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Reproductive Traits, Gonad Maturation and Spawning of Northwest Atlantic Herring *Clupea harengus harengus* L.

by

Rodney G. Bradford

Submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy

at

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The undersigned hereby certify that they have read and recommend to the Faculty of Graduate Studies for acceptance a thesis entitled: " Reproductive Traits, Gonad Maturation and Spawning of Northwest Atlantic Herring Clupea harengus harengus L.

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To

Victor and Beatrice Bradford

and to the memory of

Cecil and Madeline Thurber

My Grandparents, whose livelihood depended on the New Brunswick herring fishery.

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Abstract

Analysis of the egg weight and fecundity (egg number) traits of nw Atlantic herring (*Clupea harengus harengus* L.) reveals that egg weight remains relatively constant among populations whereas the product of egg weight and fecundity (standardized to length) varies among populations. Spring (May-June)-spawning herring mature with less gonad material than do autumn (August-September)-spawning herring. Differences in reproductive effort among populations are shown to be linked to the relative allocation of storage energy to reproductive versus non-reproductive activities during gonad maturation. Spring-spawners, having a lengthy gonad maturation, divert proportionally more energy to non-reproductive activites than do autumn-spawners with a brief gonad maturation. Analysis of herring proximate composition reveals an elaborate system of storage energy accumulation and depletion, the timing of which are specific to spawning season. Storage lipids are the primary energy source for non-reproductive activities during gonad maturation. The amount of lipid depleted therefore determines susceptibility to diversion of storage proteins from gonad to active metabolism. A lipid utilization model developed from principles of fish metabolism predicts levels of lipid depletion during gonad maturation which are consistent with observed values for both spring- and autumn-spawning herring. The known winter distributions of nw Atlantic herring are predicted from the model, with the criterion of minimizing lipid depletion through migration to low temperature habitat. Similarly, the range in latitude of herring spawning, and differences in the latitudinal range of spring and autumn spawnings are shown to be consistent with temperature-dependent energetic constraints during gonad maturation. It is concluded that the population richness of Atlantic herring is linked to the utilization of storage energy during gonad maturation.

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Fred Page helped me maintain the ability to distinguish between hypotheses and hypofantasies. I will greatly miss the daily collaboration with him. Daphne Themelis helped me recognize the light at the end of the tunnel.

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Chapter 1

Perspective and Objectives

1.1 Introduction

Losses from self-sustaining fish populations during the egg and larval stages are thought to determine both the magnitude of year-class size (Cushing 1990), and the maximum size of populations (Iles and Sinclair 1982). Consequently, much research has focussed on the degree of parental investment into reproduction and the reproductive traits of self-sustaining populations (Blaxter and Hempel 1963; 1966; Ware 1975; Rothschild 1986; Bailey and Houde 1989).

Both egg weight (egg size) and absolute fecundity (eggs·female^{-1}) in fishes vary among populations, and among species (Bigelow and Schroeder 1953; Leim and Scott 1966; Bagenal 1971, 1978; Russell 1976). Much of the variability in both egg weight and fecundity is evident as clinal trends with either latitude (Thresher 1988), or season of spawning (Hempel and Blaxter 1967; Cushing 1967; Ware 1975; Blaxter 1985; Daoulas and Economou 1986). These trends are predicted by hypotheses that link mortality through starvation and predation to the size and growth rate of both eggs and larvae (Sheldon et al. 1972; Ware 1975; Peterson and Wroblewski 1984; McGurk 1986; Nellen 1986; Tanasichuk and Ware 1987; Anderson 1988; Duarte and Alcaraz 1989). However, these assessments assume that egg weight and

fecundity are "traded-off" (Mann and Mills 1979) among populations with equal or near-equal mature gonad weights at length (also referred to from here on as either 'realized reproductive effort' or 'reproductive effort') (Ware 1975; Mann and Mills 1979; Wootton 1979; Blaxter 1985; Sinclair and Tremblay 1984; Tanasichuk and Ware 1988; Duarte and Alcarez 1989). The hypothesis of equality has rarely been tested.

1.2 Atlantic Herring and Early Life History Theory

The Atlantic herring (*Clupea harengus harengus* L.) is a key test species for the development of early life history theory (Sinclair 1988). Individual herring populations spawn within the same, relatively brief four-six week period every year (Blaxter 1985; Chadwick and Claytor 1989) but as a species herring spawn throughout the year (Iles and Sinclair 1982; Sinclair and Tremblay 1984). Reproductive traits (egg weight and fecundity) vary extensively among herring populations in association with their protracted breeding season. Among northeast (ne) Atlantic populations egg weight and fecundity vary by factors of ≈3.5 and ≈4 respectively for a standard length fish (Hempel and Blaxter 1967; Blaxter 1985).

Egg weight and fecundity exhibit inverse trends with season of spawning among populations (Blaxter 1985). Winter

(November-February)- and spring (March-May)-spawning herring have heavier but fewer eggs than summer (July)- and autumn (August-October)-spawning herring (Blaxter and Hempel 1963; Mann and Mills 1979; Sinclair and Tremblay 1984). These patterns are often interpreted as evidence that egg weight and fecundity could vary inversely among spawning seasons to optimize egg and larval survival, on the assumption that realized reproductive effort is constant among populations (e.g., Cushing 1967; Mann and Mills 1979; Rothschild 1986; Miller et al. 1988; Bailey and Houde 1989).

Northwest (nw) Atlantic herring are not well represented in descriptions of herring reproductive traits. Egg weights and gonad weights of mature fish are rarely measured. However, it is known that both summer- and autumn-spawning herring are more fecund at length than spring-spawning herring (Draganik and Rast 1970; Hodder 1972; Messieh 1976; Messieh et al. 1985; Kelly and Stevenson 1985; Bradford 1987).

Many life-history characteristics that could influence herring reproductive traits differ between ne Atlantic and nw Atlantic populations. Adult spring-, summer-, and autumn-spawning nw Atlantic herring are large bodied (asymptotic length ($L\infty$) ≥33cm; Messieh and Tibbo 1971; Anthony and Waring 1980) and when not heavily fished are long-lived (Age_{max} ≈20 years for both spring- and autumn-spawners; Lea 1919). Some ne Atlantic populations are also

large bodied and long lived, but overall both body size and life span are more variable among ne Atlantic populations (21cm $\leq L\infty \leq$ 37cm, 10 $\leq Age_{max}$(Years)$\leq$ 23; Parrish and Saville 1965, Blaxter 1985, Parmanne 1990, Cushing 1967). In the ne Atlantic, much of the variability in these characteristics occurs between populations with different spawning seasons (Beverton 1963; Cushing 1967; Blaxter 1985).

The life-history characteristics of herring with the same spawning time but from different regions of the north Atlantic can also differ. May-June spawning nw Atlantic herring are larger ($L\infty$ =33cm versus 21cm) and longer lived (t_{max} =20 years versus 10 years) than May-June spawning Baltic Sea herring. Since fecundity, and for some populations egg weights, are strongly positively correlated with fish length (Hempel and Blaxter 1967; Blaxter 1985) differences in herring reproductive traits among regions are plausible. This indicates that the reproductive traits of herring from one region may not be applicable for herring from other regions. Therefore, direct measurements of egg weight, fecundity and gonad weight at length for nw Atlantic populations are necessary for a comprehensive description of the herring's reproductive traits.

Spawning time distribution differs between ne Atlantic and nw Atlantic herring. Winter and early spring-spawning herring (December-March), which are prevalent in the North Sea (Parrish and Saville 1965), do not exist in the nw

Atlantic (Colton et al. 1979; Haegele and Schweigert 1985). Therefore, egg weights may be less variable among nw Atlantic populations than ne Atlantic populations since the eggs of winter-spawners are the heaviest recorded (Hempel and Blaxter 1967).

In spite of the above differences, several life-history characteristics are common to both nw Atlantic and ne Atlantic herring. The duration of the maturation period can differ by as much as six months between spring- and autumn-spawning herring regardless of their region of origin. Spring-spawning herring initiate gonad maturation during the previous autumn (late August-October; McQuinn 1989) and overwinter with near fully developed gonads (Iles 1964; Shatunovskiy 1970; Parsons and Hodder 1975; McQuinn 1989). The gonad maturation period is shorter for autumn-spawners whose gonads develop fully during the summer (July-August) just prior to spawning (Parsons and Hodder 1975; McQuinn 1989).

Most herring, regardless of spawning season do not actively feed beyond the initial stages of gonad maturation (Iles 1964, 1965, 1984; Shatunovskiy 1970; Parsons and Hodder 1975; Messieh et al. 1979; Crawford 1980; Linko et al. 1985). Instead, herring rely upon somatic energy stores to develop gonad in addition to fulfilling all routine and active metabolic requirements. The proportion of total fish weight accounted for by surplus energy is roughly equivalent

for both spring- and autumn-spawning populations at the onset of gonad maturation (Stoddard 1968; Hodder et al. 1973; Peturson and Rosenberg 1982). Therefore, the relative proportion of somatic energy allocated to gonad versus routine and active metabolism may be greater for populations with brief maturation periods than for populations with long maturation periods. Realized reproductive effort may not be constant for all herring populations as is commonly assumed (e.g., Ware 1975; Mann and Mills 1979; Tanasichuk and Ware 1987).

1.3 Scope and Organization of the Thesis

The general question addressed in this thesis is: "Does the timing and duration of gonad maturation influence other reproductive traits of Atlantic herring, namely egg weight and fecundity?". Evaluation of this question proceeds from assessments of specific topics addressed individually as chapters. Chapter 2 documents the egg weight, fecundity and gonad weight traits of nw Atlantic spring- summer, and autumn-spawning herring populations. Relations between egg weight, fecundity, gonad weight and length are used to determine whether egg weight and fecundity vary among populations due to a trade-off of these variables or due to variability in reproductive effort.

Chapter 3 examines whether the duration of the gonad

maturation period influences the physiological condition of spawning herring. Relationships between egg weight, spawning condition and spawning history (recruit versus repeat spawners) within populations are explored.

Chapter 4 evaluates whether surplus energy stored as lipids is utilized differently than surplus energy stored as protein by non-feeding herring. The analysis considers the cases of overwintering, maturing spring-spawning herring, overwintering, spent autumn-spawning herring, and maturing autumn-spawning herring.

Chapter 5 evaluates whether differences in the duration of the maturation period between spring- and autumn-spawning herring influences realized reproductive effort even though developmental temperatures and activity levels may differ by spawning season. Also examined is the importance of the seasonal timing of storage energy accumulation to survival in winter conditions.

Chapter 6 examines whether catch data collected from fisheries on herring spawning grounds are useful as an indicator of spawning activity. Questions which follow from this analysis include whether the spring-neap tidal cycle affects the timing of spawn deposition.

Implications for fisheries ecology theory from this study are discussed in Chapter 7.

Chapter 2.

Egg-Size, Fecundity and Gonad-Weight Variability Among Northwest Atlantic Herring Populations.

2.1 Introduction

Both egg weight and fecundity differ among Atlantic herring (*Clupea harengus harengus* L.) populations that spawn during different seasons (Blaxter and Hempel 1963). In the northeast (ne) Atlantic winter-spring- (December-March) spawning herring have larger but fewer eggs than summer-autumn (June-September) spawning herring (Blaxter and Hempel 1963). Comparisons among populations show that egg weight varies by a factor of ≈3.5 and that absolute fecundity (eggs·fish^{-1}; Messieh 1976) varies by a factor of ≈4 (Hempel and Blaxter 1967; Sinclair and Tremblay 1984). Between winter-spring- and summer-autumn-spawning populations, egg weight and fecundity vary inversely (Blaxter and Hempel 1963; Mann and Mills 1979; Sinclair and Tremblay 1984).

Extensive seasonal variability in both egg weight and fecundity in herring, and their seasonal inverse relationship among populations, are generally viewed as evidence that fish reproductive traits are selected to enhance survival during the early life period (Cushing 1967; Hempel 1965; Mann and Mills 1979; Rothschild 1986; Miller et al. 1988; Bailey and Houde 1989). The combination of heavy but few eggs is thought to maximize larval survivorship in cold waters during winter and spring when concentrations of

zooplankton are lower than during the summer or autumn (Hempel 1965; Mann and Mills 1979; Blaxter 1985; Winters and Wheeler 1987; Miller et al. 1988). Lighter but more numerous eggs are thought to be advantageous when feeding conditions are favourable but predation pressure is higher during summer and autumn (Hempel 1965; Mann and Mills 1979; Winters and Wheeler 1987). Sinclair and Tremblay (1984) have hypothesized that herring populations with long larval periods (autumn-spawning) need to be more fecund in order to offset higher cumulative larval mortalities than do herring populations with brief larval periods (spring-spawning) and lower cumulative larval mortalities.

Many interpretations of the biological significance of egg-size and fecundity variability in fishes assume that, among populations, mature gonad weight at length is constant (Ware 1975; Mann and Mills 1979; Wootton 1979; Tanasichuk and Ware 1988; Duarte and Alcaraz 1989) or varies to a lesser extent than does either egg-weight or fecundity (Sinclair and Tremblay 1984; Hempel 1965; Blaxter 1985). Empirical support for these assumptions has not been reported. However, constant realized reproductive effort among populations, regardless of spawning season, is crucial to the egg-size - fecundity "trade-off" concept (Mann and Mills 1979). Therefore, studies of egg-size and fecundity variability among herring populations should be supplemented with assessments of variability in gonad weights.

Northwest (nw) Atlantic herring are incompletely represented in surveys of egg weight and fecundity. Autumn-spawners are known to be more fecund at length than spring-spawners (Hodder 1972; Messieh 1976; Messieh et al. 1979; Kelly and Stevenson 1985; Bradford 1987), but neither egg weights nor gonad weights have been measured. A full assessment of the reproductive traits (egg weight, absolute fecundity and gonad weight) is desirable since these data could establish: 1) whether the reproductive traits of nw Atlantic herring are the same as for ne Atlantic herring, as is commonly assumed (Ware 1975; Lett and Kohler 1976; Tanasichuk and Ware 1987; Winters and Wheeler 1987; Miller et al. 1988); and 2) whether egg size and fecundity are traded off among populations with different spawning seasons.

In this chapter three hypotheses are tested regarding the nature and extent of the seasonal variability of reproductive traits among nw Atlantic herring populations. The analysis is based on data extracted from samples of nw Atlantic herring. The hypotheses are:

1) Egg weights do not vary among spring-, summer-, and autumn-spawning herring populations.

2) Egg weight varies inversely with egg number between spring- and autumn-spawning nw Atlantic herring.

3) Gonad weight, standardized to length, does not vary among herring populations that spawn during different seasons.

2.2 Materials and Methods

2.2.1 Data Base

Simulataneous estimates of egg weight, absolute fecundity, and gonad weight were not available from individual fish. Fish with freely extruded, fully mature eggs, provide the best measure of egg weight but unreliable measures of both egg number and gonad weight. Fish in near spawning condition, which do not extrude their eggs, provide both good measures of egg number and a close approximation of mature gonad weight but underestimate egg weight. Therefore, the variability of herring reproductive traits among spring-, summer-, and autumn-spawning nw Atlantic populations was analyzed using four separate data sets.

The first data set consisted of egg weight estimates for individual herring from 12 nw Atlantic populations that represented both the full range of herring spawning times, and the herring's southern and central range in the nw Atlantic (Leim and Scott 1966; Haegele and Schweigert 1985). These data were used to determine whether egg weight varied among nw Atlantic herring which spawned during different seasons (Hypothesis 1). Two other data sets, one consisting

of egg weight estimates, and the other of fecundity estimates, for the spring- and autumn-spawning southern Gulf of St. Lawrence (referred to afterwards as either 'southern Gulf' or NAFO Subdivision '4T') herring populations were used to test whether egg weight and fecundity vary inversely between populations (Hypothesis 2). The fourth data set consisted of gonad weights and fish lengths for individual mature female herring from three spring-spawning, one summer-spawning, and two autumn-spawning nw Atlantic herring populations (data source cited below). These data were used to test whether length-standardized gonad weights varied among populations which spawned during different seasons (Hypothesis 3).

2.2.2 Herring Egg Weight Variability Among Seasons and Among Populations in the Northwest Atlantic.

Preserved sections of fully mature ovaries ('ripe and running', Maturity Stage 6; Table 2.1) from herring collected during April-October, 1986 from 12 commercial fisheries (Figure 2.1), were obtained from Dr. R.L. Stephenson (Department of Fisheries and Oceans (DFO), St. Andrews, N.B.). Following previous designations (Leim and Scott 1966; Messieh and Tibbo 1971; Haegele and Schweigert 1985) herring which spawned from early April - late June (Bras D'Or Lake, Escuminac, Miminegash, Bonavista Bay, Minas

Table 2.1. The maturity scale recommended by the Herring Committee of ICES (Anon., 1962).

Stage	Description
1	Virgin herring. Gonads very small, threadlike (2 - 3mm broad). Ovaries wine red. Testes whitish or grey-brown.
2	Virgin herring with small sexual organs. The height of ovaries and testes about 3 - 8mm. Eggs not visible to naked eye but can be seen with a magnifying glass. Ovaries a bright red color, testes a reddish grey colour.
3	Gonads occupying about half of ventral cavity. Breadth of sexual organs between 1 - 2cm. Eggs small but can be seen with the naked eye. Ovaries orange; testes reddish grey or greyish.
4	Gonads almost as long as the body cavity. Eggs larger, varying in size, opaque. Ovaries orange or pale yellow; Testes whitish.
5	Gonads fill body cavity. Eggs large, round; some transparent. Ovaries yellowish, testes milk white. Eggs and sperm do not flow, but sperm can be extruded by pressure.
6	Ripe gonads. Eggs transparent; testes white; egg and sperm flow freely.
7	Spent herring. Gonads baggy and bloodshot. Ovaries empty or containing only a few residual eggs. Testes may contain remnants of sperm.
8	Recovering spents. Ovaries and testes firm and larger than virgin herring in Stage 2. Eggs not visible to naked eye. Walls of gonad are striated; blood vessels prominent. Gonads are wine red in color.

Figure 2.1. Map of nw Atlantic region from which samples were obtained for egg weight determinations.

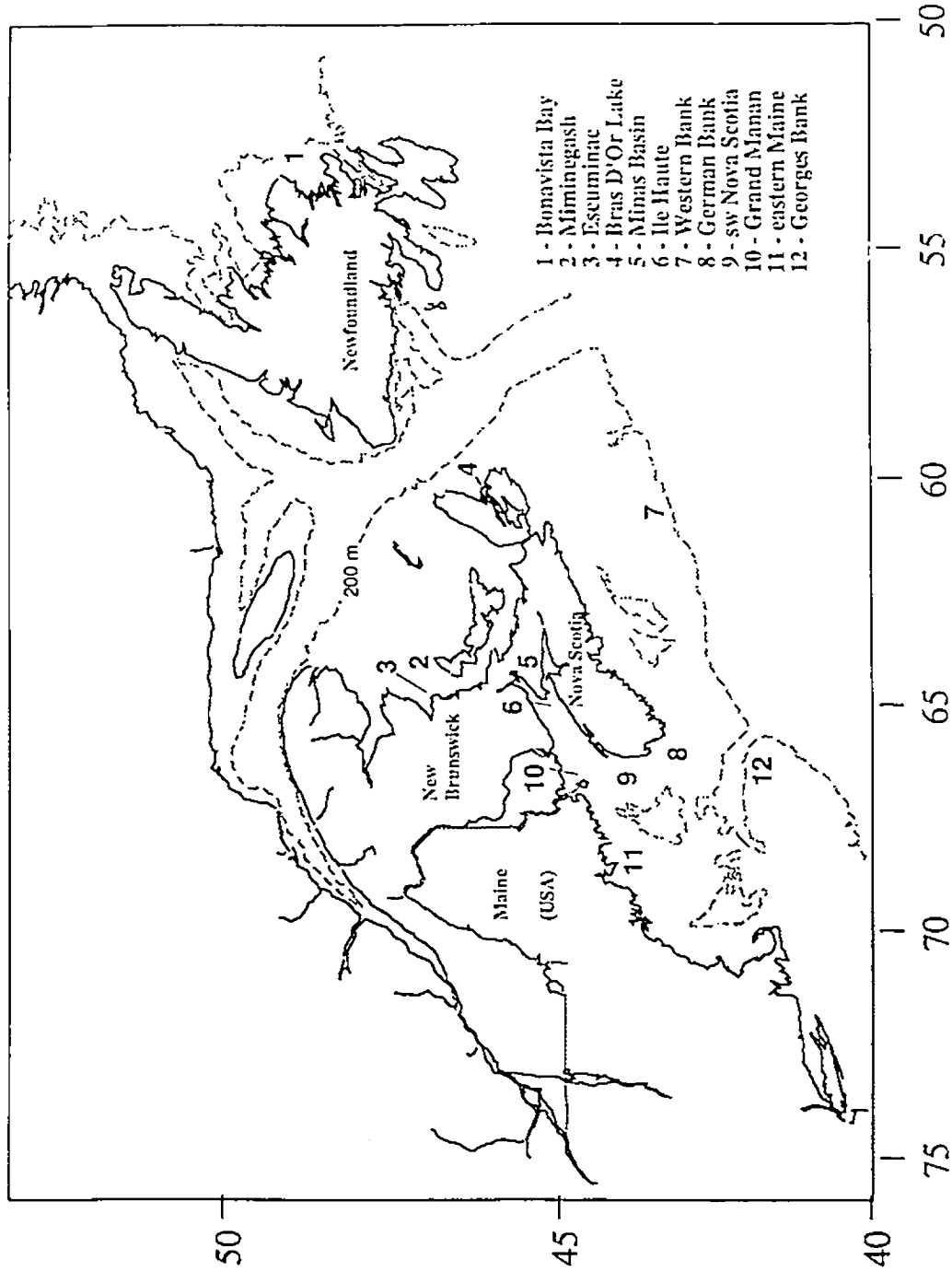
1 - Bonavista Bay
2 - Miminegash
3 - Escuminac
4 - Bras D'Or Lake
5 - Minas Basin
6 - Ile Haute
7 - Western Bank
8 - German Bank
9 - sw Nova Scotia
10 - Grand Manan
11 - eastern Maine
12 - Georges Bank
Newfoundland
New Brunswick
Nova Scotia
Maine (USA)
200 m
50
45
40
75
70
65
60
55
50

Figure 2.1

Basin), mid-July - early August (Ile Haute, eastern Maine), and mid-August - late October (southwest (sw) Nova Scotia, German Bank, Grand Manan, Western Bank, Georges Bank) were defined respectively as spring-, summer-, and autumn-spawners.

The sampling protocol is summarized from Stephenson and Gordon (1990). Both random and length stratified samples of fully mature herring were obtained from each of the above fisheries. These ensured an adequate representation of the full range in body size from each population. All samples were frozen within 2-3 hours of capture and stored for ≤6 months.

In the laboratory, fish were thawed and their total length (mm) measured. Ovaries were removed, weighed (0.01g) and an ovary section from each female was stored in Gilsons solution (Bagenal 1978) for at least 6 months. This preparation fixes the ripe eggs and allows their separation from the surrounding ovarian tissue. Upon removal from the Gilsens solution each section of ovary was placed in a 1 ℓ beaker filled with fresh water. Individual eggs were released from the ovary by gentle finger pressure on the ovary section. Tap water was alternately added to and decanted from the beaker until all of the loose ovary tissue was removed leaving only the fully developed eggs. These were transferred to small glass jars and soaked with deionized water for ≈1 hour.

Three sub-samples from each jar were placed in pre-weighed dishes and their egg number counted under a dissecting microscope at 12X magnification. Subsamples in which ovary tissues were still attached to the eggs were discarded. Eggs that were either broken or atretic (mis-shapen, grossly hydrated; Bowers and Holliday 1961) were removed. Most of the sub-samples contained between 250-750 eggs. Samples which did not provide 3 sub-samples with ≥250 eggs each, were discarded since preliminary analysis showed that the estimated mean egg dry weight estimates obtained with smaller subsamples were not accurate. All sub-samples were dried for 48 hours at 40°C, cooled to room temperature in a desiccator and reweighed (0.0001g). Sub-sample egg dry weight was determined as:

$$\frac{[(Egg\ Dry\ Wt + Pan\ Wt) - Pan\ Wt]}{Egg\ Number} \qquad (2.1)$$

The mean egg dry weight (referred to here onward as egg weight) of the 3 sub-samples was used as the measure of egg weight for each fish.

2.2.3 Egg Weight and Fecundity Variability Between Spring- and Autumn-Spawning Southern Gulf of St. Lawrence Herring.

Egg Weight Determinations

The procedure used to obtain egg dry weights for southern Gulf herring differed from that used in the previous section (2.2.2). Herring from the southern Gulf were collected fresh from commercial gill net catches during May in the vicinity of Seacow Pond, P.E.I. (Figure 2.1) and during August-September from Fishermans Bank, P.E.I. (Figure 2.1) for the years 1988 and 1989. Fully mature females (Maturity Stage 6; Table 2.1), were selected at random from the catch and measured to total length (mm). At the time of collection, a sub-sample of several thousand eggs was stripped from each female into individual vials containing Gilsens solution.

Unlike the egg samples extracted from the preserved ovary sections two sub-samples were taken with each containing between 400-800 eggs. Preliminary results showed that fewer replicates were necessary with sub-samples of this size. Sub-sample dry weights were obtained using the same methods described in Section 2.2.2 with $n = 3$. Replicates differed in mean dry weight by <5%.

Fecundity Determinations

Mature, but not spawning females (Maturity Stage 5; Table 2.1) were also collected from the Seacow Pond and Fishermans Bank fisheries. The pair of ovaries was removed from each fish, weighed (0.01g) and then placed in glass jars with Gilsens solution. All samples were stored for ≥6 weeks to break down the ovarian tissues encapsulating the eggs.

Mature eggs were collected by repeated rinsings of the preparation with fresh water through a seive. The eggs were transferred into 500ml beakers and rinsed further by decanting with tap water. Excess water was removed by inverting the preparation onto a fine meshed seive for 4 hours. This procedure has been shown to produce fecundity estimates that are both repeatable and comparable to estimates obtained by other established procedures (Bradford 1987).

Three sub-samples of approximately 200-300 eggs each were placed in tared vials and each sub-sample was weighed (0.0001g) and counted. Egg counts per sub-sample were converted to the number per gram and the mean, standard deviation and coefficient of variation calculated. Samples with a coefficient of variation >5% were discarded.

Absolute fecundity (F_a) was calculated as;

$$F_a = W_e \cdot X_n \qquad (2.2)$$

where W_e = wet weight of egg mass (g) and X_n = mean number of eggs per gram.

Additional fecundity determinations for southern Gulf spring- and autumn-spawning herring were obtained from Dr. D. Cairns (DFO, Moncton, N.B.). The analytical procedures for these samples (Messieh 1976), were similar to that described for the present study except that the separated eggs were dried at 50°C for 24 hours prior to sub-sampling. This method produces comparable estimates of fecundity to those used in the present study (Bradford 1987). The fecundity data for all years (1969-1988 inclusive) were pooled.

2.2.4 Among-Population Variability in Ovary Weight.

Records of mature female herring (Herring Maturity Stage 5; Table 2.1) were obtained from Dr. R.L. Stephenson (DFO, St. Andrews, N.B.). These fish represented routine port samples from the commercial fisheries. Information available for each fish included location and date of capture, gear type, total length (mm), total weight (0.1g), and gonad wet weight (0.01g). Samples were obtained from 6 'spawning' fisheries, each of which is currently recognized as a discrete spawning unit (Sinclair et al. 1985), and which collectively represent the known spawning times for

herring in the nw Atlantic. These include Bras D'Or Lake (April), southern Gulf spring (May-June), Minas Basin (May-June), Ile Haute (July-August), southern Gulf autumn (August-September), and southwest (sw) Nova Scotia autumn (August-September) (Figure 2.1).

Samples captured via trap nets or purse seines were used for analysis because these gear types are not size selective. Some of the samples had been captured using gill nets which capture fish differentially on the basis of body size (Hamley 1975). These were retained for analysis if a broad range of mesh sizes had been used in their capture. This procedure duplicates the length frequency distribution of samples captured with non-selective gear for herring ≥270mm in length (Winters and Wheeler 1990).

All samples had been previously frozen prior to measurement. Because freezing results in loss of length (Hunt et al. 1986), expected fresh length (mm) was calculated from the empirical relation (Hunt et al. 1986):

$$L_{FRESH} = 2.28 + 1.01 \cdot L_{FROZEN} \qquad (r^2 = .99) \qquad (2.3)$$

where L_{Fresh}= fresh length(mm) and L_{Frozen}= frozen length(mm). Ovary weight was regressed against total length for each spawning group over a common length range of 275mm-350mm using the model:

$$\ln(Ovary\ Wt) = \ln(a) + b \cdot \ln(Length) \qquad (2.4)$$

where a and b are the regression intercept and slope respectively.

2.3 Results

2.3.1 Herring Egg Weight Variability Among Seasons and Among Populations in the Northwest Atlantic

Northwest Atlantic herring egg weights (Table 2.2) varied both among populations (ANOVA, Table 2.3), and among spawning seasons (*a posteriori* tests, Table 2.3), but to a lesser degree than shown previously for ne Atlantic herring. Spring spawned eggs were only marginally heavier (1.06x) than autumn-spawned eggs in the present study (pooled mean egg weights ±1 standard deviation were 14.91±2.56mg (n =160) and 14.01±1.50mg (n =193) respectively). A seasonal pattern was evident since both spring- and autumn-spawned eggs were heavier (by 1.21x and 1.13x respectively) than summer-spawned eggs (12.35±1.47mg, n =113).

Differences in egg weight between individual nw Atlantic populations were also less than expected from analyses of ne Atlantic populations (maximum range =1.43x for Bras D'Or Lake (spring) and eastern Maine (summer); Table 2.3; Figure 2.2). Both the spring-summer and summer-autumn comparisons exhibited greater egg weight variability among populations than did the spring-autumn comparisons.

Table 2.2. Mean (±1 standard deviation (SD)) and median egg dry weights (mg/100 eggs) for nw Atlantic herring populations sampled during 1986. Also shown are the day of capture (Day), the number of samples available for each population (n), and Kolmogorov-Smirnov Z scores for tests of normality (K-S Z) and their associated probabilities (P).

			Egg Weights mg/100				
Population	Day	n	Mean	SD	Median	K-S Z	P
Brad D'Or Lake	122	19	16.50	1.43	16.57	0.514	0.95
Escuminac	127	24	14.83	1.51	14.76	0.560	0.91
Miminegash	135	26	11.96	1.83	11.59	0.603	0.86
Bonavista Bay	142	39	15.52	2.35	15.65	0.591	0.88
Minas Basin	154	31	15.15	1.70	15.52	0.573	0.90
Ile Haute	195	81	12.47	1.85	12.50	0.556	0.92
eastern Maine	218	31	11.57	1.18	11.50	0.589	0.88
sw Nova I	240	22	14.16	1.09	14.24	0.454	0.99
German Bank	240	32	13.49	0.95	13.37	0.712	0.69
Grand Manan	242	45	14.63	1.21	14.71	0.536	0.94
sw Nova II	273	23	13.93	1.41	13.71	0.482	0.97
Western Bank	283	34	14.12	1.49	14.32	0.474	0.98
Georges Bank	296	23	13.72	1.23	13.34	0.947	0.33
sw Nova I+II		45	14.05	1.25	14.00		
Totals		430	13.86	2.05			

Table 2.3. Analysis of variance for egg dry weights (mg/100 eggs) between all groups of nw Atlantic herring sampled, with a posteriori contrast tests for differences between spring- and summer-spawners, summer- and autumn-spawners, and spring- and autumn-spawners.

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Square	F	P
All Groups					
Between Groups	12	808.34	67.36	28.7	<0.001
Within Groups	435	1018.89	2.34		
Total	436	1827.24			
Spring-Summer					
Between Seasons	1	333.14	333.14	142.1	<0.001
Error	436	1021.97	2.34		
Spring-Autumn					
Between Seasons	1	48.75	48.75	20.8	<0.001
Error	436	1021.97	2.34		
Summer-Autumn					
Between Seasons	1	88.41	88.41	37.7	<0.001
Error	436	1021.97	2.34		

Figure 2.2. The mean and standard deviation of egg weight (mg) for nw Atlantic herring populations versus day of capture (day).

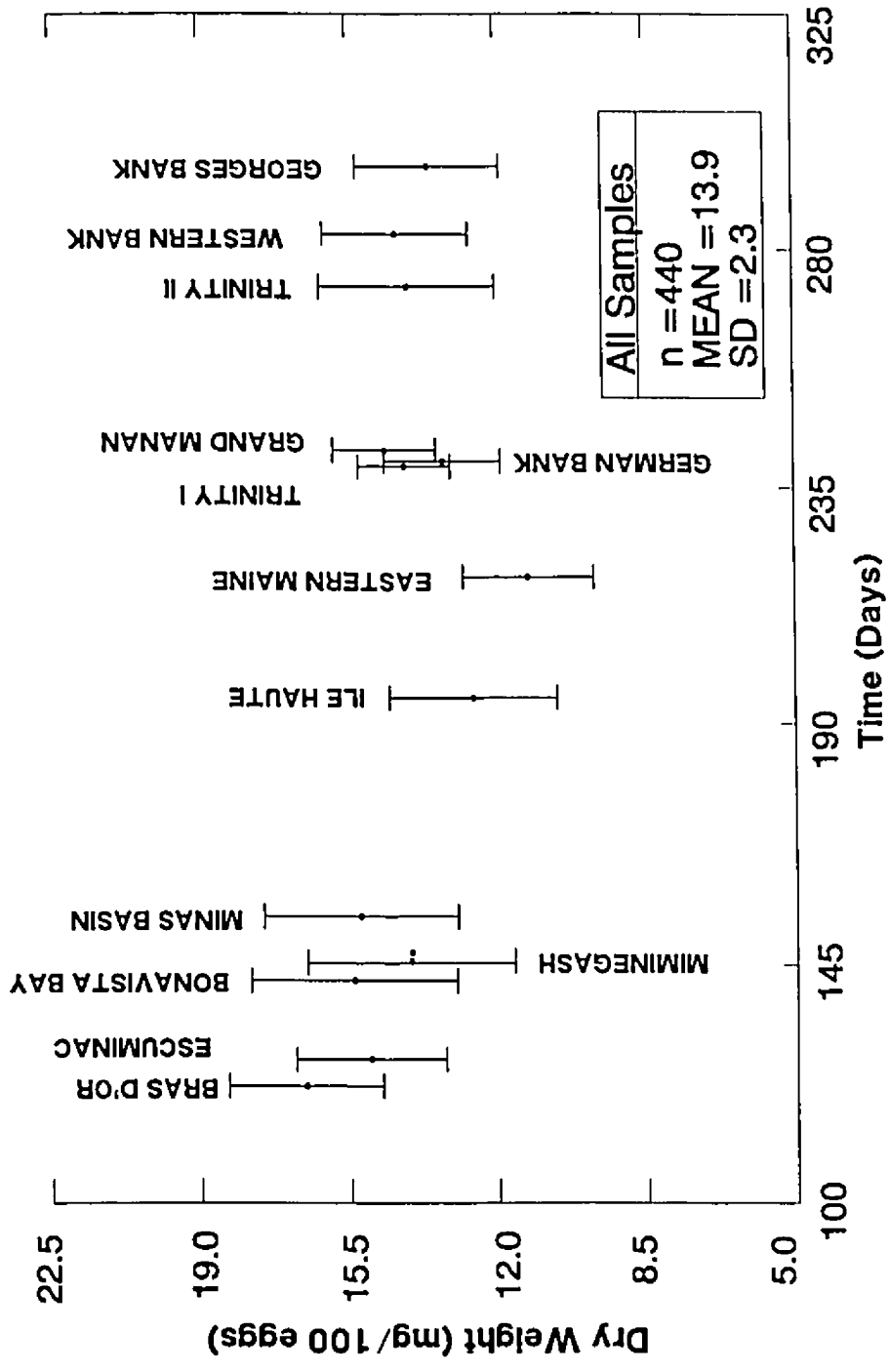
Dry Weight (mg/ 100 eggs)
22.5
19.0
15.5
12.0
8.5
5.0
100
145
190
235
280
325
Time (Days)
All Samples
n =440
MEAN =13.9
SD =2.3
BRAS D'OR
ESCUMINAC
BONAVISTA BAY
MIMINEGASH
MINAS BASIN
ILE HAUTE
EASTERN MAINE
TRINITY I
GRAND MANAN
GERMAN BANK
TRINITY II
WESTERN BANK
GEORGES BANK

Figure 2.2

Twelve of 30 possible spring-autumn comparisons were not significantly different ($P < 0.05$; Tukeys multiple between-group comparison test, adjusted for unequal sample sizes; Table 2.4). Of the 18 significantly different comparisons 12 could be attributed to 2 (of 5) spring-spawning populations (Bras D'Or Lake and Miminegash) having eggs which differed in weight from all of the autumn-spawning groups (Table 2.4). In contrast, 8 of 10 possible spring-summer and 8 of 12 possible summer-autumn comparisons differed significantly (Table 2.4). Egg weights did not vary with sampling date for sw Nova Scotia autumn-spawning herring (southwest Nova Scotia I and II sampled 34 days apart; Table 2.4).

In general, egg weights were normally distributed within populations except for German Bank and Georges Bank ($P = 0.69$ and $P = 0.33$ respectively; Kolmogorov-Smirnov Z test (K-S Z), Table 2.3). Median and mean egg weights were similar for all of the populations (Table 2.3). Egg weight was weakly but positively correlated with length for 2 of 5 spring-spawning populations (Bonavista Bay; df =37, r^2 =0.50, $P < 0.001$ and Minas Basin; df =29, r^2 =0.20, $P < 0.01$) and for none of the summer- or autumn-spawning populations.

The hypothesis that individual egg weights do not vary among spring-, summer, and autumn-spawning populations was rejected on the basis that significant differences occured

Table 2.4. Tukeys multiple between-group comaprison test adjusted for unequal sample sizes at P <0.05 (N.S. = not significantly different; Sp= spring, Su =Summer, Au =Autumn).

	Eastern Maine	Miminegash	Ile Haute	German Bank	Georges Bank	sw Nova Scotia II	Western Bank	sw Nova Scotia I	Grand Manan	Escuminac	Minas Basin	Bonavista Bay
Eastern Maine												
Miminegash	N.S.											
Ile Haute	N.S.	N.S.										
German Bank	Su-Au	Sp-Au	N.S.									
Georges Bank	Su-Au	Sp-Au	N.S.	N.S.								
sw Nova Scotia II	Su-Au	Sp-Au	Su-Au	N.S.	N.S.							
Western Bank	Su-Au	Sp-Au	Su-Au	N.S.	N.S.	N.S.						
sw Nova Scotia I	Su-Au	Sp-Au	Su-Au	N.S.	N.S.	N.S.	N.S.					
Grand Manan	Su-Au	Sp-Au	Su-Au	N.S.	N.S.	N.S.	N.S.	N.S.				
Escuminac	Su-Sp	Sp-Sp	Su-Sp	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.			
Minas Basin	Su-Sp	Sp-Sp	Su-Sp	Au-Sp	Au-Sp	N.S.	N.S.	N.S.	N.S.	N.S.		
Bonavista Bay	Su-Sp	Sp-Sp	Su-Sp	Au-Sp	Au-Sp	Au-Sp	Au-Sp	N.S.	N.S.	N.S.	N.S.	
Bras D'Or Lake	Su-Sp	Sp-Sp	Su-Sp	Au-Sp	Au-Sp	Au-Sp	Au-Sp	Au-Sp	Au-Sp	Sp-Sp	N.S.	N.S.

between more than half of the possible comparisons of individual populations with different spawning seasons. However, egg weight variability among spawning seasons is much less than expected from previous analyses of ne Atlantic populations (maximum between population differences are 1.43x and 3.5x for nw Atlantic and ne Atlantic herring respectively). Seasonal egg weight variability was least between spring- and autumn-spawning populations and greatest between spring- and summer-spawning populations.

2.3.2 Fecundity and Egg Weight Variability Between Spring- and Autumn-Spawning Southern Gulf of St. Lawrence Herring.

Autumn-spawning herring were more fecund than spring-spawning herring except for fish >365mm (Figure 2.3; Table 2.5). Analysis of covariance (ANCOVA), with length(mm) as the covariate, showed that both the intercepts and the slopes of the ln-transformed absolute fecundity - length regressions (Table 2.5) were significantly different (df= 1, 504, F= 232.22, P <0.0001 and df= 1, 503, F= 8.56, P <0.01 respectively). Egg weight (W) was weakly, positively correlated with female length (L) for spring-spawning herring (W (mg/100 eggs) = 6.56 + 0.044·L (mm), n =296, r^2 =0.15, P =0.001; Figure 2.4) but showed no relation with length for autumn-spawning herring (P >0.05)(Figure 2.4). Both southern Gulf spring- and autumn-spawning herring egg

Table 2.5. Regression statistics for Fecundity (ln Absolute) vs Length (ln)(mm) for spring- and autumn-spawning southern Gulf of St. Lawrence herring.

Group	n	a	95%CI$_a$	b	95%CI$_b$	r^2	P
Spring	283	-13.3547	0.4912	4.2705	0.4763	0.52	0.001
Autumn	224	-6.9491	0.5080	3.2308	0.5393	0.41	0.001

(Model: ln(Fecundity) =ln(a) + b·ln(Length))

Figure 2.3. Relationship between fecundity (ln absolute) and length (ln)(mm) for spring- and autumn-spawning southern Gulf of St. Lawrence herring (Years of sampling; 1969-1988).

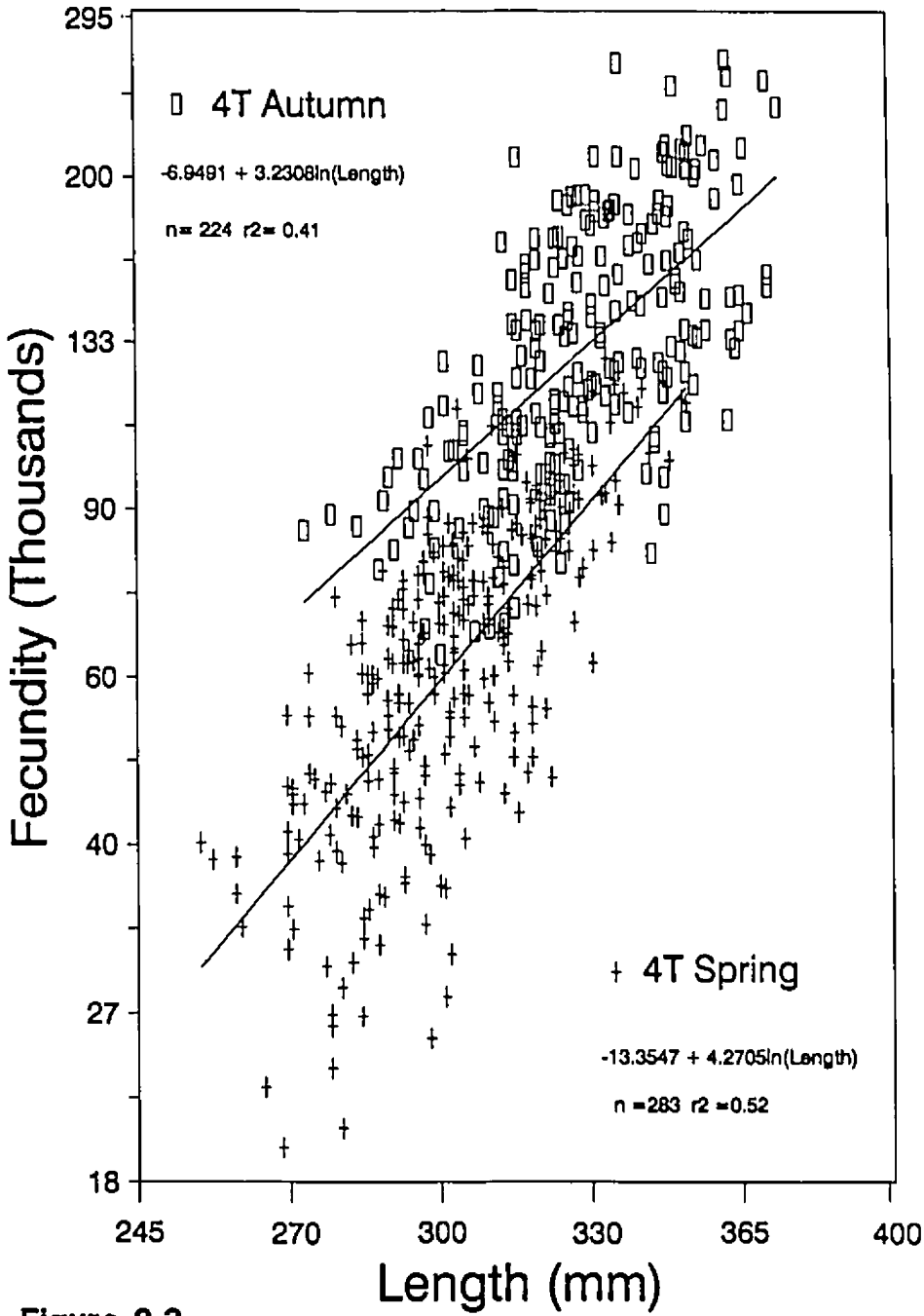
295
200
133
90
60
40
27
18
Fecundity (Thousands)
4T Autumn
-6.9491 + 3.2308ln(Length)
n= 224 r2= 0.41
4T Spring
-13.3547 + 4.2705ln(Length)
n =283 r2 =0.52
245
270
300
330
365
400
Length (mm)

Figure 2.3

Figure 2.4. Relationship between egg weight (mg) and length (mm) for a) spring- and b) autumn-spawning southern Gulf of St. Lawrence herring sampled during 1988 and 1989.

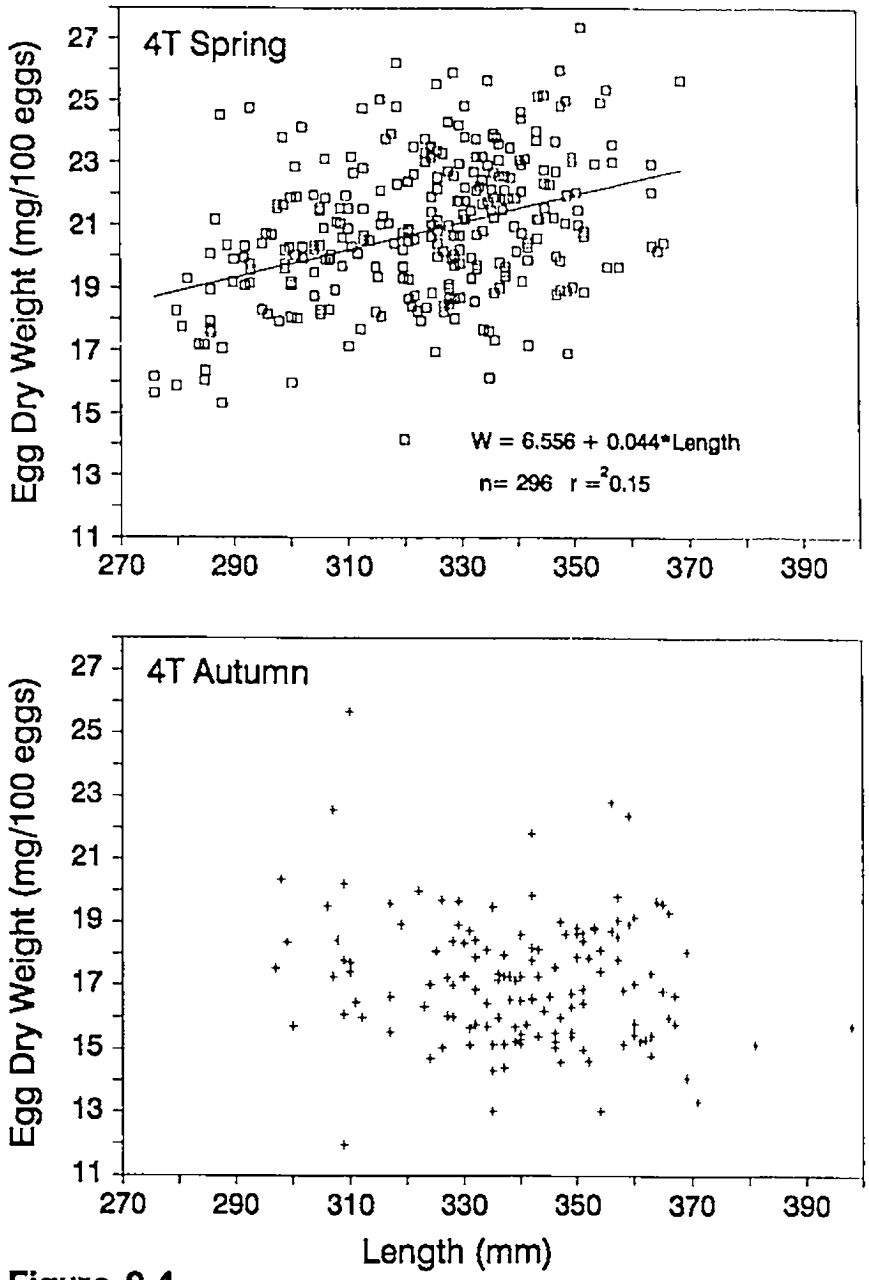
4T Spring
Egg Dry Weight (mg/100 eggs)
W = 6.556 + 0.044*Length
n= 296 r =²0.15
4T Autumn
Egg Dry Weight (mg/100 eggs)
Length (mm)

Figure 2.4

weights varied between years (Table 2.6a,b) but, egg weights differed more between populations than within populations between years (Table 2.6a,b).

Fecundity was more variable than egg weight between southern Gulf spring- and autumn-spawning herring, over a common length range. For example, fecundity (calculated from Table 2.5) differed between spring- and autumn-spawning herring by 1.76x and 1.39x at 275mm and 345mm respectively whereas egg weight (calculated from Table 2.6) differed by only 1.09x and 1.26x at 275mm and 345mm respectively. On average egg weight varied by a factor of 1.22x between spring- and autumn-spawning southern Gulf herring (Table 2.6; Figure 2.5).

Based on the above analysis the hypothesis that egg weight varies inversely with egg number between spring- and autumn-spawning nw Atlantic herring cannot be rejected. However, the degree of egg weight variability between populations is not comparable to that for fecundity.

2.3.3 Among-Population Variability in Ovary Weight

Gonad weights varied among populations. ANCOVA of ovary weight (ln) among populations with length (ln) as the covariate showed that both the intercepts and slopes of the regressions differed (df =5, 940, F =117.97, P <0.001 and df =5, 935, F= 21.02, P <0.001 respectively). In general,

Table 2.6 a) Mean egg weights ± 1 standard deviation (SD)(mg/100 eggs) and coefficients of variation (CV) for southern Gulf (4T) spring- and autumn-spawning herring sampled during 1988 and 1989. b) Twoway ANOVA for egg weight treated by spawning season and year of sampling.

a)

Season	Year	n	Mean Wt mg/100	SD	CV
4T Spring	1988	211	21.24	2.30	10.85
	1989	83	20.28	1.89	9.31
	Combined	294	20.94	2.21	10.53
4T Autumn	1988	44	16.63	1.50	9.01
	1989	95	17.48	1.83	10.45
	Combined	139	17.19	1.82	10.59

b)

Source of Variation	Sums of Squares	df	Mean Square	F	P	r^2
Season	12.081	1	12.081	298.57	<.001	0.46
Year	0.177	1	0.177	4.37	.04	
SEA·YR	1.552	1	1.552	38.35	<.001	
Error	17.359	429	0.040			

Figure 2.5. Percent frequency distributions of egg dry weight (mg/100 eggs) for southern Gulf of St. Lawrence herring (shaded bars =autumn-spawners, open bars =spring-spawners).

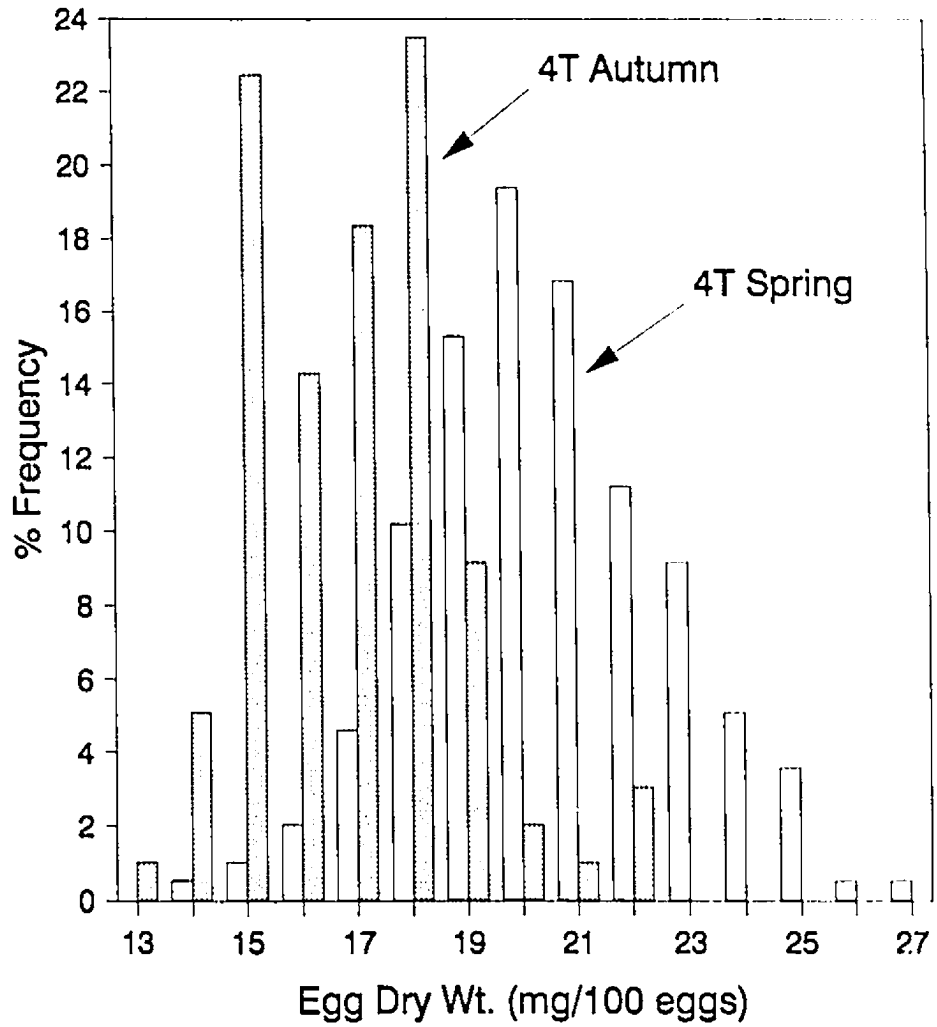
4T Autumn
4T Spring
% Frequency
Egg Dry Wt. (mg/100 eggs)
0
2
4
6
8
10
12
14
16
18
20
22
24
13
15
17
19
21
23
25
27

Figure 2.5

ovary weight variability among populations was greater at shorter lengths than at longer lengths over the common length interval (by 21.6g and 5.6g at 275mm and 350mm respectively between 4T Spring and sw Nova Scotia; Table 2.7, Figure 2.6).

The gonads of autumn-spawning fish were the heaviest of all the groups examined (Table 2.7; Figure 2.6). Between population differences (Tukeys multiple comparison test at $P < 0.05$, adjusted for unequal sample sizes), defined as differences in either slopes, or intercepts, or both (Zar 1984) were organized as follows. Five of 6 spring-autumn comparisons (not Bras D'Or Lake - 4T Autumn) showed significant differences (Table 2.8). Two of 3 spring-summer comparisons (not Bras D'Or Lake - Ile Haute) showed significant differences (Table 2.8). One of 2 summer-autumn comparisons (not Ile Haute - sw Nova Scotia) showed a significant difference (Table 2.8).

Autumn-spring ratios of both ovary weight and a reproductive index (fecundity·egg weight) at length showed that realized reproductive effort is greater for autumn-spawners than for spring-spawners in the southern Gulf (Figure 2.7). Both ratios remained greater than 1 over the common length range (270-350mm) but between-group differences became less extreme with fish length (Figure 2.7). These patterns of variability for both gonad weight and the reproductive index were the same as for absolute

Table 2.7. Regression statistics and sample size (n) for gonad wt (ln)(g) versus length (ln)(mm) for nw Atlantic herring populations (Model: ln(gonad weight) = ln(a) + b·ln(length)); CI =95% confidence interval).

Population	n	ln(a)	CI_a	ln(b)	CI_b	r^2	P
1 Bras D'Or	75	-20.7065	.3498	4.3000	.6221	.72	<.001
2 4T Spring	279	-29.8024	.4347	5.8490	.3784	.77	<.001
3 Minas Basin	98	-19.8163	.3426	4.1250	.5825	.67	<.001
4 Ile Haute	51	-19.3511	.3490	4.0710	.6920	.74	<.001
5 4T Autumn	144	-19.4981	.4553	4.0962	.7544	.45	<.001
6 sw Nova	300	-14.1344	.3359	3.1850	.3578	.51	<.001

Table 2.8. Tukeys multiple between-group comparison test adjusted for unequal sample sizes for slopes and intercepts of gonad wt (ln)(g) versus length (ln) of nw Atlantic herring populations. Numbers are q statistic values which differ significantly ($P < 0.05$) (N.S. =not significantly different).

		Bras D'Or Lake	4T Spring	Minas Basin	Ile Haute	4T Autumn	sw Nova Scotia
Bras D'Or Lake	Slope	—	5.21	N.S.	N.S.	N.S.	4.43
	Intercept	—	6.04	4.02	N.S.	N.S.	9.53
4T Spring	Slope		—	6.09	5.41	5.91	13.94
	Intercept		—	N.S.	5.98	7.74	23.44
Minas Basin	Slope			—	N.S.	N.S.	N.S.
	Intercept			—	4.91	6.86	18.82
Ile Haute	Slope				—	N.S.	N.S.
	Intercept				—	N.S.	6.14
4T Autumn	Slope					—	N.S.
	Intercept					—	8.05
sw Nova Scotia	Slope						—
	Intercept						—

Figure 2.6. Predicted relationships between gonad wt (ln)(g) and length (ln)(mm) for summer-autumn-spawning (solid line), early spring-spawning (fine dashed line), late spring-spawning feeeding (coarse dashed line), and late spring-spawning non-feeding (mixed symbol line) nw Atlantic herring populations. The numbers correspond to the populations listed in Table 2.7.

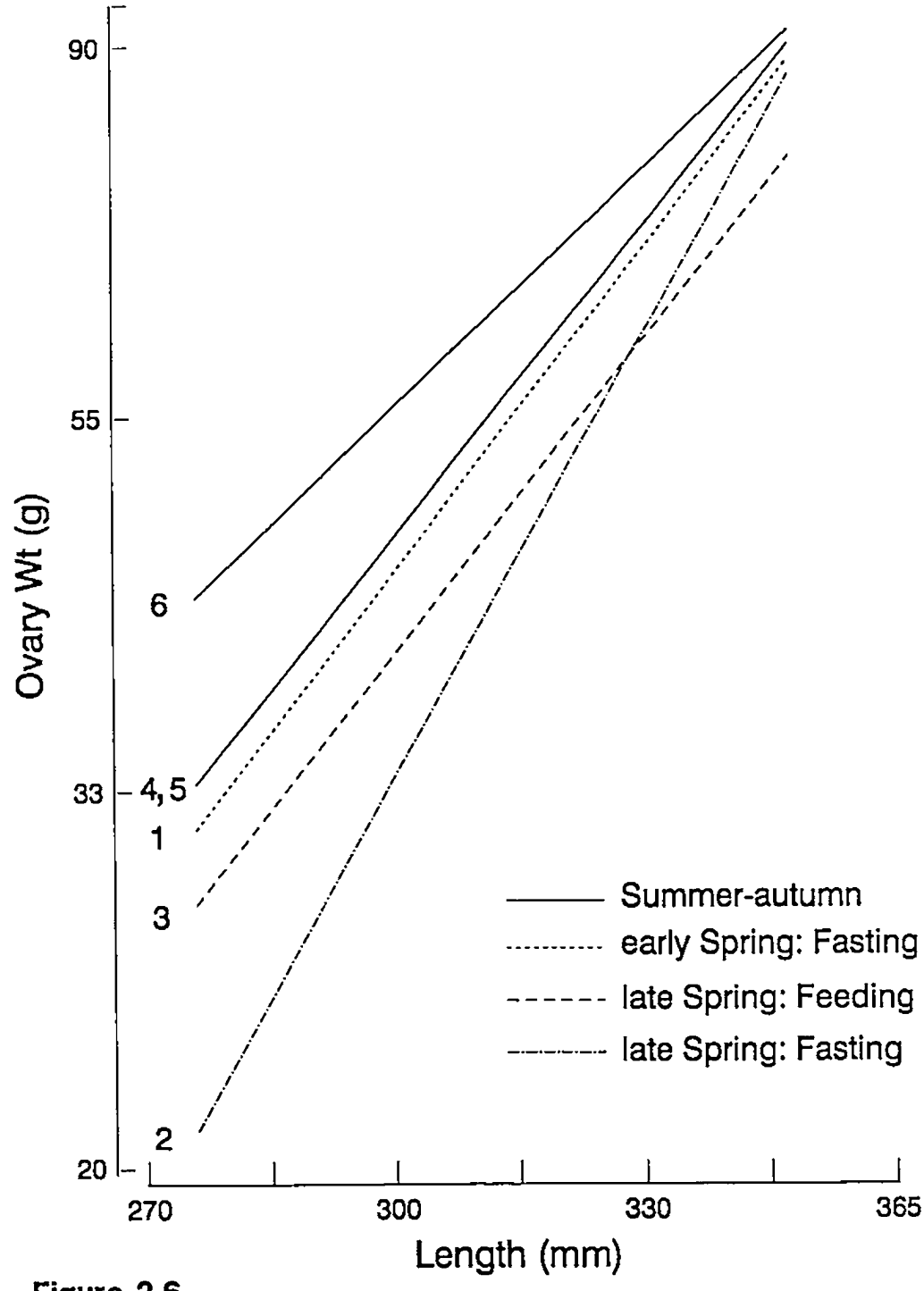
90
55
33
20
Ovary Wt (g)
6
4,5
1
3
2
Summer-autumn
early Spring: Fasting
late Spring: Feeding
late Spring: Fasting
270
300
330
365
Length (mm)

Figure 2.6

Figure 2.7. Ratios of autumn- to spring-spawning ovary weights (g) (squares) and autumn- to spring-spawning reproductive index (fecundity·egg weight (mg)) (circles) versus length (mm) for southern Gulf of St. Lawrence herring.

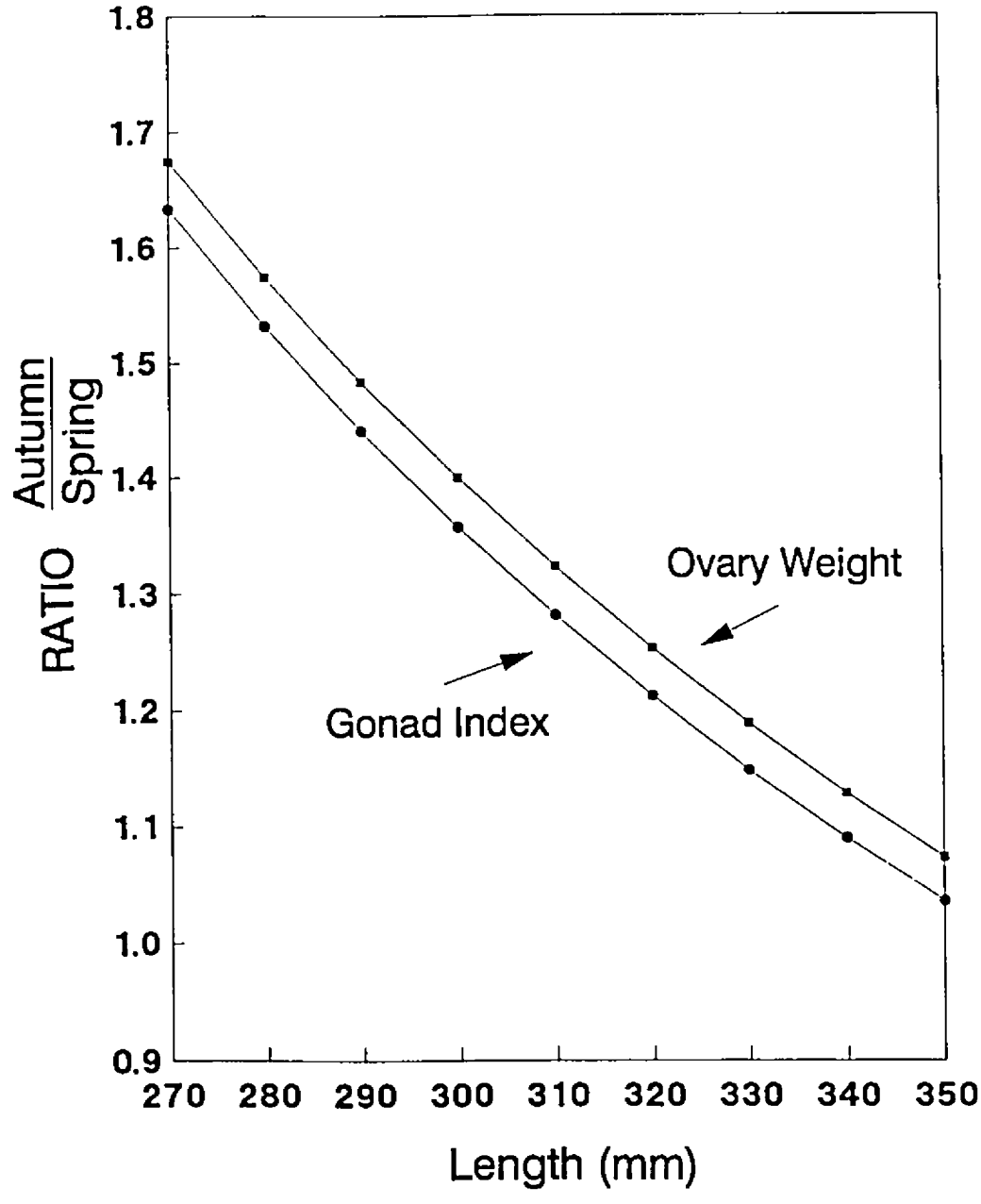
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1.0
0.9
RATIO Autumn/Spring
Ovary Weight
Gonad Index
270 280 290 300 310 320 330 340 350
Length (mm)

Figure 2.7

fecundity which also differed less extensively between southern Gulf spring- and autumn-spawning herring with length (Section 2.3.2).

The hypothesis that gonad weight, standardized to fish length, does not vary among herring populations that spawn during different seasons (Hypothesis 3) is rejected. In general, autumn-spawning herring develop heavier gonads than spring-spawning herring.

2.4 Discussion

Egg weight variability among nw Atlantic populations (1.43x) is less than one half of the egg weight variability among ne Atlantic populations (≈3.5x; Hempel and Blaxter 1967; Sinclair and Tremblay 1984). This difference is partly due to the absence from the nw Atlantic of winter-spawning populations which produce the heaviest eggs of all ne Atlantic populations (Blaxter and Hempel 1967; Almatar and Bailey 1989). For both North Sea and nw Atlantic herring, eggs weigh the least during July-August, if Baltic herring which have been treated as a discrete sub-group (possibly a sub-species; Blaxter 1958, Parrish and Saville 1965, and Blaxter 1985) are not considered in this comparison.

A salient feature of the present analysis is the

similarity in weight of spring- (late April-mid June) and autumn- (September-October) spawned nw Atlantic herring eggs (1.06x for pooled spring- and pooled autumn-spawning groups, 1.22x for mean southern Gulf spring- and autumn-spawners). These results contradict the common assumption that egg weight varies seasonally among nw Atlantic populations to a degree comparable to that for ne Atlantic herring populations (Ware 1975; Lett and Kohler 1976; Tanasichuk and Ware 1987; Winters and Wheeler 1987; Miller et al. 1988). This demonstrates that the terms 'spring-spawning' and 'autumn-spawning', which accurately summarize local spawning environments, do not embody the same physiological connotation for all populations throughout the herring's geographic range. The reproductive traits of herring from one region of the north Atlantic are not applicable to herring from other regions even when populations that spawn during the same time are compared.

The inverse correlation between fish egg weight and water temperature which is usually associated with among-population egg weight variability, including herring (Bagenal 1971; Southward and Demir 1974; Ware 1975; Markle and Frost 1985; Miller et al. 1988), does not explain the present results. Spawning temperatures differ by an average of 11 $^{\circ}$C between spring- and autumn-spawning southern Gulf herring (Appendix 2.2; Drinkwater and Trites (1988)), which is equivalent to the 11 $^{\circ}$C reported for North Sea spawnings

(Table 1 from Haegele and Schweigert 1985). However, nw Atlantic egg weight variability is less than half of that for ne Atlantic herring.

Comparisons of the length of spring- and autumn-spawned yolk-sac larvae support this interpretation. In the Bay of Chaleur (southern Gulf; Figure 2.1) both spring- and autumn-spawned larvae hatch at a length of ≈5-6mm even though water temperatures at spawning differ by as much as 10-12 °C (Jean 1956). Length at hatching is known to be strongly positively correlated with egg size (Blaxter and Hempel 1963; Miller et al. 1988; Duarte and Alcaraz 1989).

Differences in fecundity (at length) between spring- and autumn-spawning nw Atlantic herring are often assumed to reflect differences in egg weight (Ware 1975; Lett and Kohler 1976; Tanasichuk and Ware 1987; Winters and Wheeler 1987; Miller et al. 1988). This study has shown that fecundity is a poor predictor of egg size. In the southern Gulf, spring-spawned eggs are ≈22% heavier than autumn-spawned eggs (mean weights; Table 2.6) but autumn-spawning herring (320mm length) are on average ≈50% more fecund than spring-spawning herring (Table 2.5; Figure 2.4).

Both Newfoundland and southern Gulf spring-spawned eggs are heavier than sw Nova Scotia autumn-spawned eggs (by 11.4% and 6.4% respectively or ≤1.1x; Table 2.3). Predicted fecundities for Newfoundland (after Hodder 1972), southern Gulf spring (after Messieh 1976) and sw Nova Scotia autumn

(after Messieh 1976) herring are 75700, 76000, and 108800 eggs respectively for a fish 320mm in length. If gonad weight at length is assumed to be constant among populations, the expected differences in egg weights between Newfoundland and southern Gulf spring-spawners versus sw Nova scotia autumn-spawners are 43.7% and 43.1% respectively (i.e., ≈1.4x). The expected and observed differences in egg weight between spring and autumn-spawning herring are not comparable.

Differences between egg weight and fecundity in their degree of among-population variability are due to previously undocumented differences in ovary weights between-populations over a common length group (Figure 2.6). In general, gonad weight at length differs among populations on the basis of spawning season. Summer- and autumn-spawning populations have heavier ovaries, and are therefore more fecund, than spring-spawning populations. Bras D'Or Lake herring are a possible exception as their gonads are statistically as heavy as those of either the Ile Haute summer-spawners or the southern Gulf autumn-spawners (4T autumn) (Table 2.8). The ovary weight estimates for the Bras D'Or Lake group may be biased upward due to gill-net selectivity, particularly within the lower length range. However, other factors discussed below suggest the gonad weight at length data as presented for all of the populations is not spurious.

Most herring do not feed beyond the initial stages of gonad maturation (Iles 1964; Radakov 1966; Parsons and Hodder 1975; Messieh et al. 1979). Instead, storage energy is utilized to sustain all reproductive and non-reproductive functions (Iles and Wood 1965; Iles 1974, 1984; Parsons and Hodder 1975; Ackefors 1977; Winters 1977; McGurk et al. 1980; Peturson and Rosenberg 1982). This means that the relative reproductive versus non-reproductive utilization of storage energy is potentially sensitive to the duration of the maturation period. For spring-spawners, with a lengthy gonad maturation period (7-9 months, Iles 1964; Hodder et al. 1972; McQuinn 1989), non-reproductive utilization of storage energy may be greater than for autumn-spawners with a brief gonad maturation period (≤4 months, Iles 1964; Hodder et al. 1972; McQuinn 1989). These factors offer a potential explanation for why the realized reproductive effort is higher for autumn-spawners than for spring-spawners and why realized reproductive effort is higher for early spawning (April) Bras D'Or Lake herring than for populations that spawn later in the spring (May-June).

Other factors also suggest that gonad production is more limited in some populations than for others. May-June spawning Minas Basin herring, which are exceptional in that they feed intensively during the late stages of gonad maturation up to and including ovulation (Bradford 1987), produce more gonad at length than May-June spawning southern

Gulf herring which fast during the final stages of gonad maturation (Parsons and Hodder 1975; Messieh et al. 1979) (Figure 2.6; Table 2.8). Differences in gonad production between these populations are most apparent for small bodied herring (≤320mm; Figure 2.6). An inverse relation between non-reproductive utilization of storage energy during gonad maturation and body size explains similar observations for other fish species including a clupeid; American shad (*Alosa sapidissima)*, Glebe and Leggett 1981b; and a salmonid; cisco (*Coregonus artedii*), Lambert and Dodson 1990a).

This chapter shows that egg weight and fecundity vary inversely between nw Atlantic herring populations that spawn during different seasons. However, the degree of egg weight variability is less than for ne Atlantic populations (≤1.43x versus ≈3.5x). The degree of fecundity variability between spring- and autumn-spawning nw Atlantic herring (≈2x) is not fully accounted for by the seasonal inverse relation with egg weight. This is because mature gonad weight at length is not constant among nw Atlantic herring populations. Autumn-spawning herring have higher gonad weights at length than do spring-spawning herring. Differences between spring-and autumn-spawning herring in the reproductive versus non-reproductive utilization of storage energy may account for differences in gonad production between spawning seasons.

Chapter 3

Spawning Condition and Egg Weight Variability Within Spring- and Autumn-Spawning Southern Gulf of St. Lawrence Herring Populations.

3.1 Introduction

Most Atlantic herring (*Clupea harengus harengus* L.) do not feed once their gonads develop beyond the initial stages of maturation (Iles 1964, 1965, 1984; Shatunovskiy 1970; Parsons and Hodder 1975; Messieh et al. 1979; Crawford 1980; Linko et al., 1985). Instead, previously accumulated somatic stores of lipid and protein are used to fulfil metabolic needs during gonad maturation (Iles 1964, 1974, 1984; Ackefors 1977; Love 1980; McGurk et al. 1980; Peturson and Rosenberg 1982; Wallace 1986). Herring of the same size from different populations store similar quantities (by weight) of both lipid and protein prior to the onset of gonad maturation regardless of spawning season (Iles and Wood 1965; Stoddard 1968; Hodder et al. 1973; Varga et al. 1977; McGurk et al. 1980; Iles 1984). Consequently, the quantity of energy allocated to reproduction is considered to be the same among populations (Mann and Mills 1979).

This interpretation may, however, be incorrect because the relative duration of fasting and gonad maturation differs among populations (Iles 1965). Gonad maturation is accomplished in 7-9 months by spring-spawning herring but is accomplished in <4 months by summer- and autumn-spawning herring (Iles 1964; Parson and Hodder 1975; Iles 1964, 1984;

Bradford 1987; McQuinn 1989). This suggests that the length of time herring rely on somatic reserves for both their reproductive and non-reproductive energy requirements differs among spawning seasons. Whether non-reproductive utilization of storage energy during gonad maturation affects herring reproductive characters is not known. However, herring remain active (e.g. migration, schooling, predator avoidance) during gonad maturation (Winters 1977; Sinclair and Iles 1985) so the total energy cost to the fish during gonad development could vary among populations. This could explain why herring with brief maturation periods (autumn-spawners) have heavier gonads than herring with long maturation periods (spring-spawners) (Chap. 2).

Reproductive versus non-reproductive utilization of storage energy during gonad maturation affects gonad weight at length in other fish species, including clupeids. Gonad weight at length varies among populations of American shad (*Alosa sapidissima*) that migrate different distances from the sea to spawn (Glebe and Leggett 1981a,b). Similarly, both the relative reproductive effort and somatic cost of reproduction differ between sympatric species of cisco (*Coregonus artedii*) and lake whitefish (*C. clupeaformis*) (Lambert and Dodson 1990b), and sympatric species of alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*) (Crawford et al. 1986). In all of these species the non-reproductive energy cost was greater for small fish than

large fish, i.e., the proportion of the total surplus somatic energy allocated to gonad generally increased with fish length within populations.

Herring reproductive characters other than gonad weight at length may also be influenced by the relative allocation of energy to reproductive versus non-reproductive functions. For some North Sea populations, recruit herring (first time spawning) have lighter weight eggs than repeat spawning herring (Hempel and Blaxter 1967). Since recruit herring tend to be small bodied, their total reproductive investment may be proportionally less than for repeat spawning herring, thereby leading to reduced egg weights. However, this possibility requires verification through analyses of how spawning condition varies within and among populations.

The variation of egg weight within populations through time also needs to be examined. Decreases in egg weight with time have been linked to both increasing water temperature and changes in the relative proportions of recruit versus repeat spawners in Pacific herring (*Clupea harengus pallasi*) (Tanasichuk and Ware 1987; Ware and Tanasichuk 1989). Temperature does not appear to extensively influence egg weight in nw Atlantic herring (Chapter 2), but the analysis relied upon comparisons of average environmental conditions between the spring- and autumn-spawning seasons and did not consider how egg weight

varied with time within populations.

This chapter evaluates: a) whether the physiological condition of herring at spawning differs between populations with gonad maturation periods of differing duration; and b) whether among-population variability in egg weight and gonad weight at length is linked to variability in spawning condition. Both analyses assume that the fraction of stored somatic energy consumed by non-reproductive processes is directly proportional to the duration of the pre-spawning periods of fasting and gonad maturation. Since direct methods cannot be applied (samples are only available during the spawning period) the procedure compares and contrasts the physiological condition of spring- and autumn-spawning herring at spawning. Because nw Atlantic herring which spawn during different seasons have the same capacity to store surplus energy (see references above), their spawning condition should provide an indication of the relative expenditure of somatic energy by each group.

The following four hypotheses are tested in this chapter.

1) Physiological condition, as measured by somatic lipid indices of fully mature (spawning) herring, does not differ between spring- and autumn-spawning herring.

2) Spawning condition, as measured by somatic lipid indices, does not vary as a function of body size within populations.

3) Mean egg weight does not vary within populations through time.

4) Egg weight is unrelated to the spawning condition of the parent.

3.2 Materials and Methods

3.2.1 Somatic Condition of Fully Mature Spring- and Autumn-Spawning Herring

Sampling Protocol

Spring- and autumn-spawning herring populations from the southern Gulf of St. Lawrence ('southern Gulf' or NAFO Sub-Region '4T') were used for analysis. The location of their respective spawning grounds are well-documented (Ware and Henriksen 1978; Messieh 1987; Messieh 1988), and fisheries currently harvest spawning aggregations of both spring- and autumn-spawning herring (Messieh 1987), permitting samples from both populations. In addition, the general features of the life-histories of these populations are well documented (Messieh and Tibbo 1971; Parsons and

Hodder 1975; Messieh 1976).

Random samples of commercially gill-netted herring were collected during May in the vicinity of Seacow Pond, P.E.I. (Figure 3.1) and during August-September from Fishermans Bank, P.E.I. (Figure 3.1) for the years 1987, 1988, and 1989. Fish that freely extruded either eggs or milt (i.e., spawning, Stage 6; Table 2.1) were retained. Sampling during spring 1988 was extended over the entire period during which spawning herring were encountered (May 9 - May 24). Collections were made at ≈4 day intervals to provide a basis to assess the change in age distribution, length at age, somatic condition and egg weight over the course of the spring-spawning period. The number of collections per population and the number of fish of each sex retained per collection are summarized in Table 3.1.

Gill net mesh-sizes differed between the spring- and autumn-herring fisheries but for each fishery the range in mesh sizes was relatively narrow (spring, 2 1/8"-2 5/8"; autumn, 2 1/2"-3"). These factors could potentially bias the size frequency distributions of random samples as gill net selectivities are a function of body girth (Hamley 1975; Winters and Wheeler 1990). However, many herring are captured non-selectively in nets via entanglement around the mouth, operculum, and fin areas (Winters and Wheeler 1990; pers. ob.). Therefore, fish which were either ≥340mm or ≤290mm were retained for further analysis and kept separated

Table 3.1. Summary table showing total samples retained (n), number of somatic water and somatic lipid determinations, and egg dry weights for spring- and autumn-spawning southern Gulf of St. Lawrence herring by year, and sex.

Year	Date of Sampling	Sex	n	Water	Lipid	Egg Wt
1987	May 17	Male	42	37	37	---
		Female	39	37	37	37
	May 18	Female	54	0	0	0
	May 19	Male	45	0	0	---
		Female	48	10	10	20
	Aug 28	Male	39	39	39	---
		Female	40	40	40	40
	Sept 6	Male	63	40	40	---
		Female	57	38	38	38
1988	May 9	Female	16	9	9	9
	May 15	Female	77	38	38	48
	May 19	Male	28	0	0	---
		Female	63	40	40	40
	May 20	Male	26	0	0	---
		Female	57	0	0	40
	May 21	Male	15	0	0	---
		Female	20	0	0	40
	May 23	Male	42	0	0	---
		Female	43	0	0	33
	May 24	Male	4	0	0	---
		Female	37	37	37	37
	Sept 15	Male	36	36	0	---
		Female	47	43	0	47
1989	May 13	Female	85	68	0	85
	Sept 5	Female	98	61	0	98

Figure 3.1. Map of nw Atlantic region showing the locations of sampling for proximate composition analysis of fully mature spring- and autumn-spawning herring.

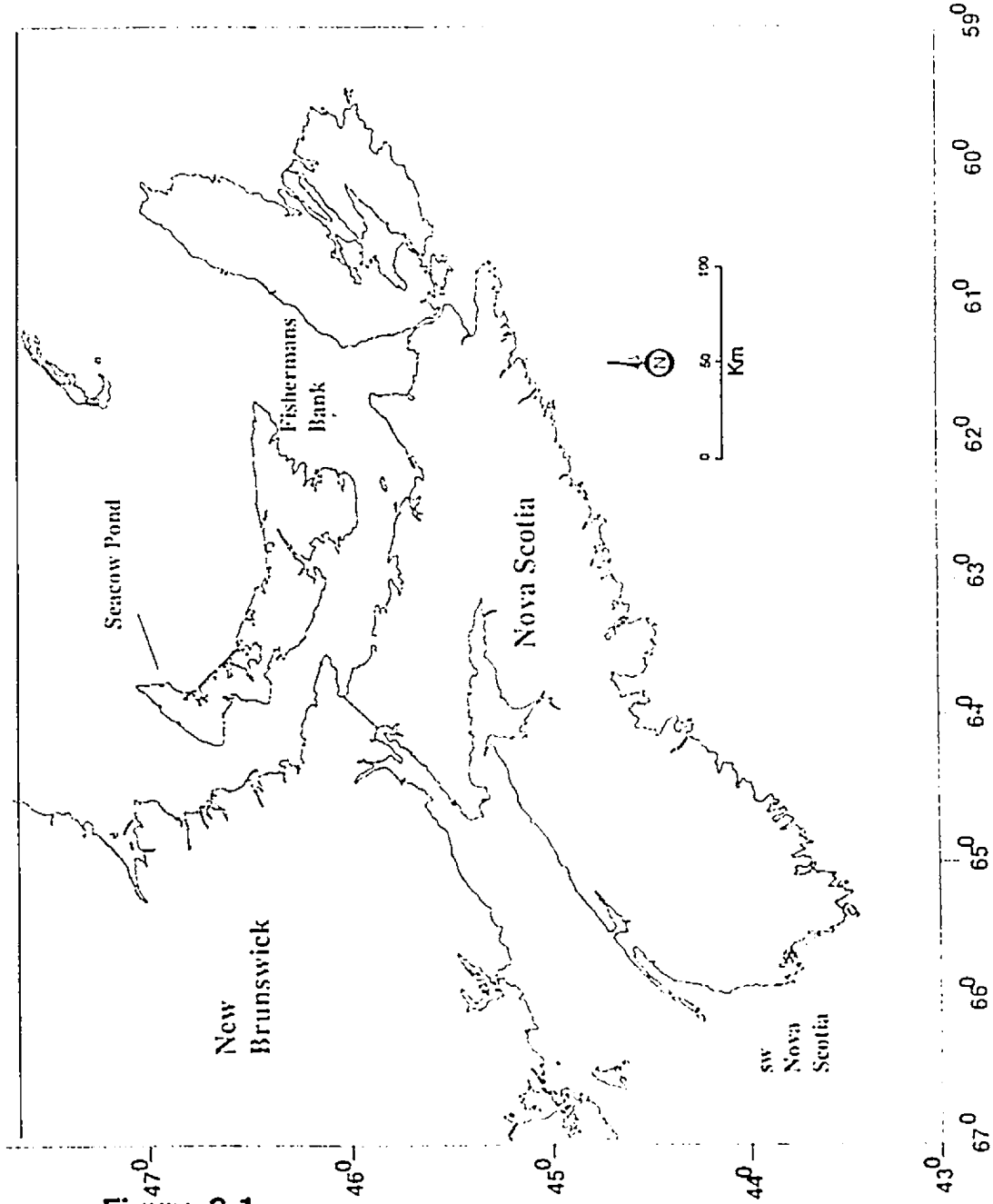
Seacow Pond
Fishermans Bank
Nova Scotia
New Brunswick
SW Nova Scotia
100
50
0
Km
N
47°
46°
45°
44°
43°
67°
66°
65°
64°
63°
62°
61°
60°
59°

Figure 3.1

from the random samples.

Samples were immediately packed on ice. Total length (mm) and total weight (0.1g) was measured for each fish within 4h. Fresh samples of extruded eggs were stripped directly into vials of Gilsens solution. A sample of the scales from the side of the fish, in the region just above the last half of the pectoral fin was removed for aging. Fish were individually wrapped in plastic bags and frozen at -25°C.

Preparation of Samples

Batches of 20-30 individual fish were removed from the freezer and packed in ice for a period of 12 hours to minimize moisture loss. Each was remeasured to total length and total weight to determine shrinkage due to freezing. The pair of sagittal otoliths was excised, cleaned in warm water and mounted in black trays. These were used to verify the scale-determined fish ages. Fish were sexed, the degree of gonad maturation assessed following the Herring Gonad Maturity Scale recommended by ICES (Anon. 1962; Table 2.1), and the gonad weighed (0.01g).

To prepare the fish for lipid and water analysis, the visceral cavity was opened, all food items were noted, the food items and gonads were removed, and the remaining tissue was diced and blended to a uniform consistency. The gonads

and resulting paste were placed in separate plastic bags and re-frozen at -25 °C. Similar procedures of sample preparation for lipid and moisture content analysis have been shown to provide reliable results for other closely related clupeid fishes (American shad (*Alosa sapidissima*), Glebe and Leggett 1981a,b; Alewife (*A. pseudoharengus*), Flath and Diana 1985; Crawford et al. 1986, and Blueback herring (*A. aestivalis*), Crawford et al. 1986).

Analysis of Somatic Lipid and Somatic Moisture

Moisture content of the tissues of each fish was determined for 2 sub-samples of 20-30g wet weight. Each subsample was dried at 80°C for 48 hours, cooled in a desiccator to room temperature, then reweighed. Percent moisture of the tissues was calculated as [(wet wt -dry wt) ÷ (wet wt)]·100. Differences in percent moisture between sub-samples were <2%. Both sub-samples were combined, ground to a fine powder with a pestle, and stored (for <1h) in a desiccator.

Lipid extraction proceeded using the Korn and Macedo (1973) solvent-column extraction procedure as modified by Meerburg (1975). This procedure provides estimates of the total extractable lipid which are comparable to those obtained using other commonly used procedures (Korn and Macedo 1973; Meerburg 1975). Extractions were conducted at

a constant temperature of 10°C. Ten grams of anhydrous sodium sulphate (Na_2SO_4) were added through the top of each of 10 chromatography columns (Dimensions: 19mm diameter, 500mm length). The dried ground tissue for each fish was mixed with 20g Na_2SO_4 and added through the top of the column, followed by a further 10g of Na_2SO_4, and then 35ml of reagent grade 1,2 trichloroethane. The extract was collected in pre-weighed beakers one hour later and the lipid was concentrated by heating at 40°C, under a fume hood, until the solvent had completely evaporated (<3h), and then reweighed.

Percent total extractable lipid (referred to from here on as percent lipid) was determined from the wet somatic tissue weights (g) and lipid weight (g) for each sub-sample as [lipid wt ÷ total wt]·100. The between sub-sample difference was 3-6%. The relation between % lipid and % water was determined via linear regression using samples with <3% variability between subsample estimates of lipid weight. Samples outside the 95% confidence interval for this regression were discarded.

Samples collected during 1989 were analyzed only for total water, and lipid predicted from the %lipid - %water relations established from the previous years samples. The dates of sampling, number of samples collected, and the analysis performed on each are summarized in Table 3.1.

The somatic lipid (%) and somatic moisture (%) content

of spawning southern Gulf herring were compared with data collected by Dr. T.D. Iles (DFO, St. Andrews, N.B.) for both maturing (Stages 4 and 5; Table 2.1) and spawning southwest (sw) Nova Scotia (NAFO Sub-Region 4WX) herring. The sampling protocol and analytical procedures for these data (detailed in Varga et al. (1977)) provide results comparable to the solvent-column lipid extraction procedure (Korn and Macedo 1973).

3.2.2 Relation Between Egg-Weight, Female Lipid Content, and Spawning Time

Average egg dry weight (referred to from here on as egg weight) per female was used as a measure of egg quality. The procedures used to determine egg weight (mg) were previously described in Chapter 2. Single and multiple regression analysis of egg weight versus the biological variables measured and time of collection was used as a basis to test for parental effects on egg quality.

3.3 Results

3.3.1 Somatic Condition of Fully Mature Spring- and Autumn-Spawning Herring.

Somatic lipid (%) was significantly and predictably ($r^2 \geq 0.92$) inversely correlated with somatic water (%) for both spawning and maturing herring (Table 3.2; Figure 3.2). The relations for spawning and maturing sw Nova Scotia (4WX) herring differed significantly ($P < 0.01$; Table 3.3a). For the other populations of spawning herring (4T and 4WX) the intercepts of the %lipid - %water relations differed ($P < 0.001$) between populations whereas the slopes did not vary (Table 3.3b).

Because neither somatic lipid (%) nor somatic moisture (%) differed between male and female spawning southern Gulf herring within populations (Table 3.4; Table 3.5), these data were pooled. On average, spawning herring were in poorer condition during the spring season than during the autumn season. Somatic moisture (%) was higher and somatic lipid (%) was lower for spawning spring-herring than for spawning autumn-herring (Table 3.4; Figure 3.3), but neither variable differed within-populations between years (Table 3.5).

Spawning condition, as measured by somatic lipid (%), increased weakly but significantly ($P \leq 0.05$) with fish length for southern Gulf spring-spawners but did not vary with length for southern Gulf autum..-spawners during both

Table 3.2. Linear regression parameters and standard errors (SE), year of sampling (Year), sample size (n), and coefficient of determination (r^2) for % somatic lipid - % somatic water relations estimated for southern Gulf (4T), sw Nova Scotia (4WX; from Iles (unpub. data) and North Sea (Iles and Wood 1965) herring (Model: %Lipid = a + b·%Water).

Group	Maturity	Year	a(95%CI_a)	b(95%CI_b)	n	r^2	P
4T	Spawning	1987	90.23(3.21)	-1.16(.04)	209	.93	.01
	Spawning	1988	90.51(1.89)	-1.16(.04)	204	.92	.01
4WX	Spawning	1975	92.25(1.66)	-1.16(.06)	132	.94	.01
	Maturing	1975	89.28(1.87)	-1.12(.02)	591	.94	.01
North Sea	Mature	1958	88.86	-1.12	276	.99	.01
	All	1958	90.45	-1.14	895	.99	.01

1: Standard errors of the slopes and intercepts were not reported by Iles and Wood (1965).

2: Data for mature (Stage 5; Table 2.1) and ripe and running (Stage 6; Table 2.1) herring were combined and reported as 'mature'by Iles and Wood (1965).

Table 3.3. ANCOVA for somatic lipid (%) between a) spawning and maturing sw Nova Scotia herring and b) spawning southern Gulf and sw Nova Scotia herring with somatic water (%) as the covariate (Gonad: either spawning or maturing herring).

Source of Variation	df	Sums of Squares	Mean Squares	F	P
a)[1]					
Gonad	1	5.71	5.71	6.62	0.01
%Water	1	10225.20	10225.20	11859.45	<0.001
Error	720	620.78	0.86		
b)					
Intercepts	1	189.39	189.38	318.94	<0.001
Error	338	200.70	0.59		
Slopes	1	0.25	0.25	0.42	N.S.
Group	337	200.45	0.60		

1: Model %Lipid= 89.57 - 1.121·%Water - 0.12·Gonad r^2= .95

Table 3.4. Percent somatic water and percent somatic lipid (1 standard deviation in parentheses) for male, female, and combined sexes for spring- and autumn-spawning southern Gulf (4T) herring sampled during 1987-1989 inclusive, and for sw Nova Scotia (4WX) autumn-spawning herring sampled during 1975 (*: 189 lipid determinations, a: 79 lipid determinations).

Year	Group	Sex	n	%Water	%Lipid
1987	4T Spring	M	37	72.06(2.30)	5.84(2.31)
		F	37	71.08(1.75)	7.25(1.88)
		M+F	74	71.57(2.09)	6.54(2.21)
	4T Autumn	M	35	67.14(2.15)	12.19(2.40)
		F	36	67.42(2.61)	12.29(2.76)
		M+F	71	67.28(2.40)	12.24(2.59)
1988	4T Spring	M	--	----	----
		F	127	71.55(2.36)	8.13(3.32)
		M+F	--	----	----
	4T Autumn	M	36	66.24(2.87)	12.17(3.27)
		F	43	66.06(2.68)	12.38(3.10)
		M+F	79	66.14(2.77)	12.29(3.19)
1989	4T Spring	M	--	----	----
		F	68	70.08(3.52)	----
		M+F	--	----	----
	4T Autumn	M	--	----	----
		F	60	66.50(2.11)	----
		M+F	--	----	----
All	4T Spring	M	37*	72.06(2.30)	5.84(2.31)
		F	258*	70.77(2.63)	8.39(2.35)
		M+F	295	70.93(2.59)	7.98(2.34)
	4T Autumn	M	71a	66.68(2.58)	12.18(2.92)
		F	140a	66.60(2.49)	12.36(2.98)
		M+F	211	66.63(2.52)	12.26(2.95)
1975	4WX	M	77	69.61(3.42)	11.17(3.69)
		F	62	69.54(3.21)	11.62(3.73)

Table 3.5. The F-ratio, degrees of freedom (df), F probability (P), and coefficient of determination (r^2) for Oneway and Twoway ANOVA of somatic lipid and somatic water content treated with sex, year of sampling, and spawning group for southern Gulf spring-, and autumn-spawning herring.

Season	Year	Variable	Treatment	F-Ratio	df	P
ONEWAY						
Spring	1987	%Water	Sex	0.004	1,134	0.95
		%Lipid	Sex	0.003	1,134	0.96
Autumn	1987	%Water	Sex	0.247	1, 69	0.62
		%Lipid	Sex	0.023	1, 69	0.88
Autumn	1988	%Water	Sex	0.081	1, 77	0.77
		%Lipid	Sex	0.080	1, 77	0.78
TWOWAY		%Water	Season	287.579	1	<0.001
			Year	1.818	2	0.16
			Sea•Yr	13.476	536	<0.001
TWOWAY		%Lipid	Season	226.681	1	<0.001
			Year	0.357	1	0.55
			Sea•Yr	9.640	409	<0.005

Figure 3.2. Relationship between % somatic lipid and % somatic water for spring (squares)- and autumn (triangles)-spawning southern Gulf of St. Lawrence (4T) herring.

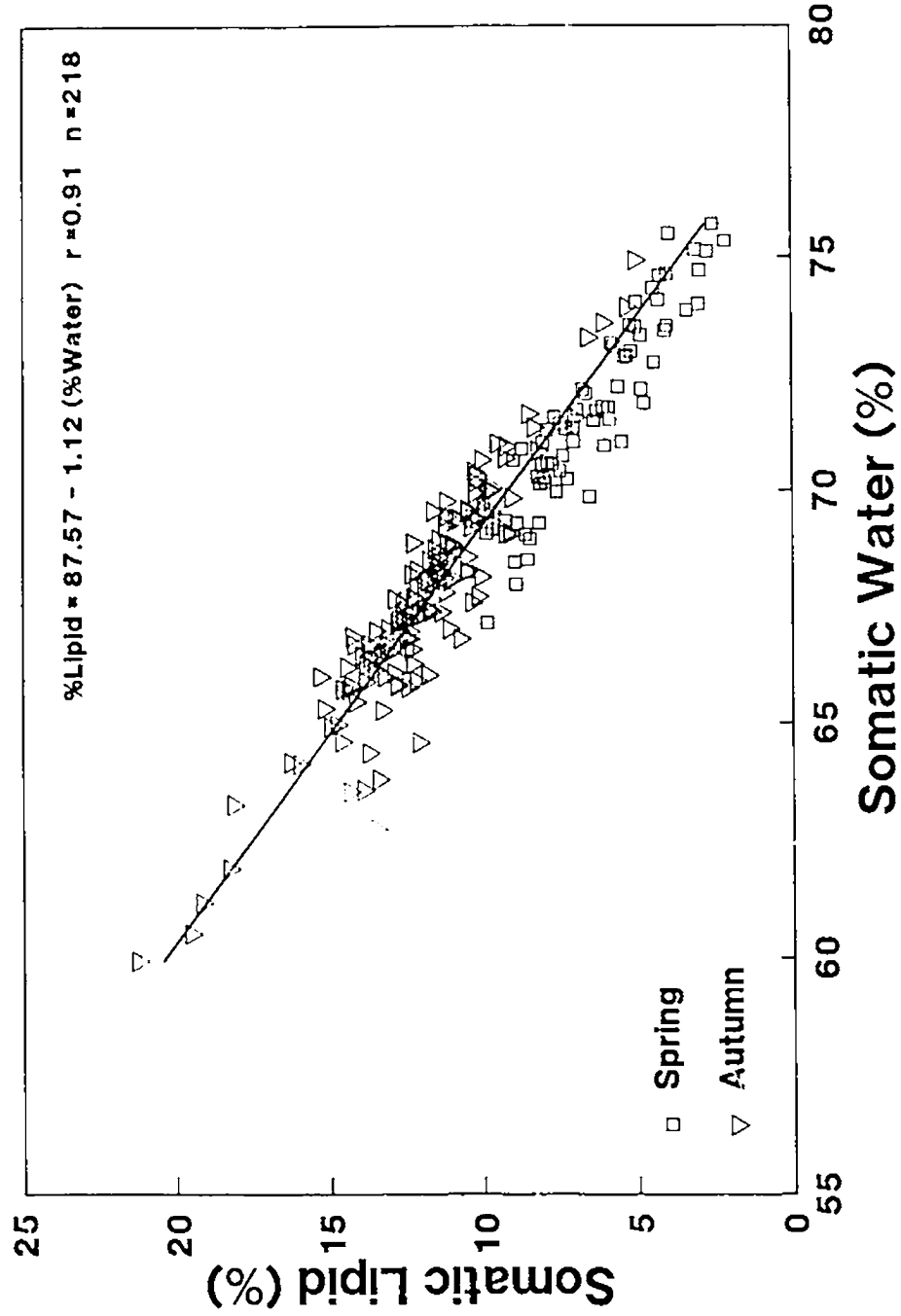
%Lipid = 87.57 - 1.12 (%Water) r =0.91 n =218
Somatic Lipid (%)
Somatic Water (%)
Spring
Autumn
0
5
10
15
20
25
55
60
65
70
75
80

Figure 3.2

Figure 3.3. Scatterplots of percent somatic lipid versus fish length (mm) for ripe and running female spring- (squares) and autumn- (crosses) spawning southern Gulf of St. Lawrence (4T) herring.

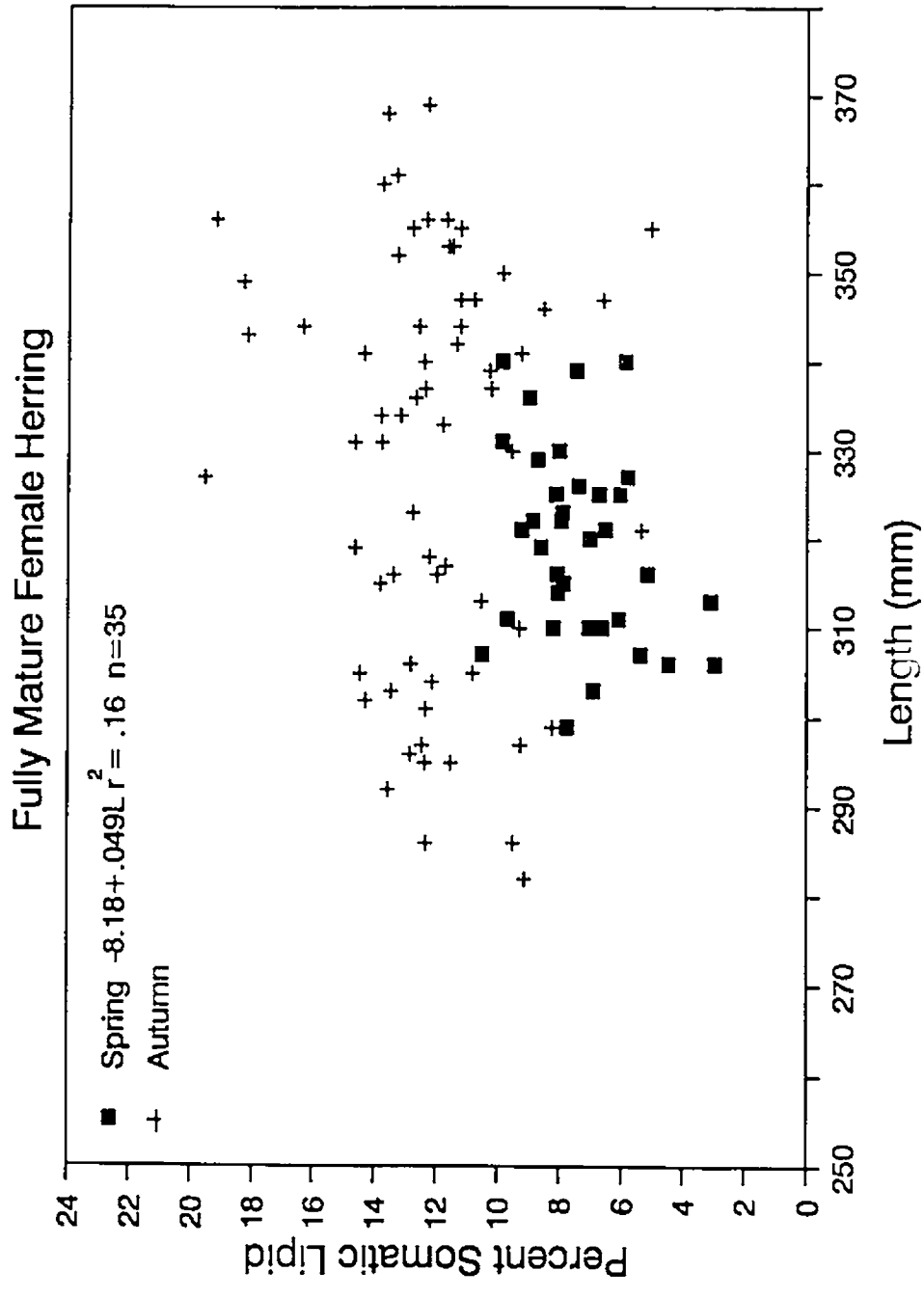
Fully Mature Female Herring
Spring -8.18+.049L r = .16 n=35
Autumn
Percent Somatic Lipid
Length (mm)
0
2
4
6
8
10
12
14
16
18
20
22
24
250
270
290
310
330
350
370

Figure 3.3

1987 and 1988 (Table 3.6; Figure 3.3). Similar between-population differences are inferred for 1989 since somatic water (%), which is inversely related to somatic lipid (%) (Table 3.3), decreases weakly with fish length for spring-spawners but shows no relationship with length for autumn-spawners (Table 3.6). Spawning condition, as measured by somatic weight minus somatic lipid weight (g) at length, also differed between spring- and autumn-spawning southern Gulf herring (Table 3.6, Figure 3.4; ANCOVA Year =1987, df= 1, 169, F =52.36, P <0.001 and df= 1, 168, F= 2.63, P >0.05 (intercepts and slopes respectively); ANCOVA Year = 1988, df =1, 204, F =226.96, P <0.001 and df =1, 203, F =8.89, P <0.01 (intercepts and slopes respectively)).

Collectively these results show that autumn-spawning herring with a brief gonad maturation period are in better physiological condition (as measured by both %somatic lipid and lipid free somatic weight) at all lengths than are spring-spawning herring with a long gonad maturation period. The hypothesis that physiological condition does not differ between spring- and autumn-spawning herring is rejected (Hypothesis 1). For populations with long maturation periods small herring have relatively less somatic lipid than large herring. The hypothesis that spawning condition does not vary as a function of body size within populations is also rejected (Hypothesis 2).

Table 3.6. Linear regression statistics of somatic lipid (%), somatic water (%), and somatic weight minus somatic lipid (Som-Lip)(g) versus fish length (mm) for spring- and autumn-spawning southern Gulf herring (Years 1987-1989; Model, Y = a + b·Length).

Season	Year	Y	a	b	n	r^2	P
Spring	1987	%Lipid	-8.18	0.05	35	.16	<.02
Spring	1988	%Lipid	-6.54	0.04	127	.09	<.01
Spring	1989	%Water	81.33	-.04	65	.06	<.05
Spring	1987	Som-Lip	-448.46	2.15	41	.75	<.001
	1988	Som-Lip	-525.68	2.37	131	.79	<.001
Autumn	1987	%Lipid	----	----	65	.01	>.50
	1988	%Lipid	----	----	77	.04	.10
Autumn	1989	%Water	----	----	61	.03	.20
Autumn	1987	Som-Lip	-546.02	2.54	131	.89	<.001
	1988	Som-Lip	-625.52	2.80	77	.89	<.001

Figure 3.4. Relationships between somatic weight minus somatic lipid weight and fish length for fully mature spring- (squares) and autumn- (crosses) spawning southern Gulf of St. Lawrence (4T) herring.

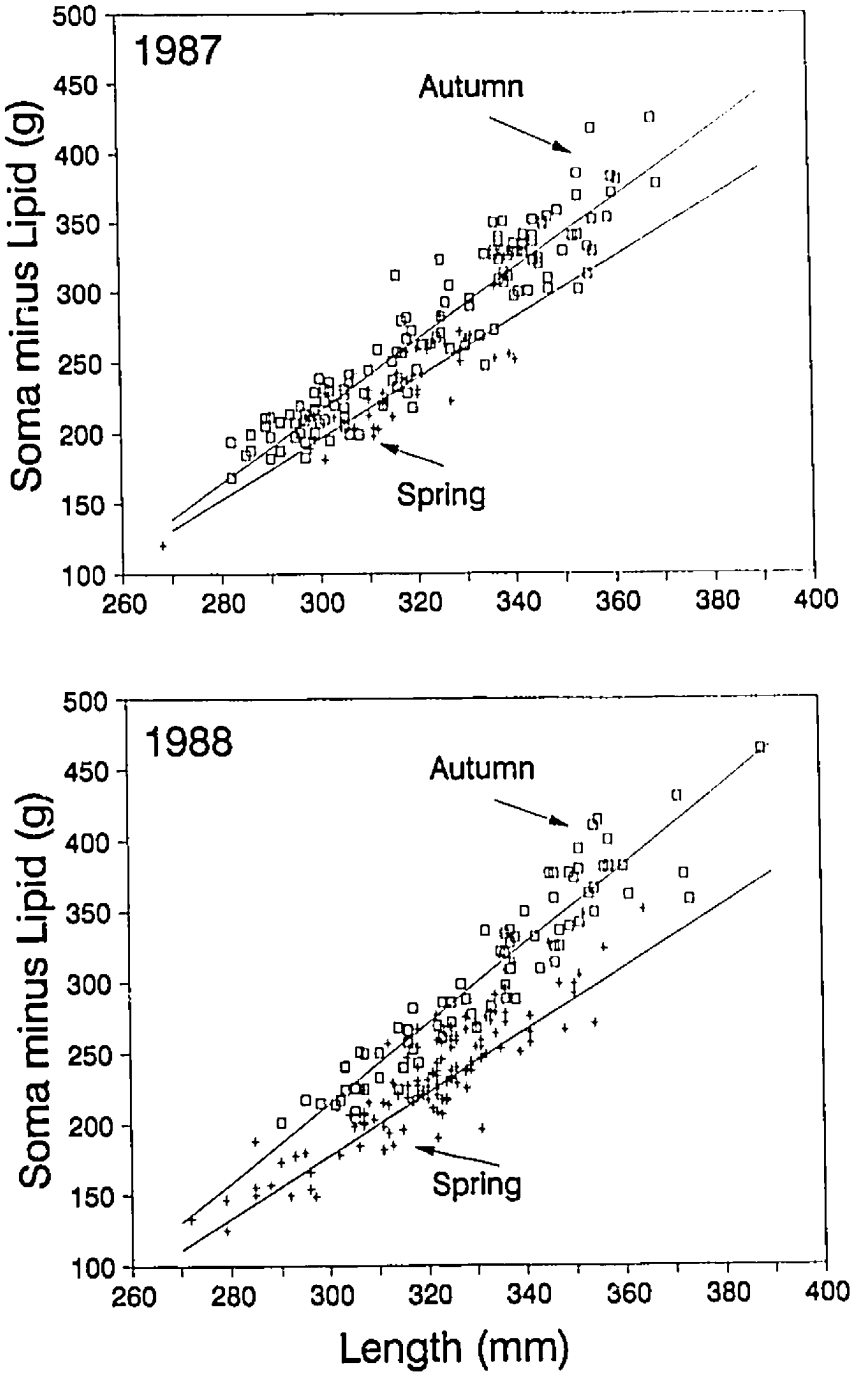
1987
Autumn
Spring
Soma minus Lipid (g)
500
450
400
350
300
250
200
150
100
260
280
300
320
340
360
380
400
1988
Autumn
Spring
Soma minus Lipid (g)
Length (mm)

Figure 3.4

3.3.2 Relation Between Egg-Weight, Female Lipid Content, and Spawning Time

Weak ($r^2 \leq 0.16$; Table 3.7), but significant declines in egg weight with time were evident within individual age classes of southern Gulf spring-spawning herring. However, factors other than day of spawning appeared to be responsible for changes in egg weight with time. For herring aged 3-5 years egg weight increased with length within age classes but length-at-age decreased with time (Table 3.7). For age 6 and older herring egg weight did not vary with length within age classes nor did length at age vary with time (Table 3.7). These patterns suggested that egg weight variability within-populations was a consequence of changes in the relative proportion of recruit spawners (ages 3-5; Chadwick and Claytor 1989) versus repeat spawners (age ≥6) with time. Because length at age decreased with time for recruit aged herring, the effect of body size on egg weight was more pronounced with time. The hypothesis that mean egg weight does not vary within-populations with time (Hypothesis 3) is therefore rejected.

Female condition, as measured by %somatic lipid, lipid free somatic weight, and %somatic water, did not appear to influence mean egg weight ($P > 0.10$; data not shown). Date of capture and fish length were the only variables which significantly covaried with egg weight as shown from multiple regression analysis (Table 3.8). The hypothesis

Table 3.7. Regression statistics for length (mm) versus date of capture, egg weight (mg) versus date of capture and egg weight (mg) versus length (mm) for spring-spawning southern Gulf herring by age class (years).

Age	Y	X	a(95%CI$_a$)	b(95%CI$_b$)	n	r^2	P
3	Length	Date	303(10)	-1.10(.50)	6	.90	.01
4			310(27)	-0.85(1.38)	15	.13	.19
5			337(19)	-1.35(1.05)	28	.21	.01
6			324(6)	0.22(.34)	86	.02	.19
7			356(22)	-0.93(1.11)	47	.06	.10
8			368(38)	-0.99(1.79)	19	.07	.26
9			337(77)	0.88(3.64)	10	.04	.60
3	Egg Weight	Date	1.911(.411)	-0.01(.06)	6	.09	>.40
4			2.048(.538)	0.00(.04)	15	.01	>.50
5			2.495(.299)	-0.02(.02)	28	.16	.05
6			2.343(.377)	-0.01(.02)	85	.08	.01
7			2.794(2.526)	-0.03(.02)	47	.12	.01
8			2.554(.456)	-0.02(.04)	19	.04	>.40
9			1.540(.389)	0.03(.06)	10	.11	>.20
All			2.380(.433)	-0.01(.02)	210	.05	.01
3	Egg Weight	Length	-2.422(.380)	.015(.03)	6	.22	>.20
4			-3.179(.469)	.018(.02)	15	.24	.05
5			-0.537(.276)	.009(.01)	28	.29	.01
6			2.278(.394)	.000(.05)	85	.01	>.40
7			0.508(.534)	.005(.01)	47	.04	.20
8			0.623(.458)	.005(.01)	19	.04	>.20
9			3.891(.399)	-.005(.02)	10	.06	.50
All			0.931(.424)	.004(.002)	210	.09	.01

Table 3.3. Multiple regression analysis of egg weight (mg) versus fish length (mm) and day of capture for samples obtained during 1988 for samples of known somatic condition (see text) (n=129) and all samples (n=210)(95%CI =(5% Confidence interval; t =t-statistic). b) ANOVA for each regression.

a)

Dependent Variable	Coefficient (95%CI)	t	P	r^2	Δr^2
n=129					
Constant	1.059(.511)	2.971	0.004	---	---
Length	0.004(.002)	3.798	<0.001	.083	.074
Day	-.015(.008)	-3.346	0.001	.157	
n=210					
Constant	1.142(.511)	4.406	<0.001	---	---
Length	0.004(.002)	4.989	<0.001	.091	.061
Day	-.015(.008)	-3.848	<0.001	.152	

b)

Source of Variation	Sums of Square	df	Mean Square	F	P
n=129					
Regression	1.009	2	0.504	11.78	<0.001
Residual	5.400	126	0.043		
n=210					
Regression	1.600	2	0.800	18.49	<0.001
Residual	8.955	207	0.043		

that egg weight is unrelated to the spawning condition of the parent (Hypothesis 4) cannot be rejected.

3.4 Discussion

In both relative (% somatic lipid) and absolute (lipid free somatic weight) terms, autumn-spawning herring are in better physiological condition, at all lengths, than are spring-spawning herring. A relationship between spawning condition and body size is apparent only for herring with long maturation periods (spring-spawners; Table 3.6, Figure 3.3). These patterns indicate that the duration of the maturation period determines, in part, the relative proportion of stored somatic energy that is allocated to reproductive versus non-reproductive functions during gonad maturation. This offers an explanation for the patterns of variability in gonad weight both within and among nw Atlantic herring populations (Chapter 2). Apparently, herring are subject to the same patterns of energy allocation to reproductive and non-reproductive functions during gonad maturation as are anadromous fishes (e.g., American shad (Glebe and Leggett 1981a,b), alewife (Flath and Diana 1985), cisco and lake whitefish (Lambert and Dodson 1990a)).

The lack of a basis to distinguish recruit herring from repeat spawning herring for nw Atlantic populations,

other than the certainty that sexually mature 3-year-old herring are first time spawners (Sinclair et al. 1982) limits the explanatory power of the present analysis. This may have obscured a relationship between egg weight and female spawning condition, which has been shown for another pelagic temperate marine fish (capelin, *Mallotus villosus*; Chambers et al. 1989), but was not evident for herring (Table 2.8). Further research is required in order to resolve whether recruit and repeat spawning herring differ physiologically at full maturity.

Despite the inability to discriminate between recruit and repeat spawning herring, strong circumstantial evidence indicates that the spawning history of herring affects egg quality. Egg weight was most strongly positively correlated with length in the age classes during which partial recruitment to the adult population is most pronounced (ages 3-5; Sinclair et al. 1982; Chadwick et al. 1989)(Table 3.7). The decline in fish length with date of sampling was also most pronounced for the partially recruited age classes (Table 3.7). Collectively these results indicate that recruit herring produce relatively small eggs and that spawning aggregations become increasingly comprised of recruit herring as the spawning season progresses. These factors, which account for changes in mean egg weight with time for southern Gulf spring-spawners, have also been demonstrated for other populations. Recruit herring from

many North Sea populations produce lighter eggs than do repeat spawning herring (Hempel and Blaxter 1967, Krivobok et al. 1970, and Almatar and Bailey 1989). Lambert and Messieh (1989) concluded from an analysis of the age frequency distributions of southern Gulf of St. Lawrence spring- and autumn-spawning herring, that the proportion of recruit herring increases with time during the spawning season.

It is generally believed that survivorship favours large larvae from large eggs (see reviews of early larval survival tactics by Parrish and Saville 1965; Blaxter and Hempel 1966; Hempel 1979; Blaxter and Hunter 1982; Rothschild 1986). Neither the decription of nw Atlantic herring reproductive traits (Chapter 2) nor the analysis of herring spawning condition (this chapter) support this view. Spring-spawned eggs do not increase substantially in weight as proportionally more stored somatic energy becomes surplus to non-reproductive functions, with increased body size. Egg number appears to be favoured over egg quality, an interpretation supported by observations (Chapter 2) that gonad weight at length increases as proportionally more energy becomes available. This energy comes from either a shortening of the gonad maturation time, increasing body size within-populations, and possibly even through active foraging during gonad maturation (e.g., Minas Basin). The increase in energy for support of non-reproductive functions

could explain why differences in gonad weight, absolute fecundity, and reproductive index (egg wt·absolute fecundity) between spring- and autumn-spawning southern Gulf herring decrease with fish length (Chapter 2).

Many conventional applications of growth theory to fishes suggest that the allocation of surplus energy to gonad and growth optimizes reproduction (Ursin 1967; Roff 1983; Ware 1980). The present analysis does not fully support this view. Autumn-spawning herring, which are more robust than spring-spawning herring, could conceivably allocate even more of their surplus somatic energy to reproduction in order to benefit either individual egg quality or absolute fecundity. However, models of fish growth usually consider the fate of energy as it is ingested and do not explicitly allow for the storage of energy which is later re-allocated to either gonad or somatic growth (Ursin 1967). Consequently, herring reproductive biology is oversimplified by fish growth models. Further investigation is required into the relation of spawning to the seasonality of feeding, growth, and gonad maturation, and how the timing of these processes varies among populations.

Chapter 4

Energy Utilization During Gonad Maturation in Spring- and Autumn-Spawning Northwest Atlantic Herring.

4.1 Introduction

Predictions from growth theory of optimal or maximal allocation of surplus energy to reproduction (Jones and Johnston 1977; Miller 1979; Ware 1980; Kozlowski and Weigert 1986) are not supported by empirical observations of northwest (nw) Atlantic herring *(Clupea harengus harengus* L.) life-history traits. Spring (May-June)-spawning herring produce less gonad material, at any length, than autumn (August-September)-spawning herring (Chapter 2). Yet, length at age, length at maturity and terminal length are similar for spring- and autumn-spawning populations (Lea 1919; Messieh and Tibbo 1971; Parsons and Hodder 1975). Autumn-spawners could conceivably invest even greater quantities of surplus somatic energy into either gonad or somatic growth than is observed (Chapter 3).

The inconsistencies between predictions from growth theory and empirical observations of herring life-history traits require explanations. Realized reproductive effort is a key component of life-history theory (Stearns 1976, 1977; Murphy 1968). Brood size (fecundity), size of gametes (egg weight), the age distribution of the mature population, and adult mortality are all potentially affected by a fish's

reproductive effort (Murphy 1968; Stearns and Crandall 1981).

The non-comparability of the predicted and observed patterns of gonad weight at length (Chapter 2) and spawning condition (Chapter 3) among populations may be due to aspects of herring growth and maturation that are not considered by the metabolic growth models. Regardless of spawning season, herring utilize energy accumulated and stored in the soma during a common feeding period (≈mid-March to late October) to fulfil all metabolic requirements during gonad maturation (Iles 1964, 1974). Spring (May-June)-spawning herring, which initiate gonad maturation 7-9 months before spawning, therefore, rely upon somatic energy stores for all metabolic requirements for a longer period of time than autumn (August-September)-spawning herring which initiate gonad maturation ≤4 months before spawning (Iles 1964; Parsons and Hodder 1975; McQuinn 1989).

Neither the re-allocation of stored energy to gonad, nor the time that metabolism is fueled by stored energy are explicitly included in metabolic growth theory (Ursin 1967, Iles 1984). Furthermore, somatic growth, and gonad maturation do not simultaneously proceed at high rates (Figure 4.1; Iles 1974, 1984) but either process can be interrupted by the other (e.g., Ile Haute, inner Bay of Fundy summer-spawning herring; Bradford 1987, Iles and Bradford unpub. data). This indicates that growth and

Figure 4.1. Idealized representation of the sequence of spawning, somatic growth, and the accumulation of energy stores for Atlantic herring populations that spawn during different seasons in relation to the feeding cycle.

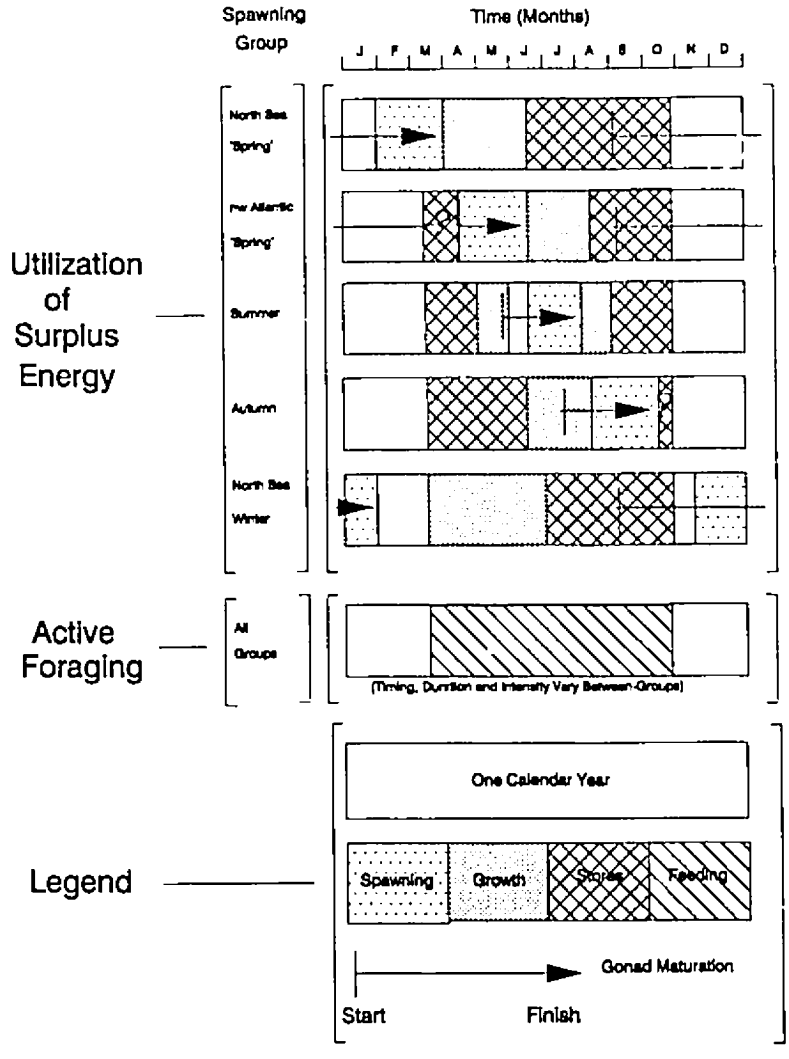
Spawning Group
Time (Months)
J F M A M J J A S O N D
North Sea 'Spring'
nw Atlantic 'Spring'
Summer
Autumn
North Sea Winter
Utilization of Surplus Energy
All Groups
Active Foraging
(Timing, Duration and Intensity Vary Between Groups)
One Calendar Year
Spawning
Growth
Stores
Feeding
Gonad Maturation
Start
Finish
Legend

Figure 4.1

reproduction are not in direct competition for energy (surplus to routine metabolism) as it becomes available through feeding.

Herring store energy in their soma either as lipid, protein or carbohydrate. Together with water these constituents of proximate composition can be expressed in either relative (%) or absolute (weight) quantities (Love 1980). Analysis of autumn- and winter-spawning North Sea herring during gonad maturation, and in winter conditions, indicates that stored somatic lipids support non-reproductive metabolic processes and stored somatic proteins support reproductive metabolic processes (Iles 1984).

The differential utilization of lipid and protein during gonad maturation may explain the more robust spawning condition of mature autumn-spawning herring, in comparison with mature spring-spawning herring (see Chapter 3). Each group has a comparable capacity for the accumulation of lipid (Stoddard 1969; Hodder et al. 1973; Peturson and Rosenberg 1982; Henderson and Almatar 1989), yet the length of time each relies solely on lipids for all metabolic processes will differ. A non-reproductive metabolic demand which exceeds lipid stores could lead to reliance on proteins, at the expense of gonad production. Northwest Atlantic spring-spawning herring may be particularly susceptible to non-reproductive protein depletion since their maturation period is the longest known for herring

(Figure 4.1).

This chapter tests whether somatic lipid and somatic protein have separate and distinct functions in Atlantic herring during gonad maturation and/or in winter conditions, as hypothesized by Iles (1984). Data gathered from spring- and autumn-spawning nw Atlantic herring, at all stages of gonad development, are used as the basis for analysis. A composite of previous analyses shows that each somatic component exhibits an annual cycle of accumulation and depletion (Blaxter and Hunter 1982). However, the phases, amplitudes and frequencies of the individual component cycles may or may not differ among populations (Wood 1958; Iles and Wood 1965; Iles 1985; Linko et al. 1985; Wallace 1986). Total protein and total lipid fractions vary synchronously with time among some populations but not others (Iles 1984). Within populations, the phases of individual somatic component cycles may differ by sex (Ackman and Eaton 1976; McGurk et al. 1980) whereas for other populations they are syncronous (Iles 1984; Henderson and Almatar 1989). The present analysis will investigate the basis for this diversity of patterns for storage energy utilization both among and within populations.

4.2 Data Analysis

Body weight is the basis for most indices of fish 'well-being' or 'condition'. Because weight is an allometric function of length the condition of fish which vary in length cannot be directly compared by a comparison of weights alone (Hile 1936; Craig 1977). Fulton's condition factor (K; Ricker 1975) allows for the comparison of different sized fish:

$$K = \frac{W}{L^3} \qquad (4.1)$$

where W= total weight (g) and L= length (mm) with K having the units $g \cdot mm^{-3}$. When W equals total weight the value of K represents the fish's 'Total Condition' (K_{TC}).

Condition factors can be partitioned into "Partial Condition Factors" (Iles (1984). The simplest partial condition factors are:

$$Somatic\ Condition\,(K_{SC}) = \frac{Somatic\ Wt}{L^3} \qquad (4.2)$$

where somatic weight = total weight - gonad weight, and:

$$Gonad\ Condition\,(K_{GC}) = \frac{Gonad\ Wt}{L^3} \qquad (4.3)$$

or:

$$K_{TC} = K_{SC} + K_{GC} \qquad (4.4)$$

These can be further partitioned into the lipid, water, protein and carbohydrate constituents either as the 'Whole Body Components' or as 'Somatic Components' and 'Gonad Components'.

Carbohydrates are a minor component of herring tissues (approximately 5% of the total weight; Love 1980; Almatar 1989) whose quantity remains constant with time (Iles and Wood 1965; Almatar 1989). Therefore, protein levels can be monitored knowing only the lipid, water and 'solid' (carbohydrate and protein) components (Iles 1984). These variables were defined as follows:

$$Whole\ Lipid\ Condition\ (K_{WL}) = \frac{Whole\ Lipid\ Wt}{L^3} \qquad (4.5)$$

$$Whole\ Water\ Condition\ (K_{WW}) = \frac{Whole\ Water\ Wt}{L^3} \qquad (4.6)$$

$$Whole\ Solids\ Condition\ (K_{WS}) = \frac{Whole\ Solids\ Wt}{L^3} \qquad (4.7)$$

Similarly condition indices for somatic lipid (K_{SL}), somatic water (K_{SW}), somatic solids (K_{SS}), gonad lipid (K_{GL}), gonad water (K_{GW}), and gonad solids (K_{GS}) were calculated. Equation 4.4 has an expanded equivalent expression:

$$\begin{aligned} K_{TC} &= K_{SC} + K_{GC} \\ &= (K_{SL} + K_{SW} + K_{SS}) + (K_{GL} + K_{GW} + K_{GS}) \end{aligned} \qquad (4.8)$$

Changes over time in all of the components were measured in absolute terms because the relative proportion (%) of any single component varies as other component(s) change (Iles and Wood 1965; Blaxter and Hunter 1982; Iles 1984).

4.3 Proximate Composition Data

Three data sets of herring proximate composition were available for analysis. The proximate composition of Atlantic herring overwintering in southwest (sw) Newfoundland (Years 1969-1971) was obtained from Hodder et al. (1973) which also detailed the sampling protocol and analytical procedures. Tagging studies (Winters and Beckett 1978; Moores and Winters 1984; Wheeler and Winters 1984a,b) and analysis of the biological characteristics of these fish (Hodder and Parsons 1971; Parsons 1972, 1973) showed that spring- and autumn-spawning southern Gulf of St. Lawrence (southern Gulf) herring represented >90% of the samples collected by Hodder et al. (1973). In total 1178 maturing, spring-spawning herring and spent, autumn-spawning herring were sampled in roughly equal proportions from November-March. Lipid and water content determinations were for whole fish only (soma and gonad combined).

McGurk et al. (1980) analyzed 292 spring-spawning herring from southeastern (se) Newfoundland. Sampling occurred on 10 occassions between March 1, 1977 and February

6, 1978. Only data for the proximate composition of the gonads was used because they defined 'soma' as the combined fillet and viscera tissues. Lipid is not homogeneously distributed throughout the body of herring (Brandes and Dietrich 1953).

Time is not a good basis for assessments of between-sex differences in gonad proximate condition, particularly for spring spawners, because the rate of gonad development varies between male and female herring. Testes develop faster and maintain an advanced stage of development for a longer period of time than do ovaries (Iles 1964; Hodder et al. 1973; McGurk et al. 1980). However, the sampling period of McGurk et al. (1980) extended from the onset of gonad maturation to near spawning. This meant that gonad development (K_{GC}) could be used as a basis to compare gonad proximate composition variability between sexes.

Somatic lipid and somatic water content data for southwest (sw) Nova Scotia (NAFO Subdivision 4WX) autumn-spawning herring, collected during 1975, were obtained from Dr. T.D. Iles (DFO, St. Andrews, N.B.). The data set included feeding (June-July), maturing, mature, and spawning (August-September) herring (Sinclair and Iles 1985; Sinclair et al. 1985). Nearly 800 fish were sampled at approximately weekly intervals. Lipid and moisture content determinations were for the whole fish minus the gonad and any food items present in the gut. The sampling protocol and analytical

procedures were previously described by Varga et al. (1977).

Partial condition factors were examined as a time series. The dates of capture were rescaled to August 15 and July 15 for maturing spring- and maturing autumn-spawning herring respectively to approximate the days from the onset of gonad maturation (see McQuinn 1989). The date of capture for overwintering, spent autumn-spawning herring was rescaled to September 15 to reflect days from spawning.

Collectively, the data sets provided data for: 1) overwintering, maturing, male and female spring-spawning herring; 2) overwintering male and female autumn-spawning herring with spent, dormant gonads; and 3) maturing, mature and spawning male and female autumn-spawning herring.

Somatic growth (a permanent increase in body length) was not apparent during the period of observation for any of the sample populations. Therefore, any changes in the proximate composition of the samples with time were due only to gonad development and/or non-reproductive activity. In these data sets, and throughout the thesis, the terms 'lipid' and 'total lipid' refer to total extractable lipid. This will include both storage lipids (principally triaglycerides (TAG)) and structural lipids (polar lipids) (Love 1980; Linko et al., 1985; Henderson and Almatar 1989). Polar lipids are incorporated into permanent membranous tissues, and therefore measures of 'total lipid' should be > zero. Since the fish studied herein were all collected

outside of the season(s) for somatic growth the absolute quantities of polar lipids are not likely to change substantially with time, with the possible exception of fish with completely depleted storage lipids. Therefore, changes in total extractable lipid with time will be due to changes in storage lipids, which account for >90% of all lipids prior to gonad maturation (Henderson and Almatar 1989).

4.4 Results

4.4.1 Overwintering, Maturing Spring-Spawning Herring.

The degree of gonad maturation attained at the time of first sampling (November, sw Newfoundland) appeared to influence the degree of change in whole solids (K_{WS}), but not whole lipid (K_{WL}) with time. Whole lipid (K_{WL}) decreased with time at the same rate for both sexes (Table 4.1a,b; Figure 4.2). Whole solids (K_{WS}) remained constant with time for males, but decreased with time for females (Table 4.1a,b; Figure 4.2). Testes were more fully developed than ovaries (K_{GC}) at the time of first sampling (Table 4.1; Figure 4.3). Testes appeared to lose weight with time, whereas ovaries gained weight with time (Table 4.1a,b; Figure 4.3).

In general, total condition (K_{TC}) decreased with time for both sexes (Table 4.1a; Figure 4.3), but at a faster rate for females than males (Table 4.1b). Somatic condition

Table 4.1. a) Sample size (n), slopes (a), intercepts (b), 95% confidence intervals of the estimates (95%CI), coefficient of determination (r^2), and probability (P) for total, somatic, and gonad condition and component lipid, water and solid condition of whole body tissues ($g \cdot mm^{-3} \cdot 10^{-6}$) versus days from the onset of maturation for male (M) and female (F) overwintering sw Newfoundland spring-spawning herring. b) Between-sex ANCOVA of slopes and intercepts for each condition factor versus days from the onset of maturation (F= F-ratio).

a) Variable	Sex	n	a(95%CI)	b(95%CI)	r^2	P
Total Condition (K_{TC})	F	127	7.773(0.424)	-.007(.002)	.21	.001
	M	125	6.908(0.350)	-.003(.002)	.06	.001
Somatic Condition (K_{SC})	F	127	7.533(0.507)	-.012(.002)	.33	.001
	M	125	5.101	-.001	.01	.405
Gonad Condition (K_{GC})	F	127	0.241(0.263)	.005(.002)	.22	.001
	M	125	1.807(0.335)	-.004(.002)	.12	.001
Lipid Condition (K_{WL})	F	127	1.837(0.224)	-.005(.002)	.30	.001
	M	125	1.663(0.248)	-.004(.002)	.23	.001
Water Condition (K_{WW})	F	127	4.502	-.001	.01	.448
	M	125	3.996(0.249)	.002(.002)	.05	.014
Solids Condition (K_{WS})	F	127	1.434(0.091)	-.002(.002)	.24	.001
	M	125	1.249	0.000	.01	.185

b)	Intercepts			Slopes		
Index	df	F	P	df	F	P
K_{TC}	1, 249	4.49	>0.05	1, 248	7.56	<0.02
K_{SC}	------	-----	-----	------	-----	------
K_{GC}	1, 249	7.28	<0.02	1, 248	46.72	<0.001
K_{WL}	1, 249	5.34	<0.05	1, 248	0.35	>0.50
K_{WW}	------	-----	------	------	-----	------
K_{WS}	------	-----	------	------	-----	------

Figure 4.2. The relationships between total condition (K_{TC}), somatic condition (K_{SC}), gonad condition (K_{GC}) and time (days from the onset of gonad maturation) for maturing, male and female spring-spawning herring overwintering off sw Newfoundland (Condition units = g tissue·length^{-3}(mm)·10^{6}).

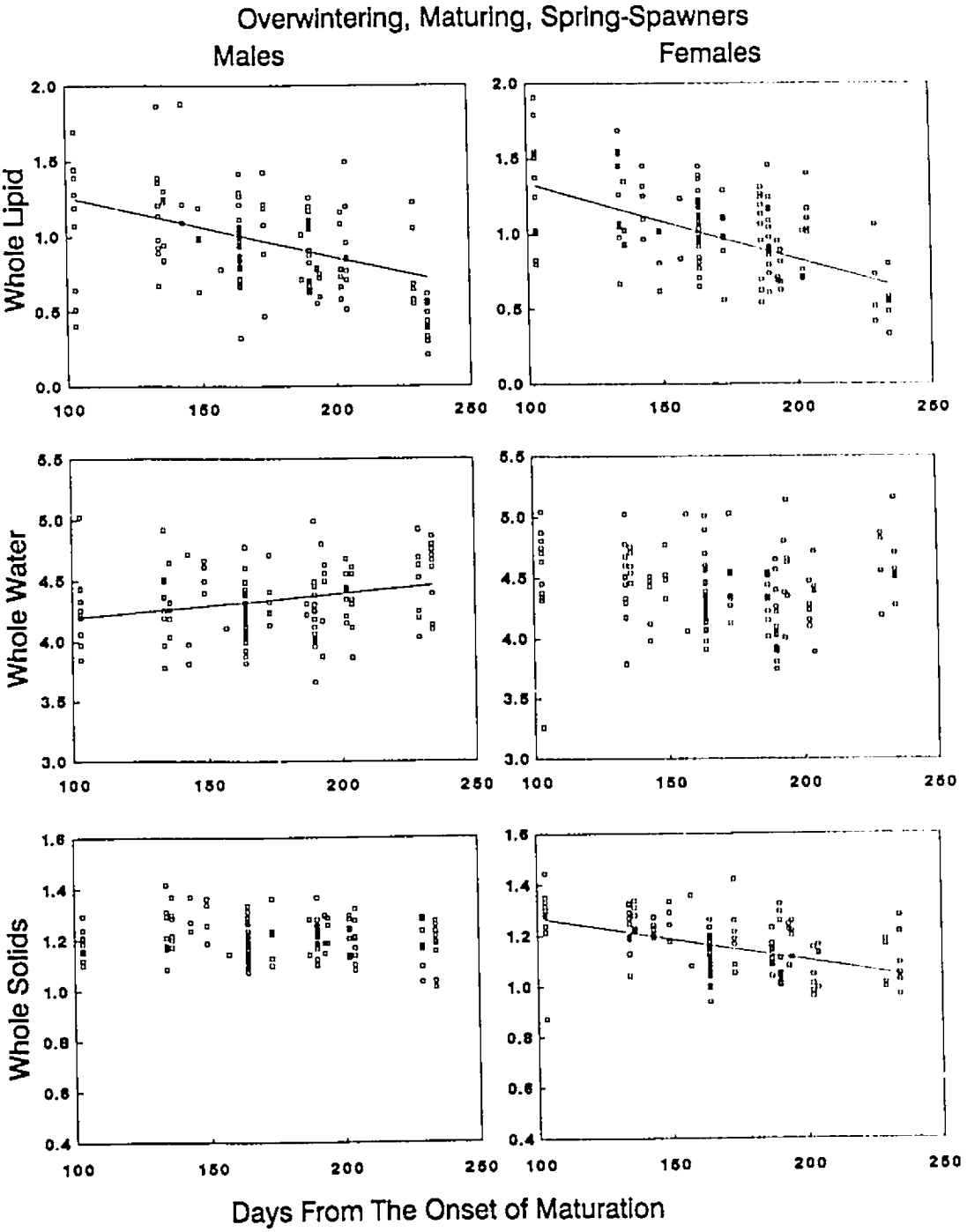
Overwintering, Maturing, Spring-Spawners
Males
Females
Whole Lipid
Whole Water
Whole Solids
Days From The Onset of Maturation

Figure 4.2

Figure 4.3. The relationships between total lipid condition (K_{TL}), total water condition (K_{TW}), total solid condition (K_{TS}) and time (days from the onset of gonad maturation) for maturing, male and female spring-spawning herring overwintering off sw Newfoundland (Condition units = g tissue·length^{-3}(mm)·10^2).

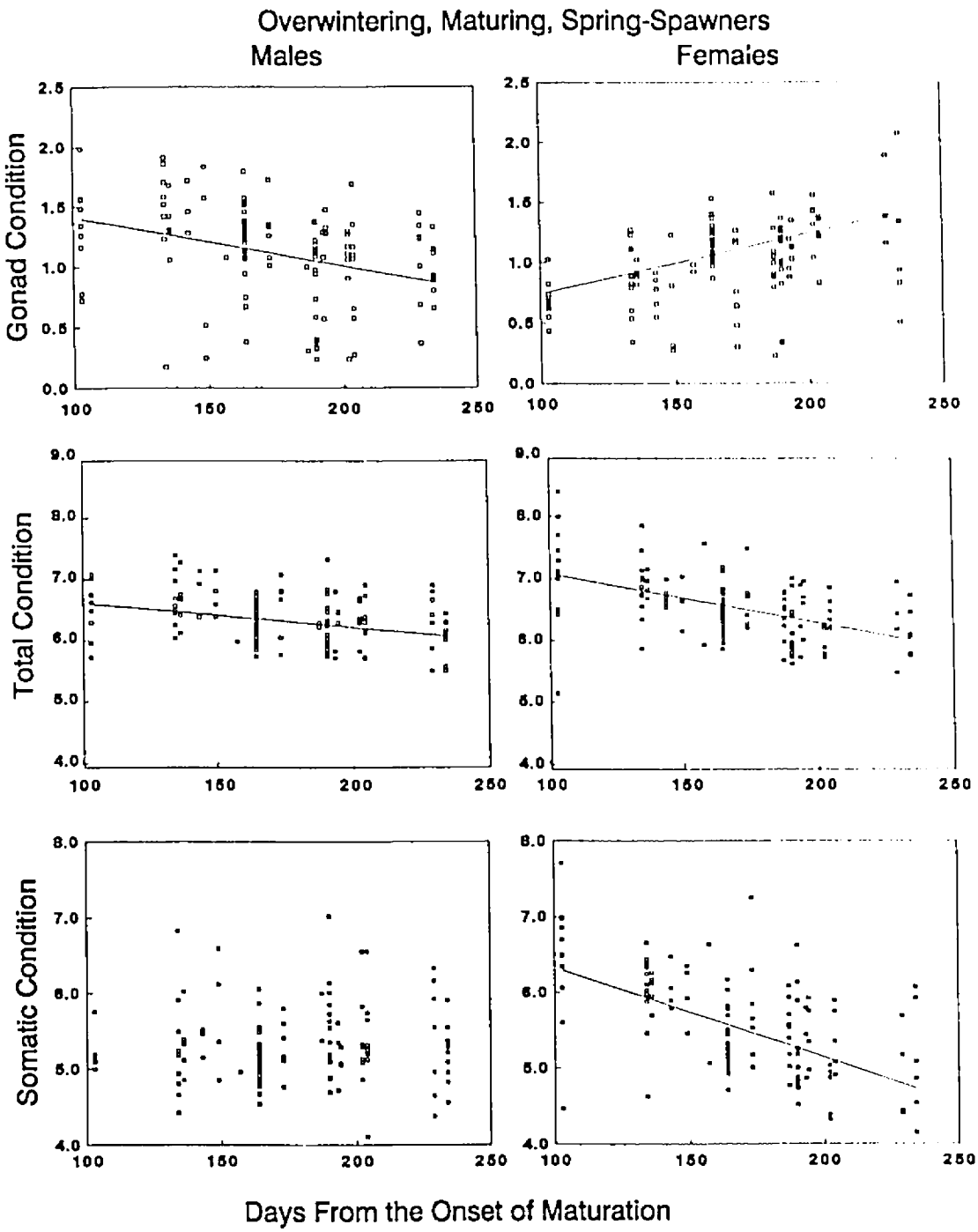
Overwintering, Maturing, Spring-Spawners
Males
Females
Gonad Condition
Total Condition
Somatic Condition
Days From the Onset of Maturation

Figure 4.3

(K_{SC}) decreased for females but remained constant for males (Table 4.1a; Figure 4.2b). Whole water condition (K_{WW}) remained constant for females, but increased for males with time (Table 4.1a,b; Figure 4.2c). This accounted, in part, for the between-sex differences in the change in somatic condition (K_{SC}) with time.

Analysis of the proximate composition of gonad tissues (se Newfoundland spring-spawners, from McGurk et al. 1980), coupled with differences in gonad maturity at the time of first sampling, substantiate the above whole fish analyses. The proximate composition of the gonads is about the same for male and female herring at the onset of maturation (Figure 4.4). With time, testes gain lipid at a faster rate than do ovaries (Table 4.2; Figure 4.4). Testes accumulate water at a slightly faster rate than do ovaries (Table 4.2; Figure 4.4). Ovaries accumulate solids at a faster rate than do testes (Table 4.2; Figure 4.4).

The above relationships (Table 4.2) indicated that the component gonad condition of sw Newfoundland overwintering, spring-spawning herring at the time of first sampling (November) was approximately as follows. Testes, being well developed (≈1.5 K_{GC} units; Figure 4.3), could be expected to have accumulated 70%, 74%, and 73% of their final lipid, water and solids respectively. Ovaries, being poorly developed (≈0.75 K_{GC} units; Figure 4.3), could be expected to have accumulated only 44%, 38%, and 31% of their final

Table 4.2. a) Sample size (n), slopes (a), intercepts (b), 95% confidence intervals of the estimates (95%CI), coefficient of determination (r^2), and probability (P) for gonad lipid (g), gonad water (g), and gonad solids (g) versus gonad condition (K_{GC}, $g \cdot mm^{-3} \cdot 10^{-6}$) for male (M) and female (F) se Newfoundland spring-spawning herring. b) Between-sex ANCOVA of slopes and intercepts for each gonad component versus gonad condition (F= F-ratio).

a) Variable	Sex	n	a(95%CI)	b(95%CI)	r^2	P
Lipid	M	47	-0.60(0.73)	1.62(0.32)	0.69	<0.001
	F	54	0.09(0.30)	0.40(0.10)	0.58	<0.001
Water	M	59	-1.66(7.17)	30.08(2.88)	0.88	<0.001
	F	63	0.03(5.94)	27.09(1.72)	0.94	<0.001
Solids	M	47	-1.65(2.92)	11.12(1.31)	0.87	<0.001
	F	54	-1.54(2.99)	15.27(0.96)	0.95	<0.001

b)	Intercepts			Slopes		
Variable	df	F	P	df	F	P
Lipid	1, 98	127.52	<0.001	1, 97	66.54	<0.001
Water	1,119	11.16	<0.005	1,118	3.37	>0.10
Solids	1, 98	232.83	<0.001	1, 97	26.00	<0.001

Figure 4.4. The relationships between gonad water (g), gonad lipid (g), gonad solids (g) and gonad condition ($g \cdot mm^{-3} \cdot 10^{6}$) for male (squares) and female (circles) se Newfoundland spring-spawning herring.

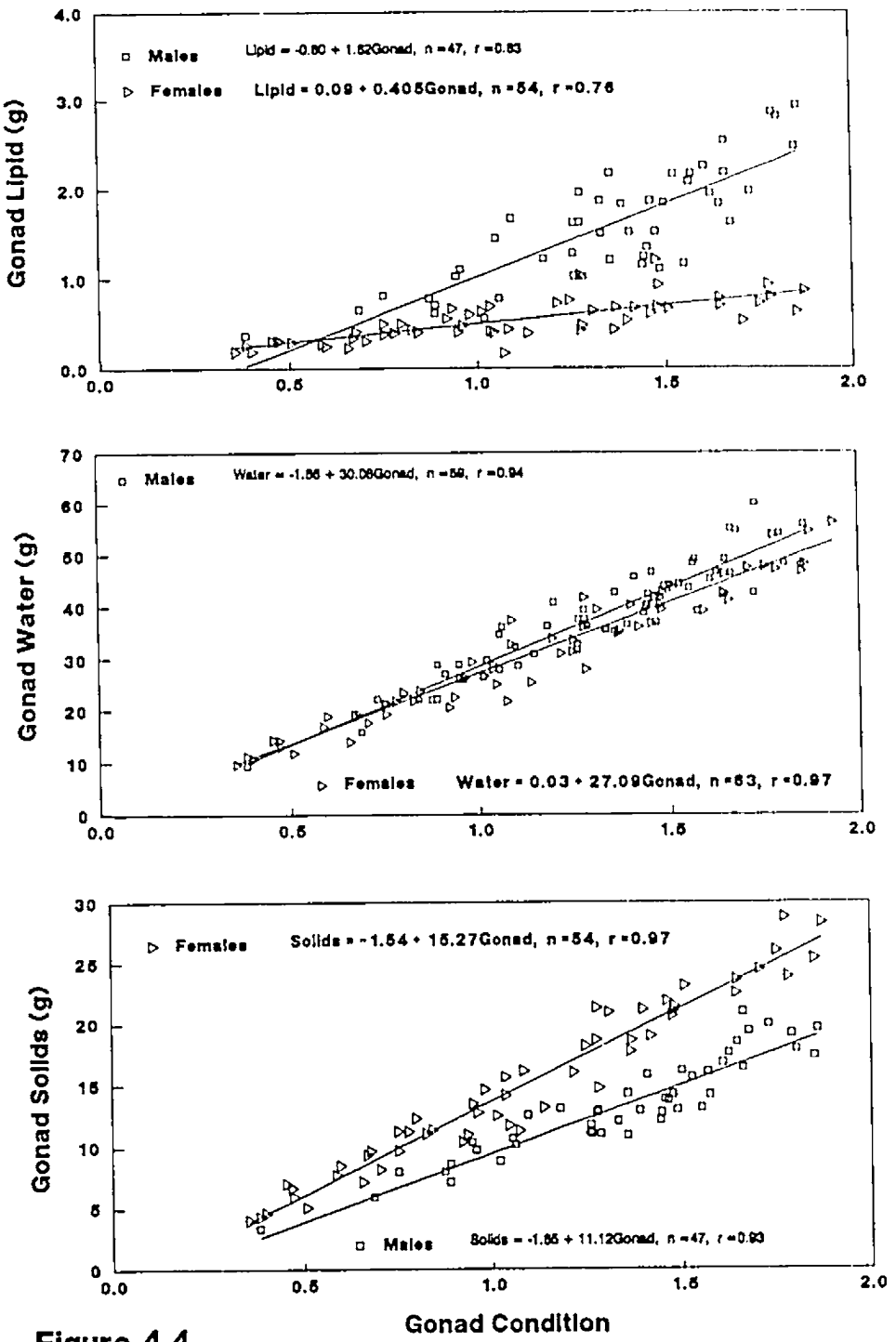
Gonad Lipid (g)
Males
Lipid = -0.80 + 1.82Gonad, n =47, r =0.83
Females
Lipid = 0.09 + 0.405Gonad, n =54, r =0.76
Gonad Water (g)
Males
Water = -1.56 + 30.06Gonad, n =59, r =0.94
Females
Water = 0.03 + 27.09Gonad, n =63, r =0.97
Gonad Solids (g)
Females
Solids = -1.54 + 15.27Gonad, n =54, r =0.97
Males
Solids = -1.55 + 11.12Gonad, n =47, r =0.93
Gonad Condition

Figure 4.4

lipid, water, and solids respectively. In general, neither testes nor ovaries contained extensive quantities of lipid at full maturity (males ≈4% and females ≈1% by weight). Solids comprised a greater proportion of mature ovaries (≈35% by weight) than mature testes (≈25% by weight). These results demonstrate that between-sex differences in the rate of allocation to gonad of somatic solids, but not somatic lipids, are indicated in the proximate composition of whole fish tissues.

4.4.2 Overwintering, Spent Autumn-Spawning Herring.

Neither gonad condition nor proximate composition differed extensively between male and female spent herring overwintering off sw Newfoundland (Gonads; ≈1.5g heavier for a 350mm female; Table 4.3a; Figure 4.5). Gonad weight increased by ≈1g during winter in both sexes (Males, df =151, r^2 =0.06, P <0.005; Females, df =148, r^2 =0.09; P <0.001). Whole lipid (K_{WL}) was the only proximate component to differ between sexes (Table 4.3a) but between-sex differences explained <3% of the variance in total lipid condition. This difference was considered to be minimal and so the male and female data were pooled for further analysis.

Declines in both total condition (K_{TC}) and somatic condition (K_{SC}) with time (Table 4.3b; Figure 4.5) were due almost completely to a decrease in lipid (K_{WL}) during the

Table 4.3. Overwintering, spent, autumn-spawners from sw Newfoundland: a) degrees of freedom (df), F-ratio (F), and probability (P) from ANCOVA of slopes (a) and intercepts (b) for male and female herring with time as the co-variate. b) Regression statistics for total (K_{TC}) and somatic (K_{SC}) condition and whole fish components (K_{WW}, K_{WL}, K_{WS}) versus days from spawning (condition units are g tissue$\cdot 1^{-3} \cdot 10^{6}$; 95%CI =95% confidence interval).

a)	Intercepts			Slopes		
Index	df	F	P	df	F	P
K_{TC}	1, 300	0.458	>0.50	1, 299	0.005	>0.50
K_{GC}	1, 300	81.538	<0.001	1, 299	0.060	>0.50
K_{WL}	1, 300	8.193	<0.01	1, 299	0.211	>0.50
K_{WW}	1, 300	1.369	>0.50	1, 299	0.005	>0.50
K_{WS}	1, 300	0.361	>0.50	1, 299	0.079	>0.50

b) Index	n	a(95%CI)	b(95%CI)	r^2	P
K_{TC}	297	6.959(0.973)	-.003(0.002)	.05	.001
K_{SC}	297	6.923(0.965)	-.004(0.002)	.06	.0001
K_{WW}	297	4.448	0	<.01	.333
K_{WL}	297	1.110(0.415)	-.004(0.0002)	.29	.0001
K_{WS}	297	1.365	0	0	.790

Figure 4.5. The relationships between total condition (K_{TC}), somatic condition (K_{SC}), gonad condition (males and females) and time (days from last spawning) for spent, autumn-spawning herring overwintering off sw Newfoundland (Condition units = g tissue·length^{-3}(mm)·10^6).

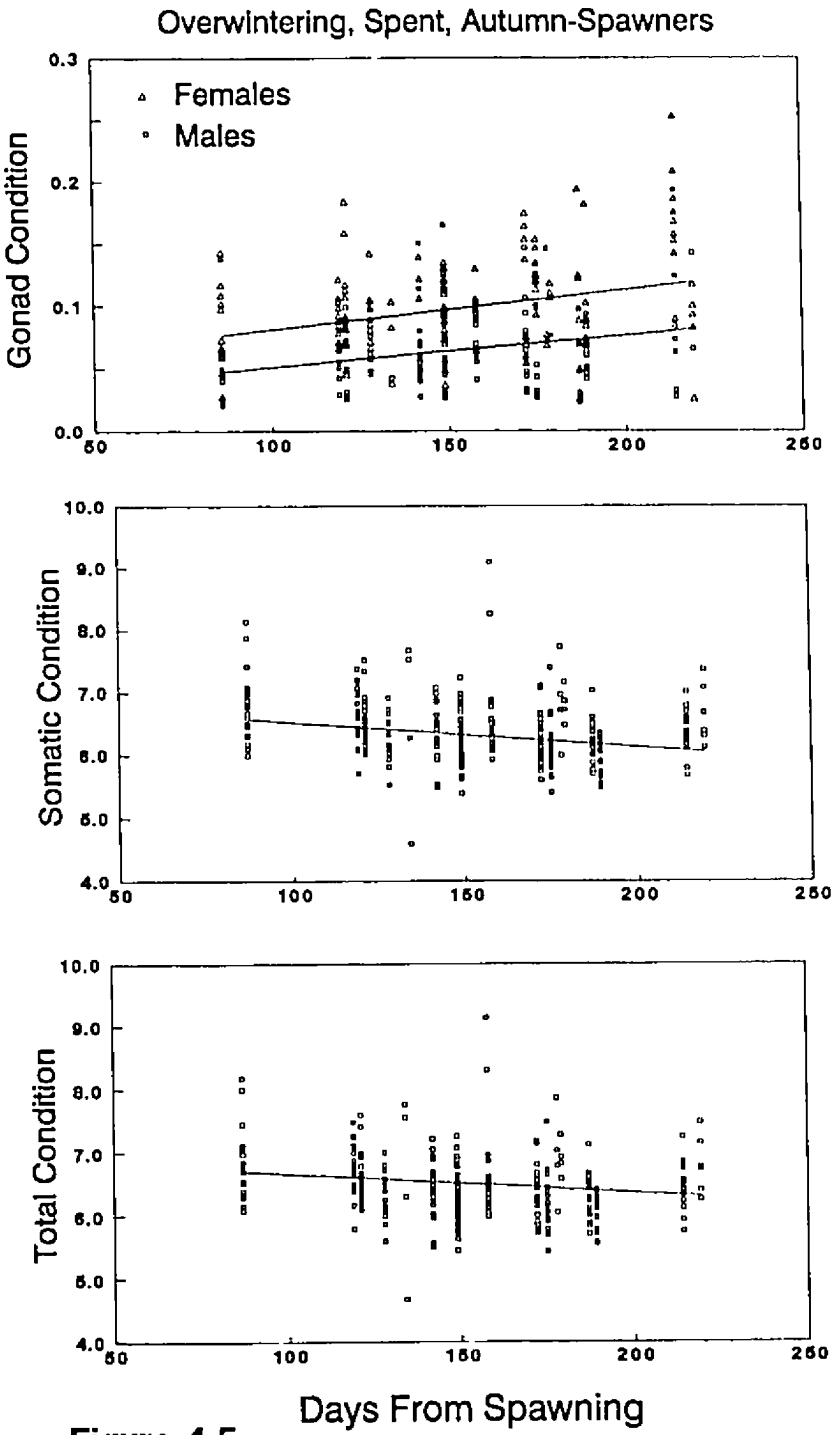
Overwintering, Spent, Autumn-Spawners
Females
Males
Gonad Condition
0.3
0.2
0.1
0.0
50
100
150
200
250
Somatic Condition
10.0
9.0
8.0
7.0
6.0
5.0
4.0
Total Condition
Days From Spawning

Figure 4.5

winter months (Table 4.3b; Figure 4.6). Neither whole water condition (K_{WW}) nor whole solids condition (K_{WS}) varied measurably with time (Table 4.3b; Figure 4.6).

4.4.3 Maturing and Mature Autumn-Spawning Herring.

Somatic condition (K_{SC}) and all of the component somatic condition factors (K_{SS}, K_{SW}, K_{SL}) decreased during gonad maturation, for both sexes, in autumn-spawning herring (sw Nova Scotia, Table 4.4; Figures 4.7 and 4.8). Gonad condition (K_{GC}) increased steadily for both male and female autumn-spawning herring once gonad maturation was initiated (Figure 4.7). The decrease in gonad condition at the end of sampling is due to the presence of individuals which had extruded milt or eggs (Stage 6; Table 2.1). Condition indices did not vary between sexes (ANCOVA, $P > 0.05$; data not shown).

4.5 Discussion

Three important features were apparent from the analysis of the proximate composition of nw Atlantic herring tissues. First, somatic lipid decreased with time for non-feeding herring captured during both the winter and summer months regardless of their degree of maturation. Second, somatic lipid and somatic solids were depleted concurrently

Table 4.4. Regression statistics of somatic condition (K_{SC}), and somatic component condition factors for solids (K_{SS}), water (K_{SW}) and lipid (K_{SL}) versus time (days from the onset of maturation) for male and female autumn-spawning sw Nova Scotia herring (4WX) (condition units are $g \cdot L^{-3} \cdot 10^{6}$, 95%CI= 95% confidence interval).

Index	a(95%CI)	b(95%CI)	n	r^2	P
Males					
K_{SC}	13.7524(1.1833)	-.0293(.0056)	96	.54	<.001
K_{SS}	2.2986(0.2044)	-.0043(.0010)	96	.46	<.001
K_{SW}	7.5420(0.6339)	-.0119(.0030)	96	.41	<.001
K_{SL}	3.9117(0.5771)	-.0131(.0028)	96	.50	<.001
Females					
K_{SC}	11.8919(1.1898)	-.0203(.0048)	95	.43	<.001
K_{SS}	2.0304(0.2349)	-.0030(.0010)	95	.29	<.001
K_{SW}	7.2626(0.6635)	-.0103(.0026)	95	.38	<.001
K_{SL}	2.5990(0.5414)	-.0070(.0022)	95	.31	<.001

Figure 4.6. The relationships between condition indices for somatic lipid (K_{SL}), and somatic water (K_{SW}), and somatic solids (K_{SS}) and time (days from last spawning) for spent, autumn-spawning herring overwintering off sw Newfoundland (Condition units = g tissue·length^{-3}(mm)·10^6).

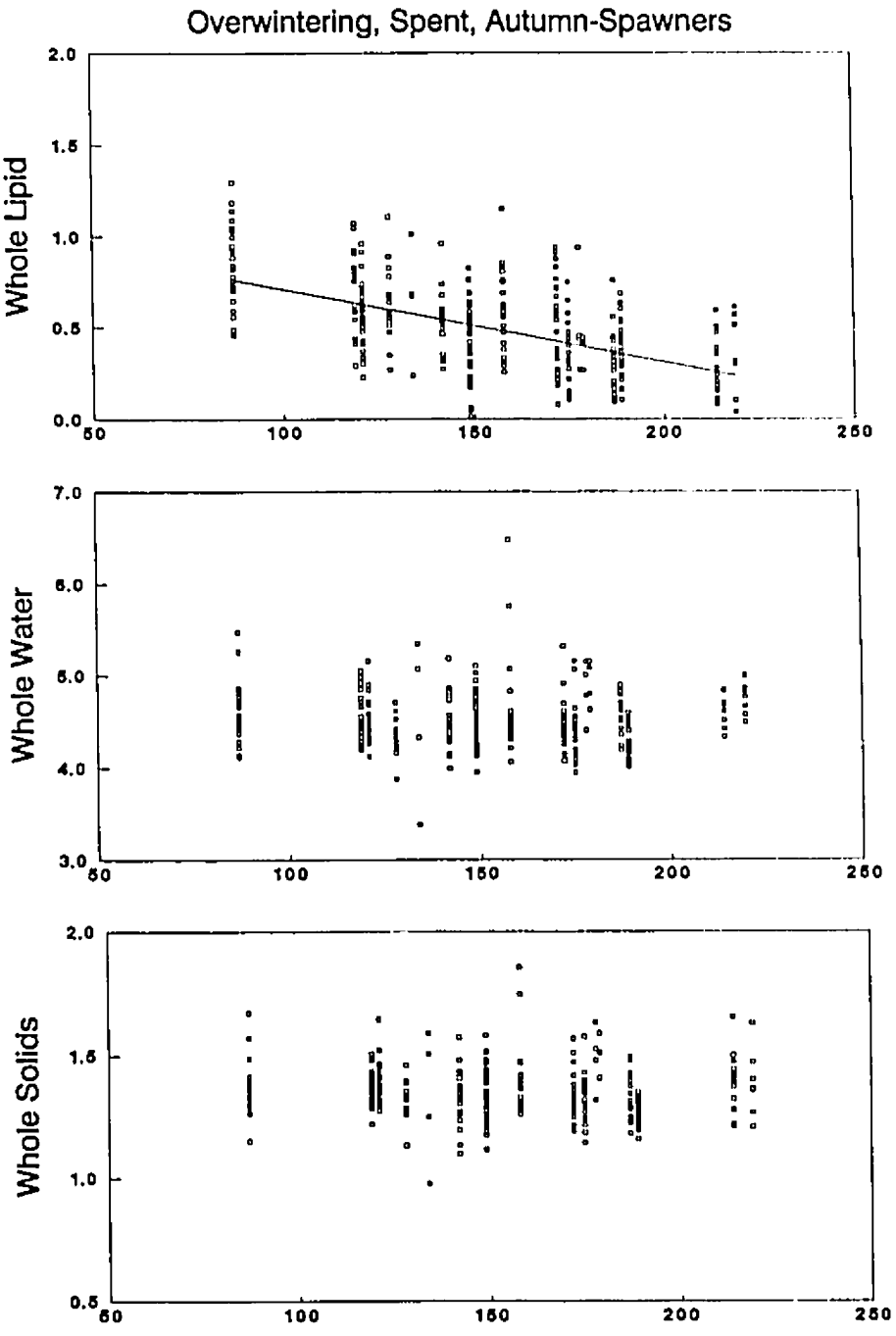
Overwintering, Spent, Autumn-Spawners
Whole Lipid
2.0
1.5
1.0
0.5
0.0
50
100
150
200
250
Whole Water
7.0
6.0
5.0
4.0
3.0
50
100
150
200
250
Whole Solids
2.0
1.5
1.0
0.5
50
100
150
200
250
Days From Spawning

Figure 4.6

Figure 4.7. The relationships between total condition (K_{TC}), somatic condition (K_{SC}), gonad condition (K_{GC}) and time (days from the onset of gonad maturation) for maturing and mature male and female sw Nova Scotia autumn-spawning herring (Condition units = g tissue·length^{-3}(mm)·10^6).

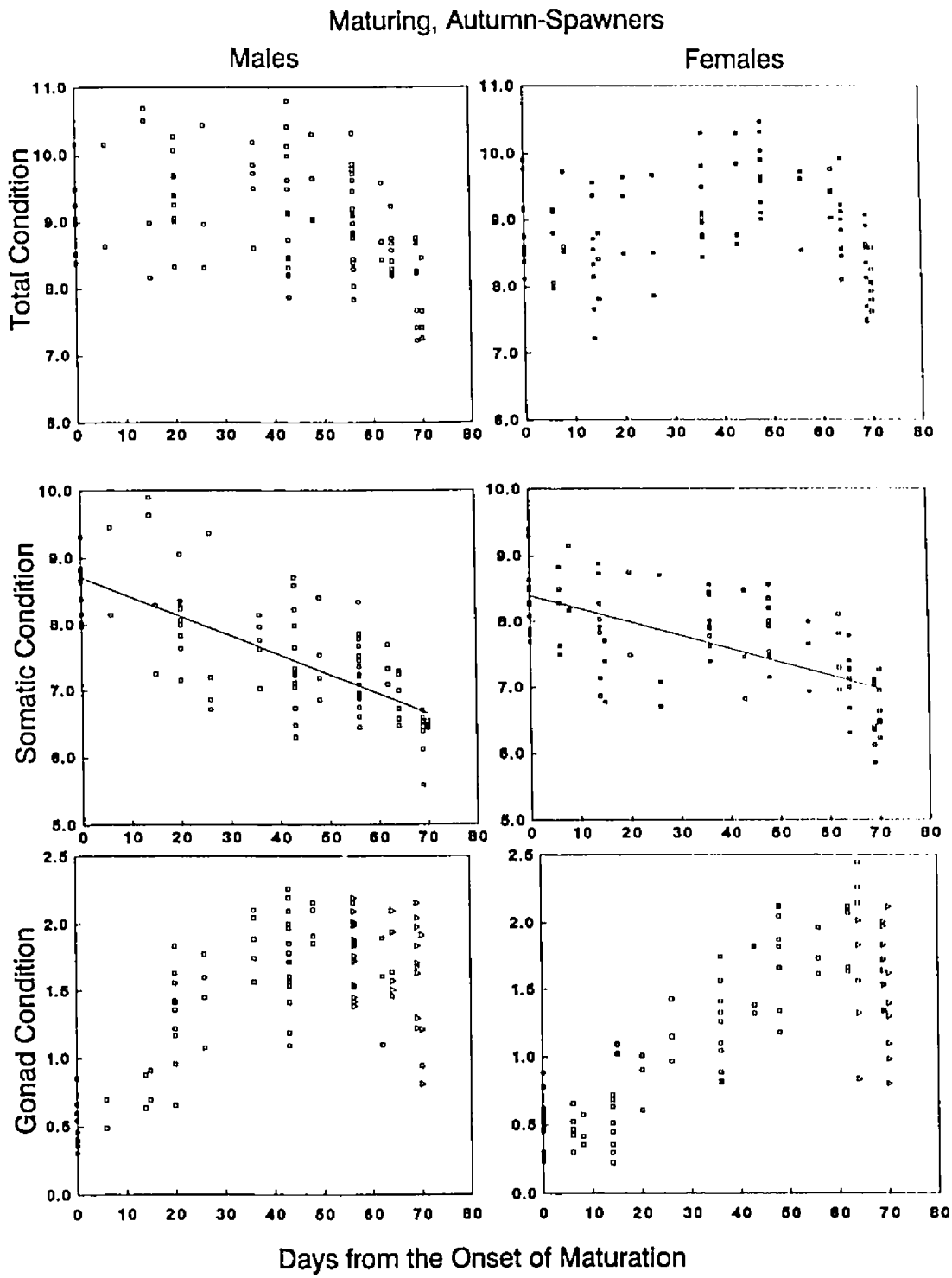
Maturing, Autumn-Spawners
Males
Females
Total Condition
Somatic Condition
Gonad Condition
Days from the Onset of Maturation

Figure 4.7

Figure 4.8. The relationships between condition indices for somatic lipid (K_{SL}), somatic water (K_{SW}), somatic solids (K_{SS}) and time (days from the onset of maturation) for maturing and mature male and female sw Nova Scotia autumn-spawning herring (Condition units = g tissue·length^{-3}(mm)·10^{8}). that none of the condition indices varied between sexes with time ($P \geq 0.15$; data not shown).

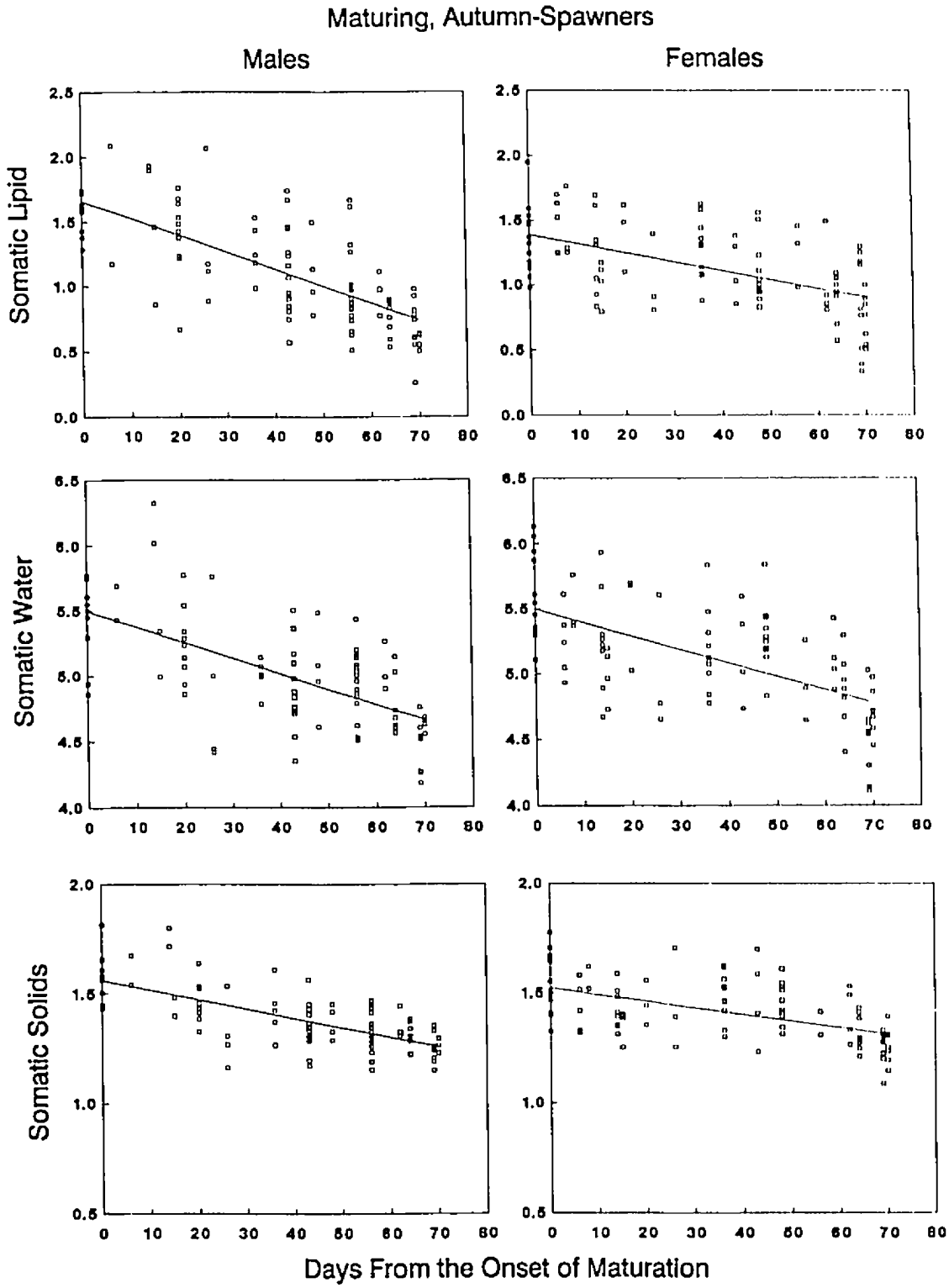
Maturing, Autumn-Spawners
Males
Females
Somatic Lipid
Somatic Water
Somatic Solids
Days From the Onset of Maturation

Figure 4.8

only for fish with gonads that measurably gained weight with time (female spring-spawners, and both male and female autumn-spawners). Third, somatic solids were never extensively depleted in herring which did not develop gonads during the period of observation, regardless of their stage of gonad development (near fully-mature male spring-spawners and both male and female spent, autumn-spawners).

These results demonstrate that somatic lipids support metabolism of fasting herring and therefore are depleted with time regardless of the degree of gonad maturation. Somatic protein is utilized for gonad development and therefore is depleted concurrently with storage lipids only during gonad maturation, as shown previously by Iles (1984). Therefore, storage lipid and storage protein are concluded to have separate and distinct fates during gonad maturation and must be treated as separate entities. The energetics of gonad maturation cannot be satisfactorily resolved solely from analyses of changes in energy density of tissues (e.g., McGurk et al. 1980).

The relation between herring reproductive traits (gonad weight at length, egg weight, fecundity) and energy utilization during gonad maturation needs to be evaluated in relation to the timing of other seasonal processes (i.e., growth, feeding and overwintering). Lipid metabolism is likely to affect differently the reproductive traits of fish that spawn during different seasons. Maturing spring-

spawning herring metabolise lipids to simultaneously offset winter conditions and gonad maturation, while not diverting protein to non-reproductive metabolism. Autumn-spawning herring metabolise lipids as gonad maturation and overwintering proceed sequentially.

The substantive depletion of storage lipids by overwintering spring-spawning herring (Chapter 3) indicates that spring-spawners are at risk of protein catabolism to support non-reproductive functions, particularly small bodied individuals. The surplus of storage lipid for fully mature autumn-spawners (Chapter 3) is irrelevant to gonad quality (e.g., gonad weight at length) beyond the fact that storage proteins are not at risk of being diverted to non-reproductive metabolism. This reasserts the importance of evaluating herring gonad maturation energetics in relation to the timing and sequencing of the seasonal cycles of the somatic components.

The significance of the surplus of storage lipid in autumn-spawners needs to be evaluated as to whether they are sufficient to maintain the fish during the ensuing winter. There are indications that some autumn-spawning herring resume feeding after spawning (Iles 1984). However, the prevalence of feeding fish in commercially caught samples suggests that feeding occurs at a low rate of intensity after spawning and ceases altogether beyond October (Parsons and Hodder 1975; Messieh et al. 1979; Crawford 1980).

Herring somatic tissues lose water as gonads gain weight with time (e.g., female spring-spawners, Table 4.1; both male and female autumn-spawners, Table 4.4; and both autumn- and winter-spawning North Sea herring, Iles 1984). This indicates that accurate and predictive measures of protein metabolism during gonad development may be possible from absolute measures of somatic tissue moisture content. Since tissue moisture content determinations are both rapid and inexpensive, a higher frequency of sampling should be possible in the future. This will provide for more comprehensive assessments of body size effects and/or spawning history effects (e.g., recruit versus repeat spawners) on protein metabolism, and therefore realized reproductive effort.

It is concluded that storage lipid and storage protein are utilized differently by herring during gonad maturation and/or in winter conditions. Lipids support non-reproductive metabolism and proteins are utilized for gonad maturation. The bioenergetics of gonad maturation must be evaluated in the context of its timing and duration in relation to the feeding, growth and winter seasons. A link between the degree of depletion of storage lipid and season of spawning is plausible. Therefore, the susceptibility of herring to protein catabolism for non-reproductive metabolism, to the detriment of gonad weight, may also vary with spawning season.

Chapter 5

Non-Reproductive Utilization of Storage Lipid by nw Atlantic Herring (*Clupea harengus harengus* L.) During Gonad Maturation and in Winter Conditions: A Model

5.1 Introduction

Both gonad weight at length and spawning condition vary among northwest (nw) Atlantic herring populations (Chapters 2 and 3). Similar observations are explained by variability among populations in the relative reproductive versus non-reproductive utilization of surplus energy during gonad maturation in other fish species (American shad (*Alosa sapidissima*); Glebe and Leggett 1981a,b, cisco (*Coregonus artedii*) and lake whitefish (*C. clupeaformis*); Lambert and Dodson 1990a, and alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*); Crawford et al. 1986). Like Atlantic herring, these species do not feed during gonad development and have population specific spawning times (see above references). However, unlike these other fish, Atlantic herring, as a species, spawn throughout the year (Sinclair and Tremblay 1984). Much of the variability in realized reproductive effort and spawning condition occurs among herring populations that spawn during different seasons. Spring (May-June)-spawning herring produce less gonad at length (Chapter 2) and are in poorer condition (Chapter 3) than are autumn (August-September)-spawning herring.

Seasonal differences in the timing and duration of gonad maturation complicates analyses of how surplus (storage) energy is utilized by herring. The duration of the maturation period varies among herring populations that spawn during different seasons (≥7 months and ≤4 months for spring-and autumn-spawning nw Atlantic herring respectively; Hodder et al. 1972; McQuinn 1989). Consequently, somatic energy stores must sustain maturing herring for varying periods of time, depending on the spawning season.

The way in which surplus energy is utilized during gonad maturation or in winter conditions depends upon its storage medium in the somatic tissues. Storage lipids, whose quantity is relatively constant among Atlantic herring populations prior to gonad maturation, support both routine and active metabolism (Iles 1984; Chapter 4). Because only protein is utilized for gonad development (Iles 1984; Chapter 4), lipids must be depleted before a herring's non-reproductive metabolic demand affects its' realized reproductive effort.

Assessments of whether the relative reproductive versus non-reproductive utilization of storage energy affects realized reproductive effort in herring requires consideration of both time and temperature. In the nw Atlantic, spring-spawners develop gonads at colder (winter) temperatures than do autumn-spawners (warm, late summer temperatures). Since herring are poikilotherms, these

temperature differences will tend to mitigate the effect that differences in the time for gonad maturation between spring- and autumn-spawners has on the respiration of storage lipid. Spring- and autumn-spawning herring could conceivably consume approximately the same amount of storage lipid during gonad maturation depending on the seasonal water temperatures.

Realized reproductive effort is potentially influenced by the temporal relation of spawning to other life-history processes (e.g., feeding, growth, overwintering). Autumn-spawning southern Gulf of St. Lawrence ('southern Gulf') herring reproduce with substantive quantities of storage energy still retained in their somatic tissues (Chapter 3). Survival in winter conditions may be as important to the integrity of autumn-spawning populations as is gonad production. Gonad maturation and overwintering proceed concurrently for spring-spawners but sequentially for autumn-spawners (Chapter 4).

Many nw Atlantic herring undertake winter migrations (Stobo 1982, 1983; Sinclair et al. 1985). The purpose of these seasonal movements is not obvious since overwintering herring do not feed (Parsons and Hodder 1975) and predation pressure remains relatively high (Winters 1977). Also, herring of different origins but which share a common distribution at some point in their life-cycles do not necessarily follow the same winter migration tract. For

example, southwest (sw) Nova Scotia herring overwinter along the eastern (e) Scotian Shelf near Chedabucto Bay (Figure 5.1)(Stobo 1982, 1983,Sinclair et al. 1985). In contrast, herring which feed with sw Nova Scotia herring during the summer, but spawn elsewhere in the Gulf of Maine, overwinter in the southern Gulf of Maine (Stobo 1982, 1983, Creaser et al. 1984; Sinclair et al. 1985). Furthermore, not all herring exhibit the same degree of fidelity to winter migration tracts. Southern Gulf herring overwinter in the southern Gulf (Stobo 1982, 1983) but, during periods of high adult population density extend their winter range northward to the sw Newfoundland coast (Winters and Beckett 1978). Southwest Nova Scotia herring appear to winter exclusively along the e Scotian Shelf (Stobo 1982, 1983).

The above among- and within population differences in winter migration behaviour need to be explained. One possibility not previously considered is that storage energy utilization may differ geographically. Winter sea surface temperatures, which could affect storage energy utilization, increase with decreasing latitude (Thompson et al. 1988). Therefore, the winter distributions of herring may reflect their degree of sensitivity to lipid depletion during winter.

This chapter evaluates whether lipid stores can fulfil the total non-reproductive metabolic demand of fasting herring during gonad maturation and/or in winter conditions.

Figure 5.1. Map of nw Atlantic region showing the location of spawning and wintering areas referred to in the text.

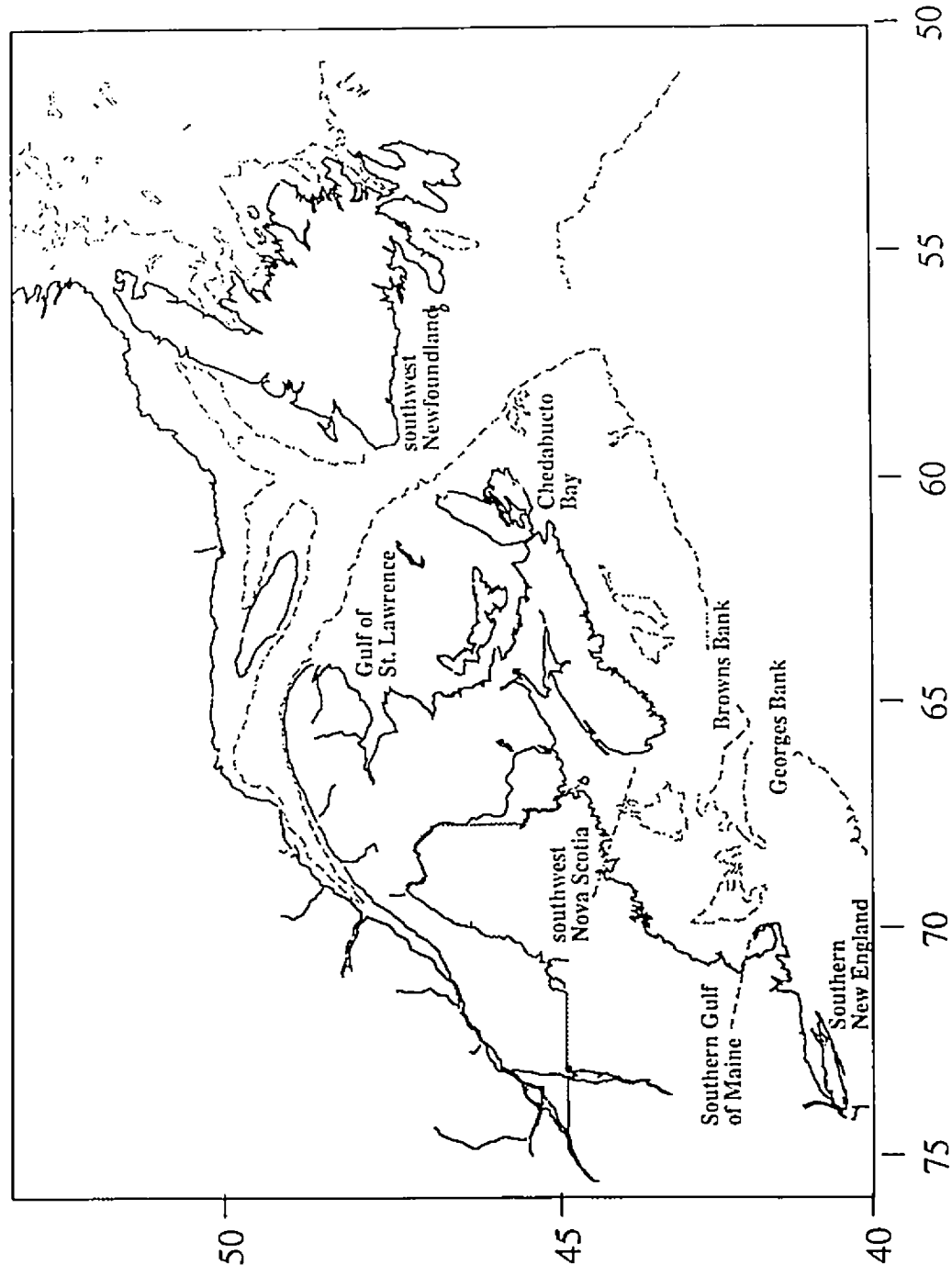
southwest Newfoundland
Chedabucto Bay
Gulf of St. Lawrence
Browns Bank
Georges Bank
southwest Nova Scotia
Southern Gulf of Maine
Southern New England
50
45
40
75
70
65
60
55
50

Figure 5.1

Maturing (overwintering) spring-spawners, maturing autumn-spawners and spent (overwintering) autumn-spawners are considered. The analysis is presented in four parts. First, a storage lipid utilization model is developed from general principles of metabolism and respiration in fishes. Simulations of how body size, time, and temperature influence both respiration and storage lipid depletion are presented. Second, the lipid depletion model is used to test whether routine respiration is higher during gonad maturation for spring-spawners than for autumn-spawners, given average gonad maturation times and average gonad development temperatures. Third, spawning condition as predicted by the storage lipid utilization model is compared with empirical spawning condition data (from Chapter 3) for nw Atlantic spring- and autumn-spawning herring. Fourth, I evaluate whether the residual storage lipid of fully mature autumn-spawning herring (Chapter 3) is sufficient to sustain their total metabolic demand during the ensuing winter.

The results from parts two through four above are used to test two specific hypotheses:

1) Non-reproductive utilization of storage lipid is the same for nw Atlantic populations that spawn during different seasons.

2) The proportion of storage lipid not utilized during gonad maturation by nw Atlantic autumn-spawning herring can support their post-spawning metabolic demand in winter

conditions.

5.2 Materials and Methods

5.2.1 Derivation of Somatic Lipid Utilization Model

For non-feeding fish, somatic weight decreases with time at the rate of respiration (R) of stored materials (Shuter et al. 1980; MacLean et al. 1981; Shuter and Post 1990):

$$R = \alpha W^{\beta} \tag{5.1}$$

where R has the units milliliters (ml) of oxygen (O_2) per hour (h), W =total weight (g), and α and β are respiration coefficients (α =0.3, and β =0.8 at 20 °C for herring sized fishes (Winberg 1956, 1961; Ursin 1967, 1979; Beyer and Sparre 1983)). Compensation for changes in temperature is necessary because respiration is temperature dependent in fish (Schmidt-Nielson 1979). This is measured as the change in respiration rate with a 10°C change in temperature (Q_{10}). For Atlantic herring $Q_{10} \approx 2$ (Ursin 1967, 1979).

$$R_T = R_{20} \cdot 2^{\frac{T-20}{10}} \tag{5.2}$$

where R_T =respiration at temperature T (°C) and R_{20} = respiration at 20°C.

Changes in somatic lipid for non-feeding herring can be estimated by converting O_2 consumption to lipid utilized (1ml O_2 =4.86 calories and 1g fat =9500 calories, Love 1980;

Winters 1977; Schmidt-Nielson 1979; McGurk et al. 1980). Therefore:

$$L_R - L_O - \sum_{t-1}^{n} [(0.3 \cdot W_t^{0.8} \cdot 2^{(\frac{T_{mm} - 20}{10})}) \cdot m_t \cdot \frac{4.86}{9500}] \qquad (5.3)$$

where L_R =somatic lipid (g) consumed by routine metabolism, W_t =weight (g) at beginning of month, L_0 =initial somatic lipid weight (g), t =time (months), m_t =hours in month (t), and T =monthly mean temperature (°C).

The lipid utilization model assumes:

1) changes in body weight are due to the depletion of somatic lipid (conversion of protein to gonad at 100% efficiency and zero translocation of somatic lipid to gonad).

2) constant Q_{10} over time.

5.2.2 Lipid Utilization by Spring- and Autumn-Spawning Southern Gulf Herring During Gonad Maturation

Physiolgical condition at the onset of gonad maturation of both spring- and autumn-spawning southern Gulf herring was defined using relations between total weight (g) - total length (mm) and somatic lipid weight (g) - total length for maturity stage 3 (Table 2.1) sw Nova Scotia herring (Table 5.1; Iles unpub. data). Predicted somatic lipid fractions were calculated from Equation 5.3 for fully mature spring- and autumn-spawning southern Gulf herring

Table 5.1. Intercepts (a), slopes (b), their associated standard errors (SE_x), and the coefficients of determination (r^2) from linear regression of somatic lipid weight (g) and total weight (g) versus total length (mm) for early maturity (Stage 3) sw Nova Scotia autumn-spawning herring. Both regressions are significant at $P < 0.01$.

Variable	a(SE_a)	b(SE_b)	r^2
Somatic lipid (g)	-113.94 (7.10)	0.51 (0.43)	0.70
Total weight (mm)	-529.33 (16.85)	2.55 (0.10)	0.91

(length 290-390mm; years 1971-1988). Monthly mean sea surface temperatures (^{o}C) for NAFO Hydrographic subregions corresponding to the approximate distribution of spring- and autumn-spawning southern Gulf herring during gonad maturation (Subregions St. Pierre and Gulf of St. Lawrence) were obtained from Dr. K. Drinkwater, Bedford Institute of Oceanography (BIO), Dartmouth, N.S. Details of the spatial coverage for each hydrographic subregion are available in Drinkwater and Trites (1988). The maturation periods for spring- and autumn-spawning southern Gulf herring were assumed to be from October 1-May 15 and from July 1-September 15 respectively (after Hodder et al. 1972; McGurk et al. 1980; McQuinn 1989).

5.2.3 Predicted Versus Observed Somatic Lipid Fractions for Spawning NW Atlantic Herring

Somatic lipid fractions based on Equation 5.3 were calculated for fully mature (Maturity Stage 6; Table 2.1) spring- and autumn-spawning southern Gulf herring (Year 1987) and for sw Nova Scotia autumn-spawning herring (Year 1975) assuming a pre-maturation somatic condition as in Table 5.1. Monthly mean sea surface temperatures from NAFO Hydrographic Subregion Yarmouth (Drinkwater and Trites 1988) were used to approximate gonad development temperatures (gonad maturation from July 1-September 1; Chapter 4).

Total respiration (R_{TOTAL}) during gonad maturation was defined as twice the routine respiration ($R_{TOTAL} = 2 \cdot R_T$; Winberg 1956; Solomon and Brafield 1972; Winters 1977).

Predicted routine and total respiration estimates for each spawning group (length 275 - 350mm) during gonad maturation were re-expressed in terms of the expected somatic lipid fraction (%) at spawning and compared to the observed somatic lipid fractions (from Chapters 3 and 4) for each group.

5.2.4 Lipid Utilization by Overwintering Autumn-Spawning Herring

Predicted lipid utilization during winter (September 1 - April 1) by both southern Gulf and sw Nova Scotia autumn-spawning herring was estimated from Equation 5.3. Initial storage lipid (L_0) was defined as the somatic lipid content (g) of fully mature, spawning herring (from Chapter 3 and Chapter 4). Initial total body weight (W_0) was estimated as:

$$W_O = W_S - W_G + 3.0 \qquad (5.4)$$

where W_S =Somatic weight (g) at length of spawning fish and W_G =gonad weight (g). A constant of 3g was added to W_0 to approximate the weight of spent (Gonad Maturity Stage 8; Table 2.1) gonads during winter (estimated from Hodder et al. 1972, 1973, and Iles unpub. data).

Predicted lipid utilization by southern Gulf autumn-spawners was estimated for two possible overwintering areas: Gulf of St. Lawrence and off sw Newfoundland (Figure 5.1)(NAFO Hydrographic Subregions Gulf of St. Lawrence and St. Pierre respectively). Similar calculations performed for sw Nova Scotia autumn-spawners assumed overwintering on Georges Bank, sw Scotian Shelf, Browns Bank, and eastern (e) Scotian Shelf (Figure 5.1)(NAFO Hydrographic subregions Georges Bank, Yarmouth, Browns Bank, and e Scotian Shelf respectively). A time period of 1 month was assumed for migration to overwintering areas. Therefore, monthly sea surface temperatures from the spawning area were used in the lipid utilization calculations for the month of September.

Whether post-spawning feeding by autumn-spawners (Parsons and Hodder 1975; Messieh et al. 1979; Crawford 1980; Iles 1984) affects their ability to conserve protein (Chapter 4) in winter conditions was assessed. Both southern Gulf and sw Nova Scotia herring were assumed to feed from September 1 - October 1 and then from September 1 - November 1, to support total metabolism (i.e., no gain of lipid or other somatic energy storage components). The model was then re-run using temperatures for the above potential overwintering areas assuming that lipid supported metabolism from either October 1 or November 1 through to April 1.

Somatic lipid condition (K_{SL}) factors (Years 1970 -

1972 inclusive) were calculated for spawning (September 1 ±14 days) and spent Scotian Shelf herring (sw Nova Scotia and eastern Scotian Shelf) as follows:

$$K_{SL} = \frac{Somatic\ Lipid}{Length^3} \cdot 10^6 \qquad (5.5)$$

with somatic lipid in grams, and length in mm (data obtained from T.D. Iles, DFO, St. Andrews, N.B.). These were plotted against time (days from September 1) to determine how somatic lipid content varied between time of spawning and the onset of winter (November 1).

5.3 Results

5.3.1 Relation of Respiration Rate and Lipid Depletion Time to Fish Length and Water Temperature

Simulations showed that respiration rate was sensitive to both fish length and temperature (Figure 5.2a). Respiration rates (ml $O_2 \cdot h^{-1}$) for 270mm and 390mm herring rose from 4.31 and 10.19 at 0 °C to 17.23 and 40.74 respectively at 20 °C. However, because the relative amount of storage lipid (g) increased with body size (Table 5.1), resistance to lipid depletion during gonad maturation also increased with body size (Figure 5.2b). In general, resistance to lipid depletion declined rapidly with temperature at all lengths (Figure 5.2b). Time (days) for 50% depletion of the initial lipids (W_0), i.e., routine

Figure 5.2. The relationship between: a) predicted respiration (ml $O_2 \cdot h^{-1}$); and b) predicted time for 50% depletion of somatic lipids (days) and fish length (mm) for given water temperatures ($^{\circ}C$) by non-feeding maturing herring with a pre-gonad maturation condition as in Table 5.1.

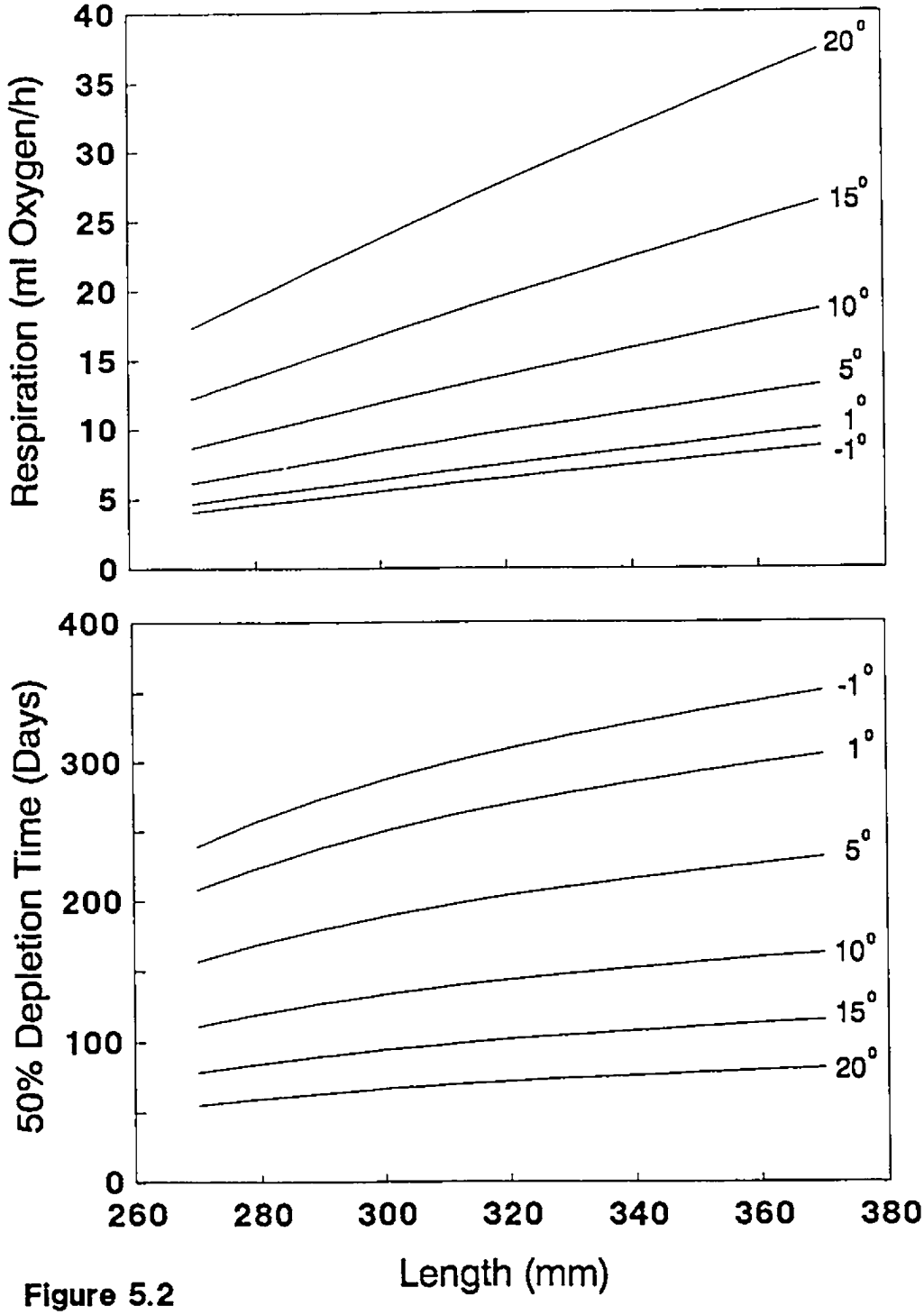
Respiration (ml Oxygen/h)
40
35
30
25
20
15
10
5
0
20°
15°
10°
5°
1°
-1°
50% Depletion Time (Days)
400
300
200
100
0
-1°
1°
5°
10°
15°
20°
260
280
300
320
340
360
380
Length (mm)

Figure 5.2

routine respiration = ½ of the fish's total respiration, were for 270mm and 390mm herring, 213 and 332 at 0 °C and 53 and 83 at 20 °C respectively.

5.3.2 Lipid Utilization by Spring- and Autumn-Spawning Southern Gulf Herring During Gonad Maturation

Predicted estimates of somatic lipid utilization (southern Gulf herring, Years 1971-1988) showed that spring-spawners would deplete relatively more storage lipid than autumn-spawners, at all lengths (Figure 5.3). The longer gonad maturation period for spring spawners affected respiration more than cooler gonad development temperatures could compensate for, particularly in small herring. Lipid was relatively more depleted for small (≤300mm) herring than for large (≥360mm) herring ($\geq 0.6L_0$ versus $\leq 0.5L_0$ respectively for both spawning groups; Figure 5.3).

5.3.3 Predicted Versus Observed Somatic Lipid Fractions for Spawning NW Atlantic Herring

Predicted and observed somatic lipid fractions (% of somatic weight) for fully mature southern Gulf spring- and autumn-spawning, and sw Nova Scotia autumn-spawning herring (Figure 5.4a-d) were in general agreement. For spring-spawning herring (n =70), 91% of the somatic lipid fraction

Figure 5.3. The relationship between the proportion of initial storage lipid predicted to be consumed by routine respiration during gonad maturation and fish length (mm) for spring (squares)- and autumn (crosses)- spawning southern Gulf of St. Lawrence (4T) herring (Years 1971-1987 inclusive).

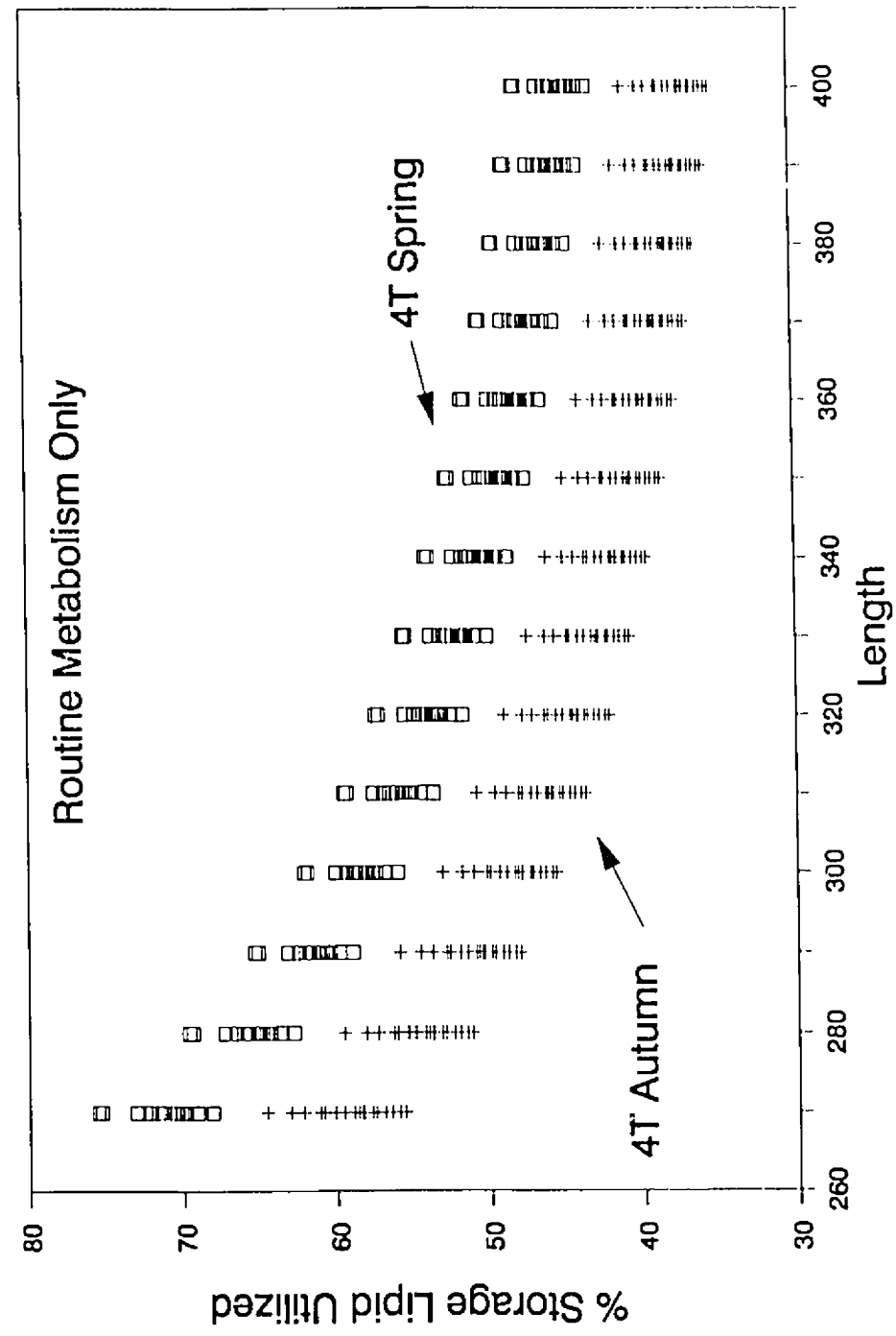
Routine Metabolism Only
4T Spring
4T Autumn
% Storage Lipid Utilized
80
70
60
50
40
30
Length
260
280
300
320
340
360
380
400

Figure 5.3

Figure 5.4. The relationship between observed (symbols) and predicted somatic lipid fractions (lines) and fish length (mm) for a) 4T spring-spawners, b) 4T autumn-spawners using monthly mean sea surface temperatures ($^{\circ}$C), c) 4T autumn-spawners at 8 $^{\circ}$C, and d) sw Nova Scotia autumn-spawners (predicted lipid remaining (% somatic weight) after routine respiration only (solid line) and routine plus active respiration (dashed line) of storage lipid).

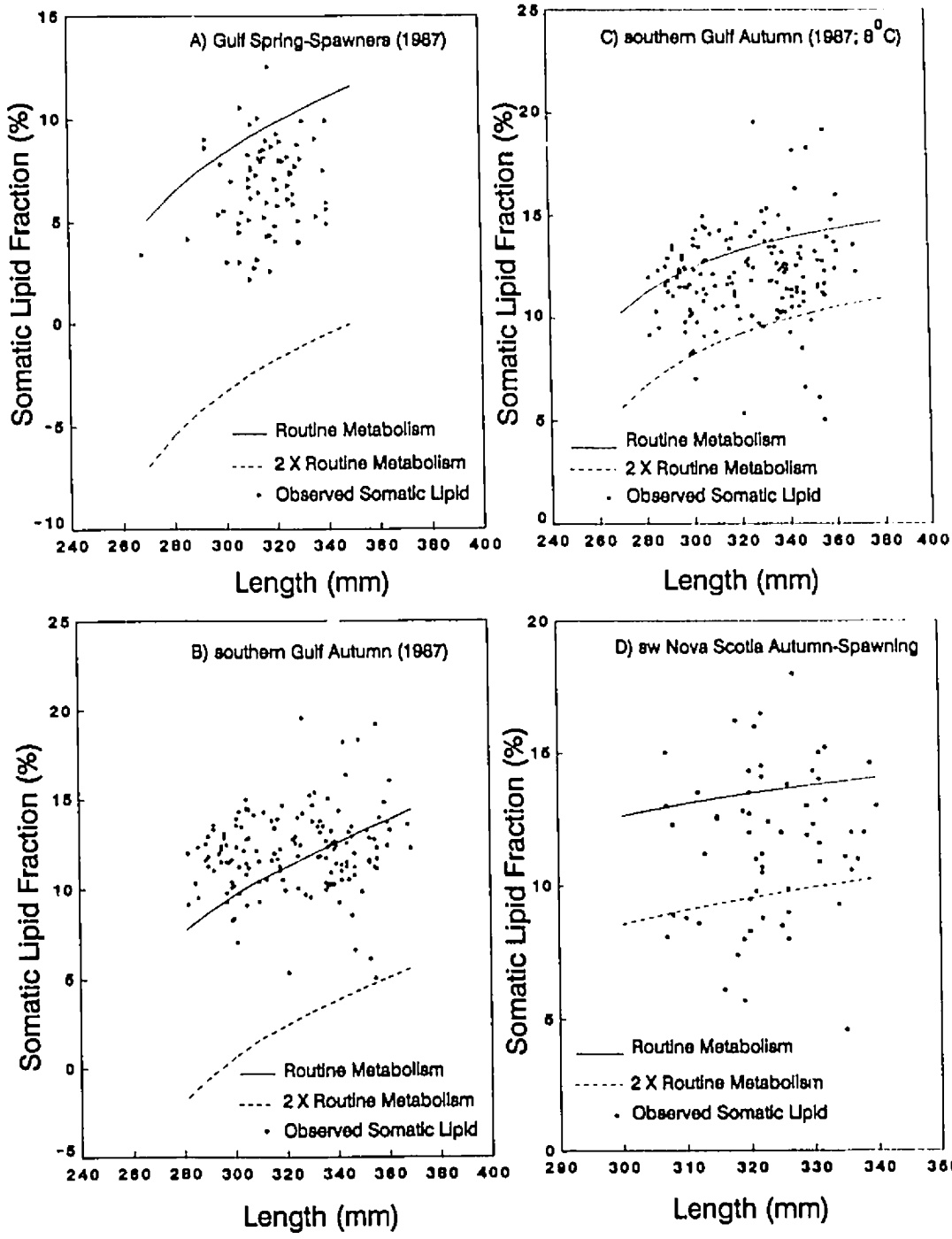
A) Gulf Spring-Spawners (1987)
C) southern Gulf Autumn (1987; 8°C)
B) southern Gulf Autumn (1987)
D) sw Nova Scotia Autumn-Spawning
Somatic Lipid Fraction (%)
Length (mm)
Routine Metabolism
2 X Routine Metabolism
Observed Somatic Lipid

Figure 5.4

determinations fell within the range predicted by their routine and total metabolic rates (Figure 5.4a). Less than half (48%) of the observed lipid fractions for southern Gulf autumn-spawning herring (n =147) fell within the predicted range (Figure 5.4b). However, sea surface temperatures are probably not representative of gonad development temperatures for these fish because the region is strongly thermally stratified during summer (Drinkwater 1987). Water temperatures can range between 6-10 °C at 20m depth in the Fishermans Bank region of the southern Gulf (Messieh and Rosenthal 1986, 1989). The lipid depletion model re-run using an average temperature estimate of 8 °C indicated that 67% of the observed somatic lipid fractions would lie within the predicted range, and 76% would lie below the predicted level of routine respiration (Figure 5.4c).

Forty-eight percent of the observed sw Nova Scotia herring somatic lipid fractions (n =60) fell within the predicted range for routine and total respiration and 77% lay below the level of routine respiration (Figure 5.4d). Sea surface temperatures are probably reasonably representative of gonad development temperatures for sw Nova Scotia herring since the water column in this region is vertically well-mixed by tidal action (Greenberg 1983).

Based on the results presented in this and the previous section it is concluded that the non-reproductive utilization of storage lipid during gonad maturation differs

among nw Atlantic herring populations that spawn during different seaons. Hypothesis 1 is rejected.

5.3.4 Lipid Utilization by Overwintering Autumn-Spawning Herring

Predicted somatic lipid content on April 1 (routine respiration only) for sw Nova Scotia autumn-spawning herring (n =83) differed among potential wintering areas (Table 5.2a). Southwest Nova Scotia herring wintering on the eastern Scotian Shelf would have more storage lipid (g) remaining on April 1, than would those wintering on Browns Bank, off sw Nova Scotia, or on Georges Bank (mean±1 standard deviation of lipid are 3.92 ±7.54g, -0.35 ±7.34g, 1.14 ±7.40g, and -2.45 ±7.25g for each group respectively). Tukeys multiple between group comparison test (equal sample sizes) showed that the mean storage lipid estimate for e Scotian Shelf differed from the other three groups whereas the Georges Bank estimate differed from that of sw Nova Scotia but not Browns Bank (Table 5.2b). Mean storage lipid estimates for sw Nova Scotia and Browns Bank did not differ (Table 5.2b).

Predicted storage lipid (g) on April 1 after routine respiration in winter conditions for southern Gulf autumn-spawners (n =129) did not differ between wintering areas (Gulf of St. Lawrence, 9.77 ±8.91g; sw Newfoundland, 8.18 ±8.73g; t_{stat} =1.461, df =256, P >0.05).

Table 5.2. a) ANOVA of lipid content (g) among sw Nova Scotia autumn-spawning herring that have overwintered on the eastern Scotian Shelf, Browns Bank, sw Nova Scotia, and Georges Bank, as determined from the lipid utilization model. b) Results of Tukeys multiple between-group comparison test (q), for equal sample sizes, of the modeled lipid contents. (df =degrees of freedom, F =F-ratio, P =Probabilility, * =differ at P <0.05)

A) Analysis of Variance

Source	Sum of Squares	df	Mean Square	F	P
Overwinter Location	1785.6	3	595.2	10.92	<0.001
Error	17870.6	328	54.5		

B) Tukeys Multiple Between-Group Comparison Results

	e Scotian Shelf	Browns Bank	sw Nova Scotia
eastern Scotian Shelf	———		
Browns Bank	4.268 *	———	
sw Nova Scotia	2.781 *	1.487	———
Georges Bank	6.371 *	2.103	3.590 *

Storage lipids at spawning (L_0) could not sustain total respiration ($2 \cdot R_T$) for either group of overwintering autumn-spawning herring, regardless of geographic location, from spawning (September 1) through to spring (April 1)(Figures 5.5 to 5.7, upper panels). Virtually all of the April 1 lipid content estimates are negative: i.e., herring would need to utilize protein to support total metabolism (Figures 5.5 to 5.7, upper panels). Feeding during September to sustain total respiration improved lipid conservation for all groups, but for all spawning group - wintering area combinations >80% of the April 1 lipid content estimates were negative (Figures 5.5 to 5.7, middle panels).

Southwest Nova Scotia herring (>72%) wintering on the e Scotian Shelf and southern Gulf herring (>95%) wintering throughout the Gulf of St. Lawrence could sustain their total respiration from November 1 - April 1 with storage lipids (L_0) (Figures 5.5 and 5.6, lower panels). The model predicts that only 35% of the sw Nova Scotia herring could winter on Georges Bank and not become depleted in storage lipid (Figure 5.7, lower panel).

A further accumulation of lipid after spawning was not evident. Somatic lipid condition (K_{SL}) of sw Nova Scotia herring was the same on November 1 for spent fish as it was on September 1 for both spawning and spent fish (Figure 5.8).

Figure 5.5. Predicted somatic lipid content on April 1 of spent, southern Gulf autumn-spawners after overwintering in the southern Gulf of St. Lawrence while fasting from a) September 1 to March 30, b) October 1 to March 30, and c) November 1 to March 30.

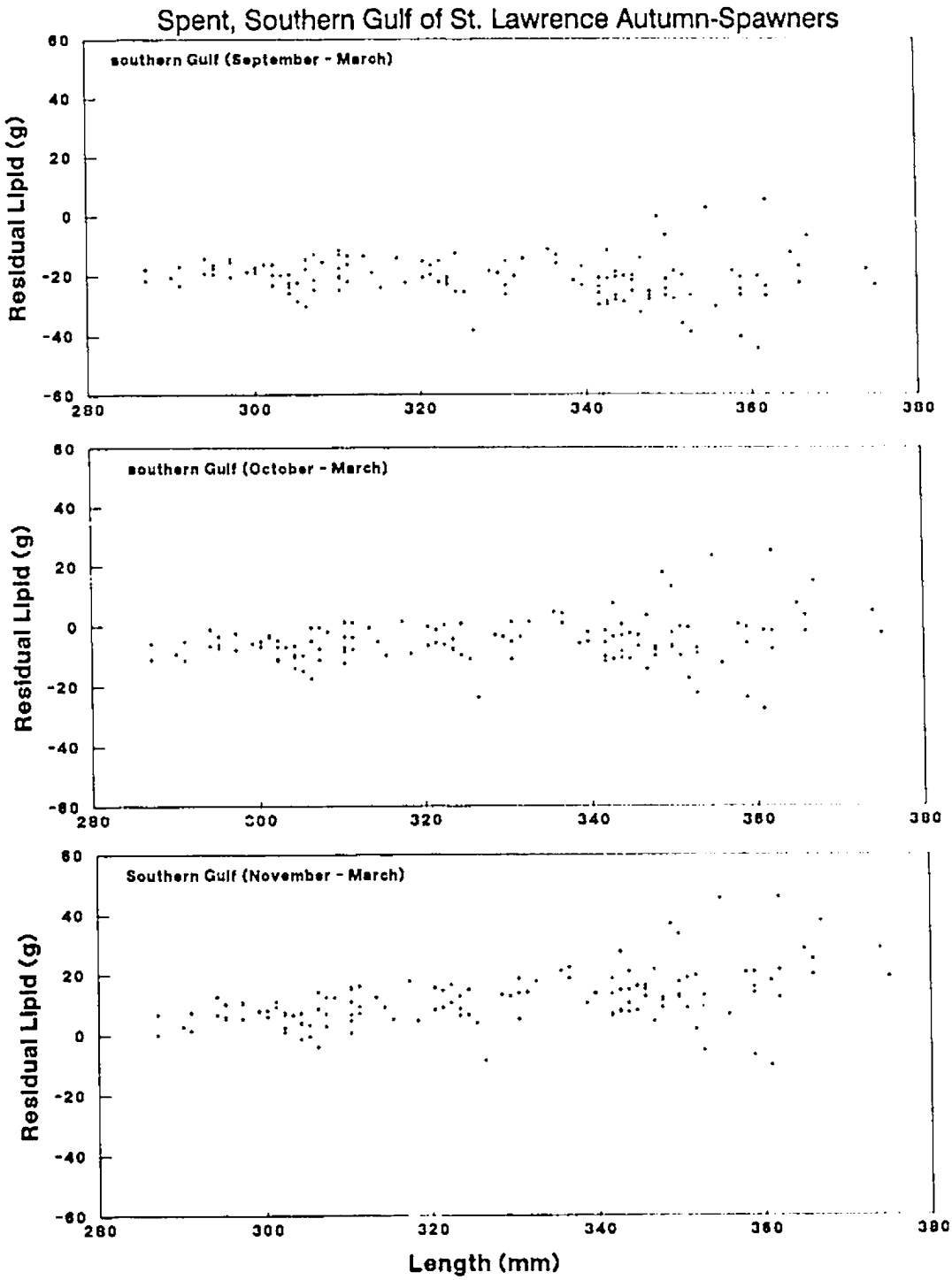
Spent, Southern Gulf of St. Lawrence Autumn-Spawners
southern Gulf (September - March)
southern Gulf (October - March)
Southern Gulf (November - March)
Residual Lipid (g)
Length (mm)
60
40
20
0
-20
-40
-60
280
300
320
340
360
380

Figure 5.5

Figure 5.6. Predicted somatic lipid content on April 1 of spent, southwest Nova Scotia autumn-spawners after overwintering along the eastern Scotian Shelf while fasting from a) September 1 to March 30, b) October 1 to March 30, and c) November 1 to March 30.

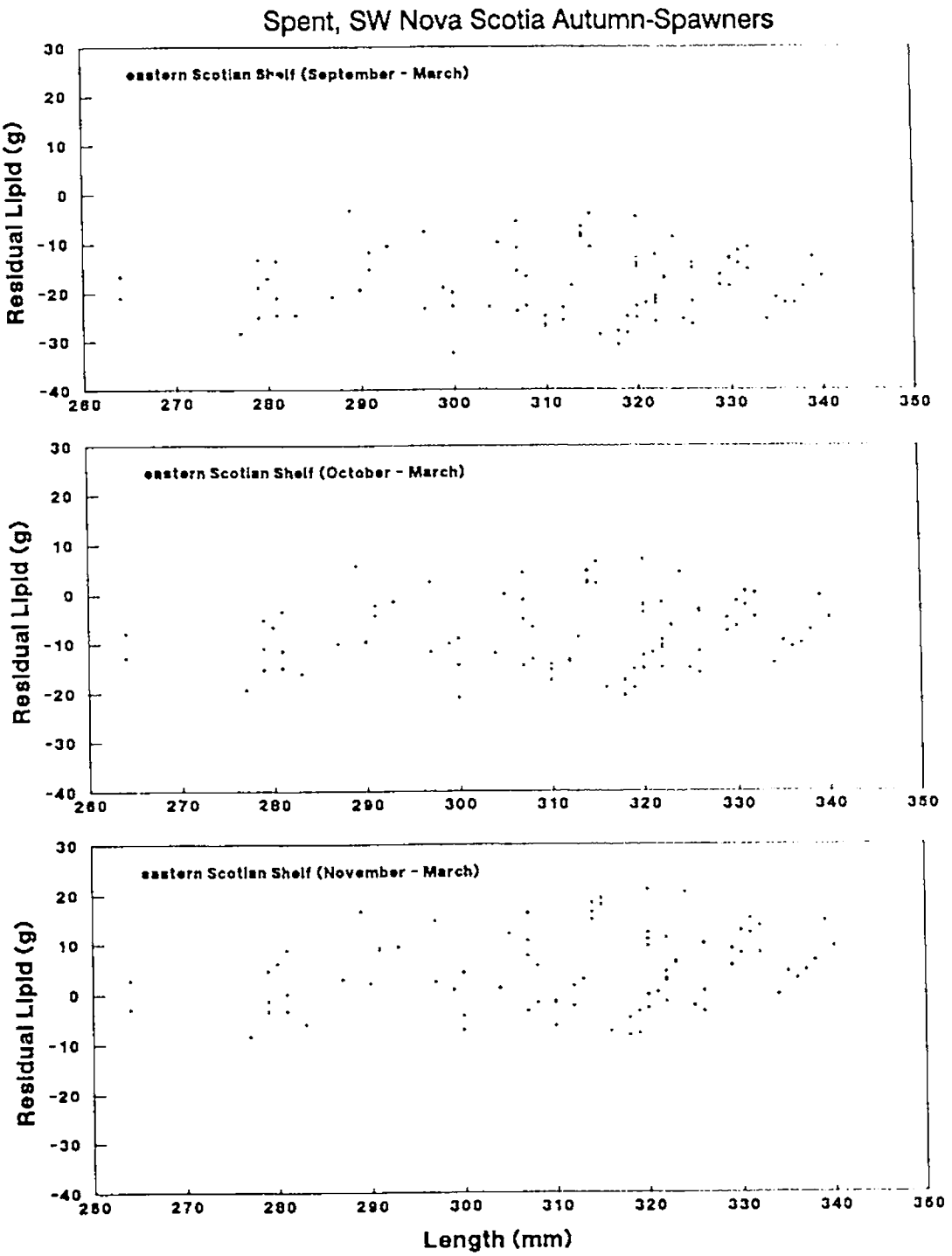
Spent, SW Nova Scotia Autumn-Spawners
eastern Scotian Shelf (September - March)
eastern Scotian Shelf (October - March)
eastern Scotian Shelf (November - March)
Residual Lipid (g)
Length (mm)
30
20
10
0
-10
-20
-30
-40
260
270
280
290
300
310
320
330
340
350

Figure 5.6

Figure 5.7. Predicted somatic lipid content on April 1 of spent, southwest Nova Scotia autumn-spawners after overwintering on Georges Bank while fasting from a) September 1 to March 30, October 1 to March 30, and c) November 1 to March 30.

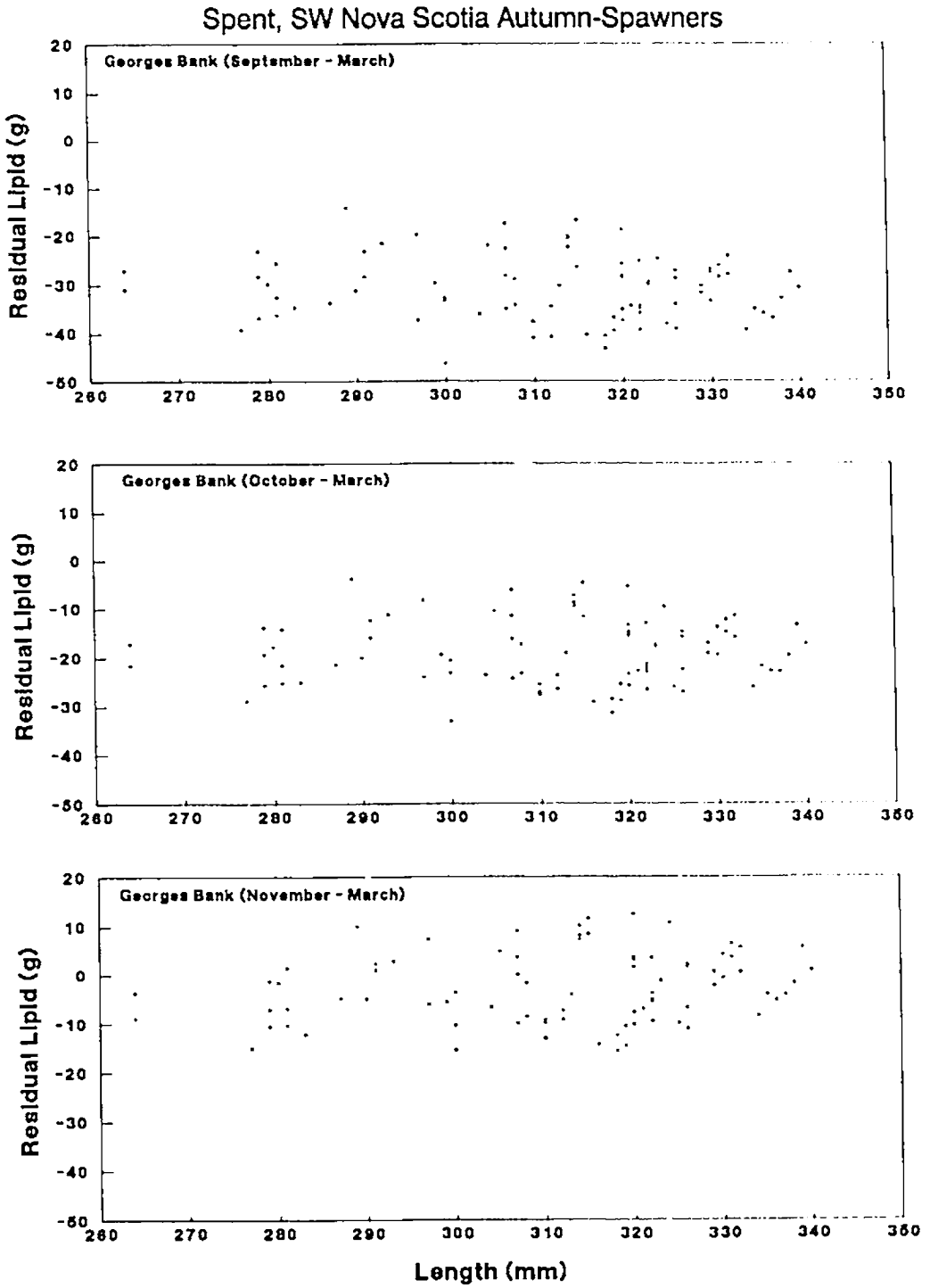
Spent, SW Nova Scotia Autumn-Spawners
Georges Bank (September - March)
Georges Bank (October - March)
Georges Bank (November - March)
Residual Lipid (g)
Length (mm)
20
10
0
-10
-20
-30
-40
-50
260
270
280
290
300
310
320
330
340
350

Figure 5.7

Figure 5.8. Somatic lipid condition (g lipid $\cdot length^{-3} \cdot 10^{6}$) of fully mature (circles) and spent (squares) southwest Nova Scotia autumn-spawners versus time (days from September 1).

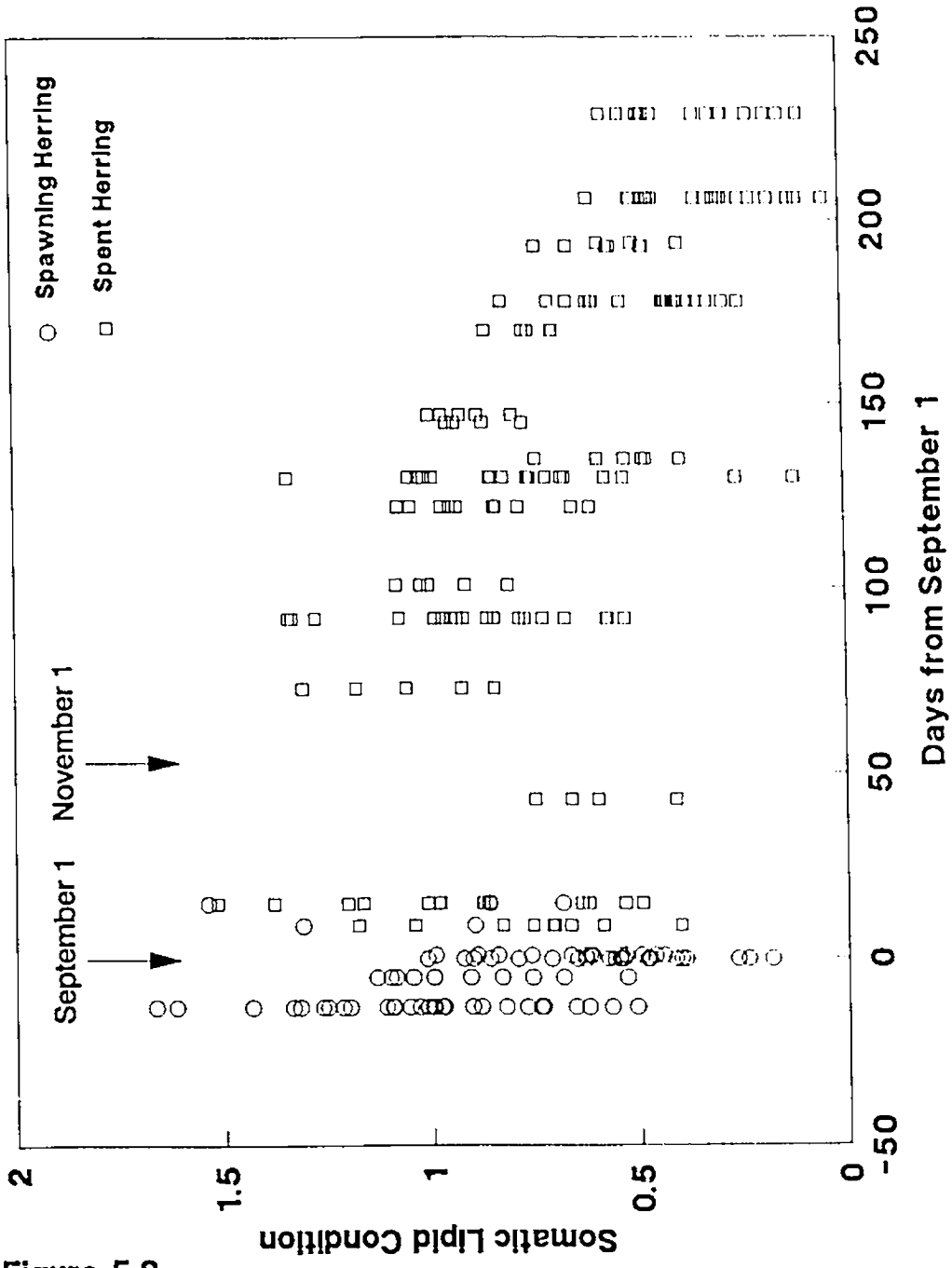
Spawning Herring
Spent Herring
September 1
November 1
Somatic Lipid Condition
Days from September 1
2
1.5
1
0.5
0
250
200
150
100
50
0
-50

Figure 5.8

This analysis indicates that the proportion of storage lipid not utilized during gonad maturation by autumn-spawning herring cannot support their post-spawning metabolic demand in winter conditions. Hypothesis 2 is rejected. However, the analysis also indicates that a further accumulation of lipid after spawning is probably not necessary provided the herring can sustain their total metabolism by feeding up to November.

5.4 Discussion

Spring-spawning herring are more susceptible to excessive depletion of storage lipid during gonad maturation than are autumn-spawning herring. Even though cooler temperatures tend to depress the rate of respiration (Figure 5.2a,b), the extensive time required for gonad maturation by spring-spawners results in a high lipid depletion relative to autumn-spawners, at all lengths (Figure 5.3). Routine metabolism alone could utilize more than 50% of the storage lipids in herring (Figure 5.3). For most herring the total non-reproductive (routine + active metabolism) utilization of storage energy will be even greater (Figure 5.4). The likelihood for a re-allocation of energy stored as protein, initially destined for gonad production, to non-reproductive functions is therefore highest for spring-spawning herring.

Gonad production is likely to be more adversely affected by non-reproductive energy utilization in small (≤275mm) herring than large (≥320mm) herring. Small herring from populations with long gonad maturation periods are particularly susceptible to non-reproductive utilization of protein (routine respiration alone could require ≈60%L_0 and >70%L_0 for ≤275mm autumn- and spring-spawners respectively, Figure 5.3). Herring are concluded to be subject to the same body size related constraints on gonad production known for other fish species that also utilize storage energy during gonad maturation (eg. American shad, Glebe and Leggett (1981a); cisco, Lambert and Dodson (1990a)).

Autumn-spawning herring probably need to feed after spawning in order to conserve protein in winter conditions, but only to maintain total respiration. Further accumulations of lipid after spawning, predicted to be unnecessary (Figures 5.5 to 5.7), apparently do not occur (Figure 5.8). However, further accumulations of lipid by herring that spawn during autumn may be problematic since zooplankton lipid content can decline from spring to autumn in association with successional changes in zooplankton species composition (Sargent and Henderson 1986). For example, in St. Georges Bay, N.S. (southern Gulf) the total lipid content of herring forage sized plankton (250 - 2000 μm) is 2x - 4x lower (depending on size fraction) during August - November than during June - July (Marine Ecology

Laboratory 1980). The accumulation of lipid by nw Atlantic herring, regardless of spawning season, is maximum during June - July (Stoddard 1968; Varga et al., 1975). This also suggests that the high pre-winter storage lipid content of spring-spawners relative to autumn-spawners (Figures 4.3 and 4.7, Chapter 4) results from differences in the timing of storage lipid utilization.

Both southern Gulf and sw Nova Scotia autumn-spawning herring resume feeding after spawning, but at a low rate of intensity (inferred from prevalences of stomach fullness indices, see Parsons and Hodder 1975; Messieh et al. 1979; Crawford 1980). Feeding virtually ceases for both groups by November (Parsons and Hodder 1975; Messieh et al. 1979). These observations are also consistent with the conclusions that post-spawning feeding (by autumn-spawners) is necessary only to sustain herring total metabolism.

Differences in winter migration behaviour between southern Gulf and sw Nova Scotia herring appear to be explained by the present analysis. Storage lipids could sustain wintering southern Gulf herring regardless of their specific geographic location within the Gulf of St. Lawrence (Section 5.3.4). In contrast, sw Nova Scotia herring will utilize less lipid by wintering on the eastern Scotian Shelf than in any other regions that are proximal to their spawning area (Table 5.2; Figures 5.6 and 5.7).

Other factors also suggest that water temperatures in

the wintering areas are important to adult herring survival. Gulf of Maine autumn-spawning populations (e.g., western Maine, Nantucket Shoals, Georges Bank) winter in the inshore regions of the southern Gulf of Maine (Stobo 1983). Feeding intensity is higher during October for Gulf of Maine herring than for sw Nova Scotia herring (Messieh et al. 1979). Gulf of Maine herring also spawn later in the autumn than do sw Nova Scotia herring (average peak spawnings for Georges Bank and Nantucket Shoals herring are October and November respectively, Boyar 1968; Grimm 1983). Herring in the region south of New England spawn during November and December (Colton et al. 1979). The combination of later feeding and later spawning delays the onset of storage lipid utilization and shortens the duration of the fasting period for the more southerly spawning herring populations, under conditions of warmer but shorter winters with decreasing latitude (Thompson et al. 1988). Similarly, populations with brief overwintering periods (December - February spawning populations, Iles 1964) dominate the southern breeding range of herring in the northeast Atlantic (Parrish and Saville 1965; Cushing 1967; Haegele and Schweigert 1985).

It is concluded that the duration of the maturation period can influence both gonad production (Chapter 2) and the physiological condition of spawning herring (Chapter 3). Patterns of within-population variability in lipid

utilization support the existence of a link between non-reproductive versus reproductive utilization of storage energy, as has been shown for other fish species. Post-spawning feeding appears to be essential for the survival of autumn-spawning herring in winter conditions, but a further accumulation of storage energy is not neccessary in order to conserve protein. Overwintering location affects lipid utilization by sw Nova Scotia autumn-spawning herring more than for southern Gulf autumn-spawning herring. Overwintering distributions of herring, determined previously by tagging studies, are predicted from the lipid utilization model with the criterion of minimizing lipid depletion.

Chapter 6

Northwest Atlantic Herring Spawning: Timing and Periodicity

6.1 Introduction

Atlantic herring (*Clupea harengus harengus L.*) have population specific spawning grounds to which individuals are thought to home each year (Harden-Jones 1968; Iles and Sinclair 1982; Wheeler and Winters 1984a). On the spawning grounds, fertilized, negatively buoyant, adhesive eggs are deposited on the sea bottom where they remain during incubation (Henri et al. 1985; Blaxter and Hunter 1982). Both the seasonal timing and geographic location of spawning by individual populations are highly predictable (Iles and Sinclair 1982; Chadwick and Claytor 1990). However, the act of spawning by individual herring (incorporation of fertilized eggs into a demersal egg matrix) remains one aspect of herring life-history that has rarely been studied directly. Most egg beds are difficult to access because spawning grounds are tidally energetic and wave-exposed (Haegele and Schweigert 1985), egg incubation periods are commonly only 5-15 days (Messieh 1988), and spawning often occurs during unsettled weather (Lambert 1984).

Herring spawning times are usually deduced from analysis of the time of arrival of herring on their spawning grounds, back-calculation of larval growth rates to their hatching date, and the capture of herring with freely

running gametes (Jean 1956; Cushing 1959; Lauzier and Tibbo 1965; Graham and Chenoweth 1973; Berenbeim and Sigajev 1978; Ware and Henriksen 1978; Crawford 1979; Grimm 1983; Lambert 1984, 1987; Messieh 1977, 1986, 1987, 1988; Chadwick and Claytor 1989). These indicators suggest that spawning for individual populations is a continuous process within the spawning season, but that spawning intensity may vary within the spawning period as either single (Blaxter 1985) or multiple 'waves' (Lambert 1984, 1987). External cues (ie. lunar-tidal influences) for spawning have been rejected for nw Atlantic herring populations based on analyses of fisheries data (Ware and Henriksen 1978; Lambert 1987). However, direct observations of the genesis of egg beds for ne Atlantic herring (e.g., Milford Haven, Clarke and King 1985) and information from fishermen (see Ware and Henriksen 1978; Crawford 1979) indicate that spawning may be related to the spring-neap tidal cycle.

Resolving which factors regulate spawning activity in herring is important to understanding herring population biology, assuming that populations are self-sustaining components (Sinclair 1988). Gonad maturation rates vary between sexes for spring (May-June)-spawners but not for autumn (August-September)-spawners (Chapter 4). Herring utilize storage energy during gonad maturation (Chapter 4) which means that gonad weight at length can be affected both by the duration of the maturation period and water

temperatures during gonad maturation (Chapters 2,4 and 5). Yet within populations, herring of both sexes must spawn at the same time and the same place while not diverting energy from gonad.

This chapter assesses what data is required to adequately resolve herring spawning biology. Two specific hypotheses are tested:

1) Catch, effort, and gonad maturity data obtained from fisheries based on spawning populations accurately predict spawning duration and location.

2) The spring-neap tidal cycle does not influence the timing of discrete egg bed deposition.

Data obtained by direct observations of egg bed deposition times for autumn-spawning southern Gulf of St. Lawrence (southern Gulf) herring is the basis for analysis.

6.2 Materials and Methods

6.2.1 Data Sources

Dates of deposition, areas (m^2), and egg abundances (eggs $\cdot m^{-2}$) for individual egg beds deposited on Fishermans Bank, P.E.I. (Figure 6.1) for the years 1985-1989 were

Figure 6.1. Map of the southern Gulf of St. Lawrence area showing the location of Fishermans Bank where spawning occurs during August and September.

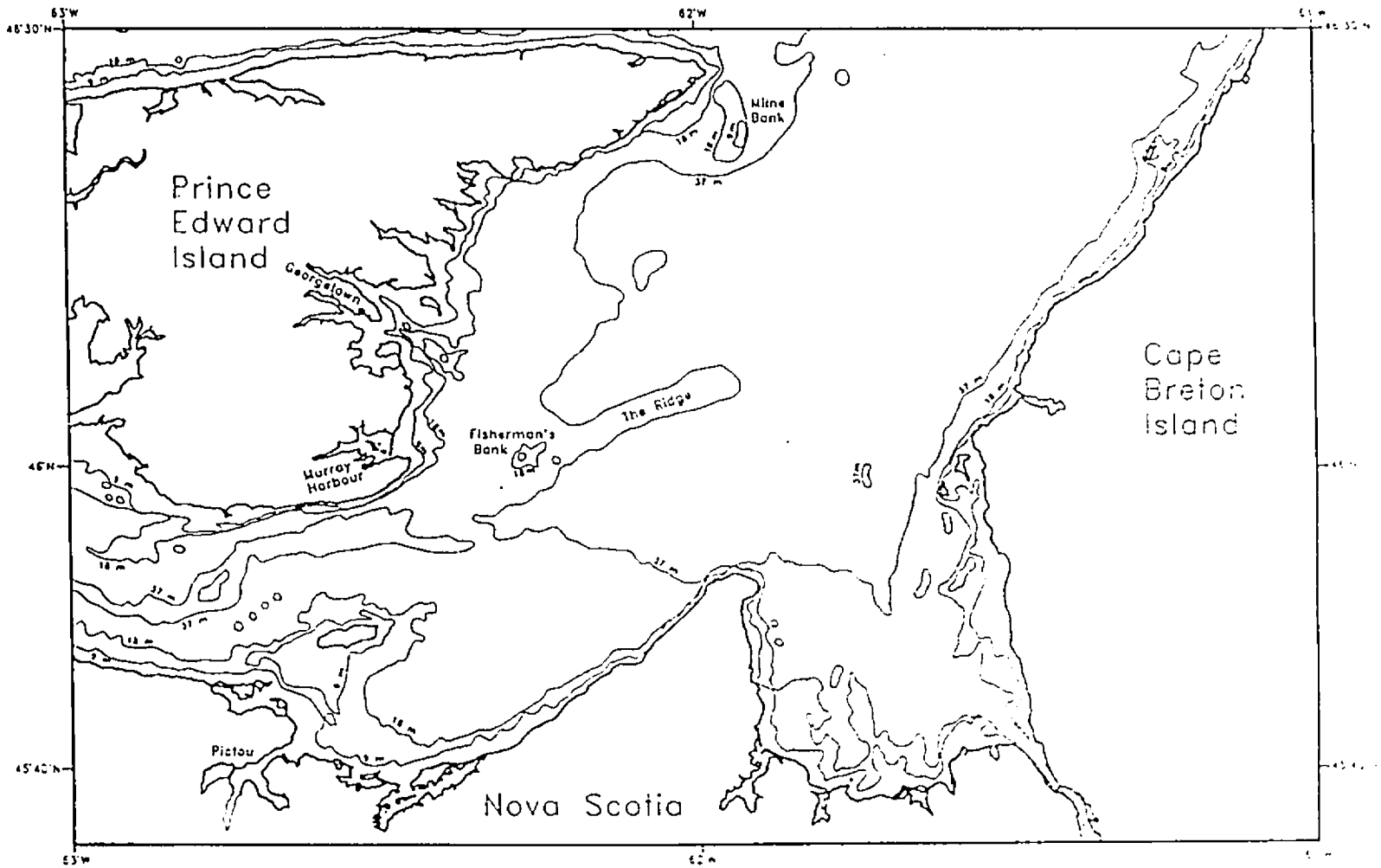
63°W
62°W
46°30'N
46°N
45°40'N
Prince
Edward
Island
Georgetown
Murray
Harbour
Fisherman's
Bank
The Ridge
Milne
Bank
Cape
Breton
Island
Pictou
Nova Scotia

Figure 6.1.

obtained from Dr D. Cairns and Dr. M. Chadwick (DFO, Moncton, N.B.) Fishermans Bank is an important regional autumn-spawning ground in the southern Gulf (Messieh 1988). Daily commercial landings and biological information from port samples from fisheries statistical district 387, which includes Fishermans Bank, were also obtained from Drs. Cairns and Chadwick.

Annual surveys, since 1985, of herring spawning beds on Fishermans Bank have shown that spawnings occur within a relatively shallow ($\approx$12 km^2) region of the bank bounded by the 30m contour (Figure 6.1). The sampling protocol is detailed in Messieh (1988). Briefly, egg beds are located using a search grid of uniformly spaced (400m) stations checked daily with an underwater video camera operated remotely from the surface vessel. Complete coverage of the bar' is possible within 1 work day (weather permitting). Second day coverage proceeds along a 400m grid offset 200m from that of the previous day. This provides a 2 day spatial resolution of 200m. The search pattern is repeated every few days for the duration of the spawning period on the bank and is considered a reliable indicator of spawning activity.

6.2.2 Usefulness of Fisheries Statistics as an Indicator of Spawning Activity.

Known dates of deposition for discrete egg beds were compared to landings and gonad maturation data to determine whether proxy variables could resolve the temporal scale of discrete spawnings. Daily landings (standardized to kg herring·trip^{-1}), for each year of the fishery from 1985-1989 were plotted against day of capture. Known, or estimated dates of deposition (from temperature-egg development data; Messieh 1988), for all detected egg beds were also plotted to determine whether a) landings were recorded for each date of deposition and b) the dates for recorded spawnings and peaks in landings were coincident.

In order to determine whether landings of spawning herring are related to known spawning activity the daily CPUE data was divided into its non-spawning, spawning and spent constituents (ICES Herring Gonad Maturity Scale; Table 2.1). If the assumption that maturity data indicates spawning activity (Lambert 1984) is robust then all daily CPUE's of 'spawning' herring should coincide with a documented egg deposition. This procedure assumed that the camera search pattern had a probability of 1 of recording all major spawning activity. This is valid as the short axis of the egg beds was in all instances >200m (the 2 day resolution of the search procedure).

6.2.3 Tidal Influences on Spawning Behaviour.

The Fishermans Bank spawning bed survey data allowed assessment of lunar-tidal related influences on spawning behaviour. This was possible because a) most beds were located while the eggs were in early development, increasing the certainty of their formation date, b) the spatial dimensions of each bed were known to within ±100m (Messieh 1988) and c) the relative proportion of the total egg production incorporated into each egg bed could be approximated from egg abundance data collected routinely over the course of the surveys (see Messieh 1988 for details of the sampling protocol).

Egg deposition dates were grouped into lunar quartiles, as listed in the *Canadian Almanac and Directory* (Bracken, Years 1985-1989). Spring tide spawnings were defined as those that occurred within ±3 days of a full or new moon. Neap tide spawnings were defined as those within ±3 days of a 1st quarter or 3rd quarter. No spawnings occurred on dates intermediate between these spring and neap tide periods. Further assessments proceeded with a) contingency table analysis of spawning on lunar quartiles and on spring tides, and b) the relative proportion of the total annual spawn production as a function of days from a new or full moon.

6.3 Results

6.3.1 Usefulness of Fisheries Statistics as an Indicator of Spawning Activity.

Daily landings fluctuated considerably, during all years, and independently of both herring abundance and spawning activity since zero landings often coincided with weekends when no fishing occurred (Figures 6.2a-d). Two of the three spawnings identified from the egg bed survey for 1985 occurred during a weekend with no concurrent fishery (Figure 6.2a). Furthermore, there was no coherence between spawning activity and CPUE even when spawning and fishing were concurrent events. Spawnings occured on nights of 'average' landings (Figure 6.2b). Peaks in daily landings did not always correspond to spawning dates although landings were generally greater within 1 or 2 days on either side of known spawning dates (Figure 6.2c,d).

Fish with freely extruded reproductive products ('ripe and running') were captured on Fishermans Bank during nights with no detectable egg bed depositions (Table 6.1), often at abundances of fish equal to or greater than those associated with detectable egg bed depositions (Table 6.1). The minimum CPUE of ripe and running herring on a known date of spawning was 3718.2 kg herring$\cdot$trip^{-1}. Landings exceeded this value on 5 of 10 nights for which no egg bed depositions were documented.

Table 6.1. Landings of herring on Fishermans Bank determined to be in spawning condition from port samples listed for dates of known spawnings and dates with no recorded spawnings (----) for the years 1985-1988 inclusive.

Date of Sampling	CPUE(MT/Trip) Spawning	Non-Spawning
Aug 22 1985	-----	2074.4
Sept 19 1986	-----	3904.5
Aug 18 1987	-----	2938.4
Aug 19	-----	2707.8
Aug 20	-----	2255.6
Aug 24	3718.2	-----
Aug 27	-----	5416.0
Aug 28	-----	5537.5
Sept 8 1988	4322.0	-----
Sept 13	-----	2154.0
Sept 15	-----	8620.8
Sept 21	-----	8458.7

Figure 6.2. Daily landings standardized to catch per unit of effort (CPUE= $kg \cdot 10^{-5} \cdot trip^{-1}$) for Statistical District 387 (including Fishermans Bank) for the years 1985-1989 inclusive. Dates for which spawnings have been documented from egg bed surveys (arrows), Sundays (dark circles), and the start and finish of the annual spawning bed surveys (dashed lines) are noted.

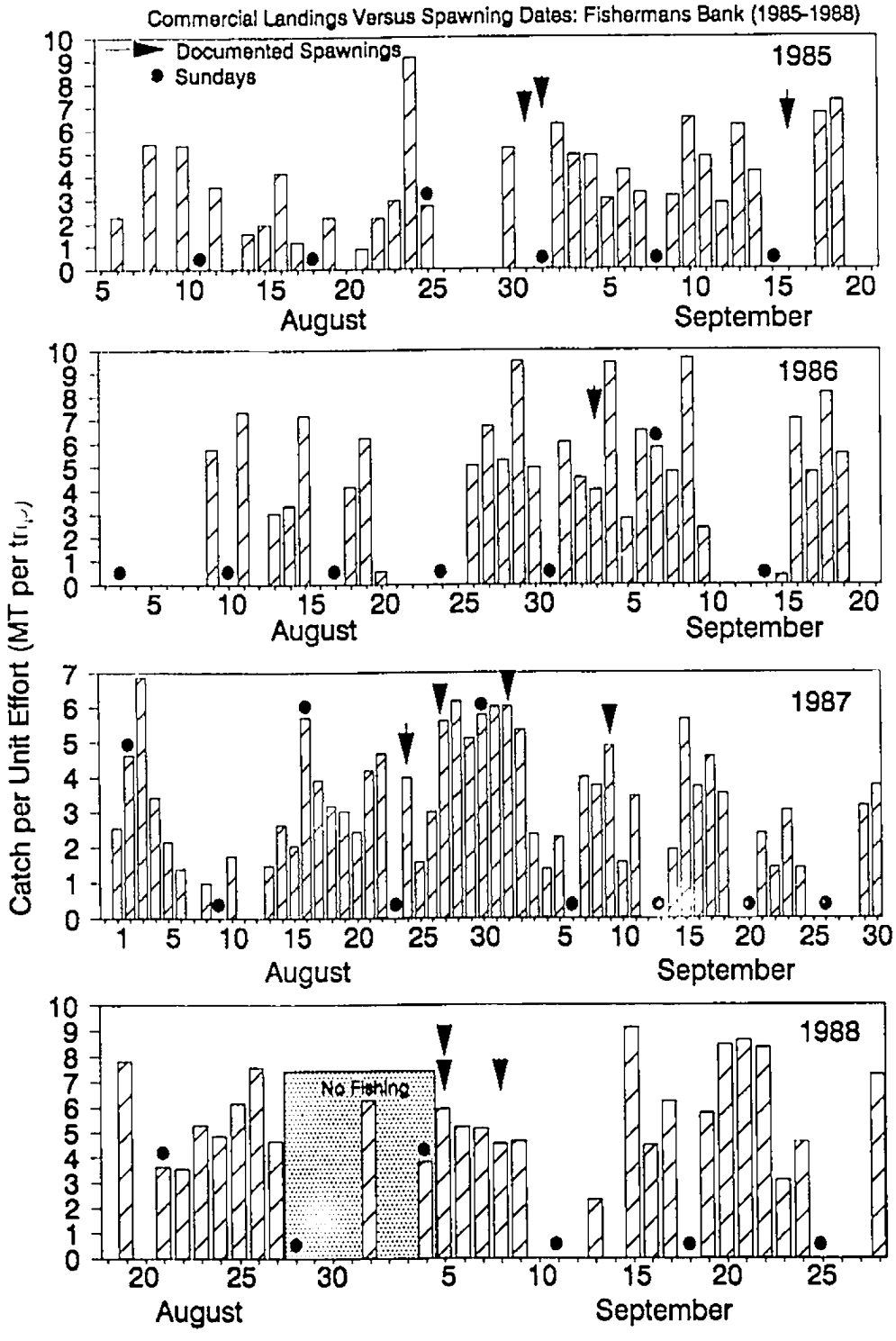
Commercial Landings Versus Spawning Dates: Fishermans Bank (1985-1988)
Documented Spawnings
Sundays
1985
1986
1987
1988
No Fishing
Catch per Unit Effort (MT per trip)
August
September

Figure 6.2

6.3.2 Tidal Influences on Spawning Activity.

Date of spawning is not statistically related to either lunar quartile (Tables 6.2 and 6.3) or the spring-neap tidal cycle (Table 6.3). However, the total estimated spawn deposited near spring tides (Table 6.4a,b), shows that spring-tide spawnings are biologically significant. For all years more than 75% of the estimated total egg production is deposited during spring tides and for all years except 1987 the magnitude of the spring tide spawnings was >90% of the estimated total egg production (Table 6.4a,b).

6.4 Discussion

Daily landings data from fisheries do not resolve spawning activity on time scales finer than that of the spawning season. Peaks in landings can be related to effort but not neccessarily to spawning activity. Most of the days with zero landings result from curtailed fishing operations on weekends. While it is not certain that all landings are taken directly on the spawning grounds, most will be from these highly localized fisheries (pers. ob.; D. Cairns, per. comm.). Runnstrom (1941) also concluded that landings data did not always reflect the relative proportion of herring present on the spawning grounds.

Gonad maturation data does not improve the resolution

Table 6.2. Known dates of individual egg bed depositions on Fishermans Bank from 1985-1989 grouped according to the corresponding lunar quartile.

Year	Lunar Quarter				Total
	Full	Last	New	First	
1985	2	1	2	0	5
1986	0	0	1	0	1
1987	1	0	2	1	4
1988	0	1	1	0	2
1989	0	0	2	2	4
Total	3	2	8	3	16

Table 6.3. Chi-square analysis of the pooled date of spawning data (Years 1985-1989) by a) lunar quartile and b) spawning on spring tides or not.

a)	Lunar Quarter				
Pattern	Full	Last	New	First	n
Observed	3	2	8	3	16
Expected	4	4	4	4	16
$[(O-E)^2/E]$	.25	1	4	.25	
	$\chi^2 = 5.5$; $\chi^2_{(.05,3)} = 7.815$				

b)	Spring	Not Spring	
Pattern	Tide	Tide	n
Observed	11	5	16
Expected	8	8	16
$[(O-E)^2/E]$	1.125	1.125	
			$\chi^2 = 2.25$; $\chi^2_{(.05,1)} = 3.841$

Table 6.4. Relative proportion of the total annual egg deposition on Fishermans Bank (1985-1989) a) for each lunar quartile, and b) in relation to the days from the nearest spring tide.

a)	Lunar Quarter			
Year	Full	Last	New	Full
1985	0.195	<0.01	0.805	0.0
1986	0.0	0.0	1.000	0.0
1987*	0.309	0.0	0.447	0.244
1988*	0.0	0.04	0.960	0.0
1989	0.0	0.0	0.780	0.12

b)	Days From Spring Tide						
Year	1	2	3	4	5	6	# Ob
1985	0.17	0.83	0.0	0.0	<.01	0.0	5
1986	1.00	0.0	0.0	0.0	0.0	0.0	1
1987*	0.10	0.66	0.0	0.0	0.0	0.24	4
1988*	0.0	0.96	0.0	0.0	0.04	0.0	3
1989	0.0	0.45	0.35	0.0	0.15	0.05	4

* - Quantitative estimates of egg abundance are unavailable. The relative magnitudes of individual spawnings have been estimated on the basis of egg bed areas.

of spawning time estimates obtained from fisheries statistics. Landings of ripe and running herring, in quantities associated with detectable egg bed depositions at other times, are reported for nights with no known spawnings. Ripe and running herring have also been captured on Georges Bank several days before egg bed depositions were detected (via benthic grab samples, Pankratov and Sigajev 1973). However, these authors did not provide daily landings information.

The results show that fishery statistics are a poor basis to evaluate the importance of external cues to spawning activity. Therefore the rejection of external cues to spawning activity cannot be justified on this basis alone, as was done by Ware and Henriksen (1978) and Lambert (1987) for southern Gulf of St. Lawrence herring. The capture of fish which readily extrude their reproductive products merely shows that some members of the population are sufficiently mature that they can ovulate when traumatized. Rigorous assessments of the timing, duration and intensity of spawning requires careful documentation of the deposition of individual egg beds. Iles (1964, 1984) proposed that the process of gonad maturation is distinct from that of spawning, with the two stages separated by the event of ovulation. The present analysis tends to support this view. Many herring of either sex would need to remain in a highly advanced stage of gonad maturation for several

days upon their arrival on Fishermans Bank if they are to ovulate and spawn on the known dates of egg bed deposition.

The dates of egg bed deposition on Fishermans Bank are not statistically related to either lunar quartiles or the spring-neap tidal cycle (Table 6.3). However, 45% or more of the total annual egg production is deposited within 3 days of a new moon (Table 6.4a) and 75% or more within 3 days of a spring tide (Table 6.4b). Evidently external cues related to tidal action are a potentially vital element of the spawning biology of some populations of Atlantic herring. Fishermans Bank herring appear to have a tendency to spawn on spring tides while herring in Milford Haven spawn predominantly on neap tides (documented by surveys of the spawning grounds, Clarke and King 1985). Therefore, it also appears that no common singular spawning time-tidal cycle relationship is to be expected for all populations.

It is concluded that Atlantic herring spawning biology is too complex to be resolved solely from fisheries statistics, as had been previously assumed. Careful documentation of discrete egg bed formation events is required to conclusively resolve which factors regulate the timing, duration and intensity of spawning. Future investigations must distinguish between time of arrival and time of spawning, and identify the factors which regulate each process. These goals should be possible by augmenting daily spawning bed surveys with intensive daily sampling of

the length and age composition of herring from their first arrival on the spawning grounds to the known days of spawning. External physical factors cannot be rejected as important determinants of spawning time and duration, but further research is required in order to substantiate their importance.

Chapter 7

Discussion and Conclusions

7.1 Introduction

The population richness (populations per species; Sinclair 1988) of Atlantic herring is one of the highest known for a marine fish (Sinclair and Iles 1988; Sinclair 1988). Utilization of storage energy to develop gonad allows herring to reproduce at times and in locations where zooplankton production is otherwise too low to sustain maturing fish (e.g., winter and early spring-spawning North Sea herring (Iles 1964; 1974)). However, this thesis has demonstrated that the decoupling of gonad maturation from simultaneous feeding imposes energetic constraints on herring reproduction. Realized reproductive effort varies among populations with different spawning seasons as a function of non-reproductive energy utilization. Spring-spawners, having a higher non-reproductive energy demand than autumn-spawners (Chapter 5), develop less gonad material than do autumn-spawners (Chapter 2). Differences in reproductive effort among herring of the same size, with different spawning seasons, has not previously been considered a limiting factor to the distribution of herring populations. This chapter evaluates whether energetic constraints on reproduction can explain some general features of the distribution of herring populations, specifically the latitudinal limits of spawning, and the

greater tendency for autumn-spawning populations in tidally energetic environments.

7.2 Latitudinal Limits of Herring Spawning

Throughout the breeding range of Atlantic herring, spring-spawning populations are most prevalent at high latitudes whereas autumn-spawning populations are most prevalent at low latitudes (Parrish and Saville 1966; Haegele and Schweigert 1985). In the nw Atlantic, both the southern limit of breeding (≈Cape Cod) and the greater prevalence of herring populations with brief maturation periods (autumn-spawners) with decreasing latitude are predictable from analysis of latitudinal differences in storage lipid utilization during gonad maturation. Equation 5.3 predicts, using average monthly sea surface temperatures (Years, 1971-1987) for NAFO Hydrographic subregions between sw Newfoundland and the mid-Atlantic Bight (Drinkwater and Trites 1988), that:

a) Lipid utilization by spring-spawning herring during gonad maturation will increase with decreasing latitude. Estimates of storage lipid depletion (percent of initial storage lipid) for routine respiration by average sized spring-spawners (320mm) range from ≈50% off of sw Newfoundland, to ≈70-75% on Georges Bank and southern New England (Figure 7.1a).

b) Lipid utilization by autumn-spawning herring during

Figure 7.1. Predicted depletion of intitial storage lipids during gonad maturation by hypothetical populations of nw Atlantic a) spring- and b) autumn-spawning herring (1, mid-Atlantic Bight; 2, southern New England; 3, Georges Bank; 4, eastern Scotian Shelf; 5, southwest Nova Scotia; 6, southwest Newfoundland).

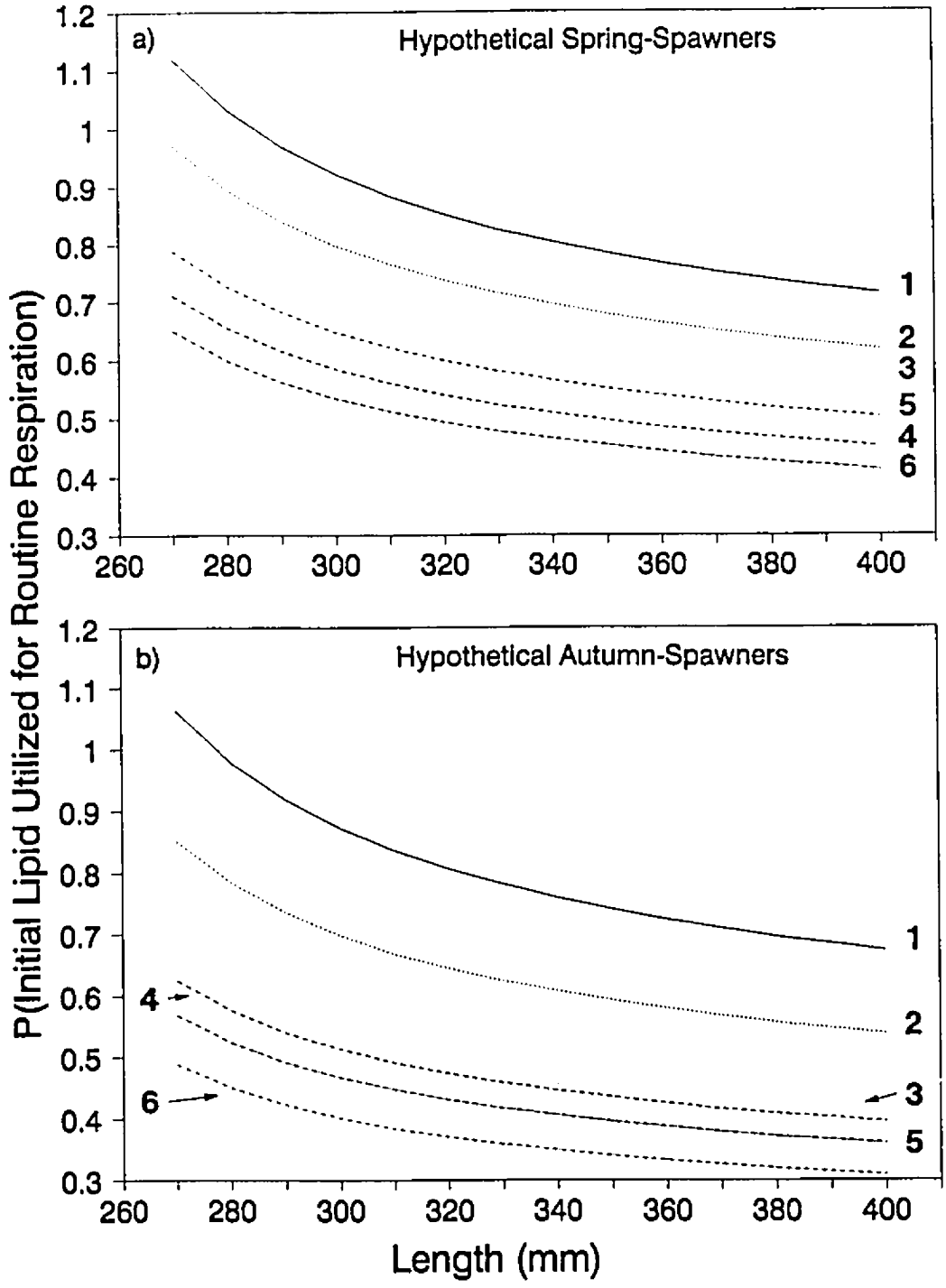
a)
Hypothetical Spring-Spawners
b)
Hypothetical Autumn-Spawners
P(Initial Lipid Utilized for Routine Respiration)
Length (mm)
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
260
280
300
320
340
360
380
400
1
2
3
4
5
6

Figure 7.1

gonad maturation also increases with decreasing latitude (Figure 7.1b). However, estimates of storage lipid depletion for routine respiration by average sized autumn-spawners within their known breeding range (<40% off sw Newfoundland, ≈50% on Georges Bank, ≈70% off of southern New England for 320mm herring) are lower than for hypothetical spring-spawning populations within the region where autumn-spaw herring are extant (see above). Routine respiration alone could utilize >80% of storage lipids in the mid-Atlantic Bight region regardless of spawning season (Figure 7.1a,b). Collectively, these calculations suggest that the broad geographic distributions of herring spawning times, and the limits to the herring's breeding range are linked to energetic constraints on reproduction.

Evaluations of the response of fish populations to temperature increases induced by anthropogenic increases in atmospheric CO_2 are currently topical. The current predicted responses of herring are of northward shifts in their breeding range (e.g., Bardach 1989; Frank et al. 1990). This thesis ideHxifies two factors which suggest that extinctions of extant populations are conceivable, and that northward shifts in herring breeding range may not be possible. First, rising water temperatures (upper most estimate of the rate of increase ≈0.8°C/decade, Vellinga and Leatherman 1989) could affect realized reproductive effort in spring-spawners and winter survival in autumn-spawners.

Increased summer temperatures could affect realized reproductive effort and/or winter survival in autumn-spawning herring.

Second, predicted changes in zooplankton community structure (Frank et. al. 1990) could affect the ability for herring to accumulate storage lipid. These lipids (principally triaglycerides (TAG)), are available in quantity only within pelagic ecosystems where diatoms are the basis of the food web (Linko et al. 1985; Sargent and Henderson 1986; Henderson and Almatar 1989). If ,as predicted, increased water column stratification shifts the phytoplankton species composition from diatoms to dinoflagellates (Frank et al. 1990), the ability for herring to accumulate storage lipid will probably decrease. This in turn could reduce their ability to conserve protein either during gonad maturation and/or in winter conditions, in conditions of already higher storage lipid utilization at warmer temperatures.

7.3 Association Between Spawning Time and the Physical Oceanography of the Early Life Environment

Variability in reproductive traits has been considered by many to be essential for ensuring the viability of the early life stages of species with broad (in time and space) spawning distributions (e.g., Blaxter and Hempel 1963; Cushing 1967, 1975; Gamble et al. 1985; Tanasichuk and Ware 1987; Ware 1975; Winters and Wheeler 1987; Duarte and

Alcaraz 1990). This thesis has provided little evidence for substantive plasticity in herring reproductive traits among nw Atlantic populations with different spawning seasons. In the nw Atlantic, egg weight remains relatively constant as gonad weight at length varies among populations (Chapter 2). Therefore, absolute fecundity differs among populations as realized reproductive effort varies, either with the duration of the maturation period, or in relation to body size related differences in the utilization of storage energy within populations. These factors suggest that for nw Atlantic herring survivorship favours increased egg number rather than increased egg quality, beyond some baseline criterion that ensures the resultant larvae are viable.

An association between absolute fecundity and the physical oceanography of larval distribution areas has been suggested for herring (e.g., Iles and Sinclair 1982; Sinclair and Tremblay 1984). In general, low fecundity herring (spring-spawning) tend to occur in vertically stratified water masses associated with low tidal mixing. High fecundity herring (autumn-spawning) occur in the same type of environment as well as in vertically homogeneous water masses associated with high tidal mixing (Iles and Sinclair 1982; Sinclair and Tremblay 1984). This pattern has been previously explained on the basis that populations with long larval periods (autumn-spawning) need to be more

fecund to offset higher cumulative larval mortalities than do populations with brief larval periods (spring-spawning) and lower cumulative larval mortalities (Sinclair and Tremblay 1984; Gamble et al. 1985). An alternative explanation is that spring-spawners, which produce less gonad material than autumn-spawners, are not capable of life-cycle closure in all environments which could theoretically sustain a viable larval population. For example, mortality through dispersal from desired larval distribution areas may require a level of gonad production that is unobtainable by populations with high non-reproductive demands on storage energy during gonad maturation.

Circumstantial evidence supports this interpretation. The species composition and size characteristics of spring-time zooplankton assemblages in regions that support autumn-spawning populations are similar to those associated with viable spring-spawning populations in other areas (e.g., southwest Scotian Shelf; McLaren et al. 1989, Georges Bank; Cohen and Lough 1983, eastern Gulf of Maine; Townsend 1983, 1984). This suggests that herring are excluded from these regions in spring for reasons other than larval feeding dynamics. Furthermore, in some regions which only support autumn-spawning herring, larval fish species are present that are spawned during the spring and which co-occur with herring larvae elsewhere during the spring (e.g., compare

spring-time ichthyoplankton assemblages in eastern Gulf of Maine (Townsend 1983, 1984), eastern Newfoundland (Frank and Leggett 1983) and Minas Basin (Bradford 1987)). This suggests that the factors restricting the access of Atlantic herring to these regions are unique to the herring species.

The life-history traits of Minas Basin herring also suggest a relationship between larval mortality and the physical oceanography of larval distribution areas. Minas Basin spring-spawning herring are one of the few populations known to feed during the late stages of gonad maturation, up to and including spawning (Bradford 1987). Perhaps not unrelated to their unusual feeding behaviour are their high (for May-June spawners) fecundities and gonad weights at length (Bradford 1987; Chapter 2). Minas Basin herring are also one of the few examples where spring-spawning is successful in tidally energetic, verticaly well-mixed physical oceanographic conditions. However, if Minas Basin larvae are food or growth limited these do not appear to affect either the duration of their larval period or their length at metamorphoses (≈4 months and ≈4.5cm respectively, both are common values; Sinclair and Tremblay 1984; Bradford 1987).

7.4 Conclusions

A re-evaluation of the factors which determine population richness and pattern is required. Regardless of whether viable populations of larvae co-occur temporally and spatially with ecologically important biological and physical variables, explanations are required for the absence of populations at other junctures in time for the same space. This thesis has demonstrated that the physiology of reproduction is potentially as powerful an influence on the distribution of herring populations as is currently assumed for the early-life history stages.

Virtually all reviews of herring biology have characterized their year-round spawning habit, as a species, as a marvelous ability for adaptation to widely differing environments (see reviews by Blaxter and Holliday 1963; Parrish and Saville 1965; Cushing 1967, 1975; Blaxter and Hunter 1982). This view has been challenged in this thesis through demonstrations that some herring populations are more limited reproductively than are others. Future research may be more appropriately aimed towards offering explanations for why the number of populations comprising a species that can spawn year-round, along two continental margins, ranges only from the tens to hundreds and not from the hundreds to thousands.

Appendices

Appendix 1.1. Summary of Statistical Procedures (sources: Sokal and Rohlf 1981; Zar 1984).

1) Analysis of Variance (ANOVA)

Null Hypothesis (H_0): population means (μ) are equal

Assumptions a) samples have normal distribution.

b) populations have equal variance (σ^2)

Test Statistic = F-ratio

2) Tukeys Multiple Between Group Comparison Test

Null Hypothesis (H_0): population means (μ) are equal

Assumptions a) samples have normal distribution

b) populations have equal variance (σ^2)

Test Statistic = q = differences between sample means divided by the standard error

Note: calculation of standard error differs between comparisons of groups with sample sizes and groups with unequal sample sizes.

3) Kolmogorov - Smirnov Test for Goodness of Fit (used in this thesis to test for deviations from normality)

Null Hypothesis (Ho): the sample came from a normally distributed population

Test Statistic = D = the maximum deviation (absolute value) from the test distribution divided by sample size (n)

4) Analysis of Covariance (ANCOVA)

Tests a dependent variable for homogeneity among group means after first adjusting for the group's differences in the independent variable (the covariate), via linear regression. Null Hypothesis, assumptions, and test statistic are the same as for ANOVA. However, ANCOVA also assumes homogeneity of slopes (no significant interaction between the covariate and treatment).

Appendix 2.2. Calculation of average spawning temperatures for spring- and autumn-spawning southern Gulf of St. Lawrence herring.

Monthly Mean Sea Surface Temperatures (°C)[1]

YEAR	APRIL T_A	MAY T_M	JUNE T_J	AUG T_{Aug}	SEP T_{Sept}
1971	1	4	9	17	11
1972	-1	2	8	15	12
1973	1	2	8	18	15
1974	-1	3	7	15	13
1975	-1	3	8	16	14
1976	0	3	8	16	14
1977	0	3	8	16	14
1978	1	5	8	17	14
1979	1	5	11	17	14
1980	1	5	10	16	14
1981	1	4	10	15	14
1982	1	4	9	15	12
1983	1	5	10	16	13
1984	0	3	8	16	13
1985	0	3	9	16	15
1986	0	4	10	16	12
1987	0	3	10	17	15
1988	0	4	8	17	14

([1] source: K. Drinkwater, BIO, Dartmouth, N.S., unpub. data)

Spring spawning season = mid April-mid June
Autumn spawning season = August-September

$$T_{Spring} = \frac{\left[\frac{(T_A + T_M)}{4} + T_M + \frac{(T_M + T_J)}{4}\right]}{2}$$

$$T_{Autumn} = \frac{T_{Aug} + T_{Sept}}{2}$$

$Mean\ T_{Spring} = 4 \pm 1^{\circ}C$ $Mean\ T_{Autumn} = 15 \pm 1.5^{\circ}C$ (1971 -1988)

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