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Comparative growth, respiration and delayed feeding abilities of larval cod (Gadus morhua) and haddock (Melanogrammus aeglefinus) as influenced by temperature during laboratory studies

By

Geoffrey C. Laurence

National Marine Fisheries Service  
Northeast Fisheries Center  
Narragansett Laboratory  
Narragansett, Rhode Island 02882  
USA



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### Abstract

Comparative growth and respiration were measured during the period hatching to metamorphosis for larval cod at 4, 7 and 10°C and for haddock at 4, 7 and 9°C. Growth was positively correlated with temperature for both species. Specific growth rates on a daily basis indicated good growth for the two species at the upper two temperatures and suppressed growth at 4°C. Respiration rates as measured by oxygen consumption were similar for both species. Variable and elevated oxygen consumption at 4°C indicated physiological stress at that temperature. Delayed feeding abilities, feeding initiation, yolk absorption and morphological development related to first feeding ability were similar for both species at 7-10°C. Larvae could survive without food and still initiate feeding until 10 days after hatching at 7°C and 8 days at 9-10°C.

### Introduction

Increasing attention in fishery science is being focused on laboratory and field studies of the extent and causes of larval fish mortality (Hunter 1976). Larval fish studies are now thought to hold some key answers in the determination of how adult populations and their resultant egg production affect eventual recruitment (stock-recruitment relationship). In addition, larval fish are good indicators of environmental quality and studies in this area are increasingly important (Blaxter 1970, Rosenthal and Alderdice 1976).

Successful feeding relationships and predators are the most probable factors controlling natural mortality during the larval fish stage. Studies of food capture and ensuing conversion for growth and metabolic processes as influenced by environmental factors show promise for determining causes of mortality in the larval stage (Laurence 1975, 1977). It is the purpose of this research to present the results of the influence of temperature on the comparative feeding, growth and respiration metabolism of larval cod, Gadus

morhua, and haddock, Melanogrammus aeglefinus, in an attempt to determine any interspecific differences between the two species that would relate to a potential and differential natural mortality. Spawning seasons for cod and haddock off the coast of North America overlap in time during winter-spring (Colton and Marak 1969), and the larvae co-exist spatially in the area from Martha's Vineyard north to the Grand Banks (Bigelow and Schroeder 1953). Under recent increased fishing intensity, stocks of haddock have become depressed and spawning success has fluctuated in comparison with cod (Grosslein and Hennemuth 1973).

### Materials and Methods

Adult cod were captured by otter trawl net in Block Island Sound, Rhode Island, and by set line approximately 18 km south of Chatam, Massachusetts. Haddock were captured by set line in the same vicinity off Chatam and approximately 20 km east of Cape Ann, Massachusetts. The adults were transported to the Narragansett Laboratory where they were separately maintained in 28,000 and 57,000 liter aquaria.

Natural spawnings were induced by standard techniques controlling temperature and photoperiod developed at the Narragansett Laboratory (Laurence 1974, Laurence and Rogers 1976). Newly fertilized embryos were collected from the experimental spawning aquaria with a 0.5 meter plankton net and placed in appropriate rearing containers.

All experiments and rearing were conducted at constant temperatures in the range of 4-10°C and at 32-34 ‰ salinity. For growth studies, approximately 1,000 newly fertilized embryos were placed in series of black 64-liter glass aquaria. The aquaria were placed in an environmental room or in water baths where the temperatures were maintained by program recorders controlling heating and cooling coils. All experimental aquaria were semiclosed systems aerated by airstones with a portion of the seawater being drained and replenished every 1 or 2 days. Illumination controlled by timers provided a 12:12 day-night photoperiod. Upon hatching, larvae were fed high concentrations of natural populations of zooplankters of 2-3 organisms per ml which were known to provide optimum growth rates (Laurence 1974). Specific zooplankters fed during experiments consisted mainly of the nauplii, copepodites and adults of the copepods Acartia clausi and Centropages hamatus with smaller amounts of Eurytemora affinis and barnacle nauplii, Balanus balanoides. All zooplankton collections were made using 0.5 meter nets with 60 or 120 mm mesh netting which were subsequently sieved through 200 or 500 mm mesh depending on the size of the larvae to be fed.

Specific methods for determining growth and respiration rates are described in detail by Laurence (1975). Briefly, growth at a particular temperature was determined on a dry weight basis once a week for individual larvae in samples of 10-25 for the entire period hatching to metamorphosis. Metamorphosis as defined in this research was when the larvae of both species developed anatomical and morphological characteristics similar to adults (i.e., fully developed fins, functional gills, "devil's thumbprint" pigmentation in haddock, etc.). This occurred at a size of approximately 1,000 µg dry weight and 10 mm standard

length for both species. Respiration as measured by oxygen consumption was likewise determined once a week for 6 replications of groups of 10, 5 or individual larvae at the constant temperature they were reared at. Oxygen consumption measurements were considered to be "routine" with larvae allowed 1-2 hrs for acclimation in the respiration flasks before results were recorded with a Gilson differential respirometer during 2 hr experimental trials.

Daily specific growth rates were calculated from the antilogarithms of the slopes of the regression equations describing the relationship of the logarithm of dry weight as the dependent variable and time in days as the independent variable (Figures 1 and 2).

Delayed feeding experiments were conducted at 7 and 10°C for cod and 7 and 9°C for haddock. These experiments were designed to ascertain the latest point after hatching that food had to be available for larvae to initiate successful feeding before starvation rendered them too weak to feed. Groups of approximately 50 larvae were placed in a series of 3.8 liter black aquaria with air-stones at the designated temperatures. The groups of larvae were fed high concentrations of zooplankters (> 2 per ml) starting at hatching and ensuing 2 day intervals. Samples of 10 larvae were taken 24 hr after feeding and analyzed for stomach contents, eye pigmentation, a functional mouth, and available yolk until it was obvious that larvae had been deprived of food long enough so as to be unable to initiate feeding. Criterion of successful feeding was if 50% or more of the sample of larvae contained food in their alimentary tracts. If less than 50% of a sample contained food they were additionally sampled every 24 hrs until it was established they could or could not feed successfully according to the criterion. All statistical and regression analyses were done according to the methods proposed in Draper and Smith (1966) and Steele and Torrie (1960).

## Results

### Growth

Cod growth was monitored weekly following hatching at constant temperatures of 4, 7 and 10°C until larvae reached metamorphosis or until complete mortality occurred in the rearing aquaria (Table 1). Complete mortality took place in the 5th week after hatching (41 days) at 4°C, while cod reached metamorphosis at 7 and 10°C in the 7th (52 days) and 6th (44 days) weeks after hatching respectively. Specific growth rates were 4.15%/day at 4°C, 6.67%/day at 7°C, and 8.75%/day at 10°C. Regression analyses of the semilogarithmic transformation of growth on time also demonstrated that temperatures strongly influenced growth rates as indicated by the increasing slopes of the regression lines with increasing temperature (Figure 1).

Haddock growth was measured weekly following hatching at 4, 7, and 9°C (Table 1). Repeated attempts to rear haddock at 10°C failed with mortalities consistently occurring 10-13 days after hatching. Rearing at 9°C produced

good growth and survival. As with cod, complete mortality of haddock occurred in the 5th week (36 days) after hatching at 4°C. Haddock larvae reached metamorphosis on the 4th week (30 days) after hatching at 9°C. Unfortunately, a malfunction took place in the haddock rearing aquarium at 7°C and all the larvae died during the 6th week (37 days) after hatching. However, the growth rate up to that time was comparable to previously reported results at 7°C (Laurence 1974) and indicated the larvae would have metamorphosed during the 6th-7th week after hatching. Specific growth rates were 3.68%/day at 4°C, 5.53%/day at 7°C, and 13.36%/day at 9°C. Regression analyses again showed the strong influence of temperature on growth with higher slope values at higher temperatures for the semilogarithmic transformation of dry weight growth on time (Figure 2).

### Respiration

The relationship of mean hourly oxygen consumption in  $\mu$ l per individual and dry body weight for cod larvae were linearized by treatment as a power function (Figure 3). Correlation coefficients indicated high statistical significance between the logarithms of oxygen consumption and body weight at 7 and 10°C ( $r = 0.80 > r$  (tabulated) = 0.33, d.f. 1,35,  $p = 0.05$  at 7°C and  $r = 0.75 > r$  (tabulated) = 0.29, d.f. 1,45,  $p = 0.05$  at 10°C).

Slight non-statistical significance was calculated at 4°C ( $r = 0.41 < r$  (tabulated) = 0.45, d.f. 1,17,  $p = 0.5$ ) indicating variable respiration with increasing body weight. Respiration rates, indicated by similar regression line slopes, were quite uniform with temperature; however, absolute respiration increased with increasing temperature as shown by the increased elevation of the regression lines (Figure 3).

The relationship of larval haddock oxygen consumption and dry weight treated as a power function showed statistically significant correlations at all 3 temperatures ( $r = 0.84 > r$  (tabulated) = 0.44, d.f. 1,18,  $p = 0.05$  at 9°C;  $r = 0.74 > r$  (tabulated) = 0.39, d.f. 1,24,  $p = 0.05$  at 7°C;  $r = 0.75 > r$  (tabulated) = 0.45, d.f. 1,17,  $p = 0.05$  at 4°C). Rates of haddock respiration and absolute values were similar at 7 and 9°C as indicated by similar slopes and elevations of the regression lines (Figure 4). The regression relationship at 4°C showed an unusually high and somewhat anomalous slope indicating, perhaps, that some stress factor was operating at this temperature.

Although absolute oxygen consumption values at a given dry weight were somewhat higher for haddock larvae at 9 and 7°C compared to cod at 10 and 7°C, 95% confidence limits about the origins and slopes of the regression lines at these temperatures revealed no statistically significant differences between the two species. Comparisons were not made at 4°C because of the variability of the data.

### Delayed Feeding Abilities

Both cod and haddock larvae were well developed at hatching with pigmented eyes, functional mouths and completed alimentary tract, and were able to initiate feeding immediately at temperatures of 7-10°C. No real differences

were noted in delayed feeding abilities of the two species (Table 2). When deprived of food, both species were able to initiate feeding as determined by the 50% feeding criterion until days 9 to 10 after hatching at 7°C and days 8 to 9 at 10 and 9°C for cod and haddock, respectively. There were no essential differences noted in yolk absorption times between the two species at comparable temperatures.

### Discussion

Larval cod and haddock growth was determined in terms of dry weights because this is the truest measure of increasing absolute size. Length measurements can be misleading since larval fishes may have allometric growth particularly when entering a metamorphosis. Additionally, weight or biomass estimates are directly applicable to trophic-energetic and productivity studies.

The successful rearing and growth of cod at 10°C and lack of success with haddock, despite several attempts is interesting. A drop of 1°C to 9°C permitted haddock larvae to survive and grow very well in spite of the fact that haddock embryos incubate until hatching reasonably well at 10°C (Laurence and Rogers 1976). This indicates that the scope for post-hatching growth and subsequent survival may be slightly temperature limited in the upper ranges for haddock larvae compared to cod. A specificity of temperature by young haddock was also noted by Tatyankin (1972) who tested the thermal preference of juvenile cod, haddock and pollack (Pollachius virens) in the laboratory. He found the haddock to be the most stenothermal of the three species.

Comparison of the rates of growth indicated by the slopes of the regression equations (Figures 1 and 2) demonstrated similar but somewhat higher rates of growth at all test temperatures for haddock larvae. Specific growth rates (Results Section) were similar for both species at 4 and 7°C, and considerably higher for haddock at 9°C than cod at 10°C. Both species showed depressed specific growth rates at 4°C and no survival to metamorphosis size under optimum feeding conditions. The general increase in growth rate with increase in temperature noted for both species has often been observed in young fishes (Shelbourn, Brett and Shirahata 1973).

Comparison of the specific growth rates recorded in these controlled laboratory studies with data extrapolated from the results of field studies of other researchers revealed some similarities. Jones (1973) reported a weight increase of 12%/day for Faroe haddock larvae which is very close to the 13.36%/day at 9°C in this study. A recalculation of Sysoeva and Degtereva's (1965) length-weight-age data for larval cod for the first 2 months of life gave an 8.5%/day specific growth rate in terms of weight. This value is in the range of the 6.67 to 8.75%/day at 7 and 10°C noted for cod in the research. Other larval species which develop at approximately the same temperatures as cod and haddock display comparable specific growth rates. A calculated 6.6%/day rate was derived from Marshall, Nicholls and Orr's (1937) data for 0-60 day post hatching, spring spawning herring (Clupea harrengus), and rates of 5.8 to 10.1%/day at 5 and 8°C were recorded for winter flounder larvae (Laurence 1975).

Respiration measurements on acclimated larvae allowed to swim freely in flasks devoid of food in these studies are considered to be estimates of "routine" metabolism according to the definition of Fry (1971). Routine metabolism is intermediate between "active" measured under conditions of forced activity and "standard" measured in a resting state with no food in the alimentary tract. Power functions describing the regression relationship of oxygen consumption and dry body weight were used because they historically have allowed comparisons between different species (Winburg 1956) and were statistically comparable in these studies with cod and haddock larvae.

The lack of statistically significant differences of respiration on a unit weight basis between the two species in the temperature range of 7-10°C indicated a physiological similarity. Also, both species showed an apparent stress situation in regards to respiration at 4°C. Cod respiration was quite variable and did not correlate significantly with dry body weight, while haddock respiration was extremely elevated. Rosenthal and Alderdice (1976) indicated that breakdown in biochemical systems of larval fishes attempting to compensate in the presence of environmental stress could result in variable or increased metabolism.

Respiration measurements of larval fishes have been scarce (Blaxter 1970) and as far as is known these studies are the first to report results for cod and haddock larvae. Studies have been conducted with juvenile and adult cod, and the slopes of the regression relationships of the logarithmic conversions of oxygen consumption/hr on body weight show values similar for larvae in this research. Saunders (1963) reported slope values of between 0.76 to 0.83 for routine metabolism in the temperature range 3-15°C, and Edwards, Finlayson, and Steele (1972) calculated a slope for cod standard metabolism of 0.82. The only known published research on haddock respiration (Tytler 1969) reported results of active metabolism at different swimming speeds for 2 year old fish and are not directly comparable to the present study.

Although no significant differences between cod and haddock larvae were seen in delayed feeding abilities, some interesting observations were made. Both species are physically advanced in regards to feeding ability potential (pigmented eyes, functional mouth, complete alimentary tract) at hatching in the temperature range 7-10 and can feed immediately well before yolk absorption. This is not generally the case with most marine pelagic larvae which, although many commence feeding while there are still some remnants of yolk left, require a certain amount of temperature dependent time after hatching to physically develop feeding capabilities (Blaxter 1970). Very early feeding ability while there is still a large supply of endogenous yolk would seem to confer a survival advantage to cod and haddock larvae if food were limited in abundance or distribution for a time around the period of yolk absorption and if prior feeding had commenced. Early feeding of cod and haddock larvae has been noted by other investigators. Stomach analyses of field caught cod and haddock larvae at hatching length sizes and with substantial yolk remaining have shown substantial numbers with food in the gut (Ogilvie 1938; Wiborg 1948; Marak 1960). Ellertsen et al. (1976) showed that more than 80% of cod larvae sampled in laboratory experiments fed the day after hatching on small flagellates.

The yolk absorption times and delayed feeding abilities of both cod and haddock larvae in this research agree reasonably well with the results of Ellertsen et al. (1976) and Tilseth and Stromme (1976). They found, respectively, complete yolk absorption of larval cod at 5°C occurring on the eighth day after hatching and delayed feeding ability ("point of no return") as defined by changes in buoyancy and activity rather than feeding criteria occurring on the eleventh day. Other studies have shown, of course, that starvation times and delayed feeding ability times after complete yolk absorption are temperature and species dependent. Detwyler and Houde (1976) found yolk absorption was complete 36 hours after hatching at 26°C for scaled sardines (Harengula pensacolae) and bay anchovies (Anchoa mitchilli), and that food was necessary by the next 12 hours to prevent starvation. Spectorova et al. (1974) determined that Black Sea turbot larvae (Scophthalmus maeoticus) absorbed their yolk 134 hours past hatching and were unable to initiate successful feeding by 182 hours at 14.6°C. Survival rates at 22°C of northern anchovy larvae (Engraulis mordax) 5 days after first being fed were much greater for groups fed prior and up to 1/2 day after yolk absorption than those fed later with complete yolk absorption occurring 1 1/2 days after hatching (Lasker et al. 1970). It is interesting to note from the present studies of cod and haddock (Table 2) and the above citations that regardless of temperature and species, the successful delayed feeding time after yolk absorption seems to be around 25% of the time from hatching to complete yolk absorption. This is a subject for further interspecific studies.

In conclusion, there appear to be no major differences in regards to comparative respiration metabolism, growth rates or delayed feeding abilities at different temperatures of larval cod and haddock in relation to survival potential. Feeding initiation times, gross anatomical development in relation to feeding ability, and ability to withstand starvation at different temperatures were virtually identical. Respiration rates and patterns were very similar at the same and comparable temperatures. The only slight and somewhat insidious differences between the two larval species were in growth potential, and these differences seemed to be offsetting in relation to survival. Haddock displayed a slightly narrower scope for successful growth in terms of temperature but slightly higher growth rates within that scope than cod. It is not known nor can it be inferred at this time if subtle differences like these during the larval stage can make a difference in the potential year class strength of a species like cod or haddock. However, these studies are important, basic components for use in a continuously developing trophic-energetic model of larval fish survival (Laurence 1977) currently utilized in on-going research.

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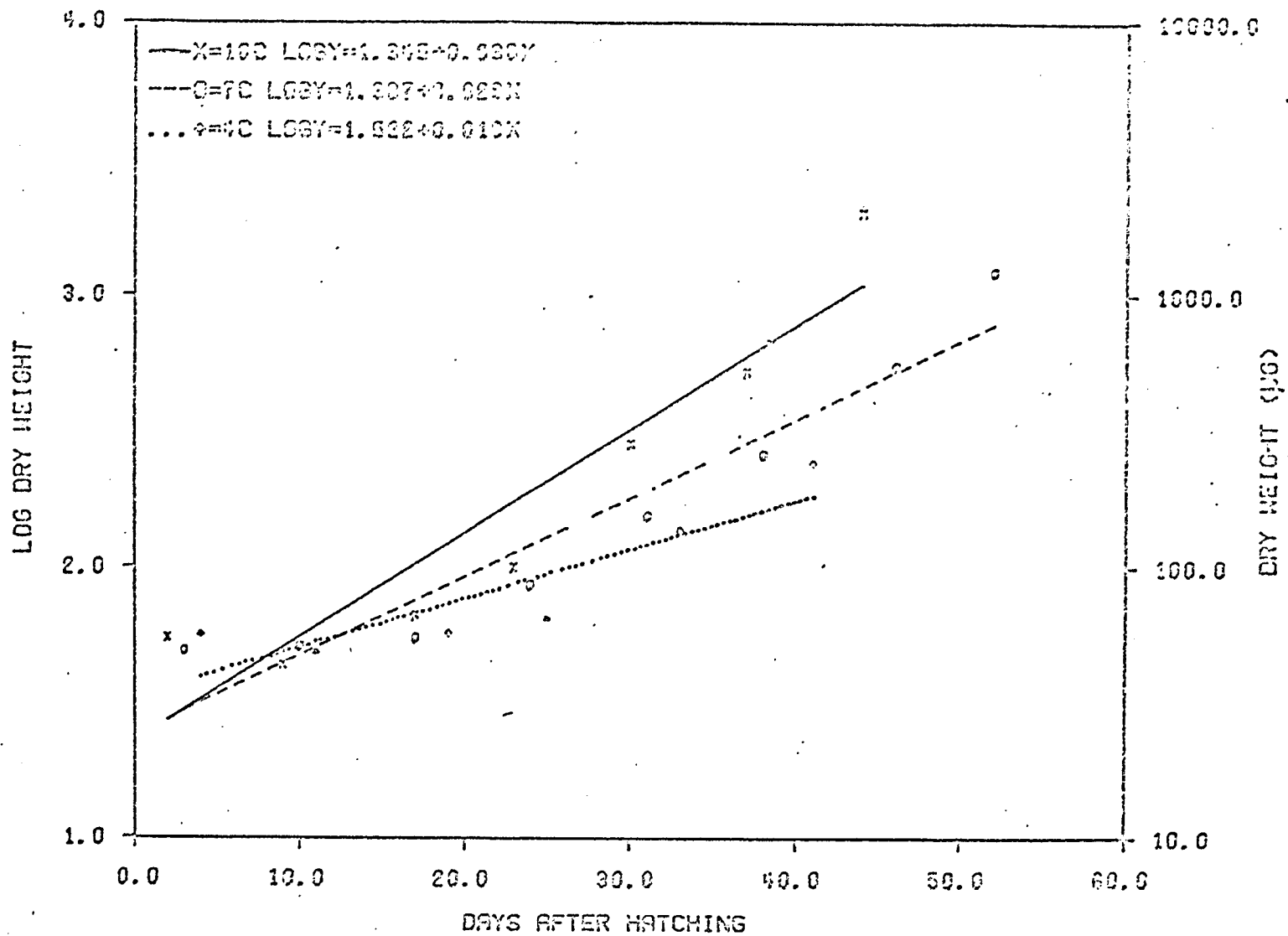


Figure 1. Dry weight growth of cod larvae for the period of yolk absorption to metamorphosis at three temperatures.

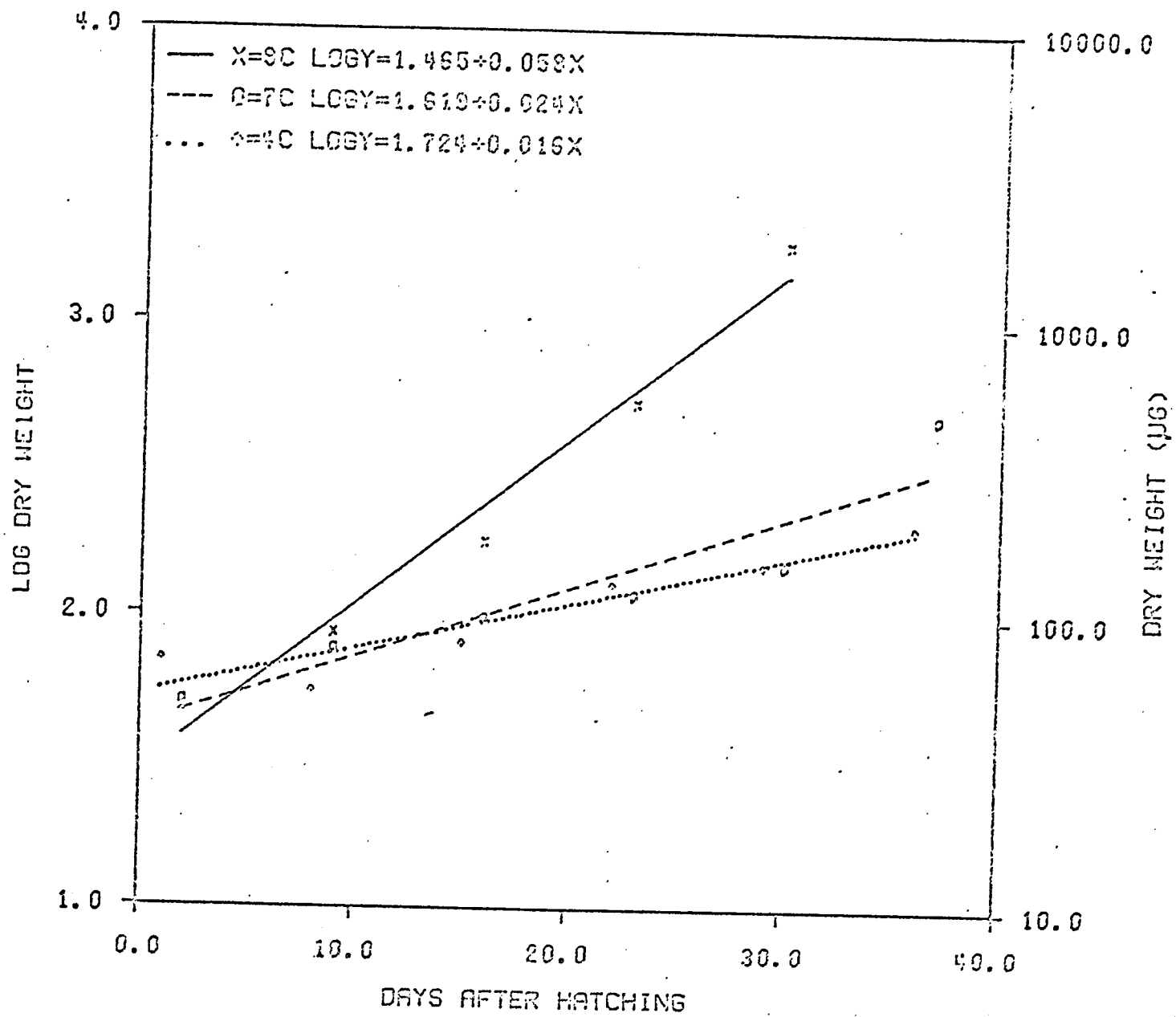


Figure 2. Dry weight growth of haddock larvae for the period of yolk absorption to metamorphosis at three temperatures.

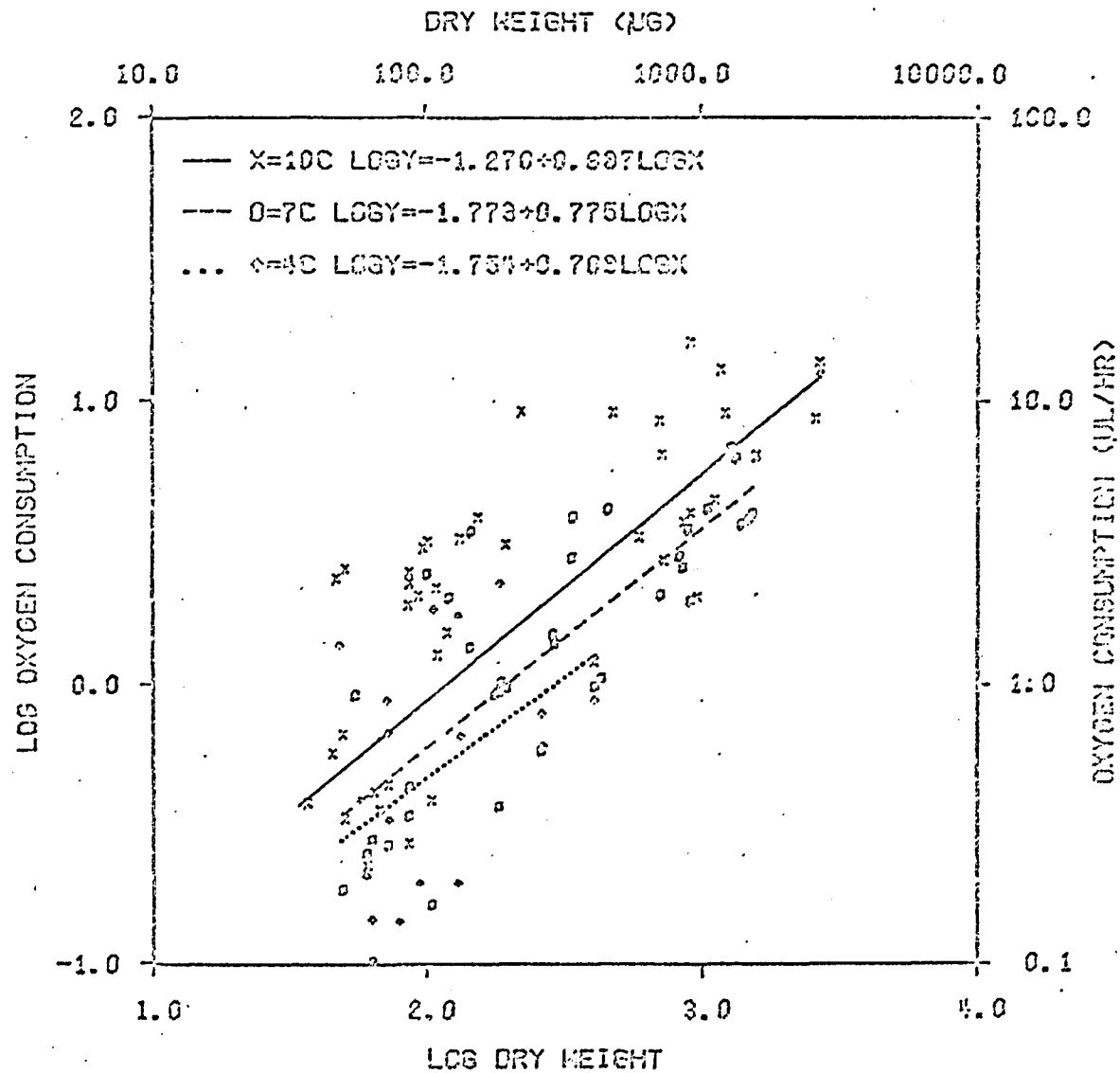


Figure 3. Regressions of hourly oxygen consumption on dry weight of cod larvae at three temperatures.

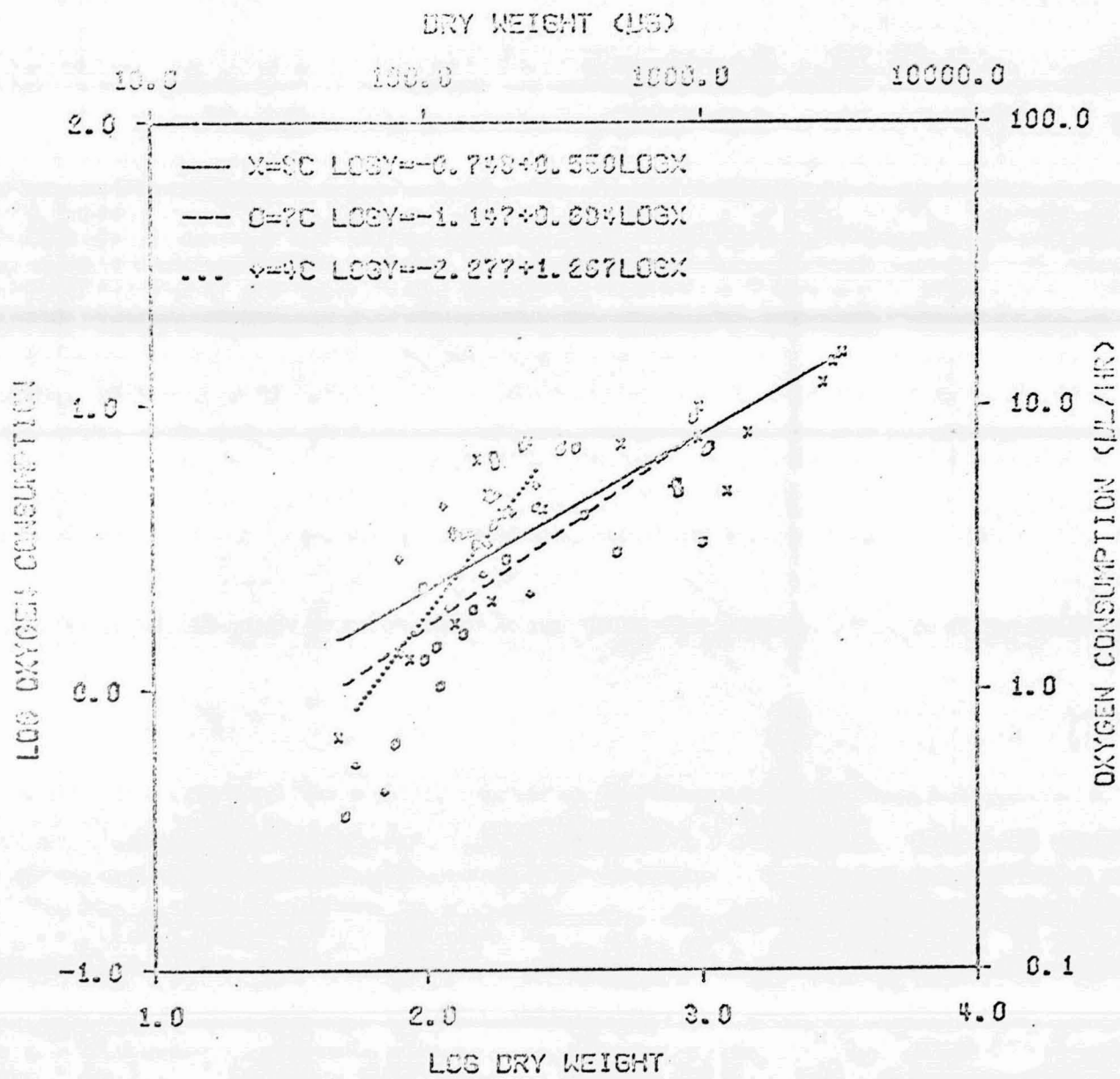


Figure 4. Regressions of hourly oxygen consumption on dry weight of haddock larvae at three temperatures.

Table 1. Mean weekly growth of larval cod and haddock at three different temperatures.

Weeks after Hatching	Mean Dry Weight Cod ( $\mu\text{g}$ )			Mean Dry Weight Haddock ( $\mu\text{g}$ )		
	Temperature			Temperature		
	4	7	10	4	7	9
0	56.5	49.2	55.0	69.8	50.3	47.6
1	48.3	51.3	43.4	55.0	76.8	86.9
2	57.3	54.7	66.5	81.0	98.3	178.6
3	64.3	85.9	100.0	129.2	119.0	532.9
4	137.1	153.8	284.0	151.2	151.0	1,858.9
5	242.7 <sup>a</sup>	200.2	520.7	205.8 <sup>a</sup>	483.8 <sup>b</sup>	
6		544.5	2,008.5			
7		1,217.4				

<sup>a</sup>Complete mortality.

<sup>b</sup>Malfunction in rearing system terminated measurements.

Table 2. Delayed feeding abilities of larval cod and haddock as indicated by the criterion of 50% feeding success.

Days after Hatching	Percentage Cod with Food in Alimentary Tract		Percentage Haddock with Food in Alimentary Tract	
	Temperature (°C)		Temperature (°C)	
	7	10	7	9
1	90	20	60	50
2	--	40	--	--
3	80	70	80	50
4	--	--	--	--
5	60	90	50	70
6	--	-- <sup>a</sup>	--	-- <sup>a</sup>
7	50 <sup>a</sup>	70	40 <sup>a</sup>	60
8	--	--	60	--
9	60	10	90	0 <sup>b</sup>
10	40	0 <sup>b</sup>	--	--
11	30		40	
12	0 <sup>b</sup>		0 <sup>b</sup>	

<sup>a</sup>Yolk absorption completed.

<sup>b</sup>> 50% mortality.