REPRODUCTIVE TACTICS AND
GROWTH OF MALE CUNNERS,
Tautogolabrus adspersus (WALBAUM),
IN NEWFOUNDLAND

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CAROLYN MARY GRAVEL

ALTERNATIVE REPRODUCTIVE TACTICS AND GROWTH
OF MALE CUNNERS, *Tautoglabrus adspersus* (WALBAUM),
IN NEWFOUNDLAND

by

© CAROLYN MARY GRAVEL, B.Sc.

A Thesis Submitted to the School of Graduate Studies
in Partial Fulfillment of Requirements for the Degree of
Master of Science

Department of Biology
Memorial University of Newfoundland

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ABSTRACT

Alternative reproductive tactics utilized in two separate populations of the Newfoundland male cunner, *Tautoglabrus adspersus*, were investigated for tradeoffs between sperm production and somatic growth. One population in Broad Cove, Conception Bay, consisted of pair spawning territorial males and nonspawning preterritorial males. A second population at Norris Point, Bonne Bay, contained group spawning nonterritorial males. The parameters measured from prespawning and postspawning samples of both populations were total length, eviscerated body weight, gonad weight, and age. These variables and a gonadosomatic index were tested for differences between the three reproductive types of males mentioned above. Results indicated that gonad weights and gonadosomatic indices per age class were significantly greater in group spawning males than in preterritorial males younger than 15 years. The same was found for gonad weight per unit body weight at age, thereby supporting the prediction that group spawners invest heavily in sex products early in life. Group spawning provides an opportunity for a female's eggs to be externally fertilized by many males, and large gonadal investments in group spawning males are probably a result of sperm competition.

Length and body weight at age of the male group spawning population at Norris Point were significantly less than those of the preterritorial male population at Broad Cove. Body size differences were slight, however, suggesting no significant tradeoff between high sperm production and decreased somatic growth rate. A tradeoff between high sperm production and reduced longevity of group spawning males was suggested by the absence of older (> 9 years) males at the group spawning site (Norris Point) as compared to high frequencies of similar aged males at the pair spawning site (Broad Cove). Age frequencies of females were the same between both populations.

Within the Broad Cove population, territorial males invested more energy in gonads than preterritorial males. Successful territorial males exhibited a faster growth rate than preterritorial males, although the maximum total lengths and body weights obtained were similar between both male types.

Since female cunners exhibit the same growth and reproductive tactics irrespective of geographic location, differences in female body size at age were used to compare the conditions for growth between the two study sites. Norris Point females were significantly smaller in length and body weight at age than those of Broad Cove, although differences were slight. These observed differences in female body growth may be related to differences in local population density between both sampling sites. Females from both Broad Cove and Norris Point were smaller sized per age class than local males (excluding territorial males). They were also heavier at length than resident males, although differences were slight between sexes in Broad Cove. A comparison of the mean total lengths at age of cunners (sexes combined) with latitude from the literature indicated no readily apparent latitudinal effect on cunner growth.

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INTRODUCTION

Species generally use a specific tactic to reproduce (Wilson 1975). Consequently, the classification of species has often been based, at least in part, on the particular reproductive tactic utilized (Howard 1984).

Recently, however, research on species-specific reproductive tactics has revealed evidence of tactical variation within species (reviewed in Austad 1984, Dominey 1984, Waltz and Wolf 1984). Alternative reproductive tactics may take the form of "sneaking" matings, in which small (young) males briefly enter territories defended by large (old) males and mate with visiting females (e.g. *Anolis* lizards, Trivers 1976; spiders, Christenson and Goist 1979); "satellite" residency in which a younger male takes position (not detected by the older defending male) in a territory and attempts to mate with receptive females (e.g. *Anolis* lizards, Trivers 1976; waterbucks, Wirtz 1982; water striders, Rubenstein 1984); or mimicking female behaviour, by which smaller males access females while avoiding aggression of large territorial males (e.g. ruffs, van Rhijn 1973; bullfrogs, Emlen 1976 and Howard 1978, 1984).

Fishes are among those animals in which alternative reproductive tactics may constitute a widespread phenomenon (e.g. Poeciliidae, Constantz 1975; Cyprinodontidae, Kodric-Brown 1977; Scaridae, Warner and Downs 1977; Gasterosteidae, Rowland 1979; Salmonidae, Gross 1985). Gross (1982) provided a detailed account of two alternative reproductive tactics (sneakers and satellites) in male bluegill sunfish (*Lepomis macrochirus* Rafinesque: Centrarchidae). Large, old territorial males build nests, attract females, remain at the colony after spawning, and show the parental care characteristic of their species. Small, young sneaker males hide behind rocks and plants, dart into a nest beneath the spawning pair, release sperm, then dart out and reposition themselves. A satellite

male (midrange in body size and age relative to territorial males and sneakers) hovers in the water column above a territorial male, descends slowly into the nest when a female is present, mimics females in colour and behaviour (i.e. thereby avoiding territorial male aggression), and positions itself with the spawning pair to release sperm.

Meyer (1977) reported both pair and group spawning by male wrasses (*Thalassoma cupido* Temminck and Schlegel: Labridae). Pair spawning involves a large territorial male (comprising less than 1% of the population) and a female. Smaller nonterritorial males spawn in groups of up to 150 individuals with a receptive female. Warner and Hoffman (1980a) also described these two tactics in the labrids *Thalassoma bifasciatum* (Bloch) and *T. lucasanum* (Gill). In addition, interference ("sneak") spawnings were observed, in which a small male rushed into a territory and joined a territorial male and female in gamete release, then quickly left the site.

Conspecifics may use one or more reproductive tactics on an individual or a population level as adaptive alternatives to the species "norm". On an individual level, alternative tactics can be genetically or ontogenetically fixed for life in each fish (Waltz and Wolf 1984). Ontogenetic changes, frequently expressed as age and/or size effects on particular reproductive tactics, may be limited in scope by environmental constraints (e.g. abundance of food in pre-maturation years). Alternative tactics can also be variable within a lifetime, or even reversible (Warner and Hoffman 1980a). Individual variability may be affected by environmental features, such as resource availability (e.g. defendability of a mating territory; availability of sites for attracting females; supply of ripe females; abundance of food), male density in a population (*ibid.*), or frequency of particular tactics used by other males (Gross and Philipp 1985). At the population level, a discrete percentage of males will adopt one particular reproductive tactic for life, while a different group of males uses an alternative (Constantz 1975). Different reproductive alternatives may even be adopted between, rather than within, populations (Campanella 1975).

Theoretical studies of species' life history evolution incorporate "tradeoffs" between life history traits (Reznick 1985). One tradeoff is the cost of reproduction, which is fundamental in predicting the optimal reproductive tactics utilized in any given environment. Although behavioural studies reveal, as noted above, the existence of alternative reproductive tactics in fish species, empirical evidence quantifying the costs (e.g. decreased growth rate, reduced parental survival) and overall benefits (e.g. increased fecundity) associated with these alternatives remains scant. Reznick (1985) described four empirical methods for measuring the costs of reproduction. Firstly, studies in phenotypic correlations would deal with naturally occurring variation in reproductive effort, presenting statistical correlations or associations between some index of reproductive effort and a potential cost to the parents. Secondly, direct experimental manipulation of some aspect of reproduction or some environmental variable which affects reproduction would allow measurement of correlated responses in adult growth and survival. Thirdly, genetic correlations could encompass variations between natural populations in addition to differences within a population, producing quantitative genetic estimates of the correlation of an index of reproductive effort with some potential cost. A fourth technique would involve an artificial selection experiment, measuring correlated changes in some index of reproductive effort and a potential cost in response to selection on some aspect of an organism's life history (e.g. an artificial reduction in adult lifespan selecting for increased fecundity at an early age plus reduced longevity).

The cunner, *Tautoglabrus adspersus* (Walbaum), a common inshore labrid fish, is an excellent subject for phenotypic correlation studies concerning alternative reproductive tactics because male cunners utilize two reproductive tactics in Newfoundland (i.e. pair spawning and group spawning; Pottle and Green 1979a, Pottle *et al.* 1981). Specifically, a territorial male (>200 mm TL) courts individual females as they swim through his territory. Courtship often culminates in a vertical (pair) spawning run with both male and female releasing gametes at the apex. Prior to establishing its first territory, a preterritorial male does not spawn, although he is sexually mature by the third year. Alternatively,

a group spawning nonterritorial male (80-180 mm TL) courts a receptive female, and is joined by an aggregation of 3 to >12 males in chasing the female along a horizontal, convoluted path. The female then initiates a vertical (group) spawning run, which terminates with all individuals releasing gametes at the apex.

Preferritorial male cunners must attain a sufficiently large body size to compete successfully with conspecifics for a mating territory (i.e. in which subsequent pair spawnings are assured). Territorial males should therefore allocate more energy to body growth (i.e. during preterritorial years) than group spawning nonterritorial males. Since establishment of a territory is unnecessary for nonterritorial males to group spawn, these cunners should not be investing heavily in body growth like preterritorial males. Given that group spawning provides an opportunity for a female's eggs to be externally fertilized by many males, group spawning males should place more energy relative to preterritorial males into gamete production. This high reproductive effort in a group spawner would increase an individual's chances of successfully fertilizing eggs in the "sperm lottery" characteristic of group spawnings. Life history theory predicts that high reproductive effort in group spawners (i.e. large investment in sex products early in life, as opposed to deferred reproduction in preterritorial males) should result in a decreased somatic growth rate and/or reduced longevity. The present study is an attempt to evaluate these predictions in an investigation of tradeoffs associated with both reproductive tactics of Newfoundland male cunners.

To accomplish this, two sampling sites were selected on the basis of previous research conducted by Pottle and Green (1979a, 1981). These authors studied a cunner population of pair spawning territorial males and nonspawning preterritorial males in Broad Cove, Conception Bay, Newfoundland (1979a). Territorial males were larger than all preterritorial males observed, and a 1:1 sex ratio was evident. No group spawning had been observed at this site during 15 years of cunner research (Green, unpubl.). Alternately, Pottle *et al.* (1981) described a population of group spawning nonterritorial cunners at Norris Point, Bonne Bay, Newfoundland. An operational female/male ratio of at least 3:1 was

suggested by the external colouration of fish observed (see Pottle and Green 1979a for details of sexual dichromatism in *T. adspersus*). Parameters measured for each male in the present study were total length, eviscerated body weight, gonad weight, and age. These variables and a gonadosomatic index were tested for differences between group spawning nonterritorial males, pair spawning territorial males, and nonspawning preterritorial cunners.

MATERIALS AND METHODS

2.1. Study Sites

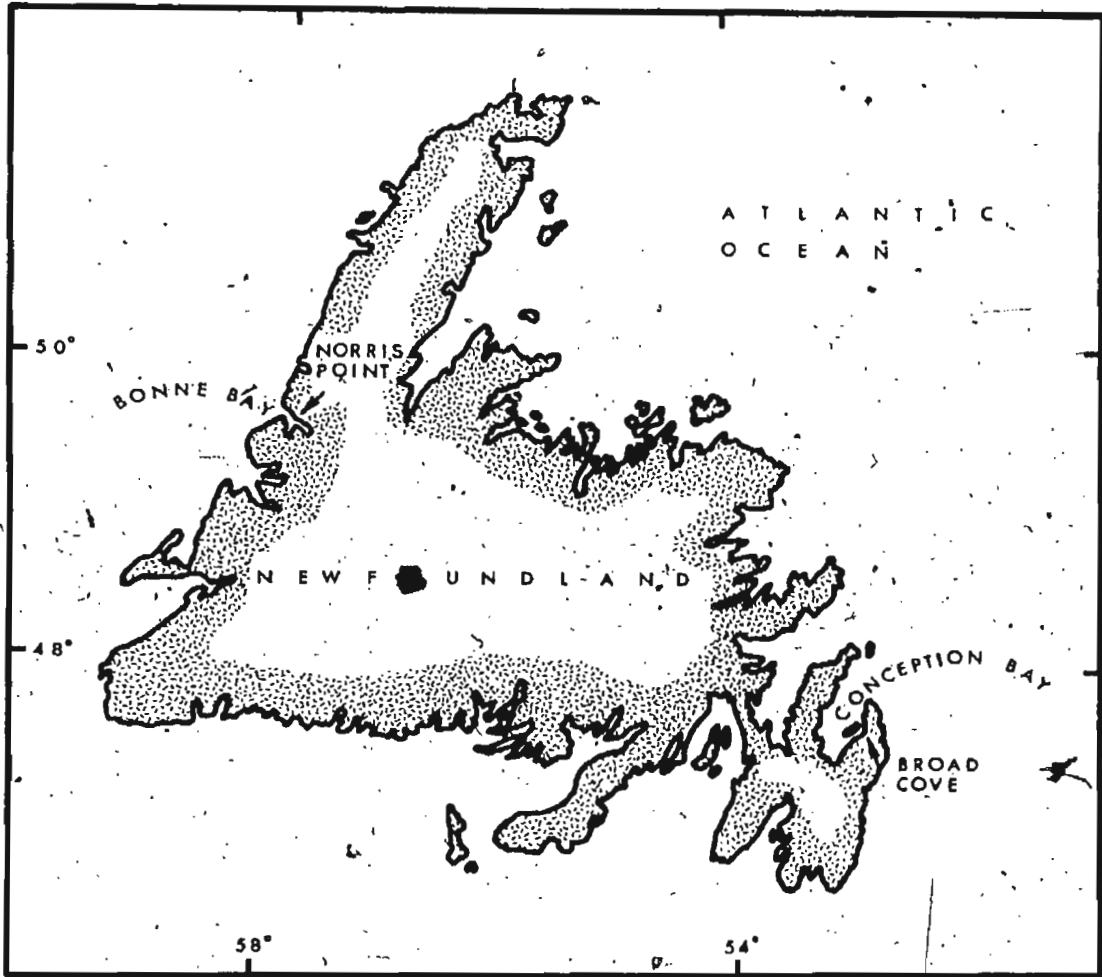
Located on the southeastern side of Conception Bay ($47^{\circ}35' N$, $52^{\circ}53' W$), Newfoundland (Figure 2-1), Broad Cove is characterized by a bottom sloping gradually seaward, with large and small boulders strewn amid bedrock outcroppings. Seasonal growth of macrophytes and benthic algae periodically blanket much of this area.

Situated on the west coast of Newfoundland (Figure 2-1), Bonne Bay is a deep, two-pronged fjord with a small percentage of littoral area. Some of this littoral zone characterizes Norris Point ($49^{\circ}15' N$, $59^{\circ}30' W$), with a flat bottom topography consisting solely of sand and pebbles. Aquatic vegetation is absent.

2.2. Sampling Procedure and Measurements

One hundred ninety-four group spawning nonterritorial males were collected just prior to spawning at Norris Point on June 24-25, 1984 (Table 2-1). One hundred ninety-six preterritorial males were obtained from Broad Cove on July 4-5, before the 1984 spawning season (*ibid.*). The gear used was a collapsible hoop net consisting of two 1 m diameter brass rings joined by 1 m of 1:3 cm (stretched) nylon mesh netting (Figure 2-2). This net was baited with freshly crushed sea urchins, *Strongylocentrotus droebachiensis* (a preferred food of cunners), lowered from a boat to rest flat on the bottom, then rapidly hauled to the surface after cunners had been attracted to the bait (approx. 2-3 min). Although territorial male cunners do not enter hoop nets, a submerged observer was present during collection of preterritorial males to ensure that no territorial fish were netted. Sixty-five territorial males (*i.e.* pair spawners) were collected by

Figure 2-1: Locations of the study sites in Newfoundland.



SCUBA divers at Broad Cove on July 6-7, 1984. All specimens were placed on ice immediately following capture and transported to freezer facilities at the Marine Sciences Research Laboratory (Logy Bay).

All samples were later processed for measurements of total length (TL ± 1 mm), body wet weight (following removal of digestive tract and gonads), and gonad wet weight. Weights to the nearest ± 0.01 g were obtained using a Mettler Precisa-512CCT digital balance. Otolith and scale samples were also extracted from each cunner (see below), and placed in standard scale envelopes for storage.

To control for possible site-specific growth differences between males from both locations (e.g. due to a longer period of warmer summer water temperatures in Bonne Bay relative to Conception Bay; Steele 1974, Hooper unpubl.), 195 female group spawners were collected in hoop nets at Norris Point on June 29-30, just prior to commencement of the 1985 spawning season (Table 2-1). Eighty-three female pair spawners were netted prior to spawning in Broad Cove on July 10-11, 1985 (*ibid.*). All Broad Cove females and 88 females from Norris Point were processed as described above.

In addition to the above data, TL (± 1 mm), eviscerated body weight (± 0.01 g), and postspawning gonad wet weight were determined for 197 male group spawners netted at Norris Point on October 2-3, 1984, and 263 preterritorial males netted in Broad Cove on September 20-21, 1984 (Table 2-1). Otoliths and scale samples were also taken for subsequent aging.

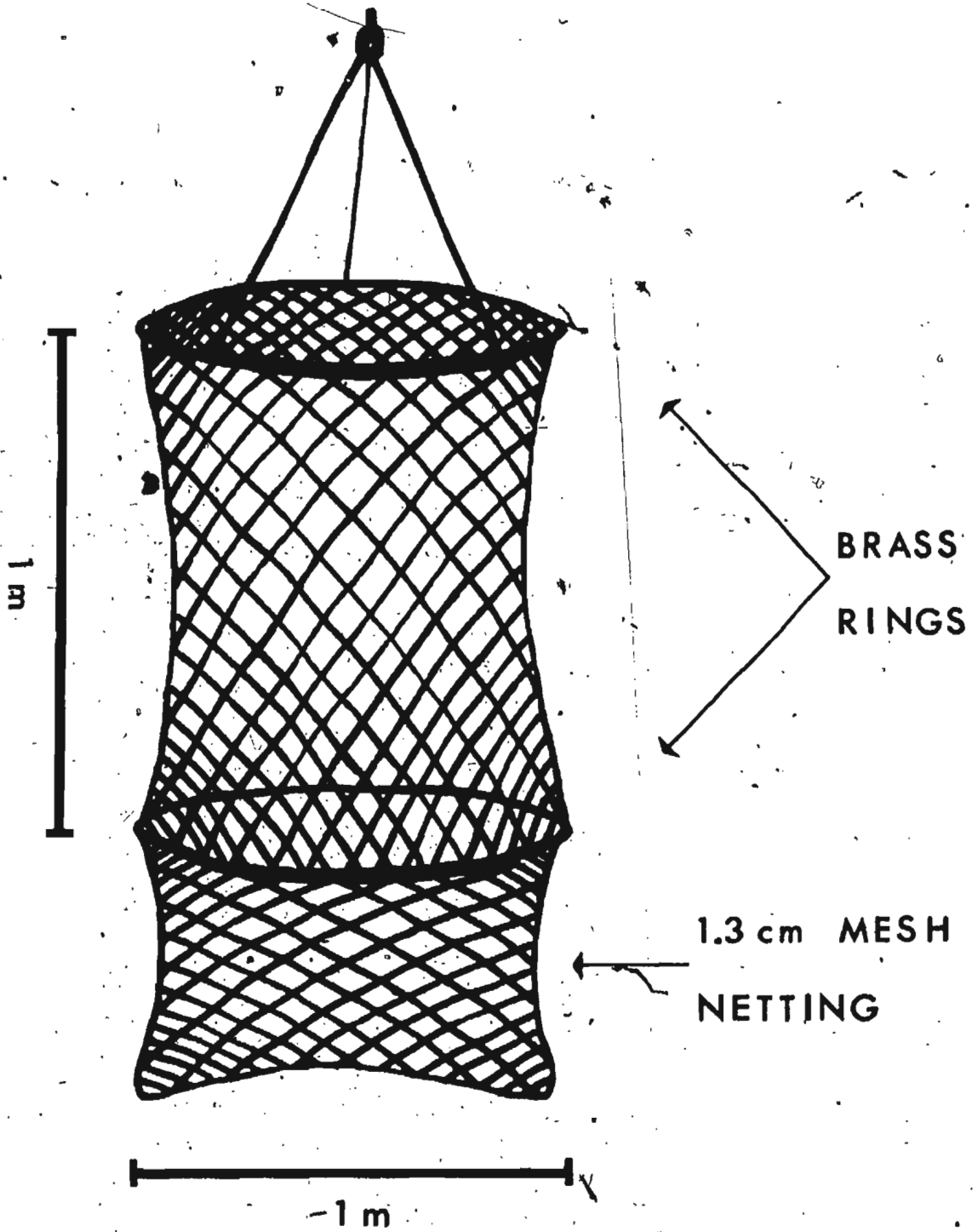
2.3. Age Determination

A high incidence of scale regeneration (approx. 80-90%) was observed for individual cunners. Consequently, five body regions on each side of 25 cunners were surveyed for nonregenerated scales. Scales valid for aging were most frequently located between rows four to six immediately above the anal fin on the left side of a fish. Scale samples were then removed from this region with forceps for all remaining fish, and each scale was gently cleaned with a 2% potassium hydroxide solution to remove adherent tissue (Serchuk 1972), prior to mounting between two glass slides. Due to the extreme difficulty in determining

Table 2-1: Description of nonterritorial cunner catches hauled in 1984 and 1985, between 0730 - 1745 h.

Location:	Sampling Date:	Total # of Males:	Total # of Females:	Sex Ratio (M:F):
Bonne Bay	June 24/84	71	789	1:12.5
	June 25/84	123	no data	no data
Broad Cove	July 4 - 5/84	196	744	1: 3.8
	Sept. 20 - 21/84	263	1052	1: 4.0
Bonne Bay	Oct. 2 - 3/84	197	3763	1:19.1
	June 29 - 30/85	22	195	1: 8.9
Broad Cove	July 10 - 11/85	no data	83	no data

Figure 2-2: Diagram of hoop net sampling gear.



Age with scales mounted conventionally from Broad Cove territorial males, permanent acetate slide impressions were made of these scales to increase readability with a Zeiss Projectina microprojector.

Left and right otoliths (sagittae) were extracted with forceps through a cranial incision, and rubbed to remove extraneous material. Relatively thick otoliths bearing unreadable surfaces were either ground down on a #149 carborundum stone or broken in half through the nucleus; in the latter instance the broken surface was read. Otolith pairs were mounted for aging in a 1:1 glycerin and water mixture on black Plasticine.

For all group spawning and preterritorial fish, age was first determined on otoliths under reflected light with a Zeiss stereomicroscope, then independently on scales with a Bausch and Lomb microprojector. Fishes with both structures intact were used for age verification between these two methods.

One hundred otoliths were also randomly reread in a double-blind study by George Fury, a technician with many years of experience aging fish at the Northwest Atlantic Fisheries Center (D.F.O. - St. John's branch, F.A.F.P. division) to obtain an estimate of observer agreement.

2.4. Statistical Analyses

All data analyses were performed using programs available in the Statistical Package for the Social Sciences (X version 2.1, SPSS Inc. 1983) on the Digital Equipment Co. VAX-11/785 computer at Memorial University of Newfoundland.

To investigate whether all Newfoundland male cunners adopt the same tactics of growth and maturation, somatic and gonadal development at age were compared between Norris Point group spawners and Broad Cove preterritorials. Fish ages were first categorized into groups; each group containing 3 age classes. Means calculated for total length (TL), body weight (W_b), gonad weight (W_g), and gonadosomatic index (GSI, see Equation 1 on next page) within each age group were tested with Student's *t* for differences between both populations.

$$\text{GSI (\%)} = \frac{\text{gonad weight (g)}}{\text{eviscerated body weight (g)}} \times 100 \quad (1)$$

* Body weight minus gonads and digestive tract. The cunner is a stomachless fish.

Linear regression using least squares was then applied to untransformed data to describe TL, W_b , W_g , and GSI over the complete age range for Norris Point group spawning males and Broad Cove preterritorial males. To stabilize heterogeneous variance in the resultant error terms (Draper and Smith 1981), all variables except GSI were natural log-transformed ($\ln = \log_e$). Multiple linear regression with a "dummy" variable representing location was used on data pooled from both sampling sites. Hierarchical F tests were utilized to test for differences in the slopes and group means of the latter descriptive equations.

To compare the proportion of energy allocated to gonad development per unit body weight by male group spawners and preterritorial males, natural logarithms of their gonad weights were regressed as above against \ln -transformed body weights. F tests were used to test for differences in the regression lines describing each male type. Length-weight relationships using \ln -transformed data were also compared.

Female data (i.e. TL, W_b , W_g and GSI at age) from both locations were analysed for differences with the statistical methods described above. Multiple linear regression required natural log (\ln) transformations similar to those done on males. Length-weight relationships and body weight-gonad weight relationships were also compared.

Within the Broad Cove cunner population, preterritorial males were investigated for similarities to pair spawning territorial males (see above for statistical techniques). Preterritorial males were then statistically compared with resident nonterritorial females. Differences between sexes in the Norris Point cunner population were analysed as well.

Group spawning males from Norris Point were studied for a tradeoff between sperm production and somatic growth. Ln-transformed W_g was regressed against $\ln TL$ within each age class containing 10 or more males (i.e. 6-12 years). A significant negative relationship at age was considered *a priori* to be indicative of a tradeoff. Male group spawners with gonadosomatic indices in the extreme range of values were also separated into two categories. One category contained males with gonadosomatic indices $\leq 10\%$; i.e. in the range of GSI values characteristic for nonspawning, preterritorial males. Males in another category had GSIs $\geq 15\%$; i.e. outside the range of GSIs representing both territorial and preterritorial males. Body weights were plotted against total lengths per age class to determine if body sizes at age were similar between both categories.

RESULTS

3.1. Age Determination

Age verification between otoliths and scales from 438 fish showed 94.3% agreement. Rereading of 93 otoliths by a second observer indicated 94.7% agreement. Where differences between readers did occur, they were generally of only 1-2 years.

The age structure of each cunner population sampled (i.e. sexes separate) is presented in Figures 3-1 - 3-4.

3.2. Sperm Production

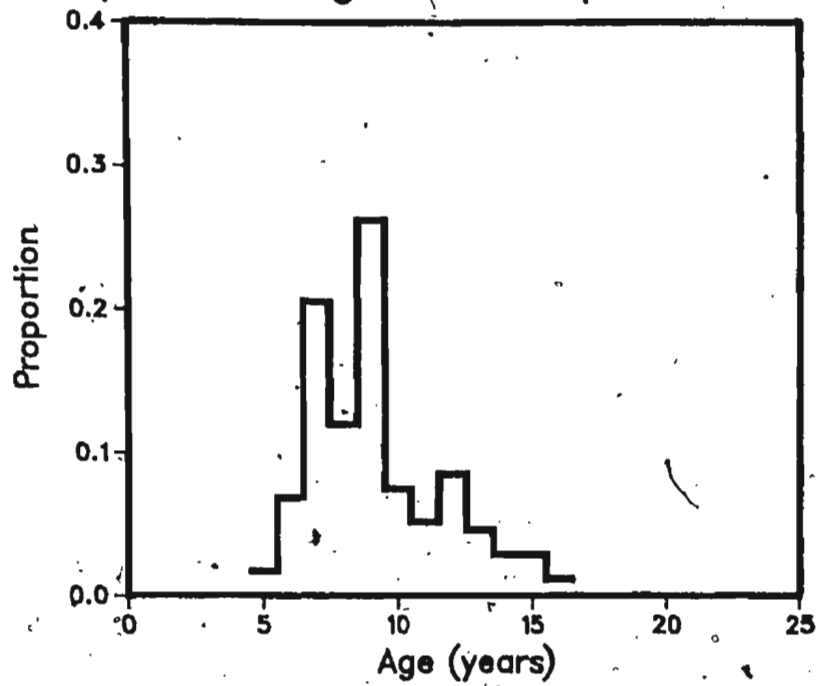
Student's t tests indicated that absolute gonad weights (W_g), across three age groups (6-14 years) were significantly greater in Norrig Point group spawning males than in Broad Cove preterritorial cunners. The proportion of gonad weight relative to body weight (i.e. gonadosomatic index: GSI) in group spawners was significantly larger than that of preterritorial males aged 6-14 years. Gonad weight and GSI did not differ between both male types ≥ 15 years (Table 3-1).

Regression analyses supported the above findings (for a summary, see Appendix A). The relationship of GSI with age was different between the two behavioural types of males younger than 15 years (Figure 3-5; $P < 0.001$). Natural logarithms (\ln) of preterritorial male age explained 62% of the variance observed in $\ln(W_g)$, whereas there was no correlation between age and W_g for group spawners. $\ln(W_g)$ regressed against $\ln(\text{body weight})$ for group spawners was not significant, although they possessed heavier gonads per unit body weight (W_b) than preterritorial males (Figure 3-6; $P < 0.001$). $\ln(W_b)$ of preterritorial males explained 61% of the variance observed in $\ln(W_g)$.

Figure 3-1: Age structure of the Bonne Bay group spawning male cunner population.

Figure 3-2: Age structure of the Broad Cove male cunner population.
Territorial males excluded.

Bonne Bay Group Spawning Male Cunners, 1984:
Proportion of Ages in the Population Sample



Broad Cove Preterritorial Male Cunners, 1984:
Proportion of Ages in Population Sample

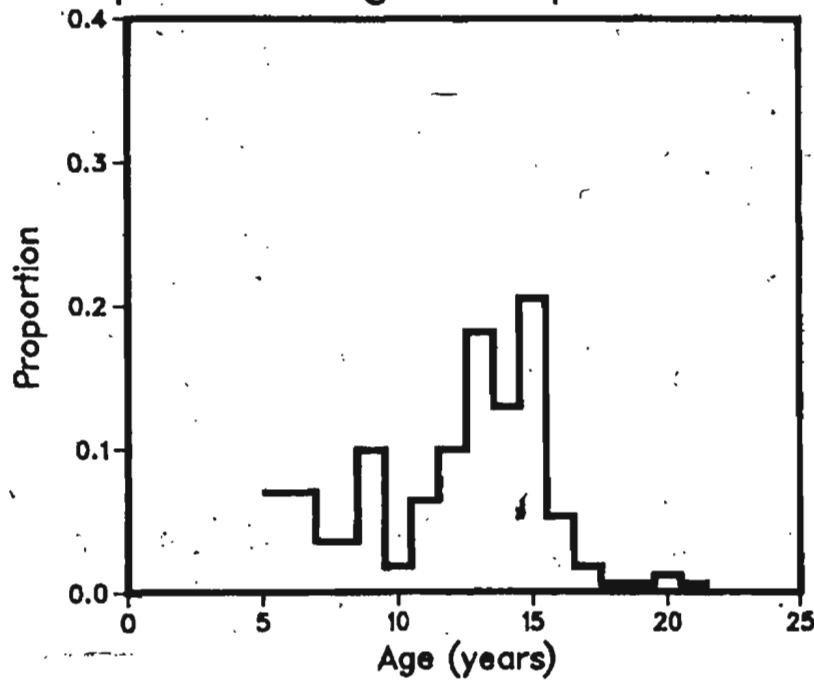
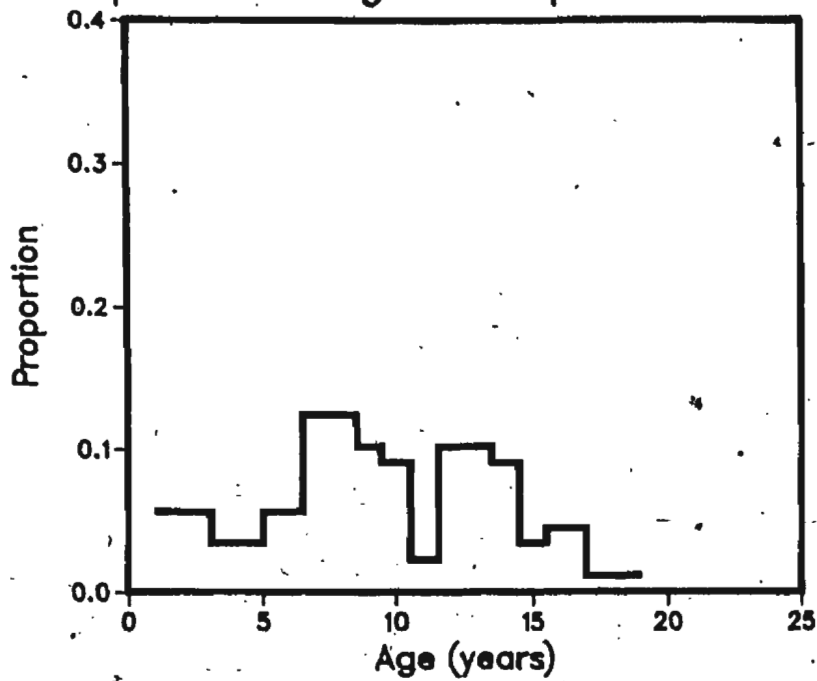


Figure 3-3: Age structure of the Bonne Bay female cunner population.

Figure 3-4: Age structure of the Broad Cove female cunner population.

Bonne Bay Female Cunnors, 1985:
Proportion of Ages in Population Sample



Broad Cove Female Cunnors, 1985:
Proportion of Ages in Population Sample

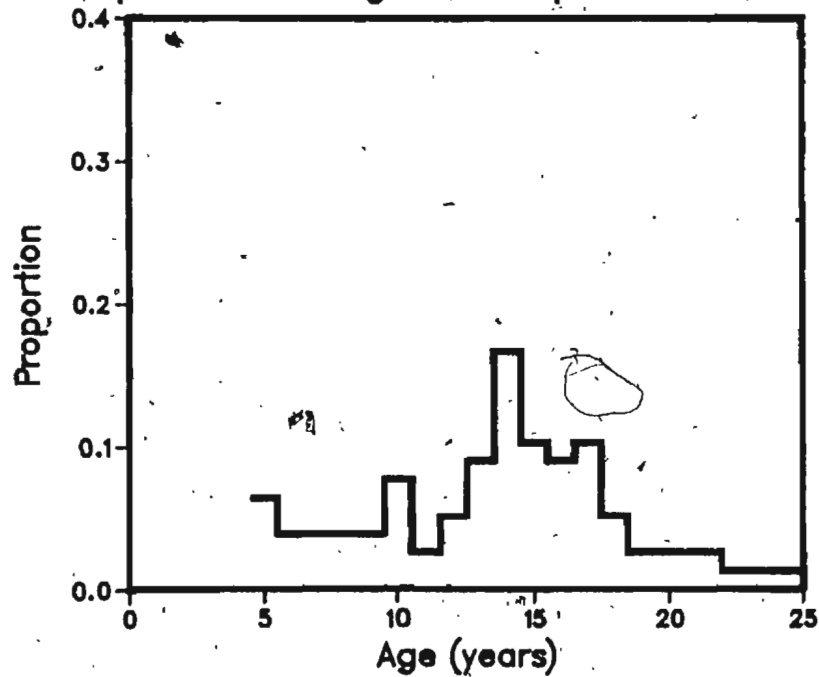


Table 3-1: Student's t tests using means of TL, W_b , W_g , and GSI between Bonne Bay group spawning males (BB) and Broad Cove preterritorial males (BC).

Age Group:	Variable Tested:	df:	t Value:	2-Tail Probability:	Result:
6-8 yrs	TL	85	-1.18	0.389	$BB\mu = BC\mu$
	W_b	85	-0.52	0.605	$BB\mu = BC\mu$
	W_g	84	6.87	0.000	$BB\mu > BC\mu$
	GSI	84	6.31	0.000	$BB\mu > BC\mu$
9-11 yrs	TL	97	-2.09	0.039	$BB\mu < BC\mu$
	W_b	96	-2.37	0.020	$BB\mu < BC\mu$
	W_g	95	4.02	0.000	$BB\mu > BC\mu$
	GSI	95	2.59	0.011	$BB\mu > BC\mu$
12-14 yrs	TL	96	-6.17	0.000	$BB\mu < BC\mu$
	W_b	96	-5.24	0.000	$BB\mu < BC\mu$
	W_g	96	3.21	0.002	$BB\mu > BC\mu$
	GSI	96	8.31	0.000	$BB\mu > BC\mu$
≥ 15 yrs	TL	56	-3.69	0.001	$BB\mu < BC\mu$
	W_b	57	-2.59	0.012	$BB\mu < BC\mu$
	W_g	55	-0.98	0.329	$BB\mu = BC\mu$
	GSI	55	1.86	0.063	$BB\mu = BC\mu$

df = degrees of freedom

μ = variable mean per age group

$\alpha = 0.05$

Figure 3-5: Regression of gonadosomatic index (GSI) on age for Bonne Bay group spawning males and Broad Cove preterritorial cunners.

Bonne Bay and Broad Cove Male Cunners, 1984:
 Regression of Gonadosomatic Index on Age
 (Symbols represent individual fish)

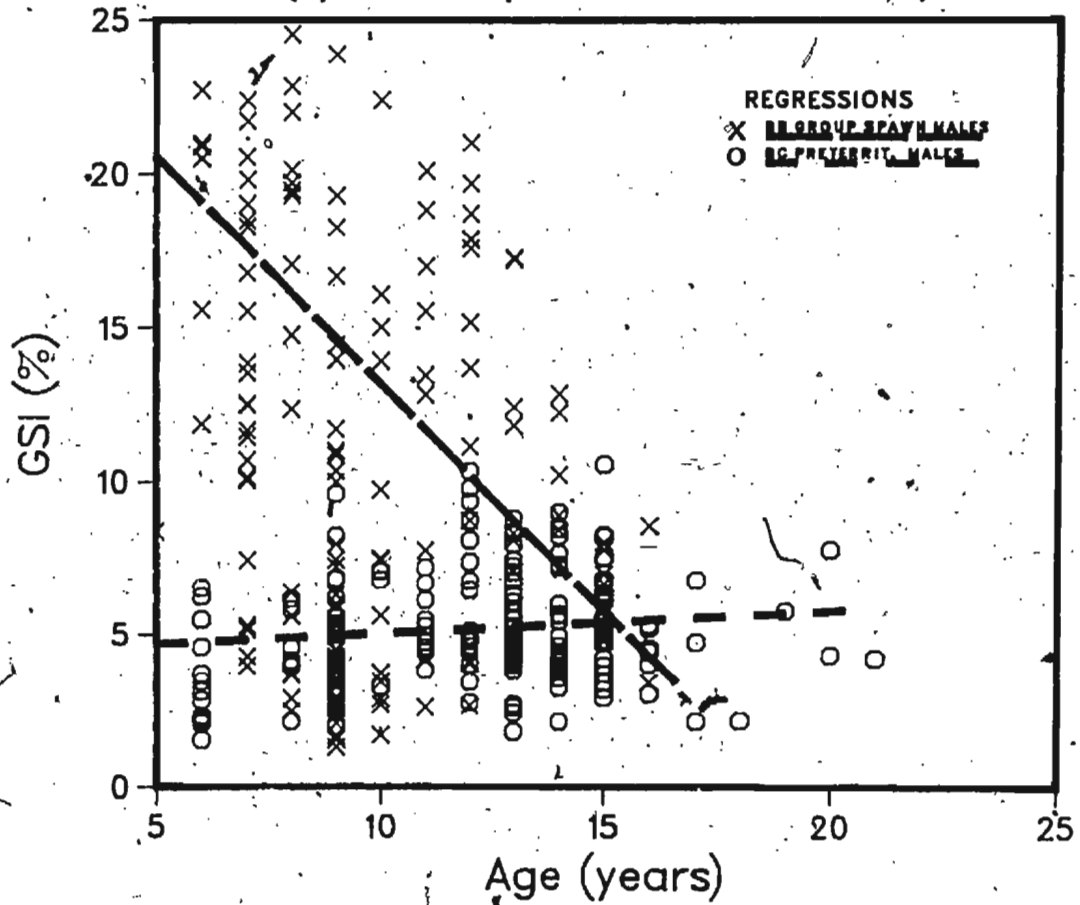
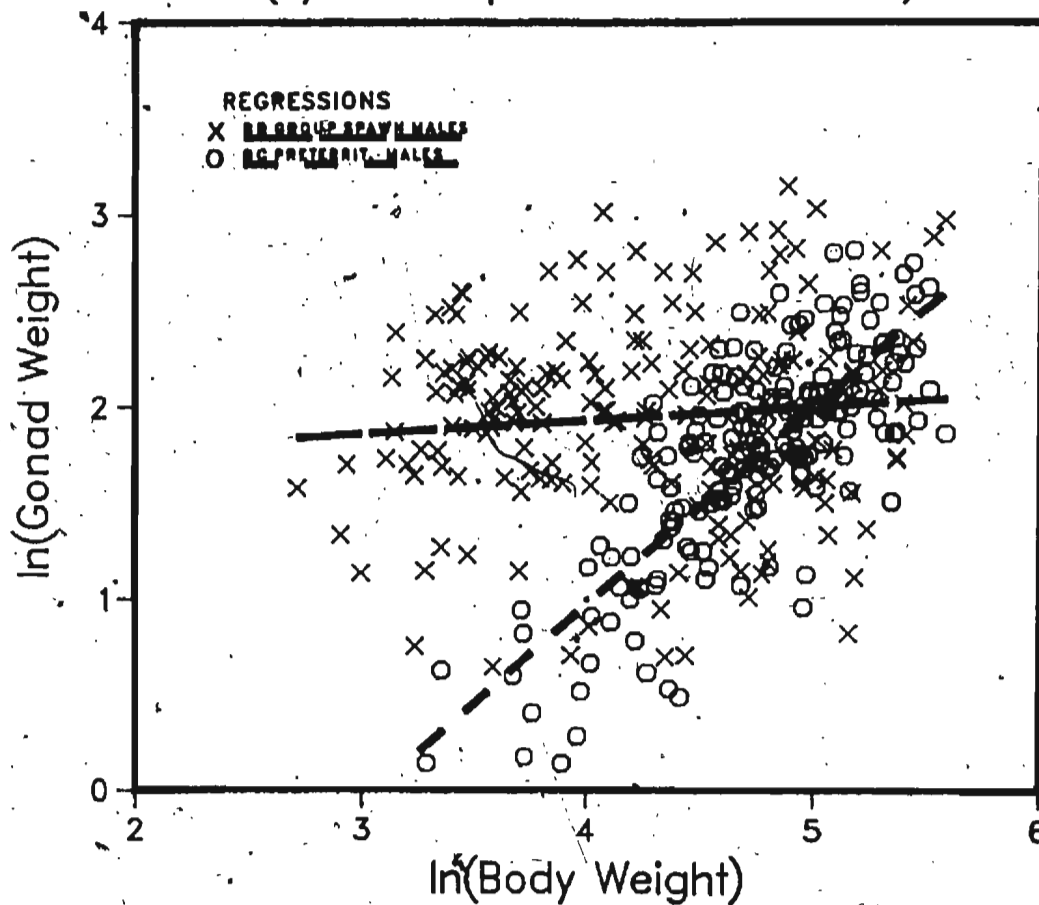


Figure 3-6: Regression of $\ln(\text{gonad weight})$ on $\ln(\text{body weight})$ for Bonne Bay group spawning males and Broad Cove preterritorial cunners.

Bonne Bay and Broad Cove Male Cunners, 1984:
Regression of $\ln(\text{Gonad Weight})$ on $\ln(\text{Body Weight})$
(Symbols represent individual fish)



Within the Broad Cove cunner population, the regressions of GSI on age for both territorial and preterritorial males were not significant, while gonadosomatic index at age was greater in pair spawning territorial males than in preterritorial males (Figure 3-7; $P < 0.01$). No correlation was found between territorial male age and W_g , although these gonad weights at age were significantly larger than those of preterritorial males ($P < 0.001$). Territorial males also allocated more energy to gonadal development per unit body weight than preterritorial males (Figure 3-8; $P < 0.001$).

3.3. Somatic Growth

Student's *t* tests revealed that total lengths (TL) and body weights (W_b) for the first age group (6-8 years) did not differ significantly between Norris Point group spawning males and Broad Cove preterritorial males. However, the mean size of group spawners was slightly less than that of preterritorial males across the remaining three age groups (≥ 9 years; Table 3-1).

Regression analyses supported the latter finding over the complete age range (for a summary, see Appendix A). $\ln(\text{age})$ of Norris Point group spawners and Broad Cove preterritorial males explained 52% and 92%, respectively, of the variance observed in $\ln(\text{TL})$ ($P < 0.01$). The same was found for $\ln(\text{age})$ and $\ln(W_b)$ (Table 3-2; $P < 0.001$). Length-weight relationships indicated that preterritorial males were heavier per length class than group spawning males (Table 3-3; $P < 0.001$).

Within the Broad Cove cunner population, regression analyses of \ln -transformed data indicated that territorial males were significantly larger in total length and body weight at age than preterritorial males (Figures 3-9 and 3-10; $P < 0.001$). Based on length-weight relationships, body weights at length were greater for territorial males (Table 3-3; $P < 0.01$).

Student's *t* tests across all five age groups indicated that Norris Point females were smaller in TL, W_b , and W_g than females from Broad Cove. Gonadosomatic index did not differ between both female groups (Table 3-4). Regression analyses of \ln -transformed data supported these results (for a

Figure 3-7: Regression of gonadosomatic index (GSI) on age for Broad Cove territorial males and preterritorial cunners.

Broad Cove Preferr. and Terr. Male Cunners, 1984:
 Regression of Gonadosomatic Index on Age
 (Symbols represent individual fish)

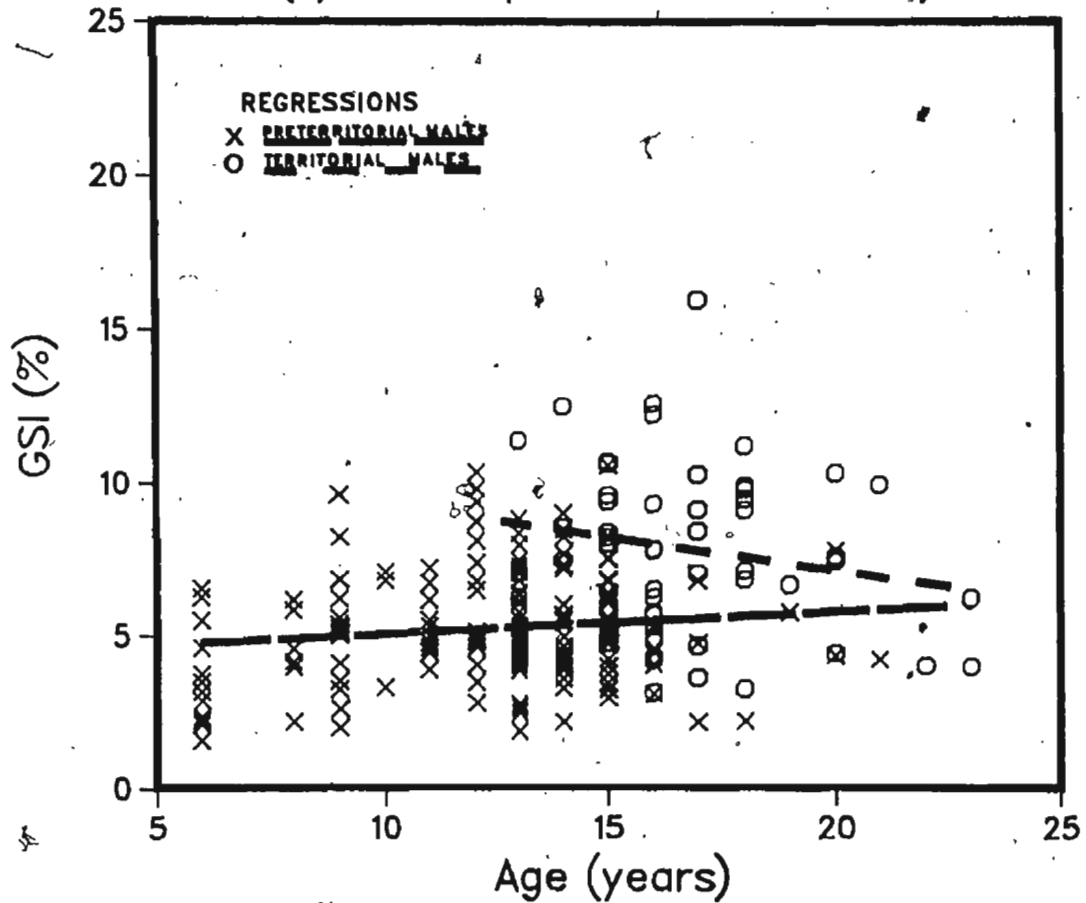
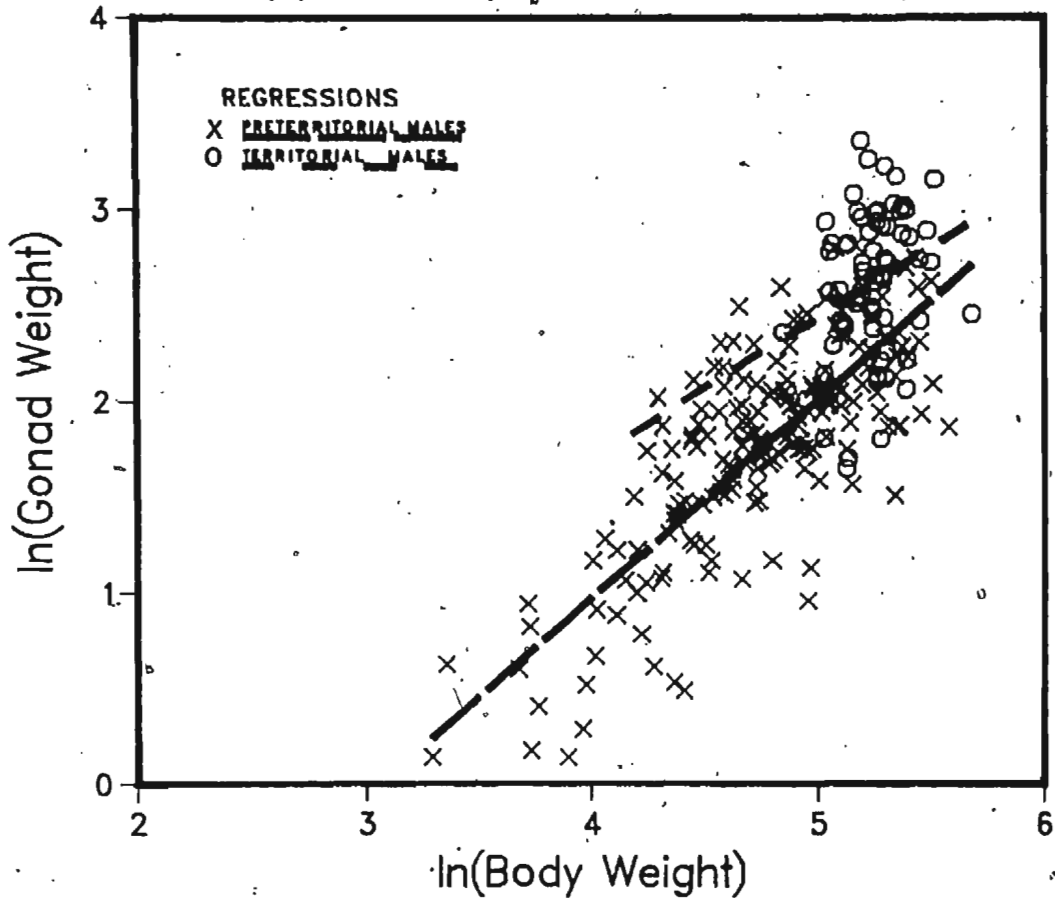


Figure 3-8: Regression of $\ln(\text{gonad weight})$ on $\ln(\text{body weight})$ for Broad Cove territorial males and preterritorial cunners.

Broad Cove Preterr. and Terr. Male Cunners, 1984:
Regression of $\ln(\text{Gonad Weight})$ on $\ln(\text{Body Weight})$
(Symbols represent individual fish)



summary, see Appendix A). The relationships of TL and W_b with age were significantly different between the two populations of females (Figures 3-11 and 3-12; $P < 0.001$), while 87% of their variability in each parameter was explained by $\ln(\text{age})$. $\ln(\text{age})$ of females from Norris Point and Broad Cove explained 80% and 84%, respectively, of the variance observed in $\ln(W_g)$, and both relationships differed significantly ($P < 0.001$). No correlation was found between age and GSI for either female group.

Linear relationships describing $\ln(W_g)$ against $\ln(W_b)$ were the same for females from both populations. $\ln(W_b)$ explained 82% and 97% of the variance observed in $\ln(W_g)$ for females from Norris Point and Broad Cove, respectively. Length-weight relationships were not significantly different (Table 3-3).

Comparisons of \ln -transformed TL and W_b at age between females and males within each population revealed that group spawning males at Norris Point were larger than resident females ($P < 0.01$). Based on length-weight relationships, females were heavier per length class than males ($P < 0.001$). Preterritorial males in Broad Cove were larger in TL and W_b at age than females ($P < 0.001$). Length-weight relationships indicated that females were slightly heavier at length than preterritorial males (Table 3-3; $P < 0.05$).

An investigation of a tradeoff between sperm production and somatic growth in Norris Point group spawning males showed that gonad weight was not related to total length within each age class (i.e. 6-12 years; $P = 0.05$). However, male group spawners with gonadosomatic indices $\leq 10\%$ (i.e. in the range of GSI values found for nonspawning preterritorial males: Cat(2)) were all large in body size at age. Group spawners with GSIs $\geq 15\%$ (i.e. outside the range of GSIs representing both territorial and preterritorial males: Cat(1)) were small in length and body weight at age (Figure 3-13).

Table 3-2: Calculated total length, and body weight relationships at age for Newfoundland cunners.

Location:	Sex:	Status:	Relationship:	r:	n:
Bonne Bay	Male	NT	$\ln(TL) = 4.1919 + 0.4256\ln(\text{Age})$.72392	175
			$\ln(W_b) = 1.1166 + 1.3914\ln(\text{Age})$.71218	175
Broad Cove	Female	NT	$\ln(TL) = 3.8178 + 0.5463\ln(\text{Age})$.93497	88
			$\ln(W_b) = 0.1877 + 1.6829\ln(\text{Age})$.92467	88
	Male	PT	$\ln(TL) = 4.1630 + 0.4541\ln(\text{Age})$.96057	170
			$\ln(W_b) = 1.1617 + 1.4282\ln(\text{Age})$.96146	170
	Female	NT	$\ln(TL) = 5.2551 + 0.0800\ln(\text{Age})$.23707	54
			$\ln(W_b) = 4.8589 + 0.1425\ln(\text{Age})$.14422	54
			$\ln(TL) = 3.7684 + 0.6068\ln(\text{Age})$.93242	78
			$\ln(W_b) = 0.0762 + 1.8504\ln(\text{Age})$.93400	78

NT = nonterritorial

PT = preterritorial

T = territorial

TL = total length (mm)

W_b = body weight (g)

r = correlation coefficient

n = number of fish in analysis

Table 3-3: Calculated length-weight relationships for Newfoundland cunners.

Location:	Sex:	Status:	Relationship:	r:	n:
Bonne Bay	Male	NT	$\ln(W_b) = -12.6703 + 3.2851\ln(TL)$ $W_b = 3.1431 \times 10^{-6} TL^{3.285}$.99131	194
	Female	NT	$\ln(W_b) = -11.6085 + 3.0871\ln(TL)$ $W_b = 9.0885 \times 10^{-6} TL^{3.087}$.99372	95
Broad Cove	Male	PT	$\ln(W_b) = -11.7128 + 3.1051\ln(TL)$ $W_b = 8.1900 \times 10^{-6} TL^{3.105}$.99403	185
		T	$\ln(W_b) = -9.5775 + 2.7072\ln(TL)$ $W_b = 6.9270 \times 10^{-5} TL^{2.707}$.89526	65
	Female	NT	$\ln(W_b) = -11.2367 + 3.0154\ln(TL)$ $W_b = 1.3181 \times 10^{-5} TL^{3.015}$.99475	84

NT = nonterritorial

PT = preterritorial

T = territorial

 W_b = body weight (g)

TL = total length (mm)

r = correlation coefficient

n = number of fish in analysis

Figure 3-9: Regression of $\ln(\text{total length})$ on $\ln(\text{age})$ for Broad Cove territorial males and preterritorial cunners.

Figure 3-10: Regression of $\ln(\text{body weight})$ on $\ln(\text{age})$ for Broad Cove territorial males and preterritorial cunners.

Broad Cove Preferr. and Terr. Male Cunnners, 1984:
 Regression of $\ln(\text{Body Weight})$ on $\ln(\text{Age})$
 (Symbols represent individual fish)

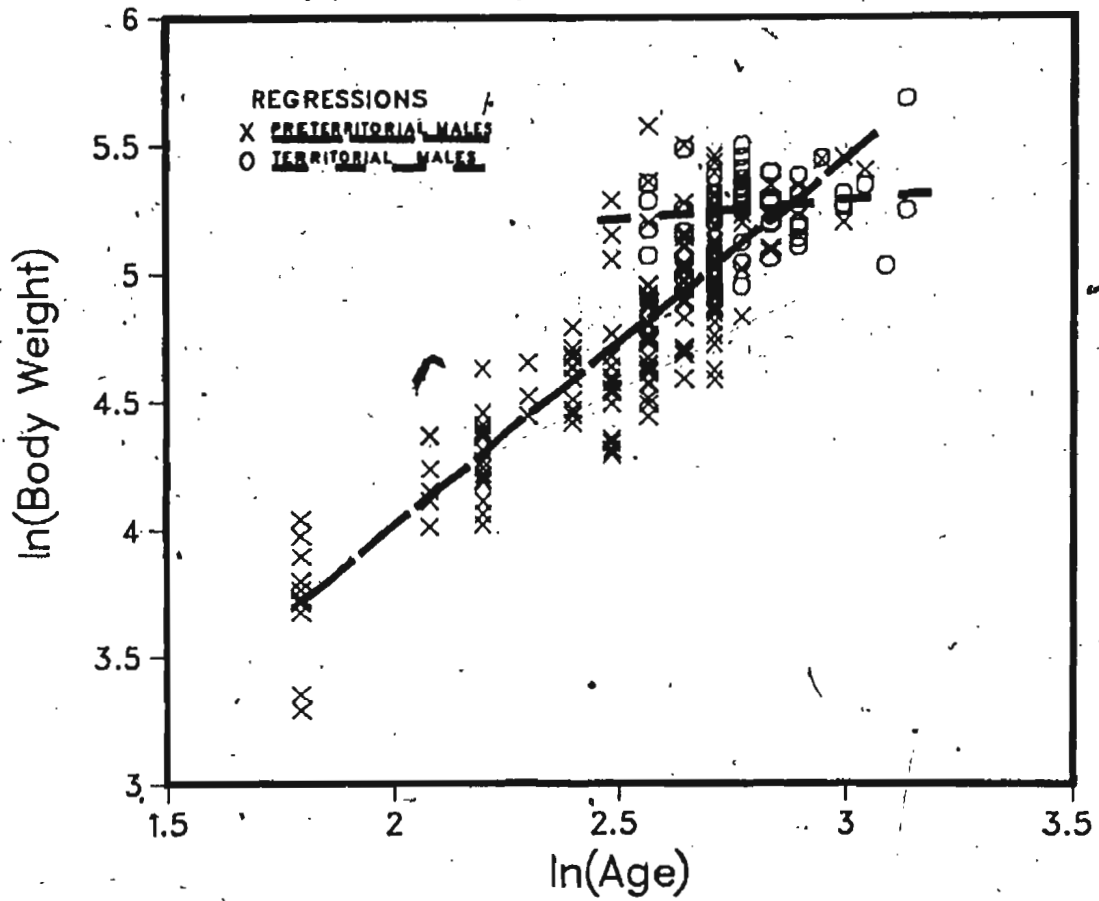


Table 3-4: Student's t tests using means of TL, W_b , W_g , and GSI between females from Bonne Bay (BB) and Broad Cove (BC).

Age Group:	Variable Tested:	df:	t Value:	2-Tail Probability:	Result:
< 6 yrs	TL	11	-2.86	0.015	$BB\mu < BC\mu$
	W_b	11	-2.86	0.015	$BB\mu < BC\mu$
	W_g	11	-2.96	0.013	$BB\mu < BC\mu$
	GSI	11	-2.99	0.071	$BB\mu = BC\mu$
6- 8 yrs	TL	31	-2.69	0.012	$BB\mu < BC\mu$
	W_b	31	-2.81	0.008	$BB\mu < BC\mu$
	W_g	31	-1.81	0.037	$BB\mu < BC\mu$
	GSI	31	0.18	0.862	$BB\mu = BC\mu$
9-11 yrs	TL	28	-3.57	0.001	$BB\mu < BC\mu$
	W_b	28	-5.33	0.000	$BB\mu < BC\mu$
	W_g	28	-4.94	0.000	$BB\mu < BC\mu$
	GSI	28	-1.20	0.239	$BB\mu = BC\mu$
12-14 yrs	TL	48	-3.06	0.004	$BB\mu < BC\mu$
	W_b	48	-2.09	0.042	$BB\mu < BC\mu$
	W_g	48	-1.56	0.025	$BB\mu < BC\mu$
	GSI	48	-0.48	0.634	$BB\mu = BC\mu$
≥ 15 yrs	TL	38	-1.56	0.000	$BB\mu < BC\mu$
	W_b	38	-0.43	0.004	$BB\mu < BC\mu$
	W_g	37	-1.36	0.001	$BB\mu < BC\mu$
	GSI	37	-4.48	0.128	$BB\mu = BC\mu$

df = degrees of freedom

μ = variable mean per age group

$\alpha = 0.05$

Figure 3-11: Regression of $\ln(\text{total length})$ on $\ln(\text{age})$ for Bonne Bay and Broad Cove female cunners.

Bonne Bay and Broad Cove Female Cunners, 1985:
Regression of $\ln(\text{Total Length})$ on $\ln(\text{Age})$
(Symbols represent individual fish)

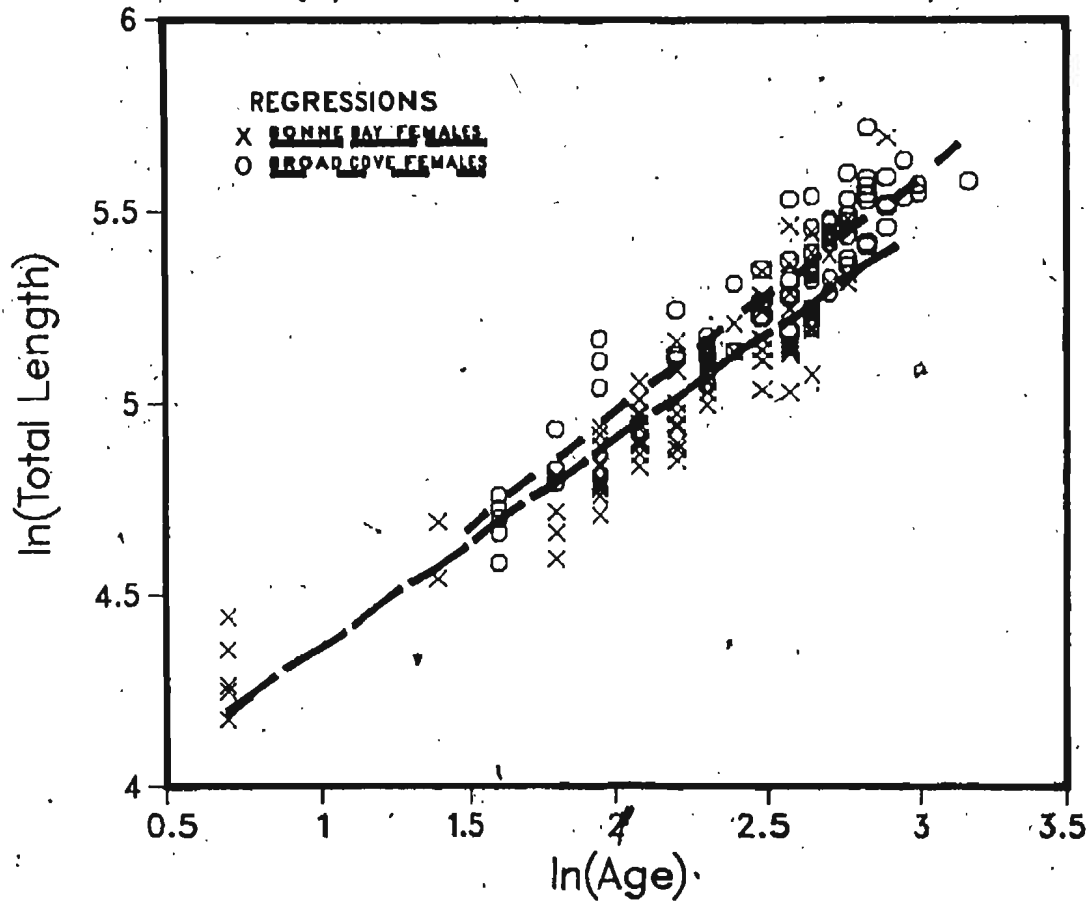


Figure 3-12: Regression of $\ln(\text{body weight})$ on $\ln(\text{age})$ for Bonne Bay and Broad Cove female cunners.

Bonne Bay and Broad Cove Female Cunners, 1985:
 Regression of $\ln(\text{Body Weight})$ on $\ln(\text{Age})$
 (Symbols represent individual fish)

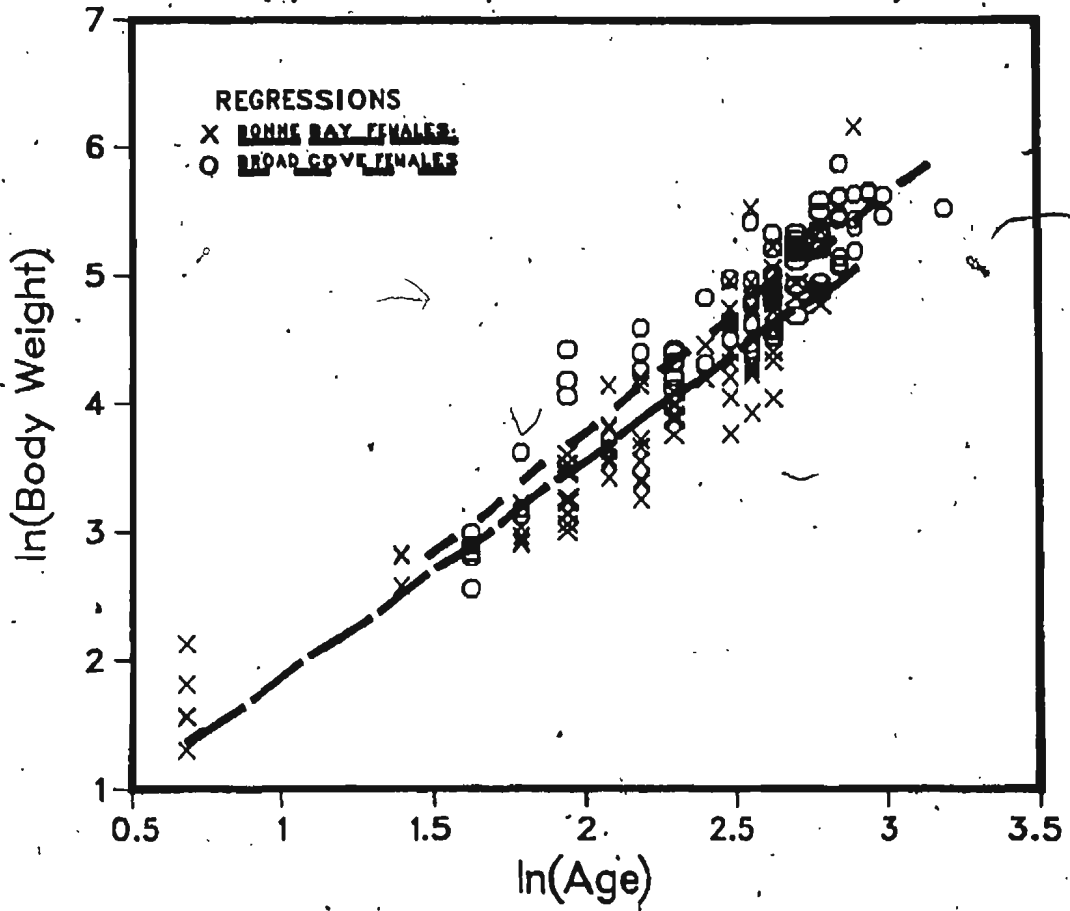
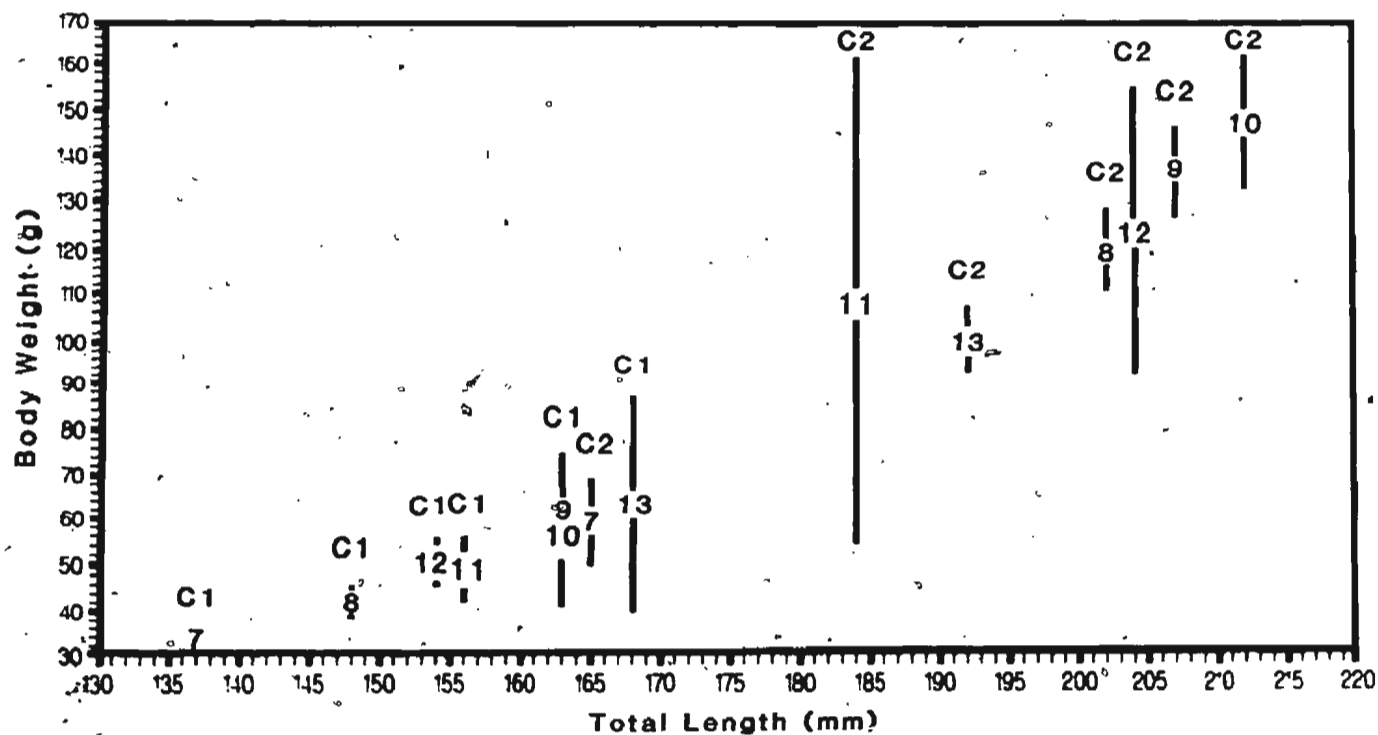


Figure 3-13: Mean body weights at length per age class of Cat(1) and Cat(2) group spawning males from Bonne Bay.

Bonne Bay Group Spawning Male Cunners, 1984: Mean Body Weight at Length for Cat(1) and Cat(2) Males.

Cat(1): Gonadosomatic Index $\geq 15\%$; Cat(2): GSI $\leq 10\%$



Each numeral indicates the specific age class of cunners.

Vertical bars represent the standard error of the mean.

DISCUSSION

A male's reproductive success primarily depends on how many of his sperm successfully fertilize eggs. Parker (1984) indicated that selection on males should favour mechanisms (*e.g.* behavioural, morphological, physiological) that increase an individual's chances of outcompeting sperm from rival males. He noted that males with external fertilization may have few alternative ways of allocating reproductive effort in intrasexual contests. As previously described, group spawning in cunners involves a large number of males simultaneously releasing gametes into the water column to externally fertilize a female's extruded eggs. Therefore, a male group spawning cunner's reproductive success is likely to be directly proportional to the number of sperm ejaculated. Sperm competition, an important intrasexual selective force in breeding systems with a high percentage of multiple paternity (Harvey and Harcourt 1984), may select for large gonadal investments in male cunner group spawners. Investing heavily in gamete production would assure numerical predominance of self's sperm in the "ensuing pelagic lottery" (Parker 1984). The present study indicates that this reasoning may well apply to male group spawning cunners, which make large gonadal investments early in life with energy allotments apparently independent of body size (Figure 3-6). Gonadosomatic index values of 25 to 46% were not uncommon for these fishes.

This high reproductive effort in group spawning males (*i.e.* large gonadal investment at an early age, as opposed to deferred reproduction in preterritorial males) should involve tradeoffs for individuals. According to life history theory (see Williams 1966, Stearns 1976), energy disbursement to one basic function (*e.g.* growth, maintenance, or reproduction) consequently decreases resources available for other processes. Length and body weight at age of the

male group spawning population at Norris Point in the present study were only slightly less than those of the preterritorial male population at Broad Cove, indicating no significant tradeoff between high sperm production and decreased somatic growth rate. Gonad weight was not related to total length within each age class for male group spawners, contrary to the negative relationship expected with evidence of such a tradeoff. However, male group spawners with gonadosomatic indices $\leq 10\%$ (i.e. in the range of GSI values characteristic for nonspawning preterritorial males) were all large in body size at age, whereas males with GSIs $\geq 15\%$ (i.e. outside the range of GSIs representing both territorial and preterritorial males) were small in length and body weight (Figure 3-13). This suggests that large amounts of energy allocated to gonads in group spawning males may reduce internal energy resources available for body growth.

In order to compare growth of Norris Point group spawning males with that of Broad Cove preterritorial males, differences in habitat (e.g. length of growing season, abundance and quality of food) between both sampling sites must be controlled for so that effects of local environment on cunner growth can then be corrected for. This procedure would allow investigation of differences in growth resulting from the different reproductive tactics used by both types of males. Female cunners exhibit the same growth and reproductive tactics irrespective of geographic location, and the present study indicates that females from both populations were allocating the same proportion of energy to gonadal development per unit body weight. Therefore, differences in female body size may reflect differences in conditions for growth between Bonne Bay and Conception Bay. For example, Bonne Bay has a longer period of warmer summer water temperatures than Conception Bay (Steele 1974, Hooper unpubl.). Norris Point females were significantly smaller in length and body weight at age than those of Broad Cove, although differences were slight.

The slower growth rate observed for Norris Point females may represent differences in one or a combination of the following factors: food habit, food availability, or local population density between sampling sites. Olla *et al.* (1975) found that the cunner's food habits vary widely with geographic location,

in addition to showing seasonal changes. Therefore, the energy content of foods consumed by Norris Point females could possibly be less than foods of Broad Cove females, but this speculation was not investigated here. Concerning local cunner population density, qualitative observations made during SCUBA dives at both sampling sites in the present study indicated that the cunner population at Norris Point was markedly denser than that of Broad Cove, although population estimates are unavailable. This observation was made *in situ* prior to cunners perceiving the presence of divers. Hart and Pitcher (1973) observed that roach (*Rutilus rutilus* Linnaeus) in the River Nene experienced better growth once its major predator (pike: *Esox lucius* Linnaeus) attained higher densities and thinned out younger roach from an initially dense population, possibly reflecting decreased intraspecific competition in roach for limited food resources. Norris Point females may also experience a similar pattern of slow growth as a result of greater intraspecific competition for food in a denser cunner population.

In addition to apparent differences in cunner population density between sampling sites, the sex ratio at Norris Point seemed greatly skewed towards females (9-19:1), as compared to the female/male ratio in Broad Cove (4:1; Table 2-1). These data are not in agreement with the findings of Pottle and Green (1979a, 1981) which indicated a 1:1 ratio in Broad Cove and at least a 3f:1m ratio at Norris Point. However, the latter authors used external fish colouration to determine sex of individual cunners, whereas gonadal products of "stripped" or sacrificed cunners were used in the present study. The observed sex ratios may have bearing on which male reproductive tactic predominates in the respective cunner population, although possible relationships were not studied here. As mentioned previously, variation in a male's adoption of a particular reproductive tactic may depend on the local supply of ripe females, in addition to other factors (e.g. the density of spawning males in a population). A large supply of females appears to be present in a male group spawning population at Norris Point, whereas there are almost equivalent numbers of females and males in a pair spawning population in Broad Cove. Dew (1970) noted a female/male ratio of 1:2.15 for cunners in Fishers Island Sound, Connecticut, but unfortunately did not report on local cunner reproductive behaviour.

A tradeoff of the high sperm production in group spawning males seems to be reduced longevity. A small proportion of males comprising the Norris Point sample was old (>9 years) relative to the large proportion of younger males (between 6 and 9 years; Figure 3-1), whereas at Broad Cove a large proportion of the males were older (from 10 to 15 years; Figure 3-2). This 'early' mortality could possibly affect the Norris Point cunner population as a whole, irrespective of reproductive effort or sex. For example, a harsher, more unstable environment in Bonne Bay (i.e. with respect to water temperature, food availability, frequency and magnitude of storms, etc.) relative to Broad Cove may increase physiological stress on all cunners, resulting in their early deaths. However, comparisons of female age distributions between both sampling sites refutes this possibility. While females older than those sampled at Norris Point were obtained from Broad Cove, the relative proportions of females at age were similar (Figures 3-3 and 3-4). Although information on food availability or stochastic climatic events is unavailable for either location, water temperature data tend to contradict a speculation that Bonne Bay is a more unstable environment than Conception Bay.

Alternately, the relative absence of old males at Norris Point may represent a migration of older males from the sampling site. If so, these males would be absent from hoop net samples. Whether older males are present in the deeper waters of Bonne Bay, and, if so, hold territories, is unknown. Olla *et al.* (1975) noted that cunners older and larger (210-420 mm TL) than those found in inshore waters inhabit offshore reefs (primarily shipwrecks). Unfortunately, sexes were not distinguished. They also speculated whether these cunners were originally recruited to offshore sites and remained there, or were members of an inshore population that moved offshore after attaining a certain size (as is the habit of a close relative of cunners: the tautog, *Tautoga onitis* Linnaeus).

Absence of territorial males at Norris Point may be a direct consequence of the density of the local cunner population. Warner and Hoffman (1980b) investigated how changes in population density surrounding the mating territory of another labrid (the bluehead wrasse: *Thalassoma bifasciatum*) affect reproductive success of resident territorial males. They found that at low

population density territorial mating success increased with increases in local population density (i.e. reflecting an increase in the supply of females). At higher population densities, time spent in territory defense increased with the number of interfering males, and the time spent in courtship was negatively correlated with time spent in territory defense. Consequently, territorial mating success declined with increasing population density. Territories remained economically defensible in this case, since reproductive success of a territory holder was higher than that of nonterritorial males. Reinboth (1973) also reported that in *T. bifasciatum* group spawning was the predominant reproductive tactic on large reefs of higher population densities, while pair spawning prevailed on small reefs of low population densities. Meyer (1977) noted that for *T. cupido* at higher densities group spawning greatly exceeded pair spawning in frequency. "At high densities of interfering males, Warner and Hoffman (1980b) found that territories became too costly to maintain: the mating success of territorial males decreased to levels below that of nonterritorial males. They observed that a defending male abandons his site at high densities and establishes a territory in a less crowded area, or that he adopts nonterritorial behaviour and remains in the densely populated region.

The above findings of Warner and Hoffman (1980b) at high local population densities may apply to the two cunner populations in the present study. The apparently high cunner population density at Norris Point relative to Broad Cove (i.e. as described previously) possibly renders territories economically undefensible in an energetic sense. Large males may consequently move from Norris Point to become territorial at other sites, or remain on site as group spawning nonterritorial males. Territorial male cunners have been observed in Bonne Bay at South Gull Rock, which lies approximately 5 km eastward from Norris Point (Pottle *et al.* 1981, this study). Those Norris Point males characterized by larger total lengths, body weights, and smaller gonads comprised the largest mode of gonadosomatic index values (i.e. between 3.5 and 6%) found in this population. This range of GSIs resembles that which predominates in Broad Cove preterritorial males, and possibly represents a territorial life history

strategy in Norris Point males. These fish may invest more energy in somatic growth to attain, at a faster rate, body sizes advantageous to their future pursuit of territories. On the other hand, Norris Point males with small body sizes and larger gonads mostly had GSIs of 16 to 21%; forming the second largest mode. These fish may follow a purely group spawning strategy for life. The third and smallest mode in GSI values ranged from 11 to 12%, and possibly represents a 'mixed' group of males following either strategy (i.e. depending upon age and body size).

Despite having larger gonads than similar sized preterritorial males, group spawning males possessed a mean length at age only slightly less than that of these nonspawning males. Coupled with the prediction that Broad Cove preterritorial males should be attempting to attain large body sizes advantageous to their future pursuit of territories, this evidence suggests the operation of growth compensatory mechanisms in group spawning males. Growth compensation refers to a tendency of smaller fish to grow more rapidly to "catch up" with larger conspecifics (Gerking 1966, Ricker 1979). Growth compensation could be achieved through alternate year spawning, in which individuals allocate energy to growth in length and weight in one year while curtailing spawning activities entirely, then become reproductively active in the following year while deferring body growth. This alternating cycle would repeat every third year, possibly until an adult body growth asymptote is attained. Therefore, some Norris Point males would possess gonads less than 1.5 g (i.e. weights characteristic of cunners in postspawning condition, irrespective of body size and age); representing their nonspawning/body growth stage of an alternate year cycle. However, all prespawning males collected at Norris Point were ripe, although whether this cunner assemblage consisted only of spawning fish is unknown.

Another mechanism for growth compensation may operate as a physiological energy 'shunt', by which some proportion of energy that 'normally' is stored in body fat or other nonreproductive tissues or organs (i.e. reflected by increases in body weight per unit length with stomach and gonads removed) is used for growth in length. The finding that male group spawners are smaller in

body weight per unit length than preterritorial males may support this possibility. Gerking (1988) observed that smaller bluegill sunfish (*Lepomis macrochirus*) of a year class begin to grow earlier than their larger companions, suggesting that growth compensation may result from the advantage in time gained by the smaller group. Data on the time of annulus formation (i.e. representing resumption of growth in length) for Norris Point group spawning male cunners are unfortunately unavailable for comparison with Broad Cove preterritorial males.

Annual ripening of gonads in preterritorial males (as observed in the present study) may serve two purposes: when a territory becomes available, the preterritorial male which acquires it is ready to pair spawn that year; ripe preterritorial males, irrespective of body size, can "sneak" spawn with pair spawners. Martel and Green (in press) observed several interference spawnings in Broad Cove, in which a preterritorial male ("sneaker") rushed into a territory and joined a territorial male and female in gamete release, then quickly left the site. As described earlier, sneak spawning is an alternative reproductive tactic used by many species, including tropical labrids (Warner and Hoffman 1980a). Hoffman *et al.* (1985) found that interference spawning with territorial males was attempted by nonterritorial male *Thalassoma bifasciatum* lacking access to mating sites for more than a few minutes.

The present study indicates that territorial males invest more energy in gonads than preterritorial males, thereby supporting a finding reported by Martel and Green (in press) concerning the reproductive success of territorial male cunners. Given that a large body size is important to a male cunner in obtaining a territory, they found that body size is not correlated with future reproductive success once a territory has been established. However, gonad size is important to a territorial male's reproductive success. With limited food resources, energy previously channelled to somatic growth by a preterritorial male (i.e. to obtain a large body size) should be redirected to sperm production once this fish has become territorial. Territorial male gonad weights per unit body weight were significantly greater than those of preterritorial males in the present study.

Furthermore, the highest frequency of territorial gonadosomatic index values ranged from 7 to 9%, whereas most preterritorial males had GSIs between 4 and 5%. A second and smaller mode was found for territorial males with GSIs between 3 and 4%. These males were 16 to 22 years old with gonad weights between 6 and 8 g. Territorial males comprising the first mode were 13 to 20 years old with gonad weights of 11 to 21 g. Within both modes, a slightly positive relationship existed between gonad weight and territorial fish size, whereas no trend was apparent for gonad size and age.

Territorial males that have gonad sizes in the preterritorial range of values (Figure 3-7) may be 'first year' territorials that acquired territories in their year of capture. The energy cost in securing a territory may prohibit an immediate changeover to higher reproductive effort within a territorial male's first year. A territorial male would therefore invest in gametes on a level characterizing its preterritorial stage, and increase its sperm production in the subsequent spawning season. This first year territorial hypothesis could be investigated through a tagging/removal field experiment. Individual territories of defending males would be marked, then their owners captured and removed before the spawning season begins. Each preterritorial male taking over a newly unoccupied territory would be tagged, and whole body wet weights per length just prior to and after the spawning season would be obtained for several years. Differences between pre and postspawning weights per annum would be compared to those of 'longer term' territorial males (*i.e.* defending males that acquired sites several years previous) and of males without territories. These indirect measurements of gonad weight would reveal any significant increases in gonadal investment per unit length of newly established territorial males between their first and second year after securing a site, while controlling for annual variability in food abundance and water temperature. Preterritorial males should show the smallest annual weight differences, while 'new' territorial males in their first pair spawning season should have gonad weights similar to those of preterritorial males. No significant differences should be found between gonad weights per unit length of new territorial males in their second pair spawning season and longer term territorial males.

According to Figures 3-9 and 3-10, preterritorial males in Broad Cove reach a total length and body weight of similar magnitude to those of territorial males. However, the rate of attaining these body growth asymptotes appears quicker in territorial males, which reach them at a younger age. This faster rate of growth in length and weight may be an important component in determining which male successfully obtains a territory. For example, a larger body size would ascribe an advantage to a preterritorial male in conflict with another for a territory recently made available for occupancy. Furthermore, the apparent three or four outliers in Figures 3-9 and 3-10 could represent a few preterritorial males possibly following the aforementioned faster growth rate. Although these fish had attained a large size at age relative to other preterritorial males, they had not yet successfully secured a territory. This latter observation may reflect a local absence of unoccupied territories, as is indicated by field observations (Green, unpubl.).

To determine whether successful territorial males have experienced a faster growth rate relative to preterritorial males in general, and if apparent preterritorial outliers have done the same, annular increments on otoliths or scales from these fish should be measured and used for back-calculations of growth. This would allow generation of individual growth curves for comparisons between territorial males, 'average' preterritorial males, and apparent outliers.

A comparison of the mean total lengths at age of cunners (i.e. sexes combined) with latitude from the literature (Table 4-1) indicates no readily apparent latitudinal effect on cunner growth. Naidu (1966) noted a decrease in the rate of growth in length of Newfoundland cunners with increasing latitude. However, length data of Serchuk and Cole (1974) in Massachusetts are comparable (if not smaller) to Naidu's rather than being significantly larger as predicted given a decrease in latitude. Johansen (1925) obtained cunners in 1917-18 from the Gulf of St. Lawrence which were similar in size to those of Serchuk and Cole (1974), and larger after age 5 than Naidu's (1966). Broad Cove cunners in the present study were smaller at age than those of Naidu from the same site in 1964.

Table 4-1: A comparison of the literature on mean total lengths (mm) at age of cunners (*i.e.* sexes combined) with decreasing latitude. Dates given represent year in which samples were caught. Known sample sizes are in parentheses. Territorial males captured in the present study are not included here.

Location and Reference						
Age (yrs):	Englee, Nfld. 1964 (Naidu)	Bonne Bay, Nfld. 1984 (This study)	Broad Cove, Nfld. 1964 (Naidu)	Broad Cove 1984 (This study)	Gulf of St. Lawrence 1917-18 (Johansen)	Massachusetts 1968-69 (Serchuk & Cole)
2	-	74 (5)	123 (6)	-	100 (160)	104 (26)
3	117 (6)	-	134 (49)	-	150 (194)	142 (35)
4	134 (26)	104 (3)	178 (17)	-	160	172 (31)
5	145 (38)	115 (3)	203 (31)	109 (5)	190	182 (22)
6	163 (18)	118 (17)	216 (26)	137 (15)	240	204 (3)
7	192 (13)	135 (47)	237 (8)	166 (3)	270	-
8	201 (4)	153 (32)	258 (3)	168 (6)	310	-
9	212 (5)	170 (55)	264 (2)	175 (20)	350	-
10	251 (4)	178 (21)	278 (1)	177 (9)	370	-
11	267 (5)	172 (11)	-	189 (13)	-	-
12	286 (6)	175 (24)	-	193 (21)	-	-
13	296 (2)	185 (17)	-	204 (38)	-	-
14	306 (2)	190 (13)	-	212 (35)	-	-
15	-	207 (8)	-	223 (42)	-	-
16	-	216 (6)	-	235 (16)	-	-
17	-	-	-	240 (11)	-	-
18	-	297 (1)	-	249 (5)	-	-
19	-	-	-	258 (3)	-	-
20	-	-	-	253 (4)	-	-
21	-	-	-	256 (2)	-	-

The above discrepancies in cunner growth across latitude may be attributable to invalid age data. For cunners apparently 7 years and older, Johansen (1925) stated, "It is, however, very difficult to decide the exact number of "winter-rings" upon scales of such old fishes". Dew (1970) noted that for Connecticut cunners, "It was difficult to interpret scales with over four annuli, and the maximum readable age was 5 years". Serchuk and Cole (1974) observed that, "Annular marks (on scales) were often difficult to discern in older fish due to crowding", and that, "the first annulus in many specimens was often indistinct and difficult to discern". Johansen also noted the latter problem. Naidu did not mention either problem in aging his samples, although both must have been present since these problems were encountered in the present study for cunner scales from Broad Cove and Norris Point. Given this great difficulty in distinguishing annuli on scales of cunners older than 7 years, lengths recorded by Johansen may actually represent much older fishes, thereby explaining their larger sizes as compared to those of this study and Naidu's. Naidu's length data may also represent older fish for this same reason. Unfortunately, Serchuk and Cole's study included only data for fish less than 7 years old.

Problems in determining annular marks on older cunner scales can usually be avoided by reading otoliths instead. Otoliths are generally far better than scales in age determinations of cunners, although previous researchers (as presented above) studying cunner neglected to use otoliths. The present study indicates that annuli are more readily distinguishable on an otolith, and its first annulus is easily found. Crowding of annuli on the margins of otoliths does not generally occur until age 15, whereas annular crowding is common on the margins of scales older than 6 years.

Johansen (1925) noted that the average body size of female cunners from the Gulf of St. Lawrence was larger than that of males. Serchuk and Cole (1974) often found that males ≥ 150 mm TL from Massachusetts were a year older than females of the same size. Naidu (1966) mentioned that females in Broad Cove (NF) grew at a slightly faster rate than males, but that variation in growth between female and male cunners from his other three sampling sites was

inconsistent. Females collected from both Broad Cove and Norris Point (NF) in the present study were consistently smaller at age than males (i.e. excluding territorial males); an observation similar to that of Dew (1970) for cunners from Fishers Island Sound, Connecticut. This result contradicts a general rule for teleostian growth: females are larger in TL at age than male conspecifics (LeCren 1958, Moyle and Cech 1982). However, Moyle and Cech (1982) also stated that in general females are smaller sized at age than males if the latter sex is territorial. The finding that female cunners were heavier at length than resident males (albeit differences were slight between sexes in Broad Cove) agrees with a second general growth pattern in teleosts (*ibid.*). This observation contrasts with those of Dew (1970), and Shumway and Stickney (1975) for Rhode Island cunners. The latter authors concluded that sex need not be considered when determining cunner weight on the basis of length.

Alternative reproductive tactics are widespread within species of the animal kingdom. Research on intraspecific tactical variation has progressed beyond identifying reproductive alternatives to hypothesizing on their theoretical implications on species' life history evolution. Armed with this theoretical groundwork, scientists must now venture further and collect empirical evidence to evaluate their predictions concerning species' life histories. Both qualitative identification and quantitative evaluation of tradeoffs between a species' life history traits should constitute the next step for research into each alternative reproductive tactic, with costs and benefits of these tradeoffs juxtaposed against environmental sources of mortality. Investigation of costs associated with each reproductive alternative will provide data fundamental to predicting which reproductive tactic, or set of alternative tactics, would be utilized by a species in any given environment. This knowledge would prove extremely important in future "mapping" and understanding of the evolution of a species' life history traits.

This study ventures one step beyond the theoretical aspects of alternative reproductive tactics by attempting to identify and evaluate the tradeoffs, or costs of reproduction, associated with each of two tactics previously noted for the Newfoundland male cunner. The empirical evidence collected in this study constitutes a basis for evaluating several predictions of life-history theory. Information obtained from scrutiny of these hypotheses forms a foundation upon which an understanding of a cunner's life history evolution can be established, once future research generates more quantitative knowledge of the physiological and biochemical aspects of tactical variation in cunners. Methodologies developed to achieve these goals with a readily studied species like the cunner can then be applied to other animals of evolutionary or economic interest.

4.1. Summary

1. The prediction of high reproductive effort in group spawning male cunners (i.e. investing heavily in sex products early in life) is supported. Gonad weights and gonadosomatic indices per age class were significantly greater in group spawners as compared to preterritorial males younger than 15 years. Group spawners allocated significantly more energy to sperm production per unit body weight than preterritorial males.
2. Group spawning in cunners involves a large number of males simultaneously releasing gametes into the water column to externally fertilize a female's extruded eggs, and large gonadal investments in male group spawners are probably a result of sperm competition. Investing heavily in gamete production would assure numerical predominance of self's sperm in the "ensuing pelagic lottery" (Parker 1984). The present study indicates that this reasoning may well apply to male cunner group spawners, which apparently allot energy to gonads independently of body size.
3. Length and body weight at age of the male group spawning population at Norris Point were significantly less than those of the preterritorial male population at Broad Cove. Body size differences were slight, however, suggesting no significant tradeoff between high sperm production and decreased somatic growth rate. Gonad weight was not

related to total length within each age class for male group spawners, contrary to the negative relationship expected with evidence of such a tradeoff.

4. Evidence suggests at least two reproductive/growth tactics occur in Norris Point male cunners. Given the presence of territoriality in Bonne Bay, males (with GSIs $\leq 10\%$) characterized by larger TL, W_b , and smaller gonads may later forego group spawning and become territorial, whereas males with smaller body size and larger gonads (and GSIs $\geq 15\%$) may remain group spawners throughout life.
5. Evidence supporting a tradeoff between high sperm production and reduced longevity predicted for group spawning males was found in the population age structure. Norris Point harboured a small proportion of old males (>9 years) and a large proportion of younger males (aged 6-9 years), whereas a large proportion of preterritorial males from 5 to 15 years old was present in Broad Cove.
6. This apparent 'early' mortality of group spawning males is not attributed to local environmental perturbations (e.g. a harsh environment would affect the Norris Point cunner population as a whole, irrespective of reproductive effort or sex). Age frequencies of females were the same between both populations.

7. Growth enhancement expected for Norris Point males (e.g. due to a longer period of warmer summer water temperatures in Bonne Bay relative to Conception Bay) was not evident. Differences in habitat between both sampling sites would be reflected in female body size, since female cunners have similar life histories irrespective of geographic location. Norris Point females were significantly smaller in length and body weight at age than those of Broad Cove, although differences were slight.

8. The slower growth rate of Norris Point females may result from one or a combination of the following factors: smaller energy content of foods consumed by these fish as compared to foods of Broad Cove females; greater food abundance in Broad Cove; or higher cunner population density at Norris Point resulting in increased intraspecific competition for limited food resources. Although information on the first two possibilities is unavailable, evidence indicates that there are differences in local population density between both sampling sites.

9. The apparently high cunner population density at Norris Point may also render territories economically undefendable, thereby explaining its lack of territorial males. Territorial cunners may move from Norris Point to defend sites elsewhere, or remain in the densely populated area as group spawning nonterritorial males.

10. Despite having larger gonads than similar sized preterritorial males, group spawning males possessed a mean length at age only slightly less than that of these nonspawning males, suggesting the operation of growth compensatory mechanisms in group spawning males. Speculation that growth compensation was achieved through alternate year spawning was unsupported, since all prespawning males collected at Norris Point were ripe. Whether this cunner assemblage consisted only of spawning fish is unknown.
11. Group spawning males were smaller in body weight per unit length relative to preterritorial males. This possibly represents a growth compensatory mechanism in the form of a physiological energy 'shunt', by which some proportion of energy that 'normally' is stored in body fat or other nonreproductive tissues or organs is used for growth in length.
12. Annual ripening of gonads in Broad Cove preterritorial males (as observed in this study) may serve two purposes: when a territory becomes available, the preterritorial male which acquires it is ready to pair spawn that year; ripe preterritorial males, irrespective of body size, can sneak spawn with pair spawners (Martel and Green, in press).
13. Broad Cove territorial male GSIs and gonad weights at age were significantly larger than those of preterritorial males. Gonad weights

per unit body weight were also greater in territorial males. These findings confirm an observation previously reported by Martel and Green (in press): body size is not important to the future reproductive success of a defending territorial male. Given the importance of a large body size to a preterritorial male in securing a territory, energy consumed from limited food resources may be redirected from somatic growth to sperm production once a male has become territorial.

14. An important component in determining which male successfully obtains a territory appears to be how quickly an individual attains a somatic growth asymptote. This is suggested by the finding that territorial males in Broad Cove reach a total length and body weight of similar magnitude to those of preterritorial males, but at a faster rate. A larger body size at age of the former male would be an advantage in conflicts with another preterritorial male for an unoccupied territory.
15. A comparison of the mean total lengths at age of cunners (sexes combined) with latitude from the literature indicates no readily apparent latitudinal effect on cunner growth. However, this absence of an inverse relationship of cunner growth with latitude may be due to invalid age data in the literature. Ages of cunners collected in previous studies have probably been underestimated.

16. Females from both Broad Cove and Norris Point were smaller sized per age class than local males (excluding territorial males); an observation, similar to that of Dew (1970) for cunners from Connecticut. This finding contradicts those of Johansen (1925) for Gulf of St. Lawrence females, and of Serchuk and Cole (1974) for many cunners from Massachusetts. Females from both locations in the present study were heavier at length than males, although differences were slight between sexes in Broad Cove. Both Dew (1970) and Shumway and Stickney (1975) had observed equivalent length-weight relationships between cunner sexes. Naidu (1968) reported no consistent variation in growth between female and male cunners from four sampling sites in Newfoundland.

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APPENDIX A

Summary table of multiple linear regression analyses and F test results for cunners from Bonne Bay (BB) and Broad Cove (BC). Territorial males included (BCt). The first F value listed per relationship refers to a test for differences between slopes of separate regression lines. The second F value, if present, refers to a test for differences between group means.

Location and Sex:	n:	Relationship:	Separate R ² :	F Value:
BB male BC male	341	GSI vs Age	0.12 ^{***} NS	F _(2,337) = 29.52 ^{***}
BB male BC male	339	lnW _g vs lnAge	NS 0.62 ^{***}	F _(2,335) = 55.22 ^{***}
BB male BC male	374	lnW _g vs lnW _b	NS 0.61 ^{***}	F _(2,370) = 116.53 ^{***}
BB male BC male	345	lnTL vs lnAge	0.52 ^{***} 0.92 ^{***}	F _(2,341) = 0.29 F _(2,341) = 5.22 ^{**}
BB male BC male	345	lnW _b vs lnAge	0.51 ^{***} 0.92 ^{***}	F _(2,341) = 0.04 F _(2,341) = 5.85 ^{***}
BB male BC male	379	lnTL vs lnW _b	0.98 ^{***} 0.99 ^{***}	F _(2,375) = 14.09 ^{***}
BCt male BC male	221	GSI vs Age	NS NS	F _(2,217) = 4.84 ^{**}

Location and Sex:	n:	Relationship:	Separate R ² :	F Value:
BCt male BC male	221	lnW _g vs lnAge	NS 0.62 ^{***}	F _(2,217) = 31.04 ^{***}
BCt male BC male	248	lnW _g vs lnW _b	0.07 [*] 0.61 ^{***}	F _(2,244) = 0.79 F _(2,244) = 32.44 ^{***}
BCt male BC male	224	lnTL vs lnAge	NS 0.92 ^{***}	F _(2,220) = 30.47 ^{***}
BCt male BC male	224	lnW _b vs lnAge	NS 0.92 ^{***}	F _(2,220) = 39.08 ^{***}
BCt male BC male	65	lnTL vs lnW _b	0.80 ^{***} 0.99 ^{***}	F _(2,246) = 5.03 ^{**}
BB female BC female	166	lnTL vs lnAge	0.87 ^{***} 0.87 ^{***}	F _(2,162) = 2.82 F _(2,162) = 35.91 ^{***}
BB female BC female	166	lnW _b vs lnAge	0.86 ^{***} 0.87 ^{***}	F _(2,162) = 2.09 F _(2,162) = 31.90 ^{***}
BB female BC female	165	GSI vs Age	NS NS	F _(2,161) = 1.51 F _(2,161) = 2.14
BB female BC female	165	lnW _g vs lnAge	0.80 ^{***} 0.84 ^{***}	F _(2,161) = 2.12 F _(2,161) = 30.55 ^{***}
BB female BC female	178	lnW _g vs lnW _b	0.82 ^{***} 0.97 ^{***}	F _(2,174) = 2.34 F _(2,174) = 2.53
BB female BC female	179	lnTL vs lnW _b	0.99 ^{***} 0.99 ^{***}	F _(2,175) = 1.91 F _(2,175) = 0.00

Location and Sex:	n:	Relationship:	Separate R ² :	F Value:
BB male BB female	263	lnTL vs lnAge	0.52 ^{***} 0.87 ^{***}	F _(2,259) = 4.67 ^{**}
BB male BB female	263	lnW _b vs lnAge	0.51 ^{***} 0.86 ^{***}	F _(2,259) = 2.45 F _(2,259) = 19.40 ^{***}
BB male BB female	289	lnTL vs lnW _b	0.98 ^{***} 0.99 ^{***}	F _(2,285) = 18.61 ^{***}
BC male BC female	248	lnTL vs lnAge	0.92 ^{***} 0.87 ^{***}	F _(2,244) = 23.68 ^{***}
BC male BC female	248	lnW _b vs lnAge	0.92 ^{***} 0.87 ^{***}	F _(2,244) = 19.73 ^{***}
BC male BC female	269	lnTL vs lnW _b	0.99 ^{***} 0.99 ^{***}	F _(2,265) = 3.55 [*]

$\alpha = 0.05$

* = P < 0.05

** = P < 0.01

*** = P < 0.001

NS = Not significant

APPENDIX B

Table of untransformed data collected for prespawning male and female cunners from Bonne Bay and Broad Cove (Conception Bay), Newfoundland. Numbers in parentheses refer to sample size. Due to missing age classes in these data, postspawning samples are included where indicated by an asterisk (*).

Location:	Sex:	Status:	Age (yrs):	Variable Measured:	Mean:	Range:	Standard Error:
Bonne Bay	Male	NT	2*	TL	81.33 (3)	74.00 - 85.00	3.67
				W _b	7.16 (3)	5.63 - 8.87	0.94
			4*	TL	104.00 (1)	-	-
				W _b	16.38 (1)	-	-
			5	TL	115.00 (3)	107.00 - 125.00	5.29
				W _b	19.73 (3)	14.98 - 25.42	3.05
				W _g	4.17 (3)	2.13 - 5.51	1.04
				GSI	23.38 (3)	8.38 - 32.44	7.55
			6	TL	125.67 (12)	112.00 - 140.00	2.45
				W _b	25.48 (12)	18.23 - 35.27	1.29
				W _g	6.44 (12)	3.12 - 10.91	0.70
				GSI	25.44 (12)	11.88 - 46.84	2.80

Location:	Sex:	Status:	Age (yrs):	Variable Measured:	Mean:	Range:	Standard Error:
			7	TL	144.78 (36)	123.00 - 195.00	2.63
				W _b	41.51 (36)	22.38 - 120.53	3.18
				W _g	7.01 (36)	1.91 - 12.12	0.46
				GSI	19.30 (36)	3.98 - 43.22	1.65
			8	TL	166.14 (21)	134.00 - 218.00	6.37
				W _b	68.41 (21)	29.64 - 160.47	8.82
				W _g	8.92 (20)	2.75 - 18.60	0.96
				GSI	17.75 (20)	2.49 - 43.52	2.65
			9	TL	195.22 (46)	141.00 - 252.00	4.39
				W _b	114.98 (46)	31.31 - 262.07	8.38
				W _g	8.18 (44)	2.01 - 20.80	0.75
				GSI	9.16 (44)	1.32 - 42.67	1.39
			10	TL	198.15 (13)	129.00 - 244.00	8.46
				W _b	121.92 (13)	24.50 - 223.77	15.26
				W _g	7.95 (13)	3.05 - 14.07	1.10
				GSI	8.64 (13)	1.72 - 22.39	1.78
			11	TL	168.11 (9)	141.00 - 242.00	10.17
				W _b	73.06 (9)	36.61 - 213.59	18.16
				W _g	7.13 (9)	2.90 - 10.49	0.90
				GSI	12.49 (9)	2.64 - 20.10	2.10

Location:	Sex:	Status:	Age (yrs):	Variable Measured:	Mean:	Range:	Standard Error:
			12	TL	168.80 (15)	132.00 - 241.00	7.09
				W _b	70.92 (15)	32.16 - 213.60	11.68
				W _g	8.78 (15)	4.02 - 20.45	1.12
				GSI	15.81 (15)	2.68 - 34.91	2.34
			13	TL	182.50 (8)	145.00 - 200.00	7.00
				W _b	86.62 (8)	39.61 - 121.09	10.62
				W _g	8.92 (8)	4.44 - 15.08	1.45
				GSI	10.92 (8)	5.00 - 17.29	1.63
			14	TL	187.60 (5)	160.00 - 232.00	13.48
				W _b	102.25 (5)	55.51 - 198.19	27.21
				W _g	10.51 (5)	4.94 - 16.71	2.50
				GSI	10.54 (5)	8.43 - 12.88	0.89
			15	TL	198.40 (5)	170.00 - 225.00	10.52
				W _b	116.23 (5)	72.16 - 175.63	18.05
				W _g	7.64 (5)	5.62 - 9.44	0.74
				GSI	6.86 (5)	4.80 - 8.04	0.57
			16	TL	210.50 (2)	180.00 - 232.00	21.50
				W _b	155.97 (2)	92.00 - 210.84	63.88
				W _g	7.73 (2)	7.57 - 7.89	0.16
				GSI	6.01 (2)	3.44 - 8.57	2.57

Location:	Sex:	Status:	Age (yrs):	Variable Measured:	Mean:	Range:	Standard Error:
Bonne Bay	Female	NT	17*	TL	262.00 (1)	-	-
				W _b	342.18 (1)	-	-
			19*	TL	243.00 (2)	242.00 - 244.00	1.00
				W _b	210.22 (2)	191.51 - 228.92	18.71
			2	TL	73.80 (5)	65.00 - 85.00	3.48
				W _b	5.54 (5)	3.66 - 8.38	0.81
				W _g	0.11 (5)	0.06 - 0.20	0.03
				GSI	1.87 (5)	1.64 - 2.39	0.14
			4	TL	104.00 (3)	94.00 - 109.00	5.00
				W _b	15.59 (3)	13.17 - 16.93	1.21
				W _g	1.15 (3)	0.60 - 1.43	0.27
				GSI	7.15 (3)	4.56 - 8.45	1.30
			6	TL	110.40 (5)	99.00 - 123.00	3.96
				W _b	20.43 (5)	18.37 - 25.00	1.23
W _g	2.05 (5)	1.27 - 2.50		0.21			
GSI	10.10 (5)	6.85 - 13.61		1.14			
7	TL	124.82 (11)	111.00 - 140.00	2.67			
	W _b	27.22 (11)	20.11 - 36.81	1.69			
	W _g	2.16 (11)	0.85 - 3.88	0.27			
	GSI	7.94 (11)	3.68 - 13.47	0.84			

Location:	Sex:	Status:	Age (yrs):	Variable Measured:	Mean:	Range:	Standard Error:
			8	TL	139.46 (11)	126.00 - 157.00	2.76
				W _b	39.98 (11)	30.61 - 62.97	2.73
				W _g	3.59 (11)	1.00 - 8.55	0.62
				GSI	8.94 (11)	2.65 - 13.58	1.20
			9	TL	145.11 (9)	128.00 - 175.00	5.03
				W _b	40.60 (9)	25.81 - 66.93	4.88
				W _g	3.57 (9)	1.55 - 92.85	0.82
				GSI	8.68 (9)	4.14 - 15.64	1.17
			10	TL	158.25 (8)	148.00 - 168.00	2.45
				W _b	50.62 (8)	42.63 - 59.73	1.82
				W _g	3.57 (8)	1.18 - 6.94	0.64
				GSI	7.02 (8)	2.21 - 11.62	1.12
			11	TL	176.50 (2)	170.00 - 183.00	6.50
				W _b	76.17 (2)	66.39 - 85.95	9.78
				W _g	3.78 (2)	3.44 - 4.12	0.34
				GSI	5.11 (2)	4.00 - 6.21	1.11
			12	TL	180.67 (9)	154.00 - 210.00	5.85
				W _b	87.06 (9)	43.08 - 142.81	10.28
				W _g	6.21 (9)	2.35 - 10.43	1.01
				GSI	7.08 (9)	3.40 - 9.57	0.75

Location:	Sex:	Status:	Age (yrs):	Variable Measured:	Mean:	Range:	Standard Error:
			13	TL	188.22 (9)	153.00 - 236.00	8.49
				W _b	108.08 (9)	50.59 - 251.31	20.15
				W _g	8.92 (9)	3.46 - 28.09	2.54
				GSI	8.04 (9)	3.98 - 11.23	1.02
			14	TL	192.50 (8)	160.00 - 232.00	8.13
				W _b	110.44 (8)	56.46 - 185.17	15.19
				W _g	10.51 (8)	3.72 - 20.43	2.14
				GSI	9.44 (8)	3.14 - 12.14	1.10
			15	TL	216.33 (3)	203.00 - 227.00	7.06
				W _b	149.80 (3)	124.53 - 184.85	18.09
				W _g	10.46 (3)	7.40 - 15.52	2.55
				GSI	6.79 (3)	5.94 - 8.40	0.80
			16	TL	221.75 (4)	203.00 - 240.00	9.47
				W _b	171.13 (4)	117.81 - 220.47	25.83
				W _g	9.46 (3)	6.20 - 14.76	2.67
				GSI	5.91 (3)	5.26 - 7.03	0.56
			18	TL	297.00 (1)	-	-
				W _b	473.10 (1)	-	-
				W _g	42.30 (1)	-	-
				GSI	8.94 (1)	-	-

Location:	Sex:	Status:	Age (yrs):	Variable Measured:	Mean:	Range:	Standard Error:	
Broad Cove	Male	PT	3*	TL	92.90 (10)	80.00 - 105.00	2.21	
				W _b	10.77 (10)	6.13 - 15.23	0.80	
			4*	TL	105.00 (1)	-	-	-
				W _b	17.66 (1)	-	-	-
			5*	TL	125.40 (15)	119.00 - 138.00	1.91	
				W _b	26.47 (15)	17.64 - 37.27	1.35	
			6	TL	145.58 (12)	131.00 - 159.00	2.61	
				W _b	42.26 (12)	26.79 - 56.91	2.50	
				W _g	1.50 (12)	0.89 - 2.57	0.16	
				GSI	3.70 (12)	1.56 - 6.54	0.48	
			8	TL	168.17 (6)	158.00 - 177.00	3.07	
				W _b	67.68 (6)	55.11 - 78.97	3.96	
				W _g	3.00 (6)	1.70 - 4.88	0.43	
				GSI	4.48 (6)	2.17 - 6.18	0.59	
9	TL	175.71 (17)	158.00 - 236.00	4.21				
	W _b	73.76 (16)	55.72 - 102.67	2.96				
	W _g	3.92 (16)	1.63 - 8.29	0.43				
	GSI	5.28 (16)	1.98 - 9.61	0.50				

Location:	Sex:	Status:	Age (yrs):	Variable Measured:	Mean:	Range:	Standard Error:
			10	TL	185.67 (3)	184.00 - 188.00	1.20
				W _b	94.01 (3)	85.20 - 104.90	5.78
				W _g	5.40 (3)	3.02 - 7.14	1.23
				GSI	5.73 (3)	3.29 - 7.09	1.22
			11	TL	191.91 (11)	182.00 - 203.00	1.99
				W _b	99.88 (11)	82.93 - 120.66	3.60
				W _g	5.23 (10)	3.50 - 6.33	0.28
				GSI	5.35 (10)	3.85 - 7.21	0.33
			12	TL	191.82 (17)	174.00 - 241.00	4.79
				W _b	105.78 (17)	73.16 - 197.47	8.80
				W _g	6.36 (17)	3.02 - 12.79	0.63
				GSI	6.26 (17)	2.78 - 10.35	0.56
			13	TL	205.26 (31)	182.00 - 262.00	2.77
				W _b	125.11 (31)	84.91 - 263.80	6.51
				W _g	6.35 (31)	2.61 - 13.50	0.41
				GSI	5.22 (31)	1.84 - 8.80	0.31
			14	TL	215.32 (22)	187.00 - 252.00	3.41
				W _b	149.38 (22)	98.35 - 245.21	6.86
				W _g	7.93 (22)	3.10 - 13.82	0.55
				GSI	5.45 (22)	2.16 - 9.00	0.39

Location:	Sex:	Status:	Age (yrs):	Variable Measured:	Mean:	Range:	Standard Error:
			15	TL	221.50 (34)	192.00 - 255.00	2.44
				W _b	156.29 (35)	98.05 - 234.69	5.84
				W _g	8.77 (33)	5.21 - 15.66	0.49
				GSI	5.61 (33)	2.94 - 10.57	0.28
			16	TL	233.00 (9)	205.00 - 240.00	4.58
				W _b	187.49 (9)	125.24 - 215.93	10.44
				W _g	7.93 (9)	5.66 - 9.82	0.50
				GSI	4.30 (9)	3.06 - 5.32	0.27
			17	TL	228.33 (3)	223.00 - 237.00	4.37
				W _b	178.25 (3)	161.63 - 209.15	15.47
				W _g	7.76 (3)	4.52 - 10.98	1.87
				GSI	4.57 (3)	2.16 - 6.79	1.34
			18	TL	249.00 (1)	-	-
				W _b	208.77 (1)	-	-
				W _g	4.54 (1)	-	-
				GSI	2.18 (1)	-	-
			19	TL	249.00 (1)	-	-
				W _b	231.20 (1)	-	-
				W _g	13.32 (1)	-	-
				GSI	5.76 (1)	-	-

Location:	Sex:	Status:	Age (yrs):	Variable Measured:	Mean:	Range:	Standard Error:
Broad Cove	Male	T	20	TL	246.00 (2)	236.00 - 256.00	10.00
				W _b	206.83 (2)	180.74 - 232.91	26.09
				W _g	12.05 (2)	10.06 - 14.04	1.99
				GSI	6.05 (2)	4.32 - 7.77	1.73
			21	TL	247.00 (1)	-	-
				W _b	221.28 (1)	-	-
				W _g	9.31 (1)	-	-
				GSI	4.21 (1)	-	-
			13	TL	235.00 (4)	223.00 - 244.00	4.60
				W _b	186.00 (4)	159.19 - 211.00	11.39
				W _g	15.13 (4)	9.91 - 23.98	3.08
				GSI	7.96 (4)	6.23 - 11.37	1.16
			14	TL	241.00 (3)	230.00 - 255.00	7.37
				W _b	202.22 (3)	174.68 - 241.45	20.14
				W _g	18.69 (3)	16.25 - 21.81	1.64
				GSI	9.49 (3)	7.46 - 12.49	1.53
15	TL	237.12 (8)	220.00 - 253.00	4.03			
	W _b	185.21 (8)	156.57 - 216.40	7.25			
	W _g	15.97 (8)	9.58 - 19.32	1.17			
	GSI	8.70 (8)	4.75 - 10.67	0.67			

Location:	Sex:	Status:	Age (yrs):	Variable Measured:	Mean:	Range:	Standard Error:
			16	TL	242.00 (14)	222.00 - 258.00	2.89
				W _b	197.31 (14)	141.12 - 244.86	7.63
				W _g	13.36 (14)	6.09 - 25.26	1.48
				GSI	6.82 (14)	3.11 - 12.58	0.77
			17	TL	235.87 (8)	223.00 - 248.00	2.94
				W _b	193.72 (8)	157.47 - 220.41	7.41
				W _g	16.42 (8)	7.89 - 28.82	2.36
				GSI	8.67 (8)	3.59 - 15.97	1.36
			18	TL	237.00 (8)	226.00 - 252.00	2.93
				W _b	184.72 (8)	164.86 - 217.48	6.50
				W _g	15.53 (8)	5.50 - 20.52	1.85
				GSI	8.32 (8)	3.23 - 11.19	0.89
			19	TL	261.00 (1)	-	-
				W _b	233.01 (1)	-	-
				W _g	15.50 (1)	-	-
				GSI	6.65 (1)	-	-
			20	TL	246.25 (4)	243.00 - 250.00	1.44
				W _b	195.15 (4)	192.00 - 202.45	2.45
				W _g	14.48 (4)	8.49 - 19.79	2.33
				GSI	7.43 (4)	4.39 - 10.30	1.21

Location:	Sex:	Status:	Age (yrs):	Variable Measured:	Mean:	Range:	Standard Error:
Broad Cove	Female	NT	21	TL	240.00 (1)	-	-
				W _b	208.80 (1)	-	-
				W _g	20.73 (1)	-	-
				GSI	9.93 (1)	-	-
			22	TL	225.00 (1)	-	-
				W _b	152.77 (1)	-	-
				W _g	6.10 (1)	-	-
				GSI	3.99 (1)	-	-
			23	TL	260.50 (2)	245.00 - 276.00	15.50
				W _b	241.66 (2)	189.84 - 293.48	51.82
				W _g	11.75 (2)	11.68 - 11.83	0.07
				GSI	5.10 (2)	3.98 - 6.23	1.12
			5	TL	108.80 (5)	98.00 - 117.00	3.25
				W _b	16.91 (5)	12.88 - 19.95	1.16
				W _g	1.36 (5)	0.91 - 1.77	0.14
				GSI	7.98 (5)	7.07 - 8.87	0.30
6	TL	128.33 (3)	121.00 - 139.00	5.46			
	W _b	28.00 (3)	22.65 - 37.29	4.66			
	W _g	2.54 (3)	1.86 - 3.62	0.55			
	GSI	8.95 (3)	8.21 - 9.71	0.43			

Location:	Sex:	Status:	Age (yrs):	Variable Measured:	Mean:	Range:	Standard Error:
			7	TL	165.67 (3)	155.00 - 176.00	6.06
				W _b	68.83 (3)	57.76 - 83.21	7.53
				W _g	5.60 (3)	4.03 - 6.95	0.85
				GSI	8.07 (3)	6.97 - 8.88	0.57
			9	TL	175.33 (3)	167.00 - 190.00	7.36
				W _b	83.49 (3)	70.88 - 98.34	8.01
				W _g	7.37 (3)	5.52 - 9.79	1.26
				GSI	8.71 (3)	7.79 - 9.96	0.65
			10	TL	168.00 (6)	156.00 - 177.00	2.94
				W _b	73.62 (6)	61.31 - 82.87	3.38
				W _g	6.82 (6)	5.25 - 9.96	0.73
				GSI	9.18 (6)	7.86 - 12.02	0.64
			11	TL	186.50 (2)	170.00 - 203.00	16.50
				W _b	99.56 (2)	74.42 - 124.70	25.14
				W _g	7.91 (2)	6.63 - 9.18	1.28
				GSI	8.14 (2)	7.36 - 8.91	0.78
			12	TL	194.50 (4)	186.00 - 211.00	5.78
				W _b	107.07 (4)	89.70 - 144.98	13.04
				W _g	9.41 (4)	7.69 - 12.57	1.14
				GSI	8.86 (4)	7.43 - 10.68	0.67

Location:	Sex:	Status:	Age (yrs):	Variable Measured:	Mean:	Range:	Standard Error:
			13	TL	203.71 (7)	179.00 - 253.00	9.59
				W _b	125.46 (7)	82.44 - 224.79	18.36
				W _g	11.39 (7)	6.03 - 24.66	2.32
				GSI	8.79 (7)	7.31 - 10.97	0.45
			14	TL	209.54 (13)	181.00 - 255.00	5.47
				W _b	132.55 (13)	91.21 - 205.48	9.04
				W _g	10.75 (13)	6.60 - 16.57	0.81
				GSI	8.12 (13)	6.84 - 11.04	0.31
			15	TL	226.13 (8)	198.00 - 240.00	5.61
				W _b	170.25 (8)	107.92 - 205.88	11.57
				W _g	14.94 (8)	8.98 - 18.39	1.00
				GSI	8.82 (8)	7.37 - 10.64	0.33
			16	TL	238.00 (7)	213.00 - 271.00	7.67
				W _b	194.21 (7)	130.92 - 267.90	19.11
				W _g	16.65 (7)	10.43 - 21.83	1.67
				GSI	8.57 (7)	7.76 - 9.89	0.30
			17	TL	252.25 (8)	224.00 - 305.00	9.72
				W _b	232.76 (8)	158.87 - 355.39	24.23
				W _g	20.54 (8)	12.11 - 28.57	2.14
				GSI	8.85 (8)	7.09 - 10.49	0.40

Location:	Sex:	Status:	Age (yrs):	Variable Measured:	Mean:	Range:	Standard Error:
			18	TL	250.25 (4)	235.00 - 268.00	6.79
				W _b	225.86 (4)	178.64 - 279.78	20.92
				W _g	19.34 (4)	12.47 - 26.72	3.05
				GSI	8.44 (4)	6.98 - 9.87	0.74
			19	TL	267.00 (2)	254.00 - 280.00	13.00
				W _b	283.69 (2)	281.24 - 286.14	2.45
				W _g	27.96 (2)	26.41 - 29.50	1.55
				GSI	9.86 (2)	9.23 - 10.49	0.63
			20	TL	260.00 (2)	257.00 - 263.00	3.00
				W _b	256.02 (2)	235.39 - 276.64	20.63
				W _g	20.58 (2)	18.27 - 22.88	2.31
				GSI	8.02 (2)	7.76 - 8.27	0.26
			24	TL	265.00 (1)	-	-
				W _b	249.75 (1)	-	-
				W _g	21.83 (1)	-	-
				GSI	8.74 (1)	-	-

NT = nonterritorial
 PT = preterritorial
 T = territorial
 TL = total length (mm)
 W_b = body weight (g)
 W_g = gonad weight (g)
 GSI = gonadosomatic index (%)



