Abstract.– Winter flounder were acclimated to two temperatures (2° and 7°C) for a period of about 7 weeks prior to spawning. Embryos produced at two acclimation temperatures were incubated through the yolksac stage at three incubation temperatures (4°, 7°, and 10°C). Both adult acclimation temperature and embryo and larval incubation temperature were found to have an effect on larval size and biochemical composition. In many cases the effects of acclimation temperature and incubation temperature were nonadditive. RNA content at first feeding indicated that larvae produced by adults acclimated to low temperature (2°C) were better suited for growth at low temperatures, while larvae produced by adults acclimated to higher temperature (7°C) were better suited for growth at higher temperatures. At first feeding larvae were larger (higher standard length) and in better condition (high protein and RNA content) when incubated at lower temperatures.

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Effects of Water Temperature on Size and Biochemical Composition of Winter Flounder *Pseudopleuronectes americanus* at Hatching and Feeding Initiation

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The effects of water temperature on the size and viability of fish eggs and larvae have been the subject of considerable interest. Water temperature is the environmental variable most often linked to recruitment in retrospective empirical analyses of recruitment variability in temperate marine fish (Sissenwine 1984). Yet in most cases causation is not established and the mechanisms involved are poorly understood. Studies of effects of water temperature prior to spawning suggest an inverse relation between water temperature and egg size in several species (Hempel and Blaxter 1967, Cushing 1967, Bagenal 1971, Southward and Demir 1974, Ware 1975, Tanasichuk and Ware 1987). The effects of water temperature during the embryonic period on larval size and yolk conversion efficiency have been examined in a variety of species (Lasker 1962, Sweet and Kinne 1964, Alderdice and Forrester 1968, May 1974, Laurence and Rogers 1976, Linden et al. 1980, Johns et al. 1981, Laurence and Howell 1981, Buckley et al. 1982). While maximum efficiency is generally achieved at intermediate temperatures within the range of thermal tolerance, the exact shape of the relation between temperature and utilization is variable (Heming and Buddington 1988). Blaxter and Hempel (1966) found that the effect of temperature on yolk conversion efficiency was dependent upon egg size in Atlantic herring *Clupea harengus*, cold temperatures favoring small eggs and warm temperatures favoring large eggs. The effects of water temperature have been examined in combination with salinity, oxygen levels, and other environmental variables. None of these studies, with the exception of Tanasichuk and Ware 1987, considered a possible interactive effect of water temperature during gamete maturation with water temperature during the embryonic and larval periods. It is widely known, however, that acclimation temperature mediates many thermal effects, including upper and lower lethal temperatures and metabolic rate (Brett 1970).

This study was undertaken to examine the effects of water temperature during the latter stages of gamete development and during the embryonic and yolksac periods on the size and biochemical composition of winter flounder larvae produced. Standard length, RNA, DNA, and protein content were determined at hatching and first feeding. These indices were chosen because of their relation to fitness, growth, and survival potential of fish larvae. Length

has been related to swimming speed and the ability to capture prey and avoid preditors (Folkvord and Hunter 1986, Miller et al. 1988). Bulk RNA content is primarily a measure of ribosomal RNA content which is an index of an organism's capacity for synthesis of protein and growth (Bulow 1987). DNA content is an index of cell number and developmental state. Protein, the primary organic constituent in fish larvae, is generally proportional to dry weight (Buckley 1979). Growth of fish larvae is primarily accomplished through protein synthesis and accumulation. Protein is also an important source of reserve energy during larval development (Buckley 1979).

The primary hypothesis tested was that water temperatures, both during gamete maturation and during embryonic and early larval development, and their interaction had an effect on the size and composition of larvae produced. It was reasoned that eggs produced by adults acclimated to low temperatures would be better adapted to low temperatures than eggs produced by adults acclimated to high temperatures. It was expected that the converse was true for eggs produced by adults acclimated to high temperatures. This study originated in part out of an earlier study indicating that winter flounder embryos produced at low temperature exhausted their yolk reserves prior to feeding initiation and appeared poorly suited for growth and survival when incubated and reared at higher temperatures (Buckley 1982). It is part of a larger study of the effects of parental and environmental factors on the size and viability of winter flounder eggs and larvae. The rationale for this larger effort is that given the high fecundity of temperate marine fishes and the high mortality rates during their early life stages, variability at the individual, brood and stock level in size and composition of fish eggs and larvae may play a large part in determining survival during the early life stages and consequently in determining recruitment success.

Methods

Mature winter flounder were caught with an otter trawl on 23 December 1980 in the West Passage of Narragansett Bay in the vicinity of Fox Island at a water temperature of 3.5°C (Table 1). Fish were randomly assigned to two groups (acclimation temperatures). One was held at 2°C, the other at 7°C. Spawning was induced by injections of carp pituitary extract administered as described by Smigielski (1975). Eggs were stripped, fertilized with the sperm of three males held at the same temperature as the spawning female, and treated with diatomaceous earth (Smigielski and Arnold 1972). Embryos from each female were randomly split into three groups of about 1500 each and incubated at 4°, 7°, and 10°C in 38-L black glass aquaria. Eggs and larvae were not incubated at 2°C because of the high mortality observed at this temperature in earlier studies (Laurence 1975, Buckley 1982). Embryos were gradually acclimated to the incubation temperatures at the rate of 1°C per 6 hours. After hatching, larvae were fed live zooplankton collected in the Narragansett Bay area and sieved to select the appropriate size fraction. Plankton densities were maintained at greater than 2 plankters per mL.

Table 1

Experimental design. Three *Pseudopleuronectes americanus* females were spawned at each of two acclimation temperatures (2°, 7°C). Subsamples of about 1500 eggs from each female were incubated in separate containers at each of three temperatures (4°, 7°, 10°C). Triplicate samples of 40 larvae each were taken from each tank for biochemical analysis.

Stage	Temperature		Time
Adults	3.5°C		Capture
	↙	↘	
	Acclimation		
Adults–Gamets	2°C	7°C	48–51 days
	↓	↓	
	Incubation		
Embryos–Larvae	4,7,10°C	4,7,10°C	13–29 days

Groups of 10 larvae were examined daily, between 0800 and 1100 hours, under a dissecting microscope to establish the day of completion of yolksac absorption and first feeding. Larvae were judged to have completed yolksac absorption when 5 out of 10 larvae had no visible yolk. Larvae were judged to have initiated feeding when 5 out of 10 larvae examined had food visible in their gut. At hatching and first feeding 10 larvae from each group (one unique combination of acclimation and incubation temperatures for each female) were measured for standard length with a filar micrometer in a dissecting microscope. Yolk volume was estimated using the equation for a prolate spheroid:

$$V = (\pi/6)\, LH^2$$

where L is the length and H is the height of the yolksac (Laurence 1973). Triplicate groups of 40 larvae each were sampled at the same times for biochemical analysis. Larvae were homogenized in 2.0 mL of ice-cold distilled water using an all-glass tissue grinder. Subsamples of 1.4 and 0.1 mL of homogenate were used for analysis of nucleic acids and protein, respectively, as outlined in Buckley (1979). Nucleic acids were determined using a modification of the Schmidt-Thannhauser method. A modification of the Lowry method was used for determination of protein. Coefficients of varia-

Table 2
Size and number of injections for individual *Pseudopleuronectes americanus* females, and percent fertility and hatch of their offspring.

Acclimation T (°C)	Tag number	Length (mm)	Weight (g)	No. injections	Fertility (%)	Incubation T (°C)	Hatch (%)	Age at hatch (d)	Age at first feeding (d)
2	335	280	290	4	98	4	85	20	9
						7	80	11	7
						10	72	7	2
2	217	301	389	4	75	4	85	17	7
						7	80	10	7
						10	70	8	5
2	218	290	315	3	96	4	85	16	7
						7	80	10	7
						10	70	7	5
7	857	245	345	2	96	4	85	15	8
						7	80	10	6
						10	70	7	4
7	067	303	373	4	98	4	80	14	11
						7	70	10	6
						10	70	7	4
7	276	357	627	3	98	4	80	14	11
						7	80	7	6
						10	80	7	6

tion (sample standard deviation as a percent of the mean) for replicate analyses on portions of a fresh or frozen homogenate run within one week of preparation were 3% for RNA, 8% for DNA, and 5% for protein.

Data analysis was done using SAS System Software for personal computers (SAS 1985). The GLM procedure was used for analysis of variance because of the unbalanced design. Differences among main effect means were tested for significance using Tukey's studentized range test.

Results

Between 48 and 51 days after capture, three females were spawned at each acclimation temperature after receiving between two and four hormone injections (Table 2). There was no significant difference in either the number of injections administered or the length of female parents between acclimation temperature groups (analysis of variance, $P \leq 0.05$). Spawning females ranged in length from 245 to 357 mm with a mean of 296 mm. Based on length-at-age data for winter flounder from the Niantic River, CT (Northeast Utilities 1987), this corresponds to a range in age of 3–6 years. Fertilization rate was high, ranging from 75 to 98% with a mean of 94%. Acclimation temperature or the number of hormone injections had no significant effect on the fertilization rate ($P \leq 0.05$). Percent hatch ranged from 70 to 85% with a mean of 78%. Hatch rates were significantly higher at the lower incubation temperatures but unaffected by acclimation temperature of the parents ($P \leq 0.05$).

At all combinations of acclimation (prespawning) and incubation (postspawning) temperature, completion of yolksac absorption occurred within one day of first feeding. Age at hatch and age at first feeding were inversely related to incubation temperature. Spawning temperature had an effect on age at hatch but not on age at first feeding. No interactive effect of adult acclimation temperature and embryo incubation temperature was observed on the rate of these developmental processes ($P \leq 0.05$).

The mean standard length and chemical content of larvae at hatching and first feeding are given in Tables 3 and 4. Standard length and DNA content generally increased over this period (Fig. 1). The decrease in protein content between hatching and first feeding indicates a net catabolism of protein during the period.

The effects of selected factors on the size and chemical content of larvae at hatching and at first feeding were evaluated using analysis of variance (Table 5). In SAS notation, the general form of the model used was:

$$Y = A\ B\ C(A)\ A*B$$

where Y is the dependent variable and A, B, and C

Table 3

Length, yolksac volume, and chemical content of *Pseudopleuronectes americanus* larvae at hatching. Values are the estimated means along with the standard deviation. For standard length and yolksac volume, $N = 30$ (10 larvae from each of 3 females). For RNA, DNA, and protein content, $N = 9$ (3 pools of 40 larvae each from 3 females). Percents in brackets are coefficients of variation of the grand mean. Where the interaction between adult spawning temperature and embryo incubation temperature was not significant, main-effects means were calculated and Tukey's studentized range test applied to these values. Where the temperature interaction factor was significant, simple main effects were tested. Values in a row with a superscrip letter in common or bracketed values in a column are not significantly different ($P \leq 0.05$).

Spawning temperature (°C)	Incubation temperature (°C) 4	7	10	$\bar{x}$
		Standard length (mm)		
2	[3.61 ± 0.15[a]	[3.45 ± 0.17[b]	3.40 ± 0.14[b]	
7	[3.33 ± 0.16[a]	[3.46 ± 0.09[b]	—	
$\bar{x}$				3.45 ± 0.18 (6.1%)
		Yolksac volume (mm^3)		
2	0.08 ± 0.04	0.05 ± 0.02	0.05 ± 0.02	0.06[a]
7	0.08 ± 0.04	0.05 ± 0.01	—	0.07[a]
$\bar{x}$	0.08[a]	0.05[b]	0.05[b]	0.06 ± 0.03 (50%)
		RNA content (μg/larva)		
2	1.32 ± 0.16	1.18 ± 0.20	1.17 ± 0.09	1.22[a]
7	1.27 ± 0.13	1.13 ± 0.08	1.05 ± 0.08	1.16[b]
$\bar{x}$	1.30[a]	1.16[b]	1.11[b]	1.19 ± 0.16 (13.1%)
		DNA content (mg/larva)		
2	[0.34 ± 0.06[a]	[0.2820.04[b]	[0.36 ± 0.04[a]	
7	[0.33 ± 0.05[b]	[0.39 ± 0.04[a]	[0.33 ± 0.03[b]	
$\bar{x}$				0.34 ± 0.06 (16.7%)
		Protein content (μg/larva)		
2	17.3 ± 2.4	15.7 ± 4.2	15.8 ± 2.7	16.2[a]
7	15.2 ± 2.2	—	15.6 ± 1.7	15.3[a]
$\bar{x}$	16.1[a]	15.7[a]	15.7[a]	15.9 ± 2.8 (17.5%)

Table 4

Length and chemical content of *Pseudopleuronectes americanus* larvae at first feeding. Values and statistics are as given for Table 3.

Spawning temperature (°C)	Incubation temperature (°C) 4	7	10	$\bar{x}$
		Standard length (mm)		
2	[4.40 ± 0.15[a]	[4.18 ± 0.30[b]	[3.96 ± 0.15[c]	4.21[a]
7	[4.35 ± 0.09[a]	[4.14 ± 0.19[b]	[4.05 ± 0.14[b]	4.19[a]
$\bar{x}$				4.20 ± 0.25 (5.9%)
		RNA content (μg/larva)		
2	[1.30 ± 0.13[a]	[1.21 ± 0.15[a]	[0.89 ± 0.01[b]	
7	[1.17 ± 0.12[a]	[1.01 ± 0.08[b]	[1.21 ± 0.15[a]	
$\bar{x}$				1.15 ± 0.18 (15.2%)
		DNA content (μg/larva)		
2	0.41 ± 0.06	0.35 ± 0.07	0.38 ± 0.02	0.38[a]
7	0.37 ± 0.03	0.43 ± 0.06	0.38 ± 0.05	0.39[a]
$\bar{x}$	0.39[a]	0.39[a]	0.38[a]	0.39 ± 0.05 (13.7%)
		Protein content (μg/larva)		
2	[13.3 ± 1.6[a]	[12.0 ± 1.8[a, b]	[11.0 ± 2.0[b]	
7	[13.1 ± 1.0[a]	[13.4 ± 0.9[a]	[11.1 ± 1.2[b]	
$\bar{x}$				12.8 ± 1.6 (12.5%)

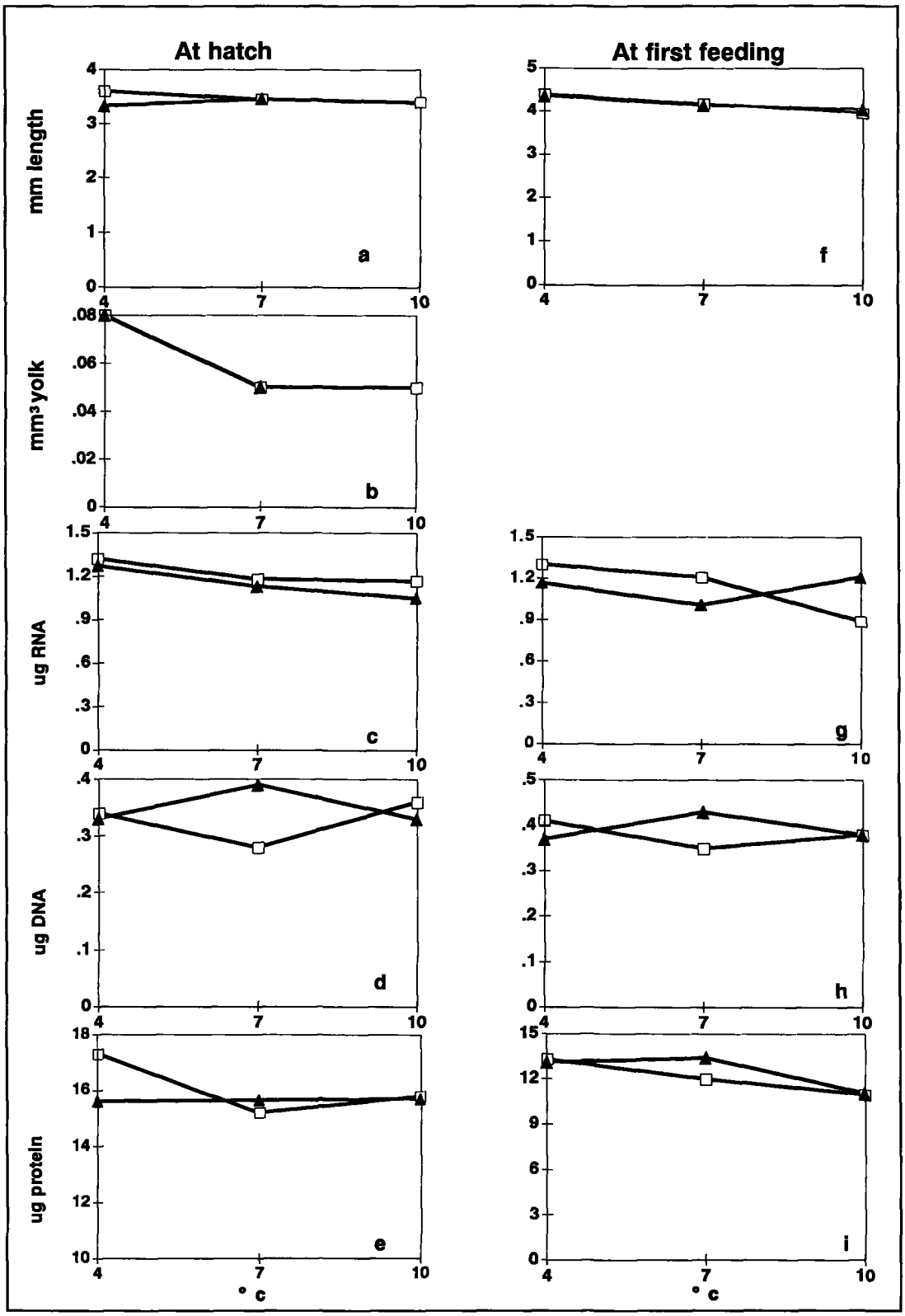

Figure 1

Standard length, yolk volume, and biochemical composition of *Pseudopleuronectes americanus* larvae at hatching and first feeding. □ Tsp = 2°C; ▲ Tsp = 7°C.

Table 5

Analysis of variance for factors affecting size and chemical content of *Pseudopleuronectes americanus* larvae at hatch and first feeding. Tsp = adult acclimation and spawning temperature; Tinc = embryo and larval incubation temperature; T x T = temperature interaction; Block = female tag number. $*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$. Where the temperature interaction is significant, F values for Tsp and Tinc are not given.

		Tsp	Tinc	T x T	Block	Total
			At Hatch			
Larval length (mm)	df	1	2	2	4	139
	F value			25.17***	13.66***	
Yolk volume (mm^3)	df	1	2	2	4	139
	F value	0.00	12.26***	0.05	2.40*	
RNA (μg/mg)	df	1	2	2	4	49
	F value	4.68*	15.94***	0.18	10.16***	
DNA (μg/mg)	df	1	2	2	4	49
	F value			24.15***	8.41***	
Protein (μg/mg)	df	1	2	1	4	36
	F value	0.00	1.11	0.01	15.59***	
			At First Feeding			
Larval length (mm)	df	1	2	2	2	169
	F value			5.07**	8.08***	
RNA (μg/mg)	df	1	2	2	4	41
	F value			40.78***	12.29***	
DNA (μg/mg)	df	1	2	2	4	39
	F value	0.27	1.38	3.13	1.90	
Protein (μg/mg)	df	1	2	2	4	34
	F value			6.32**	11.93***	

are independent class variables (SAS Institute 1985). A is the acclimation and spawning temperature (Tsp); B is the embryo and larval incubation temperature (Tinc); C is the block effect or individual female tag number (Block). This maternal factor is nested within the acclimation temperature and represents the variability among individual spawning females. This factor was added to the model to block out fish-to-fish variability. It was significant for all dependent variables tested (Table 5). $A*B$ is the interaction of acclimation and incubation temperatures.

Significant interactions between spawning and incubation temperature were observed at hatch for length and DNA content, and at first feeding for length, RNA, and protein content. In these cases, where the effects of spawning temperature and incubation temperature were nonadditive, simple main effects were tested at each spawning and incubation temperature using Tukey's studentized range test. Where no temperature interaction was observed (yolk volume, RNA, and protein content at hatch, and DNA content at first feeding) main-effects means were calculated and differences among main-effects means were tested for significance using Tukey's studentized range test.

At hatching, standard length showed a significant temperature interaction (Table 5). At a spawning temperature of 2°C, standard length decreased with increasing incubation temperature (Table 3). At a spawning temperature of 7°C, standard length was higher at an incubation temperature of 7°C than at 4°C. Yolk volume showed no significant temperature interaction, was unaffected by spawning temperature, and was highest at the lowest incubation temperature of 4°C. RNA content at hatch showed no significant temperature interaction and decreased with both increasing spawning and incubation temperature. DNA content at hatch showed a significant temperature interaction. At a spawning temperature of 2°C, DNA content was lowest at the intermediate incubation temperature (7°C). At a spawning temperature of 7°C, DNA content was highest at this intermediate incubation temperature. Protein content at hatch showed no temperature interaction and was unaffected by either spawning or incubation temperature.

At first feeding, standard length showed a significant temperature interaction. At both spawning temperatures (2° and 7°C) standard length decreased with increasing incubation temperature (Table 4). RNA content at first feeding showed a significant temperature interaction. At a spawning temperature of 2°C, RNA content was lowest at the highest incubation temperature (10°C). At a spawning temperature of 7°C, RNA

content was lowest at the intermediate incubation temperature (7°C). DNA content at first feeding showed no significant temperature interaction and was unaffected by either spawning or incubation temperature. Protein content at first feeding showed a significant temperature interaction. At both spawning temperatures, protein content decreased with increasing incubation temperature.

Discussion

Winter flounder spawn and embryos survive over a wide range of temperatures. In the laboratory, Williams (1975) observed survival of embryos between −1.8° and 15°C. Rogers (1976) reported survival between 3° and 14°C. While 2°C is close to the temperature of maximum egg production, winter flounder larvae require water temperatures above 2°C for survival to metamorphosis (Laurence 1975, Buckley et al. 1982). Spawned through the late winter and early spring, winter flounder embryos and larvae generally experience gradually increasing water temperatures. In shallow estuaries and bays, however, embryos and larvae may be subjected to large fluctuations in salinity and water temperature over relatively short periods of time, or to prolonged periods of abnormal warming or cooling. The effects of such changes in water temperature on survival and growth of the early-life stages of winter flounder are largely unknown.

Inverse relations between water temperature (during late winter and early spring) and indices of recruitment have been reported for winter flounder (Jeffries and Johnson 1974, Jeffries and Terceiro 1985, Northeast Utilities 1988). The shape of larval abundance curves, a parameter affected by water temperature, has also been related to recruitment; cold years with broad shallow abundance curves produce good year-classes (Northeast Utilities 1988).

The size and chemical composition of larvae at initiation of feeding provide useful criteria for evaluation of these temperature effects, and may provide insight into causal mechanisms. Feeding initiation is the end point of the period of reliance on endogenous energy reserves that commences at ovulation. Increased larval size confers increased potential for survival, since larger larvae are better able to avoid size-dependent predation, capture food, and survive periods of starvation (Blaxter and Hempel 1966, Rosenberg and Haugen 1982, Bailey and Battey 1984, Knutsen and Tilseth 1985). DNA content is an index of cell number and RNA content an index of the capacity for protein synthesis and hence growth (Bulow 1987). Buckley et al. (In prep.) demonstrated direct relations between size and RNA content of yolksac winter flounder larvae and survival for the first month of life in the laboratory. Size of larvae at first feeding is dependent upon egg size at spawning and the efficiency of production of larval tissue (yolk-conversion efficiency).

Based on observations of the timing of yolk absorbtion and first feeding, and the size and composition of winter larvae produced by a single female spawned at 2°C, Buckley (1982) speculated that eggs spawned at low temperatures (2°) may be poorly suited for growth and survival at high temperatures (10°C) within the range of tolerance of winter flounder. The present factorial study of six females spawned at low (2°C) and high (7°C) temperatures confirmed and extended these earlier findings. However, unlike the earlier study, first feeding occurred within one day of completion of yolk absorbtion at all combinations of adult acclimation (prespawning) and incubation temperature (Table 2). The present study, with the spawn from six winter flounders, demonstrated the importance of variability at the level of individual females in determining size and composition of winter flounder larvae (Tables 3 and 4). Adult acclimation (prespawning) temperature was important alone or in combination with embryo incubation temperature in determining length and RNA and DNA content at hatch, and in determining length and RNA and protein content at first feeding (Table 5). Embryo incubation temperature was important alone or in combination with adult acclimation temperature in determining larval size, yolksac volume, RNA and DNA content at hatch, and in determining length and RNA and protein content at first feeding. At first feeding, size and chemical content of eggs spawned by adults acclimated to 2°C were maximized at the lowest incubation temperature (4°C). Eggs spawned at 7°C produced the longest first-feeding larvae at 4°C, while DNA and protein content were highest at the intermediate incubation temperature (7°C) and RNA content was highest at the warmest incubation temperature (10°C). The largest larvae, whether measured by length or chemical content, were produced at the lowest combination of acclimation and rearing temperatures. RNA content, which is critical to protein synthesis and growth, was highest at first feeding in larvae incubated at 4°C for eggs produced at 2°C, and at 10°C for eggs produced at 7°C. RNA content was lowest in first-feeding larvae produced from eggs spawned at 2°C and incubated at 10°C. This group represented the largest difference between spawning and incubation temperature.

Hempel and Blaxter (1967) reported differences in fecundity and egg size between Atlantic herring stocks spawning at different temperatures. Stocks spawning at colder temperatures produced fewer but larger eggs. Tanasichuk and Ware (1987) working with Pacific herring found that both size-specific fecundity and egg

size, but not size-specific ovary weight, were related to seawater temperature 60–90 days before spawning. Again, fecundity increased with increasing temperature while egg size decreased.

Results from this study demonstrate that water temperatures during the latter stages of gamete maturation (48–51 days prior to spawning) and during embryo and larval development affect the size and composition of winter flounder larvae produced. Further, the interaction between acclimation temperature of adults and incubation temperature of embryos and larvae also appears to have a strong effect on size and composition of larvae. While the number of oocytes entering vitellogenesis is probably determined earlier in the reproductive cycle (Brown 1957, Dunn 1970, Tyler and Dunn 1976, Burton and Idler 1984), several important functions occur during the latter stages of gamete development, including further deposition of yolk and final meiotic division.

Our data on size and chemical composition of winter flounder at hatching and first feeding suggest a more complex relation between water temperature and larval size than observed between water temperature and egg size. These data may help explain some of the variability observed in the relation between yolk-conversion efficiency or maximum larval size and incubation temperature (Sweet and Kinne 1964, Alderdice and Forrester 1968, Laurence and Rogers 1976, Linden et al. 1980, Johns et al. 1981, Laurence and Howell 1981, Buckley 1982). Our data suggest that larval size and composition at hatch and first feeding are dependent not only upon incubation temperature but also upon water temperature during the final stages of gamete maturation and upon the interaction of water temperature during these two time-periods. This implies that the contents of the egg are modified in some way in response to water temperature prior to spawning. Most likely, this temperature response goes beyond simply producing a larger or smaller egg with components in the same proportion. The ratio of major organic components including protein, lipids, carbohydrates, and nucleic acids may be altered in response to temperature. More subtle, but possibly more significant, changes in the composition of the developing oocyte in response to water temperature may include alterations in the content, composition, activity, or stability of enzymes, hormones, maternal messenger RNA, and stable RNA (tRNA and rRNA). Any conclusions about the efficiency of yolk utilization at different incubation temperatures should take into account the thermal history of the spawning adults.

Winter flounder reproductive strategy has most likely evolved to exploit the dramatic increase in water temperature during the spring in the shallow estuaries along the northwest margin of the Atlantic Ocean. Between spawning and metamorphosis, a period of about 2 months in winter flounder, water temperatures warm an average 10°C (from ~2° to 12°C) affecting not only the abundance and composition of predators and prey but also the rates of metabolic processes (Laurence 1975, 1977). This maximizes size and condition of first-feeding larvae at low temperatures (Table 4), allows relatively long resistance to starvation at intermediate temperatures, and facilitates rapid larval and postlarval growth at higher temperatures (Buckley 1982). Mortality of late embryos and larvae at cold temperatures (≤2°C) (Laurence 1975, Buckley 1982) indicates that good survival of winter flounder is dependent upon the expected spring warming. While gametogenesis and embryo and larval development show a wide range of temperature tolerance in winter flounder, these processes appear to have been optimized for cold winter temperatures followed by gradual spring warming. Our data suggest that cold winters followed by gradual spring warming favor good survival and recruitment of winter flounder by facilitating production of the largest larvae at first feeding (high standard length and DNA content) in the best condition (high RNA and protein content). These data may explain in part the observed correlation between cold years and strong year-classes (Jeffries and Johnson 1977, Jeffries and Terceiro 1985, Northeast Utilities 1988).

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