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Reproductive Biology of Anadromous Rainbow Smelt, *Osmerus mordax*, in the Ipswich Bay Area, Massachusetts

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REPRODUCTIVE BIOLOGY OF ANADROMOUS RAINBOW SMELT, *OSMERUS MORDAX*, IN THE IPSWICH BAY AREA, MASSACHUSETTS

A Thesis Presented

By

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ABSTRACT

Reproductive biology of anadromous rainbow smelt, Osmerus mordax, in the Ipswich Bay area, Massachusetts.

By

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University of Rhode Island, 1977

The reproductive biology of anadromous rainbow smelt, Osmerus mordax, was investigated in the Parker River and Essex Bay systems from 1977 through 1979. Variations in growth and seasonal energy content of body tissue of young-of-the-year (YOY) anadromous smelt were examined to investigate their relationships to spawning of precocious (age I) fish. By late fall of their first year, YOY that will spawn precociously in the spring have developing gonads, are longer in total length and have a higher energy content (kcals/g) of body tissue than non-precocious fish. The number of fish spawning at age I increased during the spawning season, with male precocious spawners consistantly outnumbering female precocious fish.

Several aspects of the reproductive ecology of rainbow smelt were examined during the 1979 spawning season. Results from two field experiments indicated that egg survival was positively correlated with water velocity (up to 60 - 80 cm/s). Smelt spawned many more eggs (by a factor of 12 - 15) on aquatic vegetation (Podostemum ceratophyllum abrotanoides) than on two smooth-surfaced substrates (ceramic tile and gravel/rubble). Survival to hatching on the vegetation was approximately 10%

compared to a 1% rate on the other surfaces. In addition, diameter of water-hardened, unfertilized eggs was positively correlated with female total length and prolarval size at hatching. These reproductive characteristics are discussed relative to the life history strategy of anadromous rainbow smelt in the Parker River-Plum Island Sound system.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

C H A P T E R I

GENERAL INTRODUCTION

Rainbow smelt (*Osmerus mordax*) are distributed along the east coast of North America from Labrador, Canada to the Delaware River, Pennsylvania (Bigelow and Schroeder 1953). During the past 70 years, the range of this species has been extended to the Great Lakes watershed (Scott and Crossman 1973). Smelt are utilized in both marine and freshwater environments as forage, and in commercial and sport fisheries (Kendall 1927; McKenzie 1964; Chesmore et al. 1973). Overexploitation, spawning habitat destruction and pollution have greatly reduced smelt numbers, especially in marine environments, and resulted in much recent interest in their population biology. The Massachusetts Division of Marine Fisheries is investigating the occurrence of *Glugea hertwigi*, an internal parasite that has reduced several freshwater smelt populations in Canada and New Hampshire (Delise 1969; 1973). An egg stocking program for several Massachusetts coastal streams is underway, trying to re-establish areas that historically supported spawning.

Very few smelt studies have dealt with the biological problems outlined above. There are some notable exceptions in recent literature on smelt population dynamics (Murawski and Cole 1978) and movement patterns of spawning adults (Murawski et al. in press). The present two-part investigation was performed to provide more, basic life history information on anadromous smelt. The first part deals with growth and energetics of young-of-the-year (YOY) in relation to precocious (age I) spawning, providing possible explanations of how precocious gonadal development relates to differential growth and seasonal energy content of body tissue. The second part of the study deals with the reproductive ecology of smelt in the Parker River-Plum Island Sound system. Two previous theses have addressed some aspects of anadromous smelt reproduction (Crestin 1973; Clayton 1976); my study estimates egg survival relative to several biological and physical parameters. The results should be of interest to population and environmental impact modelers, and to management agencies. The last section of the thesis presents some suggestions for future research.

CHAPTER II

VARIATION IN GROWTH AND SEASONAL ENERGETICS OF ANADROMOUS RAINBOW SMELT IN RELATION TO PRECOCIOUS SPAWNING

Introduction

Precocious gonadal maturation has been noted in several salmonids (Robertson 1957; Saunders and Henderson 1965; Lee and Powers 1976; MacKinnon and Donaldson 1976), but has not been investigated for rainbow smelt. During the 1974, 1975 (Murawski and Cole 1978) and 1979 anadromous smelt spawning runs in the Parker River, Massachusetts, numerous precocious (age I) spawners were observed. Murawski and Cole (1978) indicated that Parker River fish were partially recruited to the spawning population at age I and fully at age II, and that growth in length was greatest during the first year. The present study investigates growth and seasonal energetic content of YOY to follow the development of precocious gonadal maturation. These results are discussed relative to the optimization of life history characteristics.

Methods

Precocious smelt were collected with a fyke net in the Parker River-Plum Island Sound system during the 1979 spawning run. These fish were preserved by freezing and aged in the laboratory using the 'shiny line' formed on the scales during the winter slow-growth period (McKenzie 1947). Juveniles used for growth analysis were obtained from Essex Bay in 1977 and 1978 using beach seines and a small otter trawl. Most were preserved in 10 % formalin. Others were frozen for energetic studies. Gonadal development was followed for YOY during late fall, 1978. Maturing males had thick, white testes taking up approximately the same proportion of the body cavity as in older (age II^+) males at the same time of year. No maturing females were found, although some females do spawn at age I (Murawski and Cole 1978).

Calorific determinations were made using a Parr Model 1221 adiabatic oxygen bomb calorimeter (Parr Instrument Company 1960). Frozen YOY were thawed, weighed (to 0.01 g) and measured (to 0.1 mm). Fish were combined in five-millimeter (total length-TL) groups and dried at 80^{o}C. Whole-body samples were then ground into a coarse powder using a Wiley mill. Calorific determinations were made for each size category using three subsamples (0.2 g each) of the dried body tissue. Corrections for unburned wire and HNO_3 were made.

Results

Spawning in the Parker River commences in mid-March and extends to mid-April (see also Murawski and Cole 1978). Smelt usually start spawning in Cart Creek around mid-April and continue until the end of April. There was an increase in relative number of precocious male spawners (X) as the 1979 run progressed (Y= day of run; Y= 10.41 + 1.31X; $\underline{r}$= 0.76; $p<0.01$; n=26). Consequently, the percentage of spawning age I fish was much greater in Cart Creek than in the Parker River during 1979 (Table 1). No clear relationship could be established between number of precocious females and day of run in 1979, since few precocious females were found (n=5).

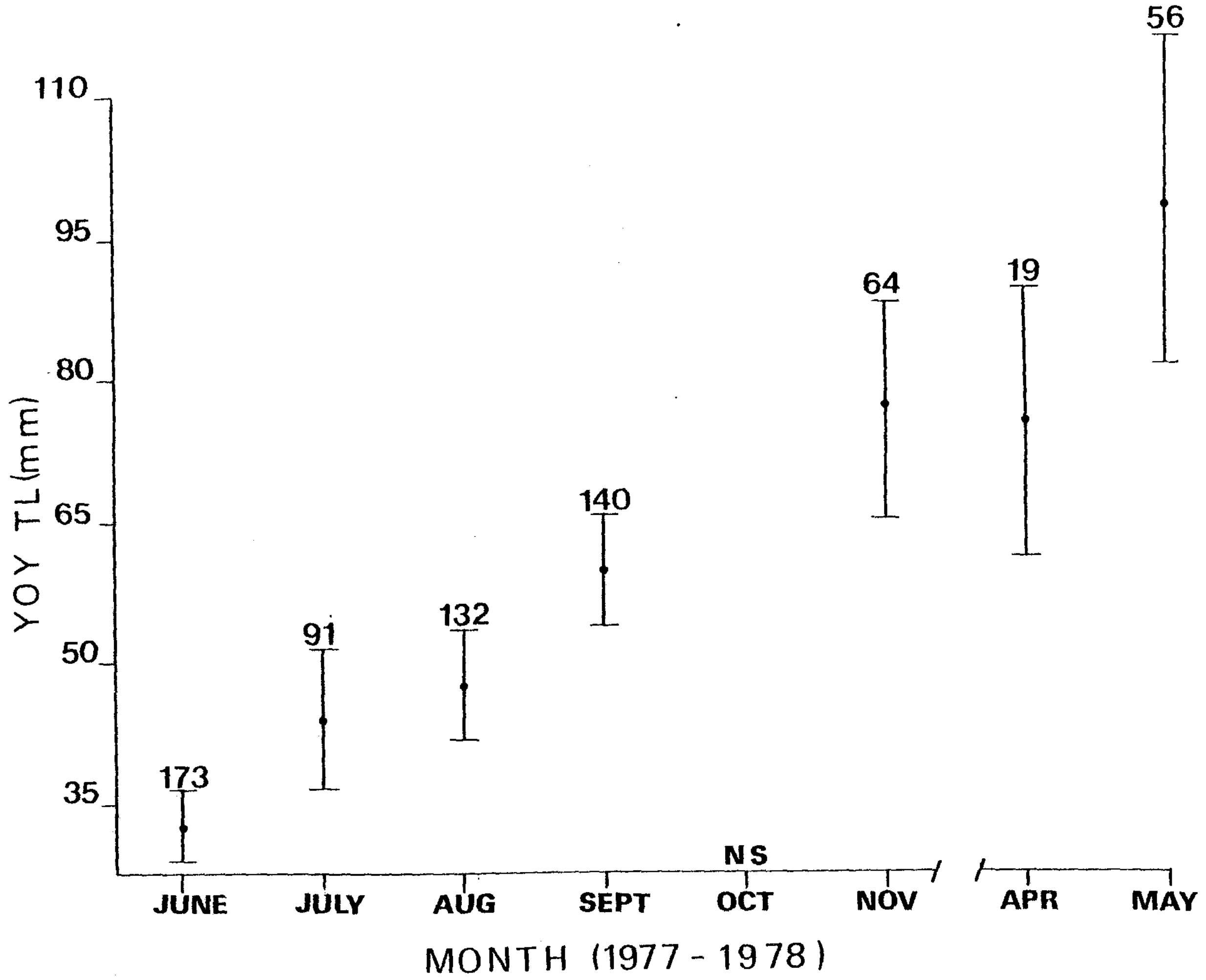
Growth of rainbow smelt from Essex Bay for the first year of life is summarized in Figure 1. Similar patterns of growth were noted in YOY from three other Massachusetts estuaries (Sutter et al. in prep). During June (n=6), August (n=9) and September (n=12), no significant relationships were found between total length and calorific content of YOY body tissue ($p>0.25$; n=27). However, during November, about 3.5 months prior to the spawning season, there was a significant difference ($p<0.01$) in the calorific value of body tissue between small fish (57-80 mm; $\bar{x}$= 5042.4 cal/g; S.D.= 36.5 cal/g; n=12) and large fish (81-103 mm; $\bar{x}$= 5203.0 cal/g; S.D.= 62.8 cal/g; n=9).

The difference in calories per gram of body tissue between small and large YOY smelt may be related to gonadal maturation and ultimately to precocious spawning. When YOY from 1 December 1978 were examined for gonadal development (gross internal inspection), only males had maturing

Table 1. Number of male and female precocious spawners as a percentage of total number of ripe fish, taken with fyke net, in the Parker River-Plum Island Sound spawning areas (1974 and 1975 data from Murawski and Cole 1978). Numbers of fish collected are in parentheses.

Year	Spawning Location	Percent Male	Percent Female
1974	Parker River	33.1 (491)	2.0 (70)
1975	Parker River	8.8 (1205)	0.4 (153)
1979	Parker River	1.5 (978)	0.2 (103)
	Cart Creek	12.5 (217)	1.6 (30)

Figure 1. YOY smelt growth in Essex Bay, Massachusetts from 1977-1978. Monthly measurements indicate mean total length and S.D.. Sample sizes are given above each month's data point and NS indicates no sample taken.



YOY TL(mm)
110
95
80
65
50
35
173
91
132
140
NS
64
19
56
JUNE
JULY
AUG
SEPT
OCT
NOV
APR
MAY
MONTH (1977 - 1978)

gonads, although in the 1974, 1975 and 1979 spawning runs, both male and female precocious spawners were found (Table 1). The relationship between male size (TL) and sexual maturity is reflected in the percentages of smelt (by size class) with developing testes in the December samples: 6.25 % (81-86 mm), 20 % (87-92 mm), 75 % (105-110 mm) and 100 % for males more than 110 mm (maximum size= 112 mm; n=96). In addition, maturing males had significantly higher calorific value of body tissue ($p<0.01$) compared with fish of the same size (TL=87-92 mm) without developing gonads (maturing males: $\bar{x}$= 5496.9 cal/g; S.D.= 17.4 cal/g; n=3; immature males: $\bar{x}$= 5282.8 cal/g; S.D.= 30.6 cal/g; n=3). Fish with maturing testes in December would probably spawn precociously during spring since maturation of testes is usually complete by January (Chen 1970).

A positive relationship between body length and maturation of gonads is further supported by comparing lengths of age I fish from the 1974, 1975 and 1979 spawning runs to age I fish that did not spawn, but remained in the estuaries. The smallest fish found spawning ranged from 120-124 mm (present study; Murawski 1976), showing that considerable growth had occurred since December. No fish collected in the Essex River estuary (56-103 mm; n=19) or the Parker River estuary (55-102 mm; n=51; Clayton 1976), at the same time of year, were this large.

Discussion

Anadromous rainbow smelt in the Parker River-Plum Island Sound and Essex Bay areas clearly displayed a positive relationship between length, sexual maturity and caloric content of body tissue. Visual inspection of gonads and calorific determinations indicated that larger fish (>80 mm, TL) collected in late fall were becoming sexually mature. The effect of size on maturity was not absolute, but with increasing length there was a corresponding increase in percentage of maturing males. A relationship between sexual maturation and size (length) or faster growth rate has also been noted for several other fish species. Donaldson (1969) and Burrows (1970) found that larger hatchery-reared sockeye and coho salmon tended to mature earlier. MacKinnon and Donaldson (1976) suggested that male pink salmon must attain a specific size before the initiation of gonad (testicular) development. Similarly, Schiefer (1971) indicated that faster growth rates affected precocious gonadal maturation of male Atlantic salmon. Bowering (1976) speculated that size rather than age was more related to maturation of witch flounder. A critical size may exist for YOY smelt from Essex Bay corresponding to the 80 mm energetic and gonadal maturation threshold noted above.

Smelt maturing precociously apparently have a higher energy content stored in the body tissue (higher energetic potential) than fish remaining immature at age I. This energy difference may be expressed in differential fat content. Fat is closely related to gonadal maturation (Love 1970; Shul'man 1974; DeVlaming et al. 1978), supplying the major source of energy for gamete production in fish (Shul'man 1974). Fat for germinal tissue growth of Esox lucius must be drawn from somatic and/or liver tissue (Medford and MacKay 1978; Diana and MacKay 1979). Winters (1970) found that the fat content of immature capelin (Mallotus villosus) was much lower than mature capelin. The higher caloric content of maturing male smelt can probably be accounted for by increased fat.

Relative number of precocious spawners increased as the Parker River and Cart Creek runs progressed. Photoperiod and temperature have been suggested as triggering mechanisms for sexual maturation in precocious Pacific salmonids (MacKinnon and Donaldson 1976; Schmidt and House 1979). It seems probable that a lengthening photoperiod and warmer water temperatures also may account for the increase in number of precocious smelt arriving at spawning sites later in the seaosn.

Percentage of age I male smelt spawning was consistently greater than percentage of precocious females (Table 1). This has also been found for Atlantic salmon (Lee and Power 1976), steelhead trout (Schmidt and House 1979), chinook salmon (Robertson 1957) and pink salmon (MacKinnon and Donaldson 1976), and would be expected since more time and energy are required for oogenesis than for spermatogenesis (Shul'man 1974). Foltz and Norden (1977) determined that the change in gonadal energetic content of Lake Michigan rainbow smelt from post-spawning to pre-spawning was 6.5 times greater in females than males.

The physiological strategy of any organism is to balance energy allocations between growth, maintenance and reproduction, and between survival and egg production (Cody 1966; Holgate 1967; Gadgil and Bossert 1970). Female age I smelt (which have a higher energetic requirement for gonadal maturation) may be delaying reproduction more often in favor of somatic growth, and possible higher survival and later reproduction at age II. Delayed reproduction will be selected for only when it will increase the probability of a higher reproductive potential. An organism must decide how much of its current available resources to commit to reproduction at a particular age (eg., age I or age II for first reproduction of smelt) relative to future efforts so that the optimum progeny will be produced and survive (Williams 1966a,b).

Theoretical consideration of age at first reproduction has involved discussion of optimization within different environmental and biological constraints (see Stearns 1976 for review). A population's reproductive age structure will affect the whole life history of an organism, as indicated for several fish species (Murphy 1967; 1968; Schaffer 1974a; Schaffer and Elson 1975). Age of reproductive maturity is influenced by various biological and environmental parameters, eg., differential growth rates (Schiefer 1971; and others), food availability (Bagenal 1969; MacKinnon 1972), and latitudinal variations (Leggett and Carscadden 1978) that involve a complex of environmental factors. In addition, incidents causing increasing mortality of adults or juveniles will shift first reproduction to younger or older ages, respectively (Murphy 1968; Schaffer 1974b).

Life history variables are usually considered to be adaptive and influenced by natural selection (Cole 1954; Murphy 1968; Schaffer and Elson 1975; Leggett and Carscadden 1978), and have been shown under experimental conditions to have varying degrees of heritability (Elson

1970; Schaffer and Elson 1975). Robertson (1957) and MacKinnon and Donaldson (1976) indicate precocious gonadal maturation of chinook and pink salmon may be under genetic control, and Schmidt and House (1979) suggest a sex-linked trait to explain low frequency of female precocious spawners. Although these studies suggest a high degree of heritability for precocious spawning phenotypes, this must be experimentally verified to determine the importance of precocious spawning to the life history of smelt. The degree to which reproductive characteristics are genetically determined or due to environmental variation expressed by the diversity of the phenotype must also be determined (Schaffer and Elson 1975).

CHAPTER III

REPRODUCTIVE ECOLOGY OF ANADROMOUS RAINBOW SMELT IN A NEW ENGLAND ESTUARINE SYSTEM

Introduction

Determining relationships between fish reproduction and environmental parameters is an important part of effective fisheries management (Leggett and Carscadden 1978). Anadromous populations of rainbow smelt in New England have been reduced due to spawning habitat destruction, pollution and overfishing (Bigelow and Schroeder 1953), thus intensifying the need for understanding environmental factors affecting reproductive success. A critical part of this assessment is estimating egg survival. Studies of salmonid populations have generated information on physical and biological factors that affect egg survival (Wickett 1954; Shumway et al. 1964; Koski 1966; Mason 1976; Hausle and Coble 1976), but research addressing these problems for smelt is lacking, especially for anadromous populations (Rothschild 1961; Rupp 1965; 1968). Therefore, the effect of two environmental parameters, substrate and water flow, on survival of smelt eggs from fertilization through hatching was evaluated.

The present investigation also examined, using field experiments, selectivity of spawning sites by smelt. Smelt are generally thought to be non-selective in choice of spawning habitat (Rupp 1965; Hulbert 1974). However, smelt eggs are adhesive and possess a specialized stalk formed by the inverted outer coat, so that attached eggs are suspended in the current (McKenzie 1964). Presumably the stalk insures adequate water circulation. This adaptation suggests specialization relative to spawning habitat.

The objectives of this study were to investigate smelt reproductive biology to obtain information that can be used to develop optimal smelt egg stocking techniques for restoration. This information should aid in the understanding of their reproductive tactics, enabling a better evaluation of perturbation on systems containing anadromous smelt.

Study Areas

Investigations were conducted in two spawning locations as well as in two areas where spawning no longer occurs. Parker River and Cart Creek spawning sites were used because of predictability of smelt runs and existence of background data for this area (Clayton 1976; Murawski and Cole 1978; Murawski et al. in press).

Smelt spawning has not been reported in the Essex River since 1969. Substrate of the historically-utilized spawning site was predominantly rubble and boulders, with some gravel and sand, similar to the Parker River and Cart Creek. At present, the Essex River lacks the aquatic vegetation that is abundant in the Parker River and Cart Creek. Chesmore et al. (1973) discussed hydrographic data for this area (see map in Kelso 1979). The site in Bull Brook, Rowley, Massachusetts (approximately 9 km southeast of the Parker River and Cart Creek spawning areas) consisted of a series of pools and small falls (made of railroad ties) about 50 m long, 2-3 m wide and 30-90 cm deep, leading from Bull Brook Reservoir to the Egypt River (one of four rivers leading into Parker River-Plum Island Sound).

Methods

Artificially fertilized eggs placed in experimental cages were used to measure egg survival. Eggs from six ripe females collected from the Parker River on 21 March 1979 were artificially spawned onto the rough side of 36 11.5 cm ceramic tiles and placed in shallow metal pans filled with stream water. Milt from several males was added until the water was discolored, then left for 30 minutes allowing eggs to water-harden. Half the plates were put in the Parker River and half in the Cart Creek area. After 24 hours, eggs remaining on the plates were counted with a hand held counter, magnifying lens and grid laid over the tile. Several other similarly-treated tiles were taken to a field laboratory on Cart Creek and placed in four-liter aquaria with a natural photoperiod. Water temperature in these aquaria was kept the same as the Cart Creek spawning area ($\pm 1^{o}C$) by supplying them with a constant flow of water via a submersible pump in the stream. Eggs in aquaria allowed careful, daily inspection of egg development that could not be done in the field.

Tiles in both the Parker River and Cart Creek were placed into 20x 20x10 cm cages that inhibited smelt from adding eggs to the known number on each tile. Cages were constructed of 1 mm mesh nylon screen stapled on a wooden frame with the bottom embedded into cement to prevent cages from being washed away. The top was secured with two rubber bands allowing easy access to the plates. Although cages prevented additional eggs from being deposited on the plates, they also prevented egg predation, decreased physical damage and reduced flow over eggs. Phillips and Koski (1969) noted similar problems in estimating salmonid egg survival using porous containers. To evaluate the cage effect on estimates of egg survival, two sets of four control plates were placed in Cart Creek above a 0.5 m waterfall that marked the upstream limit of spawning.

Egg development was followed daily in both the stream experiment and field laboratory. When laboratory egg development indicated that hatching in the field was 3-5 days away, the number of 'late-eyed' eggs on all field plates were counted. When pre-hatching larvae exhibited eye movement and body jerks, plates were removed from the two streams and placed in shallow plastic containers. Prolarvae were counted as they hatched, which started within 24 hours of being removed from the field. These experiments provide estimates of percent survival to late-eyed stage (number of late-eyed/initial number of eggs) and to hatching (number of prolarvae/ initial number of eggs) for the Parker River and Cart Creek (caged and controls). Similar procedures were followed to determine survival of artificially fertilized eggs from the Parker River that were placed in Essex River. No cages were used to prevent additional egg deposition, since there has been no smelt run in Essex since 1969. The Essex River experiment also provides egg survival data in the absence of cage effects.

Preliminary estimates of effect of water current on egg survival were made in Cart Creek and Bull Brook. Artificially fertilized eggs from four females were placed on 16 plates without cages and arranged in four areas of Cart Creek representing relatively high water velocity (3 plates), moderate velocity (4 plates in two areas) and low velocity (5 plates) as measured daily. Equal numbers of plates were originally used in each area, but some plates were washed away during a spring flood. This experiment was terminated after eggs reached early-eyed stage (12 days) due to an unexpected night of spawning over some of the plates. A separate, but comparable, estimate of the effect of stream flow on egg survival was made in Bull Brook. Trays made of leaves pressed between chicken wire held by a wooden frame lined with metal were placed in the Jones River, Massachusetts. After several days of smelt spawning, trays containing eggs were removed by the Massachusetts Division of Marine Fisheries and put into Bull Brook and several other coastal streams. Monitoring of the 23 egg-covered trays in Bull Brook began on day of stocking (13 April 1979) and continued to 30 April 1979 when, before hatching occurred, the trays were destroyed by flooding. On 13 and 20 April, 35 mm photographs were taken of each of the 23 plates. Current speed, dissolved oxygen and water temperature were taken over every plate after each photographic sequence. An estimate of egg survival from 13 and 20 April was made by randomly selecting 10 of the trays, then dividing the two photographs of those trays into 130 equal areas and counting eggs from 15 random areas. The decrease in number of eggs over time was related to water velocity using linear regression.

To determine substrate-related egg survival and substrate preference of spawners, a site was cleared of loose rock and vegetation in Cart Creek. Two experimental areas were constructed, each consisting of two natural and one artificial substrates: aquatic plants (river moss, *Podostemum ceratophyllum abrotanoides*), gravel/rubble (5-20 cm diameter of a type typical to most New England streams) and ceramic tiles. Each substrate type covered 1125 cm^2 of the cleared bottom. Smelt were allowed to spawn over the experimental area for one night, and the next day the numbers of eggs on each substrate were counted. Development was followed to late-eyed stage only on plants. Survival on ceramic tiles had already been estimated, and since tile and gravel/rubble subtrates present a similar surface to eggs laid on them, survival of these substrates was assumed equal. Shortly before hatching, late-eyed eggs still on river moss were brought back to the laboratory, counted and placed in an aerated four-liter glass jar. Number of prolarvae were counted over three days of hatching to estimate percent hatching. An approximation of overall egg survival was made by multiplying percent hatching by number of late-eyed eggs and dividing the result by initial number of eggs.

Relationships between length of spawning female, diameter of eggs and resultant prolarval length were determined to provide more insight into factors influencing size of eggs and prolarvae. Five ripe females were obtained from the Parker River run, artificially spawned into five separate four-liter glass jars and fertilized with 3-5 males per jar. Water in each jar was aerated and changed daily. Water temperatures in the jars was kept the same as the spawning area by placing the jars in a large water bath supplied with a constant flow of Cart Creek water. When eggs hatched, prolarvae were measured to the nearest 0.01 mm (TL, from the anterior tip of the lower jaw to the distal tip of the urostylar vertebra). The relationship between diameter of eggs (water hardened and unfertilized) and total length of female was found by subsampling eggs from the above experiment, and from another 24 females of various sizes from the Parker River run. Egg size was taken as the mean of two measurements of diameters. All eggs and prolarvae were measured using a microscope and micrometer.

Results

Mean egg survival to hatching over all five treatments (Table 2) was 1.02 % (S.D.= 0.35 %). Comparison of caged treatments and uncaged controls indicates little cage effect in Cart Creek. A 50 % lower than mean survival-to-hatching rate was found for eggs in the Parker River. In this stream, algae grew quickly on cages and had to be removed daily. Lower survival in the Parker River may have been due to clogging of the nylon screen that restricted water flow into the cages and reduced available oxygen.

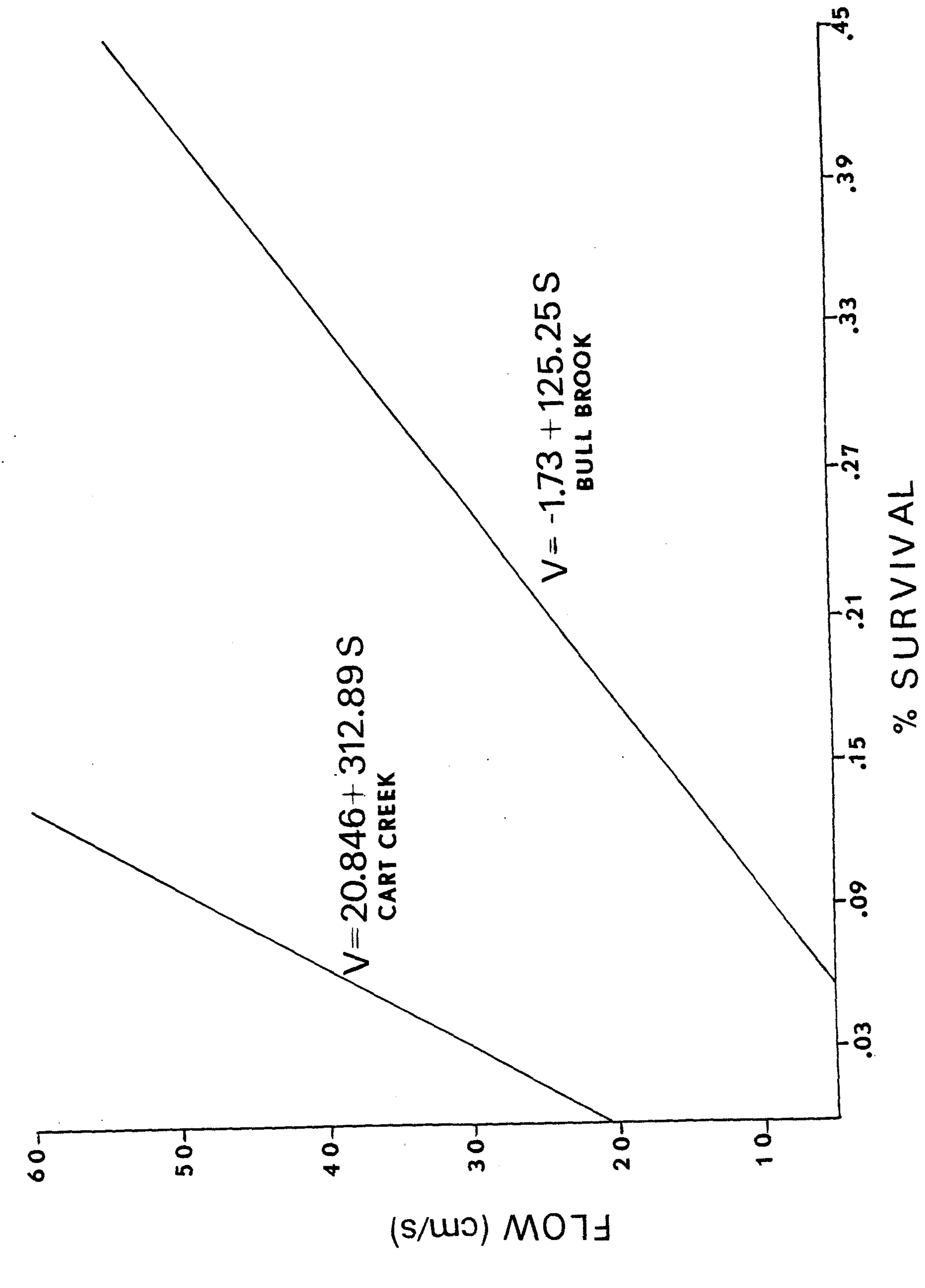
Egg survival was correlated with average water velocity over the restoration stocking trays in Bull Brook ($\underline{r}$= 0.92; $p<0.01$; Fig. 2). Since most estimates of water velocity over the trays were around 40 cm/s, with few higher or lower values (range 25-80 cm/s), more data would be needed to confirm the relationship between flow and survival. Similar results were obtained in another experiment in Cart Creek. Eggs placed in high ($\bar{x}$= 60 cm/s; 3 plates; 2965 eggs), moderate ($\bar{x}$= 40 cm/s; 8 plates; 6875 eggs) and low water velocity ($\bar{x}$= 15 cm/s; 5 plates; 4818 eggs), resulted in a significant relationship between survival to early-eyed stage and flow rate ($\underline{r}$= 0.70; $p<0.01$; Fig. 2). Slopes of the regression equations differ, but this may be attributable to Bull Brook eggs being at least one week old before starting the experiment (which lasted only eight days), while survival was followed from fertilization to early-eyed stage in Cart Creek (twelve days). However, both experiments indicate a positive relationship between water velocity and egg survival.

Substrate type influenced numbers of eggs deposited by naturally

Table 2. Percent survival of eggs to eyed stage and hatching in experimental cages in the Parker River and Cart Creek, uncaged controls in the upper area of Cart Creek and for the historically utilized area of Essex River during 1979.

Location	Number of Plates	Date Started	Hatching Dates	Initial Egg Number	% Survival	
					Eyed Stage	Hatching
Parker River (caged)	18	3-21	4-23,24	9577	2.76	0.42
Cart Creek (caged)	18	3-21	4-23,24	8976	3.01	1.02
Cart Creek (control 1)	12	3-23	4-24,25	5567	4.10	1.33
Cart Creek (control 2)	5	4-19	5-4,5	3804	2.30	1.10
Essex River	10	4-4	4-30,5-1	5042	4.46	1.21
				Mean survival	3.33	1.02

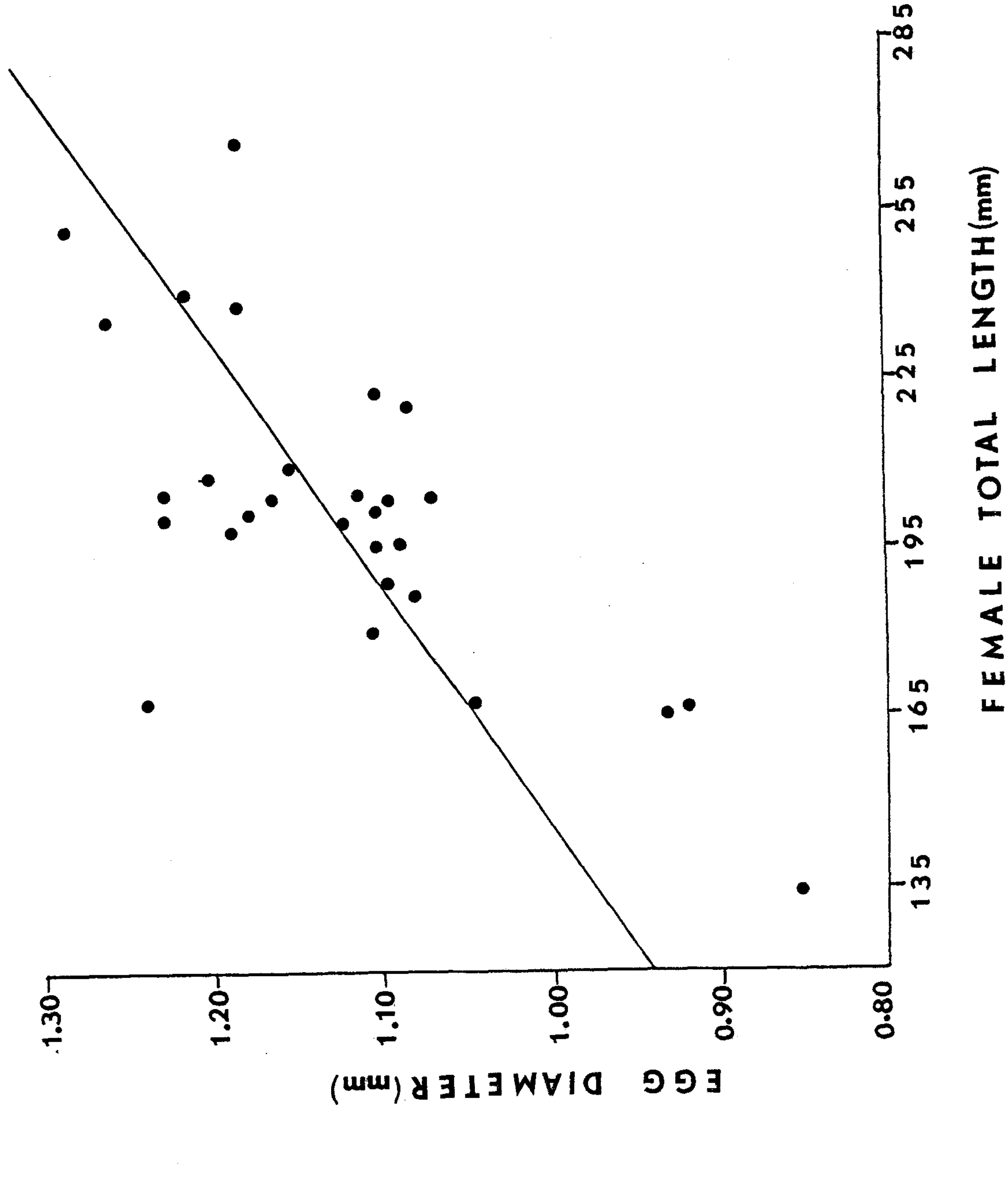
Figure 2. Relationship between water flow and smelt egg survival in Cart Creek (16 ceramic tiles with a maximum flow of 60 cm/s; 12 days) and in Bull Brook (10 stocking trays with a maximum flow of 80 cm/s; 8 days).


V= -1.73 + 125.25 S
BULL BROOK
V=20.846+ 312.89 S
CART CREEK
% SURVIVAL
FLOW (cm/s)
.03
.09
.15
.21
.27
.33
.39
.45
10
20
30
40
50
60

spawning smelt and subsequent egg survival. During the Cart Creek instream experiment, where equal bottom areas were covered by three types of spawning substrate, approximately 12-15 times more eggs were deposited on river moss (n= 7000) than either ceramic tiles (n= 629) or rocks (n= 375). On aquatic vegetation, egg survival from fertilization to late-eyed stage was 11.6 %, compared with 2-4 % on tiles (Table 2). An 87.5 % hatching success rate was found for late-eyed eggs brought to the field laboratory, for an overall estimate of 10.1 % survival from fertilization to hatching. This compares to only 1 % survival on the two dimensional surface of ceramic tiles.

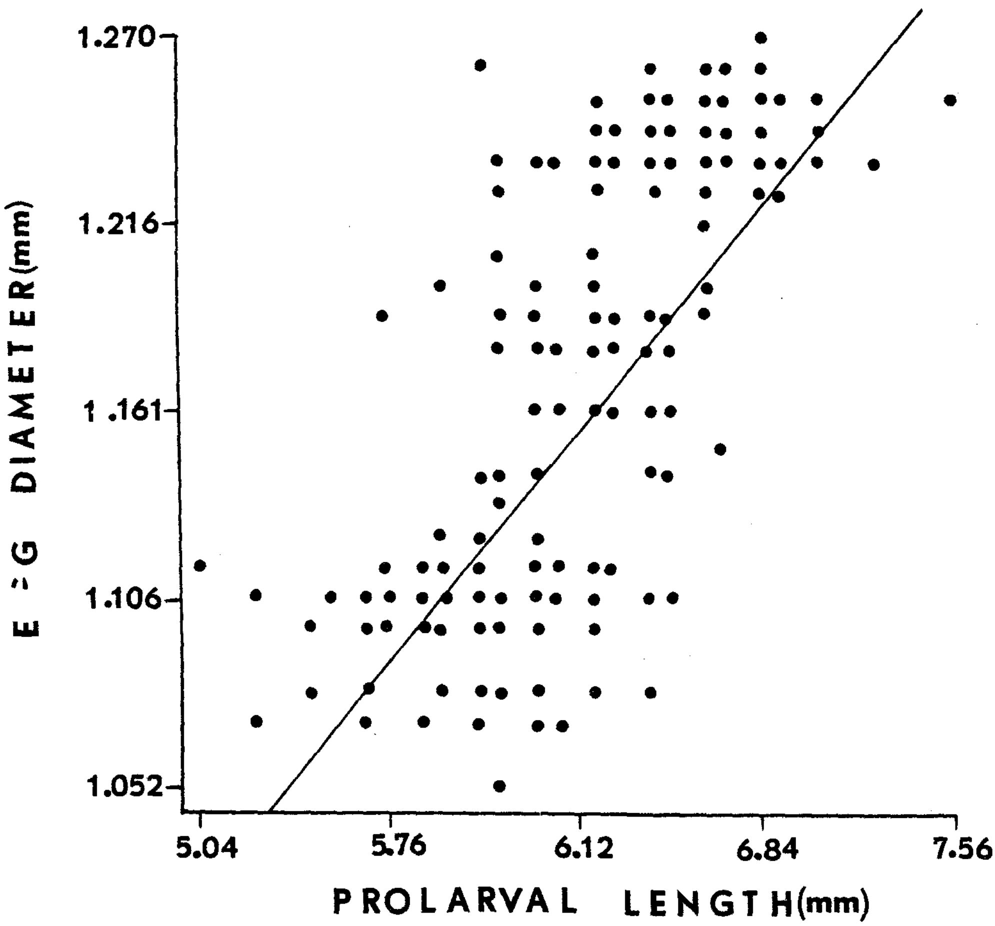
Regression of mean diameter (E) of water-hardened, unfertilized eggs on female total length (TL) gave the following equation: $E = 0.66 + 0.0023\ TL$ ($\underline{r} = 0.66$; $p<0.01$; $t=4.54$; $p<0.01$; Fig. 3). Although the relationship was significant, there was large variation in egg size. Laboratory investigation of relationships between egg size and prolarval length revealed significant differences in egg diameters among the five experimental jars, when all data were pooled ($p<0.01$; n= 375); with eggs in a particular jar being statistically the same size. Partitioning jar effects with Duncan's range test showed no difference between egg diameters of jars 1 and 5 ($p>0.05$). Hatching lasted four days with the majority of prolarvae emerging on days 2 and 3. Covariate analysis indicated that within any jar, prolarvae hatching on the third day were significantly larger ($p<0.05$ for each jar, 1-4; n=30). Duncan's range test on prolarval size (day 3 hatch) indicated that each jar was significantly different from all others ($p<0.01$). The relationship between egg diameter (E) and pro-

Figure 3. Relationship between mean diameter of water hardened, unfertilized eggs and total length of the respective female (n=29).


EGG DIAMETER (mm)
1.30
1.20
1.10
1.00
0.90
0.80
135
165
195
225
255
285
FEMALE TOTAL LENGTH (mm)

larval length (PL) from day 3, over all jars was: $E = 0.301 + 0.135\ PL$ ($\underline{r}=0.78$; $p<0.01$; $t= 23.74$; $p<0.01$; Fig. 4).

Figure 4. Relationship of Day 3 post-hatching prolarval length to pooled egg diameters (n=375).


1.270
1.216
1 .161
1.106
1.052
E :G DIAMETER(mm)
5.04
5.76
6.12
6.84
7.56
PROLARVAL LENGTH(mm)

Discussion

McKenzie (1964) followed anadromous smelt egg deposition and prolarval production over several years in the Miramichi River, Canada, and found 0.8 - 1.8% hatching success. A mean survival rate of 1.06% from final egg deposition to hatching was determined for freshwater, shore spawning smelt (Rupp 1965). Rothschild (1961) studied a stream spawning population of freshwater smelt and used canvas covered ceramic tiles as substrate to collect eggs. He found 24% survival to prehatching, with survival to prolarval stage only 0.55%. Measurements of egg survival on ceramic tiles in the present study (Table 2) were consistant with results from these studies. However, none of the previous estimates of egg survival led to an ecological interpretation since they did not account for specific effects of physical and biotic variation within the spawning streams.

General trends in survival of fish eggs after spawning can be correlated with characteristics of the aquatic environment (Dahlberg 1979). Survival rates are generally low in freshwater species that do not guard their demersal eggs, with rainbow smelt as an example. Egg survival is much higher in fish providing some parental care, such as freshwater and anadromous fish that construct redds (summary in Breder and Rosen 1966). Marine demersal eggs can also exhibit high survival rates (Gjosaeter and Saetre 1974) compared to much lower survival of pelagic eggs. These examples serve only to illustrate broad scale environmental effects on reproduction. To understand micro-environmental effects, studies must examine intrapopulation variation in egg/fry production in relation to specific environmental factors (Kynard 1979).

In the present investigation, a positive relation between flow and egg survival was found in both Cart Creek and Bull Brook. Also, general observations indicated more eggs were laid in areas of higher water velocity (present study; Rothschild 1961; Hulbert 1974). Rate of water exchange has been found to be an important component of salmonid egg survival (McNeil 1966). Closely associated with flow rate is the amount of dissolved oxygen available to developing eggs, as illustrated by studies of salmonid redds (Wickett 1954; Coble 1961; Phillips and Campbell 1962; Avery 1974; Silver et al. 1963; Mason 1969). Variation in dissolved oxygen concentration may also effect the size of the emerging fry (Shumway et al. 1964). In the present study, silt accumulation was evident in some cages located in areas of slower moving water and might have caused total mortality if it were not removed daily. Smelt eggs spawned in low current areas (< 15 cm/s) would be subject to heavy siltation and lower dissolved oxygen. Such conditions would probably cause increased mortality, similar to that noted in salmonid redds by Koski (1966), Burns (1970) and Dill and Northcote (1970).

Substrate characteristics are important for salmonids that bury their eggs (Larkin 1977; Hausle and Coble 1976), and have a significant effect on smelt egg survival, even though smelt have stalked, adhesive eggs which are not buried. Hulbert (1974) found a significant, but limited effect of substrate type on smelt prolarvae production. He incubated eggs in glass jars with four substrates: sand (with low prolarvae production), large and small gravel and an artificial substrate (all having equal effect on hatching success). Variable survival was also noted on different substrates for walleye, with more eggs spawned in the areas of better survival (Johnson 1961). Anadromous smelt in Cart Creek also appear to have spawning substrate preferences and place significantly more eggs on plant material, where survival is higher. Evidence for substrate preference was not expected since smelt are generally portrayed as nonselective spawners (Rupp 1965, 1968).

Egg predation can be a major source of mortality for many fish species (Dahlberg 1979), especially for broadcast spawners that have no specialized protective mechanisms. Predation on smelt eggs by spawning adults was found by Creaser (1925) and Hoover (1936), while Rupp (1959) described egg predation by larval and nymphal insects. Common mummichogs (Fundulus heteroclitus) and sticklebacks (Apeltes quadracus), known egg predators, were captured below both Cart Creek and Parker River spawning sites. However, none contained smelt eggs nor were collected in the faster moving water over the actual spawning grounds. In addition, if egg predation had been a significant source of egg mortality in the present study, survival estimates would have been much lower on the unprotected tiles in Cart Creek and Essex River relative to the caged plates, instead of having equivalent or higher survival (Table 2).

Rothschild (1961) noted fungus on many large freshwater smelt egg masses, stating that the mycelia may prevent escapement of prolarvae, thereby reducing survival. Fungus was noted on many ceramic tiles and it probably contributed to the lower egg survival observed in the Parker River. It may be significant that no eggs with fungus were found on any plants examined for smelt eggs, despite higher density of eggs on plants relative to that on tiles. Therefore, biotic and physical characteristics that affect smelt egg survival cannot be investigated separately, since many of these parameters have complex interrelationships (e.g., flow affecting dissolved oxygen levels and siltation rate, the latter also affected by rainfall, vegetation substrate, etc.).

Egg survival should be viewed relative to other aspects of anadromous smelt reproductive biology. Spawning females were larger (older) at the beginning than at the end of both the Cart Creek and Parker River 1979 runs. A decrease in female total length during the 1974 and 1975 Parker River runs was also noted by Murawski (1976). Total length of female rainbow smelt was positively correlated with diameter of unfertilized, water-hardened eggs (Figure 3). Koski (1966) and Winters (1970) noted similar positive correlations between size of female and corresponding egg size in coho salmon and capelin. The above results would account for the seasonal decline in fertilized egg size observed during the 1974 and 1975 Parker River spawning runs (Clayton 1976). Bagenal (1971) found a general seasonal decline in egg and spawner sizes for many marine fishes, indicating that as the season progressed, eggs would contain less yolk (a factor in larval growth and survival).

The positive relationship of egg diameter and length of resultant prolarvae is well established (Dahl 1919; Mason and Chapman 1965; Blaxter and Hempel 1963, 1966; Bagenal 1969b) and is supported by the results of the present study (Figure 4). Size of prolarval smelt in the five experimental jars increased from the second day of hatching to the third and maintained a close association between size of egg and corresponding prolarval length. A significant increase in size of coho salmon fry as emergence progressed was also found by Mason (1976). In addition, size of fry is related to survival time without an exogenous food source (Blaxter and Hempel 1963, 1966; Bagenal 1969a,b).

Seasonal variability in quality and quantity of food affects fish reproductive characteristics (Nikolsky 1969; Shul'man 1974; Tyler and Dunn 1976; Kramer 1978; Wooton et al. 1978). Differential energy intake may explain variation in fecundity of some salmonids (Scott 1962; Bagenal 1969b; Martin 1970) and seasonal decrease in egg size of herring (Cushing 1967), plaice (Riley 1966) and trout (Bagenal 1969a). Variation in the distribution of energy to gonads, relative to the amount of food ingested, is affected by the size of female plaice (MacKinnon 1972) and by geographic location of American shad (Leggett and Carscadden 1978) and may be reflected in smelt egg size and number, as well as survival of prolarvae.

The reproductive strategy of anadromous rainbow smelt within the Parker River-Plum Island Sound, as concluded from this and other investigations, is that larger fish, with larger eggs, spawn earlier than smaller, less fecund fish with smaller eggs (Clayton 1976). This produces large larvae in early spring when primary production is probably lower than late spring (when the smaller eggs hatch).

Within each stream spawning area, more eggs are placed on aquatic vegetation and in areas of high water velocity (present study; Hulbert 1974). This study found that eggs laid on plants had higher survival than those laid on other substrates. Eggs on plants may be afforded more protection from predation (eggs are harder to obtain from a complex, moving, three dimensional substrate than from a static, two dimensional surface like ceramic tile or rock), are less likely to have problems with fungal growth, which was abundant on eggs on tiles, and in high density situations, have the best contact with water due to higher surface area of the vegetation. Due to lack of plants and large numbers of spawning fish, eggs are often laid on any available type of substrate. Spawning in fast moving water in early spring, when water temperatures are low, may also serve to avoid possible egg predation. An individual female may utilize two or more spawning areas within the Parker River system (Murawski et al. in press) thereby spreading reproductive effort into different stream environments. This may optimize the number of progeny produced, especially if environmental variations causing egg mortality are unpredictable from year to year (i.e., 'bet-hedging' in conditions of uncertainty; Mountford 1973; Stearns 1976).

The timing of smelt reproduction in early spring may, in part, be the result of inter-species competition for limited spawning substrate. When alewives (migrating through the Parker River area) and blueback herring (which spawn in the exact area as smelt) became abundant during the 1979 run, smelt spawning shifted completely (from the Parker River to Cart Creek) thereby avoiding physical and possible gametic contact. Hulbert (1974) also mentioned the possibility of inter-specific interaction between alewives and smelt causing differential spawning stream usage.

Results of this study should be of interest to modelers assessing the impact of various perturbations in systems containing smelt and to agencies attempting to re-establish, or enhance existing, smelt runs by egg stocking procedures. Placing smelt eggs in high flow areas (60-80 cm/s), on substrates with high surface areas will probably enhance hatching success, and increase the efficiency of stocking programs. However, egg survival should not be the only factor considered in management of egg stocking programs. Although egg survival in the Essex River was good and many ripe fish are collected by an annual ice-fishery each year (below the historical spawning area), no spawning has been documented in the Essex since 1969. It seems that the problem with smelt production in this river may rest with adults avoiding the Essex River in spite of adequate habitat quality for survival of eggs, and indicates the need for further research in this area.

CHAPTER IV

SUGGESTIONS FOR FURTHER RESEARCH

Based on the information collected during this study, several future research problems became apparent. Some of these are:

1. Further examination of the reproductive characteristics of anadromous rainbow smelt by:

   a) Investigation of the use of artificial substrates with high surface areas (e.g., plastic strips attached to rocks or cement bricks) to enhance spawning substrate in the Parker River and Cart Creek and for use in stocking in various coastal streams;

   b) More extensive experimental testing of flow and substrate in different areas of Cart Creek, the Parker and Essex Rivers and in heavily utilized areas (e.g., the Jones River). In addition, expansion of experiments to include other environmental and biological factors;

   c) Observation of spawning to elucidate any behavioral selection of substrate or flow;

   d) Obtaining an extensive predator collection in the field and verifying, via laboratory experiments with different predators and substrates, the effects of various predators;

   e) Collection of larvae as they emerge from spawning sites to confirm the hypothesis that large eggs, that are spawned first, hatch first.

2. Investigate possible relationships between alewives and blueback herring spawning with smelt. In addition, study the possibility of

habitat partitioning between smelt, tomcod, blueback herring and white perch (all of which use the Parker River for spawning) and compare their reproductive strategies with those found in systems which do not contain all these species.

3. In the Essex River, examine the possibilities of sonic tags on fish in the ice-fishery to determine whether smelt are spawning in sub-optimal habitat (i.e., brackish water) or are moving to the Parker River-Plum Island Sound (see Murawski et al. in press).

4. Determine how complete the homing instinct is for smelt in this system, especially in collaboration with Murawski et al. (in press). This may help answer questions about Essex River fish homing to the Parker or Merrimack Rivers or some other location (possible use of choice chambers, electric fields etc.).

5. Concerning precocious spawners:

   a) Identify the role of age I spawners in the spawning run (i.e., see if there is age specific egg survival, if these fish do spawn and try to identify the possible ecological significances of spawning precociously);

   b) Sample runs north and south of the Parker River-Plum Island Sound to see if the percentage of precocious fish increases in the southern populations and decreases in the northern ones (see Leggett and Carscadden 1978).

6. Use the liver-somatic index (see Heidinger and Crawford 1977; Bulow et al. 1978; DeValming et al. 1978; Wootton et al. 1978) as an indicator of food quality intake relative to the size of the developing

eggs to try to determine factors that influence egg size and investigate the results of such an index using field data.

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