Time to hatch and larval size in relation to temperature and egg size in Atlantic cod (*Gadus morhua*)

P. Pepin, D.C. Orr, and J.T. Anderson

Abstract: We report on the effect of temperature and egg diameter on the development rates of Atlantic cod (*Gadus morhua*) eggs and yolk-sac larvae from experiments in which individuals were followed from fertilization until death. Temperature was the only variable to consistently and significantly affect development rates. Egg size had no consistent effect on transition times during the egg phase, but there was a significant increase in the time to yolk absorption as well as the time until death with increasing egg diameter. Larval length at hatch was significantly greater in larger eggs, but only a small proportion of the variance in length at hatch was explained by egg size (6%). Increasing temperature resulted in a significant increase in the size at hatch and may reflect the overall metabolic load placed on the embryo as temperatures decrease below 1–2°C.

Résumé : Nous rendons compte des effets qu'ont la température et le diamètre de l'oeuf sur le taux de développement des oeufs et des larves vésiculées de la morue franche (*Gadus morhua*), à partir d'expériences qui consistaient à suivre des individus depuis la fécondation de l'oeuf jusqu'à la mort. La température est la seule variable à avoir affecté régulièrement et de façon significative les taux de développement des oeufs. La taille de l'oeuf n'a pas eu d'incidence régulièrement observable sur les périodes de transition au cours de la phase de l'oeuf; par contre, nous avons observé qu'une augmentation du diamètre de l'oeuf entraînait une augmentation significative du temps écoulé jusqu'à la résorption du vitellus, de même que jusqu'à la mort. La longueur des larves à l'éclosion était plus importante pour les oeufs de plus grande taille et ce, de façon significative, mais seule une faible part de la variance observée dans la taille à l'éclosion s'expliquait par la taille de l'oeuf (6%). Une hausse de la température a entraîné une augmentation significative de la taille à l'éclosion, ce qui pourrait refléter la charge métabolique globale que subit l'embryon lorsque les températures baissent au-dessous de 1–2°C.
[Traduit par la Rédaction]

Introduction

Early development of poikilotherms is determined by factors that limit the rate of biological production, the total amount of energy allocated to each offspring, and the interaction between these components which ultimately defines the overall conversion efficiency. Development of the nonfeeding early life stages of fish is significantly influenced by both temperature and egg size (Pauly and Pullin 1988; Pepin 1991). Increased temperature, within the optimal range for a species, results in faster development, and increased egg diameter results in longer times to hatch and increased larval size (Pepin 1991). Intraspecific studies have also noted a strong relationship between the size of eggs and the temperature of the environment in which they are spawned (Blaxter and Hempel 1963; Bagenal 1969; Ware 1975). Ecological and evolutionary arguments suggest that these relationships may represent an adaptation of different stocks or species to their available food resources (e.g., Ware 1975). Such relationships are also believed to extend within the spawning season of individual stocks because of the observations that egg size decreases as the environmental temperature increases (e.g., Ware and Lambert 1985; Miller et al. 1995).

Although the apparent consistency of the size–temperature relationships between and within stocks suggests that increased body size is beneficial in colder temperatures and that this principle applies even at the individual level (Pauly and Pullin 1988; Pepin 1991), the lack of supporting laboratory observations limits the rigour of such an extrapolation (Pepin and Miller 1993). The significance of body size to physiological processes during the egg and larval stages is well established (e.g., Miller et al. 1988; Houde 1989; Pepin 1991) as is the variability in offspring size among females (e.g., Chambers et al. 1988; Kjesbu 1989; Buckley et al. 1991) and in relation to differences in environmental conditions (e.g., Blaxter and Hempel 1963; Bagenal 1969; Ware 1975; Ware and Lambert 1985; Miller et al. 1995). However, because environmental temperature and egg size are correlated, it is difficult to determine the influence that each variable has on the development and potential survival of eggs and larvae. Only under laboratory conditions is it possible to make strong inferences (sensu Platt 1964) about the influence of temperature and size on the development of fish eggs and larvae.

The following study was designed to determine the effects of incubation temperature and initial size on the development (e.g., time to hatch, yolk absorption, starvation) and charac-

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Table 1. Description of egg stages as defined by Laurence and Rogers (1976) and Markle and Frost (1985).

Laurence and Rogers 1976	Markle and Frost 1985
Stage I From fertilization until the formation of a complete blastodermal cap	Stage I From fertilization until the visible formation of an embryonic axis about the midgastrula.
Stage II From the formation of a complete blastodermal cap through the development of the segmentation cavity to the first appearance of the germinal ring and embryonic axis	Stage II From the formation of the embryonic axis until the embryo is halfway around the yolk, approximately the time of blastopore closure
Stage III From the first appearance of the germinal ring and embryonic axis to the closure of the blastopore	Stage III From the end of stage II until the tip of the tail reaches or could reach the snout
Stage IV From the closure of the blastopore to hatching	Stage IV From the end stage III until hatching

teristics of individual eggs and yolk-sac larvae of Atlantic cod (*Gadus morhua*). The range of temperatures was chosen to reflect those that occur during the spawning of cod on the northeast Newfoundland shelf (Templeman 1981). We use event analysis to ascertain the effects of temperature and body size on the timing of developmental stages, as suggested by Chambers and Leggett (1989), which provides a method for determining treatment effects on event dispersion.

Materials and methods

Experimental protocol

A broodstock of 30–50 adult cod (40–80 cm TL) was maintained under natural light and temperature regimes at the Ocean Sciences Centre, Memorial University, St. John's, Nfld. The fish had been captured using a bottom trawl and held in captivity for at least 6 mo during which time they were fed a mixture of dry feed and capelin (J.A. Brown, Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, NF A1C 5S7, Canada, personal communication). The physiological condition of fish during the spawning season was not recorded. Eggs and sperm were collected from two to four ripe female and three to five running male cod. Only females that yielded eggs freely (i.e., with little or no pressure on the vent) were used in these experiments. We did not determine if the same individuals were used in the different experimental trials of this study. Eggs and sperm were combined in filtered seawater at ambient temperature (1–3°C). After approximately 6 h postfertilization, 150 viable zygotes were separated into individual 30-mL sterile vials filled with UV-sterilized filtered (0.45 μm) seawater. Thirty vials were transferred to each of five water baths which were maintained at −1, 1, 3, 5, or 7°C using Neslab RTE-220 flow-through controllers. Seawater in each vial was replaced every 2 d throughout the experiment. Eggs were treated with a solution containing 100 mg streptomycin·L^{-1} and 60 mg penicillin·L^{-1}. Vials were checked daily to determine the stage of development, as described below. The experiment was repeated three times starting on 1 May 1991, 9 May 1991, and 23 May 1991.

To extend our analysis beyond events associated with the larval stage (i.e., hatch, yolk absorption, death), two descriptive staging schemes were used to monitor development during the egg stage. Each scheme divides development of the egg into four stages (Table 1). The scheme used in all experimental trials was that of Laurence and Rogers (1976), which has similarities to that of Thompson and Riley (1981). During the third experimental trial, we also used the staging scheme of Markle and Frost (1985). The former scheme places greater emphasis on separation of the early developmental stages whereas the latter provides a more even separation of stages through the period from fertilization until hatch. Both schemes provide information that permits age determination of field sampled eggs, given environmental temperatures and information on development rates. In both schemes, the end of stage IV represents hatch. In addition to the time until the end of the four egg stages, we noted the time until yolk absorption as well as time of death. Death occurred during all stages of development and was due principally to developmental abnormalities during the egg stage, and to the exhaustion of energy reserves during the larval stage.

During the second and third trials, individual egg diameter on the day of fertilization and length of the larva at hatch were measured to the nearest 0.1 mm using an image analysis system mounted on a Wild M3C dissecting microscope with an S-type mount fitted with a 0.5× objective.

Analysis

The analysis of transition times (i.e., age at the end of a stage) for early life history stages was performed using a technique for event analysis, wherein the entire distribution of event times, rather than only the mean or median, is used to depict the schedule of transitions from one stage to the next. Details of methods for event analysis are available from Cox and Oates (1984) and applications to early life history development were given by Chambers and Leggett (1989).

A Weibull distribution was selected to model event data in this study. The survival function of the Weibull distribution is defined as

$$(1) \quad S(t) = e^{[-(t/\alpha)^{\gamma}]}$$

where t is time, α is the scale parameter in units of time (i.e., days),

and γ is a dimensionless shape parameter. Equation 1 is modified into an accelerated failure time model by including treatment variables, described by a vector $\nu' = (\nu_1, \nu_2, ..., \nu_k)$ such that

$$(2) \quad S(t; \nu) = e^{[-(t/\alpha)^{\gamma} e^{\nu'\beta}]}$$

assuming that the elements of ν interact through a linear function, $\nu'\beta$, where the parameters, β_i's, are estimated.

Analysis involves the logarithmic transformation of event times which yields the standard extreme value distribution that is multiplied by a scale factor (analogous to the variance of a normal distribution) and translated by a location parameter (β). Observations of event times are related to explanatory variables as

$$(3) \quad Y = V\beta + \sigma\epsilon$$

where Y is the vector of ln-transformed event times, V is the matrix of explanatory variables, β is the vector of coefficients to be estimated, σ is the scale parameter to be estimated, and ϵ is the extreme value distribution in the case of the Weibull distribution. In this case, σ is equal to the inverse of the Weibull shape parameter γ. The first column of V is typically a unit vector such that β_1 estimates the intercept which in this context is the location parameter of the extreme value distribution. In equation 3, the explanatory variables act additively on Y, the ln-transformed time, leading to an acceleration or deceleration of event times. The explanatory variables considered in our analysis were temperature and the ln-transformed egg diameter. We transformed egg diameter because we had no a priori expectation that transition times were exponentially related to egg diameter. The effect of sequential trial numbers is excluded from the analysis because of the small number of observations available (i.e., three) relative to the spawning period of individual fish (Kjesbu 1989) and because we used several male and female fish to obtain and fertilize the eggs for each trial. Analysis was performed using maximum likelihood.

The Pth percentile of the cumulative distribution function for age-at-stage transition can be estimated as

$$(4) \quad \hat{y} = \beta_1 + \nu\beta_i + u_p\sigma$$

where $y = \ln(t)$, β_1 is the location parameter, ν are the covariates (temperature and egg diameter) and β_i are their coefficients, σ is the scale parameter of the extreme value distribution, and $u = \ln[-(\ln(1 - P)]$ is the Pth standard extreme value percentile.

The relationships between survival rates and temperature and between egg diameter and larval length were evaluated using general linear models fitted by least squares. Such models were also used as complementary alternatives to event analysis in order to assess the relative effects of egg diameter and temperature on transition times in instances where both were considered to have a significant effect based on maximum likelihood approximations.

Results

Increased temperature led to faster transition times and was the only variable to have a consistently significant effect on development rates of cod eggs and yolk-sac larvae (Table 2). Although there was some variation in the slope of the response of development rates to changes in temperature (Table 2), the effect appeared to have little impact on the uniformity of development among stages at the different temperatures when all experimental trials were combined (Fig. 1). The average ratio of development rates expected for a 10°C change in temperature (Q_{10}) was 3.7. The staging scheme of Markle and Frost (1985) yielded similar results (Q_{10} = 3.9), but because only one experimental trial was available to estimate the parameters, we will restrict all further discussion to the results obtained using the staging scheme of Laurence and Rogers (1976).

Age-at-death was the only process not significantly influenced by temperature (Table 2; Fig. 1). As a result, the distribution of mortalities tended to move towards later stages of development as temperature increased. Consequently, overall survival to hatch was significantly influenced by temperature ($F_{1,12}$ = 10.9, $p < 0.01$) (Fig. 2). Despite the scatter, it is clear that mortality to hatch decreases with increasing temperature, within the range of conditions used in these experiments.

Egg diameter had a significant influence on age-at-transition for the stage II eggs only ($\chi_{[1]}^2$ = 9.96, $p < 0.01$). Increasing egg diameter led to longer development times. The age-at-transition for the other egg stages (I, III, IV) was not significantly influenced by egg diameter.

In addition to having no apparently strong and consistent effect on stage-specific transition times during the egg phase, egg diameter did not have a significant effect on the probability of hatching (Fig. 3). Although the two trials for which we had information on egg size had notably different distributions of diameters, we found no evidence of a consistent difference in the probability of hatching for a given size between the two experiments. Furthermore, there was no evidence that the size-dependent probability of hatching changed in relation to temperature.

Although egg diameter had no notable effect on transition times during the egg phase, egg diameter did significantly effect time to yolk absorption ($\chi_{[1]}^2$ = 8.64, $p < 0.01$) (Fig. 4) as well as the age-at-death ($\chi_{[1]}^2$ = 7.17, $p < 0.01$) (Fig. 5; Table 2), both of which increased for larger eggs. If instead of using event analysis we use an ANCOVA to assess the relative effects of temperature (T) and egg diameter (ϕ) on time to yolk absorption (t) ($\ln(t) = a + bT + c\ln(\phi)$, where a, b, and c are parameters to be estimated), we find that egg diameter explains only an additional 3% of the variance in individual development rates ($F_{1,82}$ = 4.1, $p < 0.05$) after taking into account the effect of temperature which explains 56% of the variance ($F_{1,82}$ = 105, $p < 0.001$). Although temperature did not significantly influence age-at-death ($F_{1,280}$ = 0.2, $p > 0.5$), egg diameter explained only 3% of the variance ($F_{1,280}$ = 9.1, $p < 0.01$).

Larval length at hatch was significantly positively related to egg diameter ($F_{1,75}$ = 5.2, $p < 0.05$). However, as with the effect of egg size on time to yolk absorption or age-at-death, only a small proportion of the variance in length at hatch was explained by egg size (6%) (Fig. 6). Increasing temperature resulted in a significant increase in the size at hatch ($F_{4,75}$ = 2.53, $p < 0.05$) resulting in a 1.2-mm increase in average length of larvae for an increase in temperature of 8°C (Fig. 7). We used an ANCOVA where temperature was treated as a classification variable because we had no a priori expectation of the functional form of the relationship between length at hatch and temperature.

The scale parameter of equation 3, σ, which provides a measure of the spread in the distribution of observations, tended to decrease with increasing development. This suggests that the stage-specific transition times were most variable for the transitions from stage I to II and from stage II to III and decreased thereafter as embryos and larvae

Table 2. Stage-specific fit to the accelerated failure time model (equation 3), with ln-transformed observations of transition times for the staging schemes of Laurence and Rogers (1976).

	Parameter estimate	SE	χ^2	$p <$
Stage I				
Location, β_1	2.39	0.13		
Temperature, β_2	-0.17	0.009	371	0.001
Egg diameter, β_3	-0.41	0.35	1.35	0.3
σ	0.36	0.016		
Stage II				
Location, β_1	2.08	0.19		
Temperature, β_2	-0.15	0.015	108	0.001
Egg diameter, β_3	1.59	0.50	10.2	0.01
σ	0.43	0.020		
Stage III				
Location, β_1	2.70	0.12		
Temperature, β_2	-0.13	0.009	215	0.001
Egg diameter, β_3	0.12	0.31	0.14	0.8
σ	0.24	0.013		
Stage IV				
Location, β_1	3.56	0.075		
Temperature, β_2	-0.13	0.007	389	0.001
Egg diameter, β_3	0.15	0.19	0.63	0.5
σ	0.13	0.011		
Yolk Abs.				
Location, β_1	3.84	0.099		
Temperature, β_2	-0.16	0.012	152	0.001
Egg diameter, β_3	0.67	0.23	8.87	0.01
σ	0.11	0.008		
Mortality				
Location, β_1	2.15	0.22		
Temperature, β_2	0.021	0.017	1.62	0.3
Egg diameter, β_3	1.66	0.61	7.36	0.01
σ	0.74	0.034		

Note: The equation was fit to the combined data from the three experimental trials. Egg diameter was ln-transformed. The χ^2 statistic tests the null hypothesis of no effect of temperature (i.e., $\beta_2 = 0$) or egg diameter (i.e., $\beta_3 = 0$) with df = 1.

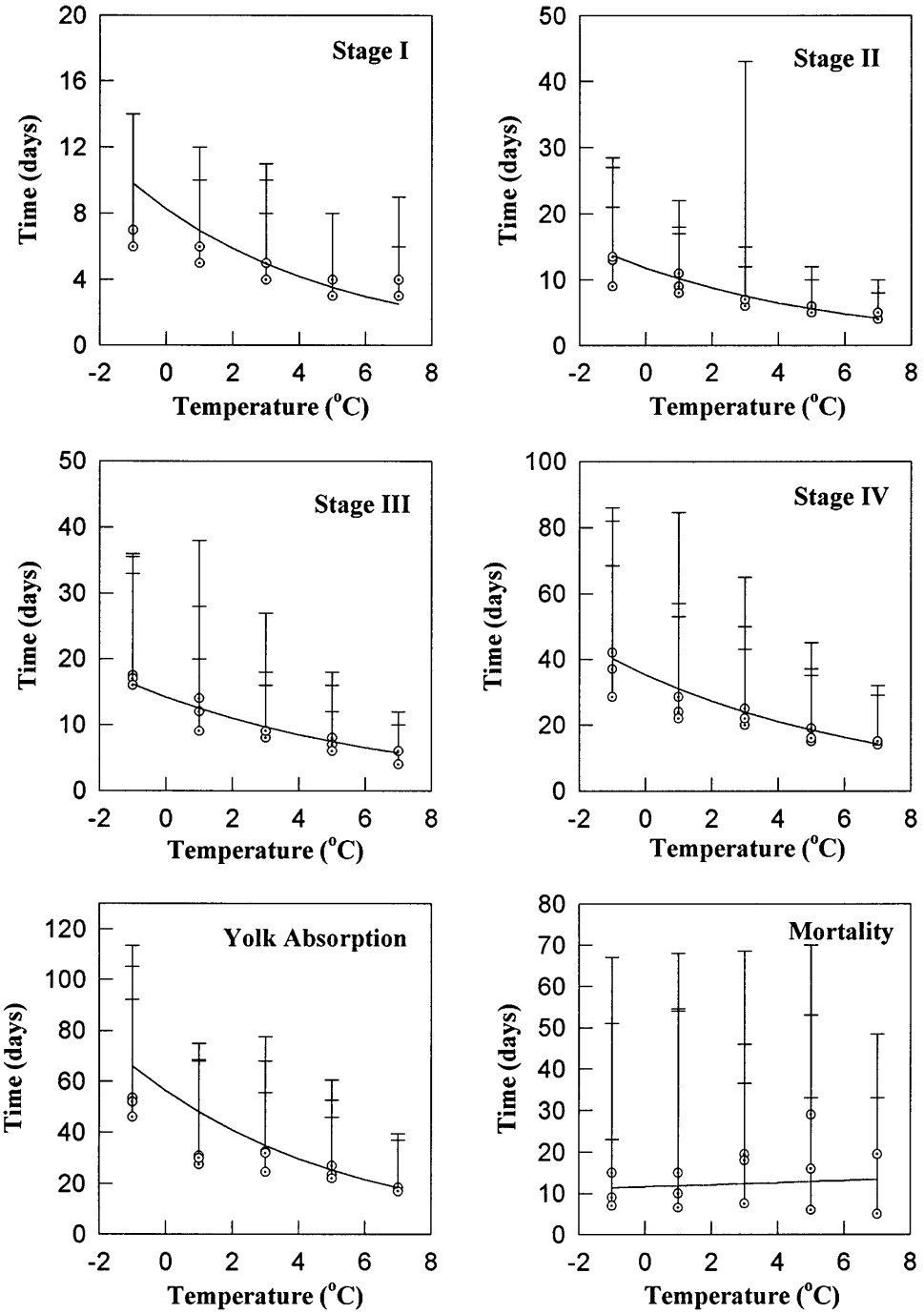
approached the time to hatch and of yolk absorption (Fig. 8), respectively.

Discussion

Temperature proved to have a greater influence on development rates of cod eggs and yolk-sac larvae than egg size. Although there is evidence that metabolic processes, such as respiration rates, increase with increasing body size during embryonic stages (e.g., Davenport and Lønning 1980; Rombough 1988), there may be relatively little impact on development rates caused by the variation in embryo size, at least prior to hatch. As a result, the temperature dependence of the biochemical reactions that govern metabolism is likely to be the dominant factor governing early development in cod. The strong temperature dependence of embryonic development rates may prove to be useful by giving added reliability to ageing of eggs from field collection without having to be overly concerned about possible influences of initial size.

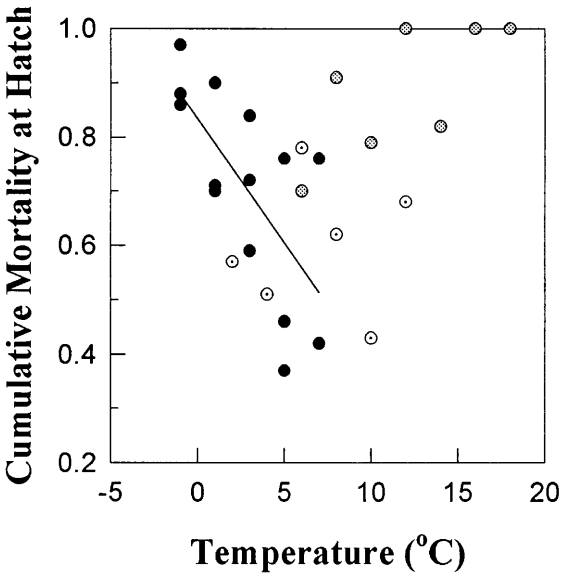
The magnitude of the temperature effect observed in this study shows some disparity with previous work on cod. Data from both Laurence and Rogers (1976) and Thompson and Riley (1981) indicate a Q_{10} of 2.3 and 2.7 in times to hatch, respectively, whereas our results yield a Q_{10} of 3.7, and Page and Frank (1989) obtained a value of 4.6 in their review, which excluded data from Thompson and Riley (1981). Part of the difference in the temperature effect may stem from the lower temperature limit of the different studies. Both Lau-

Fig. 1. Estimated age at which 50% of individuals reach the end of individual developmental stage of cod eggs and yolk-sac larvae in relation to temperature for the staging schemes of Laurence and Rogers (1976) (solid line) for the experimental mean egg size of 1.42 mm. Parameters are listed in Table 2. Open dotted symbols represent the 50th percentile of the data for each experimental trial and the capped error bar represents the range up to the 95th percentile of the data. Note that the fitted relationships were based on the distribution of number of individuals that transited each stage at each temperature regime and not on a single estimate of location for each experimental trial.



rence and Rogers (1976) and Thompson and Riley (1981) limited their experiments to temperatures of 2°C or more. Page and Frank's (1989) fig. 6 indicates a sharp discontinuity in the rate of increase in hatch times at temperatures below 2°C, largely due to works by Earll (1878), Dannevig (1895), and Brice (1898). These results would suggest that the lower limit of thermal tolerance in the development of cod eggs may occur at temperatures below 1−2°C. However, we found no evidence of such a sharp discontinuity in our general analysis (Fig. 1). This may reflect local adaptations to environmental conditions due to genetic isolation of cod on the northeast Newfoundland Shelf from other stocks (Carr and Marshall 1991), but further research is required to properly address this issue. Alternatively, this may reflect differences

Fig. 2. Cumulative mortality to 50% hatch in relation to temperature from this study (solid symbols). The solid line represents the least squares regression line $Y = 0.83 - 0.046X$, where Y is the cumulative mortality to 50% hatch and X is temperature. Each point represents an experimental trial. Data from Laurence and Rogers (1976) (open dotted symbols) and Iversen and Danielssen (1984) (shaded symbols) are included for comparison (see discussion).

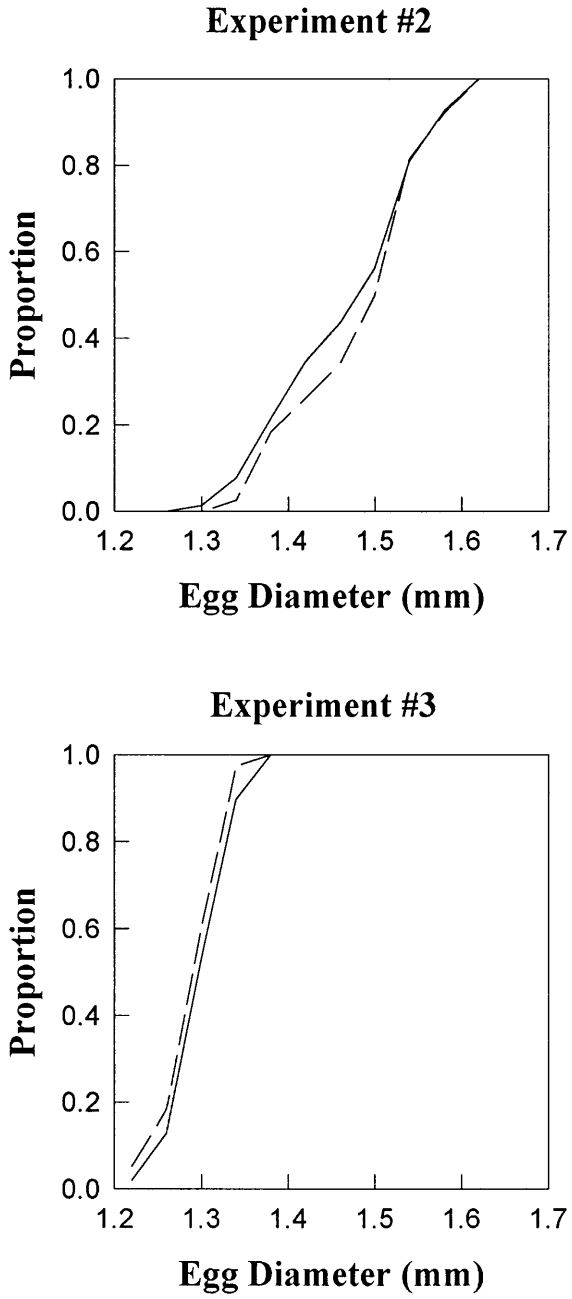


in experimental or analytical approaches between this and earlier studies.

We have demonstrated that cod eggs from the northeast Newfoundland shelf stock can develop normally at ocean temperatures as low as −1°C although there was high mortality during early development. This extends the lower tolerance limit for normal development in this species. In comparison, Thompson and Riley (1981) found that death occurred in the early stages of cleavage at temperatures below 1.5°C in cod from the southern North Sea. Although we found mortality increased with decreasing temperatures, a comparison with work by Laurence and Rogers (1976) and Iversen and Danielssen (1984) suggests that the cumulative mortality during development reaches a minimum in the 5–10°C range and increases above and below that (Fig. 2). The implication is that for cod eggs on the northeast Newfoundland Shelf, production early in the spawning season, before surface waters have warmed, can lead to low overall survival during this stage of development.

Although egg size did not have an important influence on development during the egg stage, there was a significant effect on the characteristics of yolk-sac larvae. As in previous studies (e.g., Blaxter and Hempel 1963; Chambers et al. 1988; Buckley et al. 1991), body length at hatch was correlated with egg size but this relationship was weak. However, our observations are consistent with Miller et al.'s (1995) results which showed that the egg – larval size relationship was highly variable within surveys of cod on the Scotian Shelf. They noted that a stronger egg – larval size relationship was obtained when data from a broad range of environmental conditions were combined. A similar contrast with previous studies was apparent when we considered the relationship

Fig. 3. Cumulative distribution of egg diameters at the start of the second and third experimental trials (solid line) and of the eggs that successfully hatched (broken line).



between egg diameter and time to yolk absorption. Although Blaxter and Hempel (1963) found that increased egg size is associated with a longer time until endogenous resources are completely utilized, our results indicate that the overall effect of individual egg size was weak. Much of the contrast between our findings and previous studies may arise from the basis for comparison. Many of the principles pertaining to the effects of both egg and larval size on physiological processes during the early life history of fish are derived from a comparison of group averages or distributions, whether these groups represent species, stocks of a species, or families within stocks (Pepin and Miller 1993). We focus on the vari-

Fig. 4. Relationship between time to yolk absorption and egg diameter. The key indicates the temperatures at which the eggs were incubated. The broken line shows the expected time to 50% yolk absorption, based on maximum likelihood estimates (Table 2), in relation to egg diameter. The line is based on the average overall mean temperature of 4.7°C, estimated for all the observations shown (n = 83).

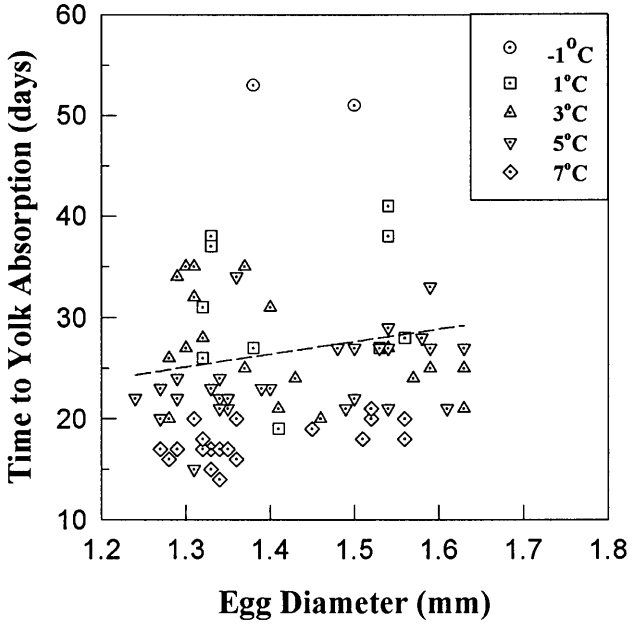


Fig. 5. Relationship between the age-at-death and egg diameter. The key indicates the temperatures at which the eggs were incubated. The broken line shows the expected time to 50% death, based on maximum likelihood estimates (Table 2), in relation to egg diameter. The line was based on an average overall mean temperature of 2.7°C, estimated for all the observations shown (n = 281).

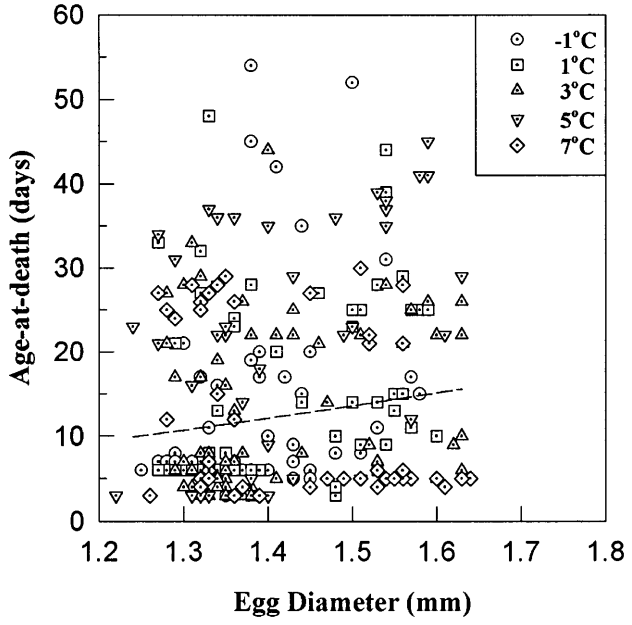
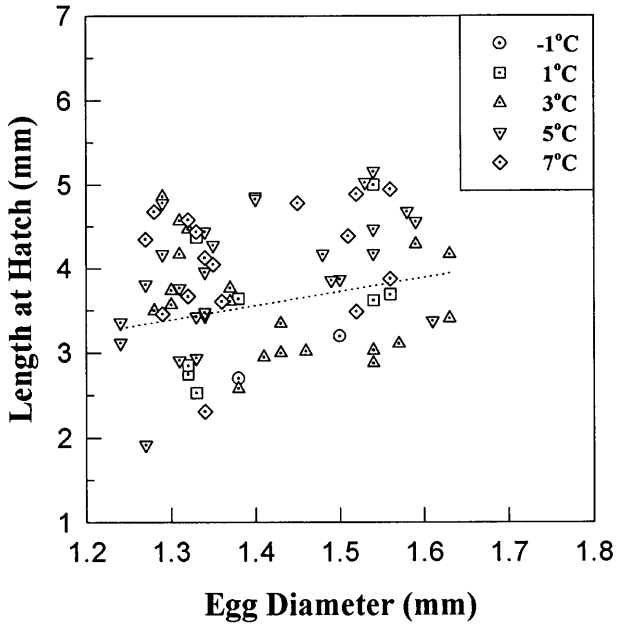


Fig. 6. Relationship between length at hatch of cod larvae and the diameter of the egg. The legend indicates the temperatures at which the eggs were incubated. The dotted line represents the expected length at hatch, estimated for a temperature of 3°C using an ANCOVA in which temperature was treated as a classification variable, in relation to egg diameter.



ability among individuals produced under similar conditions. Thus, we reduce potentially confounding factors, such as differences in physiological history of individual parents or gross differences in environmental conditions, that may lead to size-correlated trends in developmental features without necessarily having a size-dependent influence on the individual larva. We propose that the effect of body size on the early development characteristics of fish may in fact be substantially less important than previously suggested. It is possible that much of the variance in size-dependent developmental constraints of eggs and yolk-sac larvae may represent the overall influence of environmental features characteristic of spatial or temporal variations within or among ecosystems.

The effect of both temperature and egg size on the length of larvae at hatch was an unexpected finding of our study. Ware and Lambert (1985) noted a strong negative relationship between the average size of fish eggs and the temperature of the environment in which the eggs are caught. As well, Miller et al. (1995) found a strong positive relationship between the size of cod larvae and the egg from which each individual hatches. The conclusion from such studies has been that large eggs are produced in colder waters and yield larger larvae. Our results indicate that for a restricted number of experimental trials, the relationship between size at hatch and temperature is opposite to that noted under field conditions by Miller et al. (1995). Part of the contrast may be due to the generally weak relationship between egg size and size at hatch noted within experiments (this study) or within sampling periods (Miller et al. 1995). The inverse relationship between size at hatch and incubation temperature obtained in this study may be the result of the overall metabolic load placed on the

Fig. 7. Estimated average larval standard length at hatch in relation to temperature. The error bars represent standard errors estimated from an ANCOVA in which temperature was treated as a classification variable. The average egg size used for the estimate was 1.42 mm.

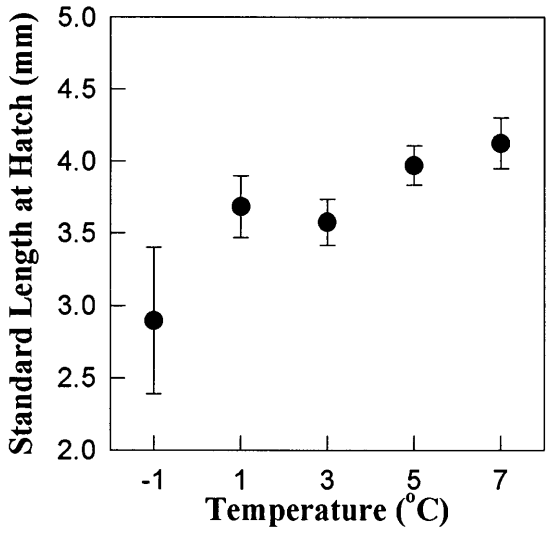
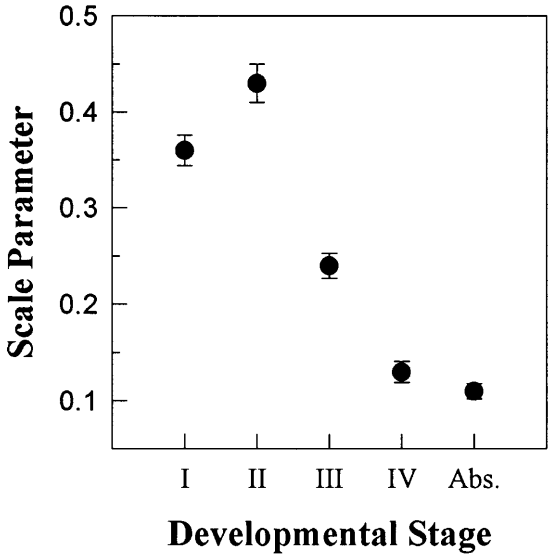


Fig. 8. Scale parameter (σ), with estimated standard errors, in relation to developmental stage from which cod eggs or larvae were transiting. The end of stage IV corresponds to hatch.



embryo as temperature decreases. The Q_{10} of decreasing incubation time with increasing temperature from this and previous studies (Laurence and Rogers 1976; Thompson and Riley 1981; Page and Frank 1989) ranges from 2.3 to 4.6 (average = 3.3). This contrasts with an average Q_{10} of 2.7 for the increase in respiration rate (micrograms O_2 per gram weight per hour) with increasing temperature for nonsalmonid species listed in Rombough's (1988, table IV) review. The implication is that the overall metabolic load (i.e., total respiration from fertilization to hatch) increases with decreasing temperature. This would result either in smaller energy reserves or a smaller individual at hatch for a given egg size. Alternatively, differences in the effect of temperature on developmental characteristics may occur in different populations or over a broader range of conditions. Chambers et al. (Huntsman Marine Science Centre, St. Andrews, NB E0G 2X0, Canada, personal communication) observed a dome-shaped relationship in the average length at hatch, for a given average egg diameter, in relation to incubation temperature. The range of temperatures used in this study corresponds to the lower range of conditions in Chambers' (personal communication) treatments whereas the average conditions encountered during Miller et al.'s (1995) surveys correspond to the middle to upper range used by Chambers. Consequently, the contrasting results observed in this and Miller et al.'s (1995) study may represent observations along the ascending and descending limb of a dome-shaped relationship between length at hatch and environmental temperature. The paucity of information pertaining to the determinants of egg size in highly fecund fish does not permit us to reject any hypothesis that could reconcile the contrast between field and laboratory observations of the relationship between egg diameter, temperature, and length at hatch. It appears that one must be cautious in the interpretation of relationships between body size and environmental factors unless the functional response has been carefully established over the full range of conditions that a species may encounter.

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References

Bagenal, T.B. 1969. Relationship between egg size and fry survival in brown trout *Salmo trutta* L.J. Fish Biol. **1**: 349–353.

Blaxter, J.H.S., and Hempel, G. 1963. The influence of egg size on herring larvae (*Clupea harengus*). J. Cons. Int. Explor. Mer, **28**: 211–240.

Brice, J.J. 1898. A manual for fish-culture, based on the methods of the United States Commission on Fish and Fisheries. Appendix to U.S. Comm. Fish. Rep. **23**(1897): 1–340.

Buckley, L.J., Smigielski, A.S., Halavik, T.A., Caldarone, E.M., Burns, B.R., and Laurence, G.C. 1991. Winter flounder *Pseudopleuronectes americanus* reproductive success. II. Effects of spawning time and female size on size, composition and viability of eggs and larvae. Mar. Ecol. Prog. Ser. **74**: 125–135.

Carr, S.M., and Marshall, H.D. 1991. Detection of intraspecific DNA sequence variation in the mitochondrial cytochrome *b* gene of Atlantic cod (*Gadus morhua*) by the polymerase chain reaction. Can. J. Fish. Aquat. Sci. **48**: 48–52.

Chambers, R.C., and Leggett, W.C. 1989. Event analysis applied to timing in marine fish ontogeny. Can. J. Fish. Aquat. Sci. **46**: 1633–1641.

Chambers, R.C., Leggett, W.C., and Brown, J.A. 1988. Variation in and among early life history traits of laboratory-reared winter flounder (*Pseudopleuronectes americanus*). Mar. Ecol. Prog. Ser. **47**: 1–15.

Cox, D.R., and Oates, D. 1984. Analysis of survival data. Monographs on statistics and applied probability. Chapman Hall. London.

Dannevig, H. 1895. The influence of temperature on the development of the eggs of fishes. Rep. Fish. Board Scotl. **13**: 147–152.

Davenport, J., and Lønning, S. 1980. Oxygen uptake in developing eggs and larvae of cod, *Gadus morhua*. J. Fish Biol. **16**: 249–256.

Earll, R.E. 1878. A report on the history and present condition of the shore cod fisheries of Cape Ann, Mass., together with notes on the natural history and propagation of the species. U.S. Comm. Fish. Rep. **6**(1878): 685–740.

Houde, E.D. 1989. Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. Fish. Bull. U.S. **87**: 471–496.

Iversen, S.A., and Danielssen, D.S. 1984. Development and mortality of cod (*Gadus morhua* L.) eggs and larvae in different temperatures. *In* The propagation of cod *Gadus morhua* L. *Edited by* E. Dahl, D.S. Danielssen, E. Moksnes, and P. Solemdal. Flødevigen Rapp. **1**: 49–65.

Kjesbu, O.S. 1989. The spawning activity of cod, *Gadus morhua* L. J. Fish Biol. **34**: 195–206.

Laurence, G.C., and Rogers, C.A. 1976. Effects of temperature and salinity on comparative embryo development and mortality of Atlantic cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus* L.). J. Cons. Int. Explor. Mer, **36**: 220–228.

Markle, D.F., and Frost, L.-A. 1985. Comparative morphology, seasonality, and a key to planktonic fish eggs from the Nova Scotian Shelf. Can. J. Zool. **63**: 246–257.

Miller, T.J., Crowder, L.B., Rice, J.A., and Marschall, E.A. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Can. J. Fish. Aquat. Sci. **45**: 1657–1670.

Miller, T.J., Herra, T., and Leggett, W.C. 1995. An individual-based analysis of the variability of eggs and their newly-hatched larvae of Atlantic cod (*Gadus morhua*) on the Scotian Shelf. Can. J. Fish. Aquat. Sci. **52**: 1083–1093.

Page, F.H., and Frank, K.T. 1989. Spawning time and egg stage duration in Northwest Atlantic haddock (*Melanogrammus aeglefinus*) stocks with emphasis on Georges and Browns Bank. Can. J. Fish. Aquat. Sci. **46**(Suppl. 1): 68–81.

Pauly, D., and Pullin, R.S.V. 1988. Hatching time in spherical, pelagic marine fish eggs in response to temperature and egg size. Environ. Biol. Fishes, **22**: 261–271.

Pepin, P. 1991. The effect of temperature and size on development and mortality rates of the pelagic early life history stages of marine fish. Can. J. Fish. Aquat. Sci. **48**: 503–518.

Pepin, P., and Miller, T.J. 1993. Potential use and abuse of general empirical models of early life history processes in fish. Can. J. Fish. Aquat. Sci. **50**: 1343–1345.

Platt, J.R. 1964. Strong inference. Science (Wash., D.C.), **146**: 347–353.

Rombough, P.J. 1988. Respiratory gas exchange, aerobic metabolism, and effects of hypoxia during early life. *In* Fish physiology. Vol. XI. The physiology of developing fish. Part A. Eggs and larvae. *Edited by* W.S. Hoar and D.J. Randall. Academic Press, San Diego, Calif. pp. 59–161.

Templeman, W.T. 1981. Vertebral numbers in Atlantic cod, *Gadus morhua*, of the Newfoundland and adjacent areas, 1947–1971, and their use for delineating cod stocks. J. Northwest Atl. Fish. Sci. **2**: 21–45.

Thompson, B.M., and Riley, J.D. 1981. Egg and larval development studies in the North Sea cod (*Gadus morhua* L.). Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **178**: 553–559.

Ware, D.M. 1975. Relation between egg size, growth and natural mortality of larval fish. J. Fish. Res. Board Can. **32**: 2503–2512.

Ware, D.M., and Lambert, T.C. 1985. Early life history of Atlantic mackerel (*Scomber scombrus*) in the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. **42**: 577–592.