#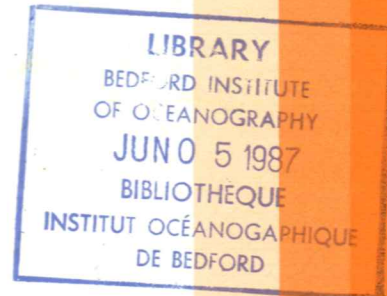 The Development and Early Growth of Embryos and Larvae of the Atlantic Mackerel <u>Scomber scombrus L.</u>, at Different Temperatures

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Canadian Technical Report of
Fisheries and Aquatic Sciences

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CANADIAN TECHNICAL REPORT OF

FISHERIES AND AQUATIC SCIENCES NO. 927

February 1980

THE DEVELOPMENT AND EARLY GROWTH OF EMBRYOS AND LARVAE OF THE

ATLANTIC MACKEREL, SCOMBER SCOMBRUS L., AT DIFFERENT TEMPERATURES

by

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ABSTRACT

Lanctot, Marthe. 1980. The development and early growth of embryos
and larvae of the Atlantic mackerel, Scomber scombrus L.
at different temperatures. Can. Tech. Rep. Fish.
Aquat. Sci.: 927, 77 pp.

The development of mackerel embyros obtained from St.
George's Bay, in Nova Scotia, was monitored at four temperatures
ranging from 8 to 23°C. A staging key, based on approximately
equal developmental increments, was devised for stages from
fertilization until exhaustion of the yolk supply. There were
two series of experiments, one dealing with partially developed
eggs taken from nature and the other with artificially fertili-
zed eggs. Differences in mortality were found between the two
series, probably due to the higher sensitivity of the stages
before blastopore closure. A method is proposed for estimating
the time to hatching at different temperatures for partially
developed eggs taken from nature. The times to hatching
obtained in this study were shown to agree rather closely with
those reported for mackerel from Woods Hole (Worley, 1933) and
from the Bay of Biscay (Lockwood et al., 1977). The range of
temperatures over which hatching occurred differed, however,
possibly due to the previous thermal history of the eggs. The
size of the larvae at exhaustion of the yolk supply was nega-
tively correlated with temperature and this appears to be
adapted to the variations in size and abundance of the available
food. This adaptation favors a higher success for first-
feeding mackerel larvae and reduces the importance of mortality
at this particular stage.

RESUME

Lanctot, Marthe. 1980. Le développement et les premières phases de la croissance des embryons et des larves du maquereau bleu, Scomber scombrus L. à différentes températures. Rapport techn. pêches et sciences aquat. Canada. 927, 77 pp.

On a surveillé le développement d'embryons de maquereau, pris dans la baie St. George's (Nouvelle-Ecosse), à quatre températures différentes allant de 8 à 23° C. On a conçu une grille comportant des stades évolutifs à peu près égaux pour les phases de développement, depuis la fécondation jusqu'à l'épuisement du vitellus. Deux séries d'expériences ont été menées, l'une avec des oeufs partiellement développés fécondés naturellement et l'autre avec des oeufs fécondés artificiellement. Les deux séries ont donné des résultats différents en ce qui a trait à la mortalité, ce qui est probablement dû à la plus grande sensibilité des spécimens au cours des phases qui précèdent l'occlusion du blastopore. L'auteur propose une méthode d'évaluation du temps d'incubation à différentes températures pour les oeufs partiellement développés pris dans leur milieu naturel. Les périodes d'incubation obtenues dans le cadre de la présente étude concordent à peu près avec celles qui ont été enregistrées pour le maquereau de Woods Hole (Worley, 1933) et celui de la baie de Biscay (Lockwood et al., 1977). La gamme des températures sous lesquelles l'éclosion s'est produite présentait cependant des variations imputables peut-être aux divers degrés de chaleur auxquels les oeufs avaient été précédemment soumis. La corrélation entre la taille de la larve à l'épuisement du vitellus et la température était négative. Cela semble plutôt adapté aux variations dans la taille et à l'abondance de nourriture disponible. Cette adaptation laisse présager un plus grand succès en privilégiant d'abord l'alimentation des larves de maquereau et réduit le taux de mortalité à ce stade particulier.

LIST OF ABBREVIATIONS AND SYMBOLS

cm   centimeter

mm   millimeter

μm   micrometer

ml   milliliter

hr   hour

PVC   polyvinylchloride

°C   degree Celsius

n   sample size

SD   standard deviation

L_{∞} asymptotic length

l_t length at time t

C   parameter of the Brody-Bertalanffy equation, L_{∞} - C being the hypothetical length that a fish would have been at t = 0 if it had always grown according to the equation

K   constant determining the instantaneous relative decline in growth rate, referred to as the Brody-Bertalanffy growth coefficient

t   time

t_0 hypothetical age at which a fish would have been zero length if it had always grown according to the Brody-Bertalanffy equation

S_{∞} asymptotic stage of development

S_t stage of development at time t

C' parameter of the modified Brody-Bertalanffy equation, S_{∞} - C' being the hypothetical stage at which

a fish would have been at t = 0 if it had always

developed according to the equation

K'   constant determining the instantaneous relative

decline in development rate, referred to as the

development coefficient

I   time to hatching

$\hat{I}$ estimated time to hatching

T   temperature

α temperature-scale correction factor

r^2 coefficient of determination

ACKNOWLEDGEMENTS

INTRODUCTION

The study of larval fish ecology has drawn the attention
of many fisheries scientists in recent years, largely because
of its relevance in fish population dynamics. It seems to
be generally accepted that high mortality in the embryonic
and larval stages is an important factor in determining the
success of a year-class, and thus the recruitment to the
fishery (Blaxter, 1974). Hjort (1914) hypothesized that food
availability for first-feeding larvae was probably the most
important cause of mortality and this critical period con-
cept has been referred to in many studies (eg. Bannister *et
al.*, 1974; Ryland and Nichols, 1975; Ware, 1977). However,
most survival curves for larval fishes collected at sea do
not provide convincing evidence for this phenomenon (see re-
views by Marr, 1956; Farris, 1960; May, 1974), although
Dragesund and Nakken (1971) reported a 94% mortality at time
of yolk sac absorption for Norwegian herring. Some field and
experimental studies have shown that starvation may be an im-
portant cause of larval mortality after the yolk supply is
exhausted (Shelbourne, 1957; Blaxter and Hempel, 1963; Lasker
et al., 1970; Jones, 1972), but the relation between this fac-
tor and the strength of a year-class remains unclear. Fur-
thermore, there appear to be species-specific differences in
the susceptibility to starvation (May, 1974). Mortality can
also strongly affect the developing eggs through other factors,
such as temperature, salinity, mechanical disturbance, and the

early stages before blastopore closure are often reported to be very sensitive in this respect (Southward and Demir, 1974; Brewer, 1976; Guma'a 1978). In view of these considerations, May suggested that the important question should not be "does a critical period exist?" but rather "how do the characteristics of reproduction and early development reflect the overall adaptation of the species to its environment?" (May, 1974, page 14). This more global approach is worth pursuing in larval fish studies.

Surveys of eggs and larvae are used, together with data on time to hatching at different temperatures, for resource management of various fish species (Tanaka, 1974; Bannister *et al.*, 1974; Lett *et al.*, 1975). In the case of the Atlantic mackerel (*Scomber scombrus* L.), data on the duration of embryonic development at different temperatures are available from Worley (1933), who obtained mature fish from Woods Hole, Massachusetts, and from Lockwood *et al.* (1977), whose fish came from the Bay of Biscay, west of France. The two sets of observations agree rather well on incubation time, but the ranges of temperatures for successful hatching do not completely overlap. The mackerel population in Canadian waters has not yet been studied in this respect, although ecological studies dealing with egg distributions and biological characteristics, such as meristic counts, growth rates, feeding habits, etc., are available (Sparks, 1929; MacKay, 1967; Arnold, 1970; Moores *et al.*, 1975). The aim of the present study was to compare the temperature tol-

erance and duration of embryonic development of mackerel
from St.George's Bay, in the southern Gulf of St.Lawrence
with those reported for other mackerel populations. The
influence of temperature on development and growth of embryos
and yolk-sac larvae was also investigated in view of May's
(1974) approach.

MATERIALS AND METHODS

The mackerel eggs used in this study came from St. George's Bay, off Northumberland Strait, Nova Scotia. Spawning in this bay takes place from the beginning of June to mid-August, with peak spawning around July 1 (Ware, 1977). Two series of experiments were performed in this study, the first one using eggs caught by plankton tows and the second with artificially fertilized eggs.

The experimental set-up consisted of a large tank with a cooling unit maintaining the water temperature slightly below 8°C, three heating containers where the 8°C water was raised to the appropriate test temperature (13,18 and 23°C) by immersion heaters connected to temperature control relays, and four fiberglass rearing tanks of approximately 80 liters capacity in which the incubators were kept. Because the room temperature was around 20°C, all tubing was insulated and the rearing tanks were covered by 7.6 cm thick styrofoam through which the incubators were suspended. The incubators were made of PVC pipe 11.5 cm in diameter and 15 cm high with a Nitex screen bottom of 405 µm mesh size. There was a continuous flow of water from the heating containers into the incubators, ensuring proper aeration of the water. The water from the rearing tanks was returned to the cooling reservoir where it was filtered, cooled to 8°C and sent back into the system. Water levels in each tank were controlled by siphons. Filtered local seawater was used.

Continuous temperature records were kept and temperature

usually described a sinusoidal path in time, with an amplitude of ±2°C. However, on a few occasions, siphon blockage caused water from the heating containers to flow directly into the rearing tanks, thereby maintaining the temperature 2 or 3°C higher than the set temperature for a few hours until detected and fixed. Lighting was not regulated except that tanks were in shadow and protected from the fluorescent lights.

On June 21, 1978, mackerel eggs were obtained by surface plankton tows using a 3/4 meter diameter net of 782 μm mesh size. The surface water temperature was then 9.5°C. The eggs were transported to the laboratory in a styrofoam box and eight samples of approximately one hundred eggs were placed in jars filled with 10°C seawater. The eight jars were placed in the four rearing tanks (2 per tank) and water was allowed to equilibrate for about one hour before the eggs were poured out of the jars into the incubators.

Ripe mackerel (one female and four males) were caught on July 6, 1978 by hook and line. The mature eggs and milt, stripped from these fish, were kept in separate jars in an insulated box for about five hours before artificial fertil- ization was carried out. The surface water temperature when the fish were caught was 14.5°C. Artificial fertilization was done in the laboratory by mixing the eggs and milt back and forth between two jars. Water was added to the jars after fifteen minutes and the eggs were kept at 10°C for one hour. They were then rinsed with fresh seawater a few times, counted in groups of approximately one hundred, and placed in small

jars in the incubators. (Live eggs can easily be recognized because they float at the surface whereas the dead ones sink to the bottom.) After another hour, the eggs were poured out of the jars into the incubators. A sample of unfertilized eggs was preserved. Three more attempts at artificially fertilizing eggs were made from July 19 to July 26, but they did not succeed.

Davidson's solution has been used for preserving salmonid embryos because it contrasts the translucent yolk with the white embryonic structures (Battle, 1944). It was used in this study as a means of facilitating staging. This solution is made of 86 ml of 40% formaldehyde, 91 ml of glycerine, 91 ml of glacial acetic acid, 273 ml of ethanol and 459 ml of seawater. After 3-24 hr, specimens were transferred to a second solution consisting of 1 part 40% formaldehyde, 1 part glycerine, 3 parts ethanol and 5 parts seawater. However, formalin is more commonly used for preserving embryos and, in order to compare my results with those of other studies, I preserved half of my samples in 5 to 10% formalin. In the first series, samples of five specimens were taken daily from each incubator, those from incubator A being kept in formalin, those from incubator B in Davidson's solution. In the second series, specimens were picked up at every 12 hr for the first 85 hr and 24 hr apart thereafter. However, samples from each incubator were not taken simultaneously but at 6-hr or 12-hr intervals, in order to provide a more continuous picture of development. Dead eggs were picked up at the end of the ex-

periments.

The preserved samples were examined under a stereomicroscope at 40 X magnification, and staged according to the key developed for this purpose (see Stage Classification). The stage of a sample was defined as the mean stage of the five specimens. Eggs with partially or completely opaque perivitelline space were considered dead, but it is not possible to determine whether this opacity was due to a natural cause or to the effect of the fixative. An embryo or larva was considered abnormal if it showed deformities most likely to cause death. The most common ones were curvature of the spinal cord, incomplete finfold, embryos developing eye pigmentation and tail growing past the nape while still in the egg envelope (failure to hatch), and the like.

The sizes of the egg and oil globule were measured with an ocular micrometer at a 40 X magnification. The extent of the perivitelline space was determined by adding the dimensions of the space on each side of the yolk when the ocular micrometer was oriented through the center of the egg, and dividing this value by the egg diameter. A drawing tube fixed to the stereomicroscope was used to trace embryos and larvae at a 40 X magnification, from which their size was estimated. The shape of the yolk reserves gradually changed from a sphere to a prolate spheroid and back to a very small sphere as the larva was using its supply. The yolk volume was estimated from the measures of diameter or of major and minor axes, according to the particular form.

STAGE CLASSIFICATION

The study of egg development of fish is greatly
facilitated by a staging system appropriate to the species
under consideration. In this study, I was interested in
a key representing equal increments in development as
much as possible, because of the way in which the data
were analysed. I also wanted a key which was easy to use
and which did not require tedious counts or precise mea-
surements. Furthermore, since this study is concerned
with the development of the embryos to resorption of the
yolk sac, larval stages needed to be incorporated into
the key.

The two most suitable keys under these conditions
were those of Worley (1933) and of Garside (1959). The
first is concerned with stages for developing mackerel em-
bryos. It has a series of eighteen stages from fertilization
to hatching. The early stages are finely separated (i.e.
periblast nuclei, periblast ridge, "Randwulst", germ ring,
. . .) and require very detailed observations in order to
ascribe a precise stage to an embryo. The stages defined
in relation to the number of somites also involve tedious
counts, whereas the last divisions up to hatching are based
on the length of the embryo in relation to the yolk mass,
a criterion easily observed. Worley's key therefore does
not completely meet my requirements for simplicity and
ease of identification for the early stages, but the last

part of his classification is adequate.

The key presented by Garside (1959) deals with lake trout embryos. It is based on external anatomical features easily observed in preserved embryos. The early stages (small blastodisc, large blastodisc, germ ring, 1/4, 1/2 and 3/4 epiboly) are clear-cut and young embryos are easily staged. Later stages however, are mostly based on vitelline venation and eye pigmentation, two characters not observed in mackerel embryos. By combining the two classifications, I obtained a key which is easy to use with live or preserved specimens and which represents approximately equal increases in development. This last affirmation has to be accepted here as an assumption. The subsequent "predictions" of such increments by my procedure will be discussed. That is, my key comprises the early divisions of Garside (1959) up to blastopore closure, whereas the length of the embryo around the circumference of the egg, as described by Worley (1933), defines the later stages up to hatching. As a final modification, Worley's stages 4/5 and 5/6 of the circumference were omitted because they represent a very small increase and are difficult to distinguish.

No stages have been proposed for mackerel larvae yet. Berrien (1975) described early mackerel larvae from different points of view but did not propose any stage classification. I included in my key three larval stages, mostly based on mouth morphology. These represent a continuous gradation and classification is therefore more arbitrary

and not as clear-cut as for the embryonic stages. For the last two stages, measurements of the eye, the lower jaw and the distance from the snout to the back of the eye, are given as further aids to classification. The following descriptions are from formalin-preserved specimens.

Description of stages

The mackerel egg is spherical with a clear egg membrane. It contains a single oil globule which is found on the edge of the yolk reserves. The perivitelline space takes up approximately 18% of the egg diameter. Eggs obtained from plankton tows, raised in the laboratory and preserved in formalin, had a mean diameter of 1.252 mm ± 0.072 SD (n=69). The diameter of the eggs from the second series (therefore from a single female) averaged 1.235 mm ± 0.027 SD (n=63) while the oil globule had a mean diameter of 0.309 mm ± 0.030 SD (n=62). These values are compared with those published by other workers for European mackerel, mean egg diameter = 1.26 mm ± 0.03 SD, mean oil globule diameter = 0.34 mm ± 0.01 SD (Lockwood *et al.*, 1977), for Atlantic mackerel, mean egg diameter = 1.13 mm (Berrien, 1975) and for mackerel from the southwestern Gulf of St.Lawrence, mean egg diameter ranging from 1.3 to 1.1 mm over the spawning season (Ware, 1977).

1. *Small blastodisc* (Fig.1a)

The first stage, called small blastodisc, covers the early cleavage divisions. It is recognized by a multicellular cap bulging on the yolk mass opposite the oil globule. Its

Figure 1.   Developmental stages 1 to 7.   32 X magnification.

        a. Small blastodisc, side view.
        b. Large blastodisc, side view.
        c. Germ ring, side view.
        d. 1/2 epiboly, side view.
        e. 1/2 epiboly, top view.
        f. 3/4 epiboly, side view.
        g. 3/4 epiboly, top view.
        h. Blastopore closure, top view.
        i. Blastopore closure, bottom view.

a.

b.

c.

d.

e.

f.

g.

h.

i.
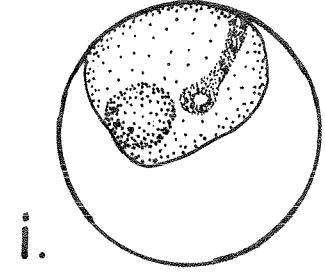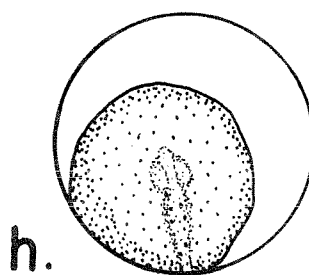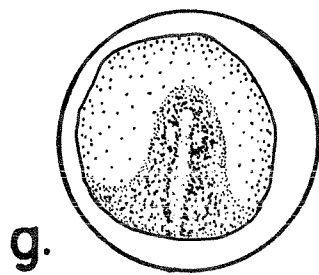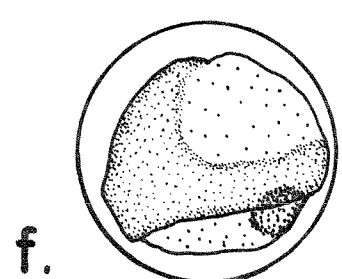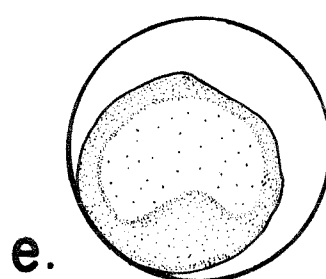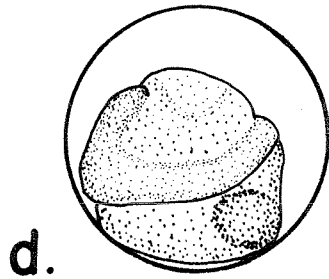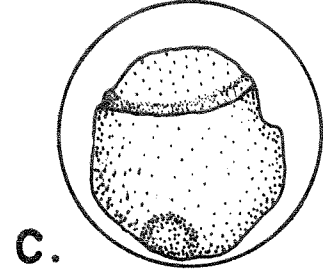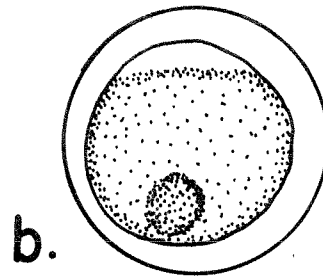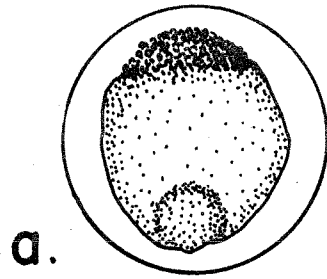
outline is clearly delimited and individual cells are readily distinguished at 40 X magnification.

2. *Large blastodisc* (Fig. 1b)

The large blastodisc, the next stage, is a much flattened, undifferentiated white cap. The boundary is not as clear now as previously since the blastodisc is flat on the yolk mass, but the difference in color (white against the more translucent yolk) indicates the margin. Individual cells are no longer observable.

3. *Germ ring and embryonic shield* (Fig. 1c)

As the peripheral cells thicken, they form the germ ring. At one pole of the ring, opposite the oil globule, a mass of cells starts growing inward in the shape of a broad triangle: this is the embryonic shield. The germ ring is then just on top of the yolk mass and the blastocoel can be seen under the shield.

4. *One-quarter epiboly*

The germ ring has overgrown one-fourth of the yolk. The embrynic shield is elongating but shows no differentiation yet.

5. *One-half epiboly* (Fig.1d,e)

The blastoderm has extended halfway around the yolk. As the embryonic cells thicken, the shield appears more opaque and is more clearly seen. It continues to elongate and the head region starts to widen.

6. *Three-quarters epiboly* (Fig. 1f,g)

The germ ring has overgrown three-quarters of the yolk

and the embryonic shield is easily distinguished.The sites of the optic cups as well as the neural tube appear more opaque than the rest of the embryo. As epiboly proceeds to completion, the area of yolk exposed gradually decreases until there is only a small drop-shaped area remaining.

7. *Blastopore closure* (Fig. 1h,i)

The germ ring is now closing around the drop-shaped area of exposed yolk and the embryonic shield covers slightly less than half of the yolk circumference. The posterior part of the developing embryo is making the transition from spreading in the germ ring to ending in a node. Faint melanophores appear over the body and a few are found on the oil globule and in the yolk around it. The tail of the embryo does not reach the oil globule.

8. *Half circle embryo* (Fig. 2a,b)

The length of the embryo covers one-half of the circumference of the yolk. The optic cups are well differentiated and the lenses are formed. The nasal sacs appear as tiny structures in front of the optic cups. Melanophores form two dorso-lateral rows over the trunk and many are scattered over the anterior part of the body. They are less numerous posteriorly and none is found in the caudal area. The tail does not reach the oil globule but now clearly ends in a node.

9. *Two-thirds circle embryo* (Fig. 2c,d,e)

The embryo extends in length over two-thirds of the yolk circumference. The optic cups as well as the lenses

Figure 2. Developmental stages 8 to 11.   32 X magnification.

          a. 1/2 circle embryo, side view.
          b. 1/2 circle embryo, top view.
          c. 2/3 circle embryo, side view.
          d. 2/3 circle embryo, top view.
          e. 2/3 circle embryo, bottom view.
          f. 3/4 circle embryo, top view.
          g. Full circle embryo, side view.
          h. Full circle embryo, top view.

a.

b.

c.

d.

e.

f.

g.

h.
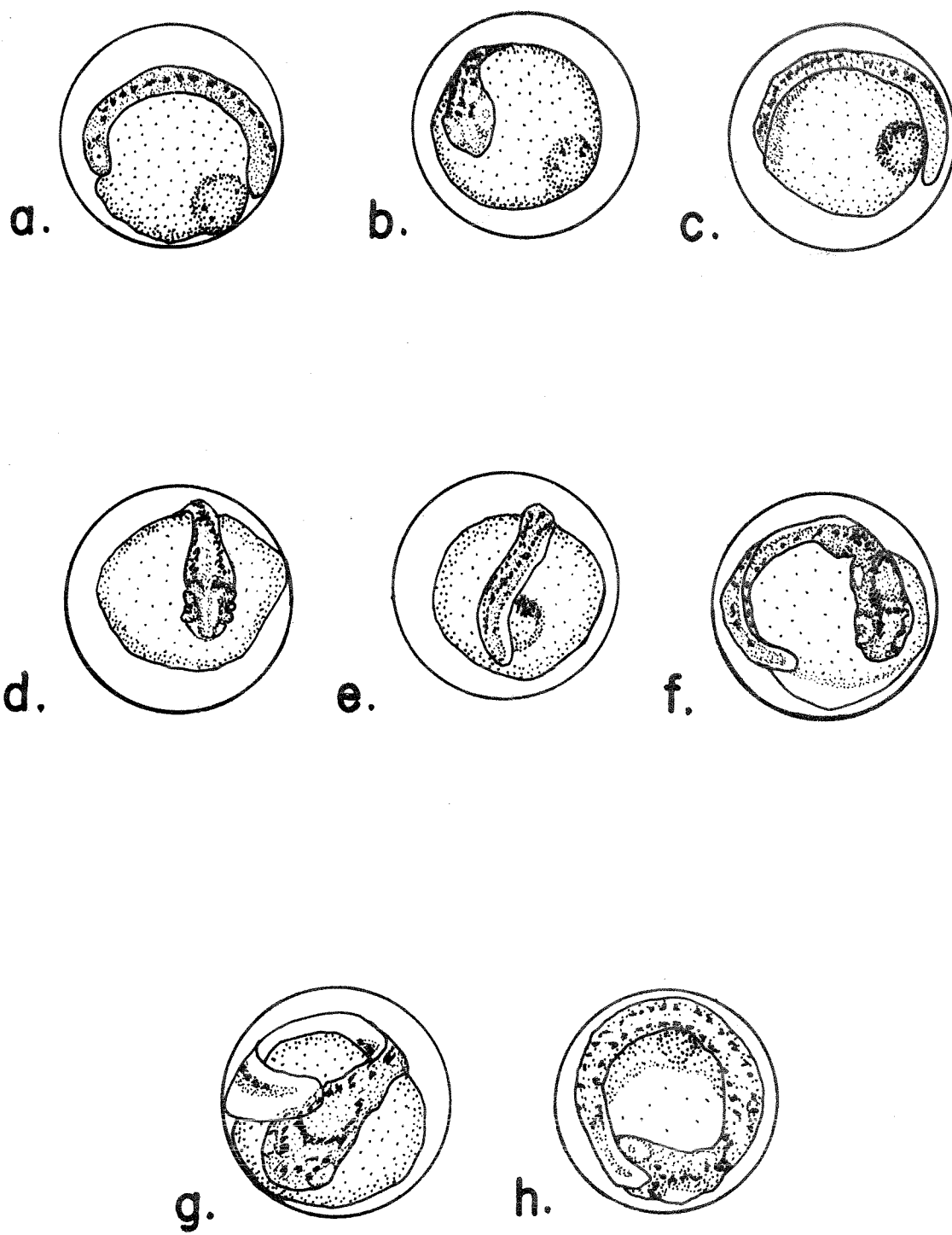
are clearly differentiated, but they are still unpigmented.
The auditory placodes are now visible just behind the eyes,
whereas the nasal sacs remain fairly small. The tip of
the tail has reached the oil globule and is free from the
yolk. The tail starts to curve to one side of the embryo,
usually to the left. A narrow finfold is apparent over
the posterior third of the body. A melanophore pattern
over the head has been called the "two-bridge pattern" as
it suggests two connections lying parallel to each other
and joining the two dorso-lateral rows of melanophores
which extend over the whole body, except for the tail. The
first of these "bridges" is just behind the eyes while the
second stretches over the nape. There are also a few
melanophores around the eyes, but the eyes themselves are
still unpigmented.

10. *Three-fourths circle embryo* (Fig. 2f)

The embryo encircles three-fourths of the yolk cir-
cumference as the tail has passed the oil globule and is
curving back toward the head. The tail is now flat on the
yolk sac, lying on its side. The finfold extends over
slightly more than the posterior half of the body. The
intestine is visible as it stretches from the body to the
oil globule. In addition to the nasal sacs and auditory
placodes which are expanding, the pectoral buds are start-
ing to develop along the sides of the nape. Body pigmenta-
tion still includes the two lateral rows of melanophores
and the "two-bridge pattern" as well as a few more pigment

cells scattered over the head. The oil globule is half
covered by melanophores.

11. *Full circle embryo* (Fig. 2g,h)

The tail reaches the eye and often covers the head
before the embryo hatches. It lies flat on its side but it
is not touching the yolk. The finfold extends to the nape
and widens. The eyes are still unpigmented, but there
are a few melanophores on the snout. Two ventro-lateral
rows of melanophores have also been added to the "two-
bridge pattern" and to the two dorso-lateral rows still
present. The digestive tube extending to the oil globule,
now covered by dendritic melanophores, is visible. The
three main brain divisions, forebrain, midbrain and hind-
brain, are individually recognized.

12. *Newly hatched larva* (Fig. 3a,b,c)

This stage is easily recognized by the large yolk sac
which extends under the head of the larva. The elongate
head assumes a curved position, being attached to the round
yolk envelope. As the brain develops, the anterior part of
the body will expand in depth rather than in length. The
eyes are completely unpigmented and the heart is distin-
guished as a small vesicle in the jugular region. The
pectoral buds are spreading along the sides of the trunk,
increasing their attachment surface. The intestine runs
from under the pectoral buds to the anus, and the oil
globule is found at the posterior end of the yolk sac.
The previous pigmentation patterns (the "two-bridge", two

Figure 3. Developmental stages 12 and 13. 32 X magnification.

      a. Newly hatched larva, side view.
      b. Newly hatched larva, dorsal view.
      c. Newly hatched larva, ventral view.
      d. Mouth outline, side view.
      e. Mouth outline, dorsal view.
      f. Mouth outline, ventral view.

a.

b.

c.

d.

e.

f.
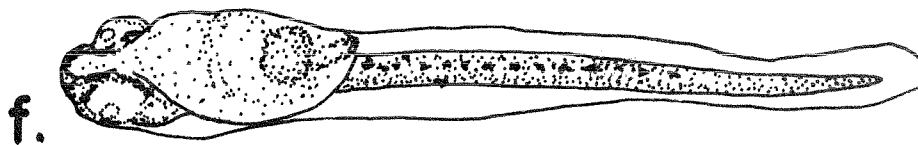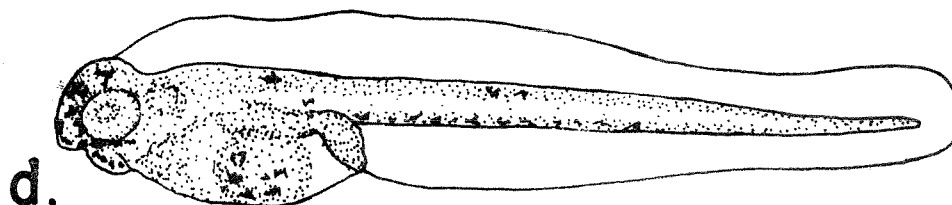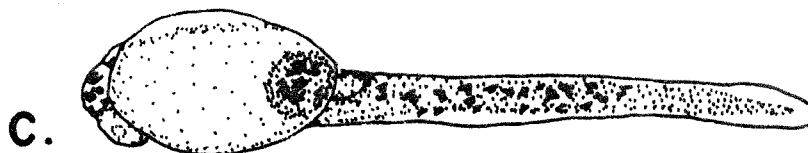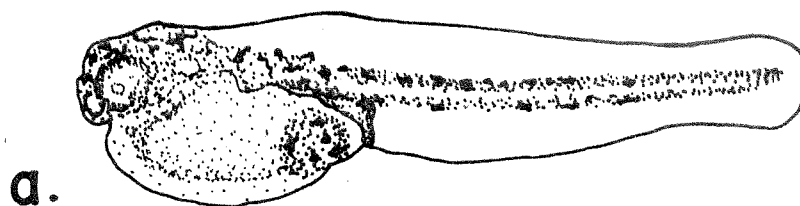
dorso- and two ventro-lateral rows) are still observed, but more pigment cells are scattered over the snout, sometimes covering the nasal sacs. The body is often slightly curved as the larva is slowly straightening out of the curled position it had inside the egg envelope.

13. *Mouth outline* (Fig. 3d,e,f)

As soon as the outline of the mouth appears, this marks a separate stage which lasts until the gill arches are distinguished. Anteriorly, the yolk sac does not extend farther than the back of the eyes. The bulging brain and the ventral mouth give a round appearance to the head and snout. The yolk reserves have diminished and the sac does not reach the anus anymore. The pectoral buds are expanding laterally. The auditory vesicles of oblong shape are becoming more prominent, and the digestive tube is enlarging and is slightly curved above the oil globule. Melanophores are marking the outline of the mouth as well as those of the nasal sacs and optic cups. The "two-bridge pattern" is not clearly recognizable anymore. On the dorsal side, the melanophores are now few and scattered, whereas the two ventro-lateral rows have merged into a single ventral row. Pigment cells are also found along the dorsal side of the intestine, on the yolk sac and all over the oil globule.

14. *Well formed mouth* (Fig. 4a,b,c)

This stage is characterized by a well formed lower jaw and easily distinguished gill arches. The mouth moves

Figure 4.   Developmental stages 14 and 15.   32 X magnifi-
             cation.

             a. Well formed mouth, side view.
             b. Well formed mouth, dorsal view.
             c. Well formed mouth, ventral view.
             d. End of yolk sac, side view.
             e. End of yolk sac, dorsal view.
             f. End of yolk sac, ventral view.

a.

b.

c.

d.

e.

f.
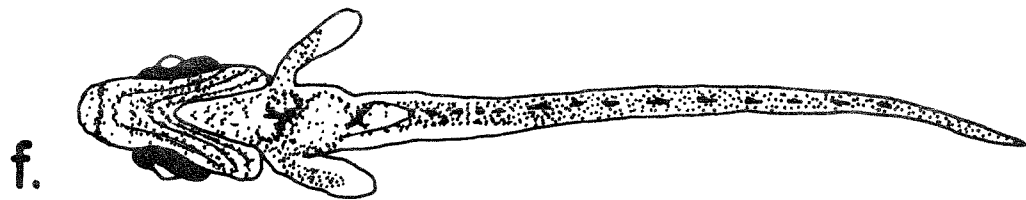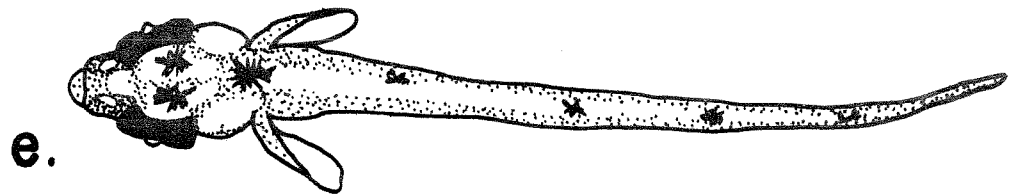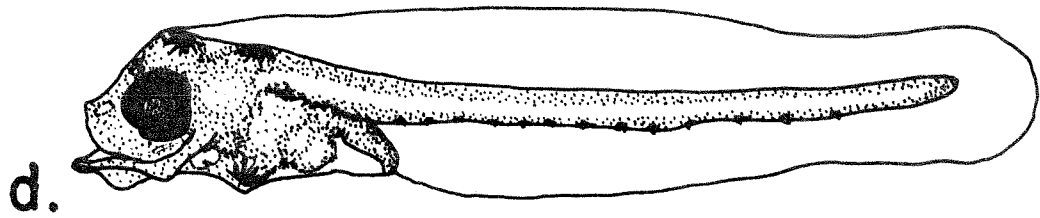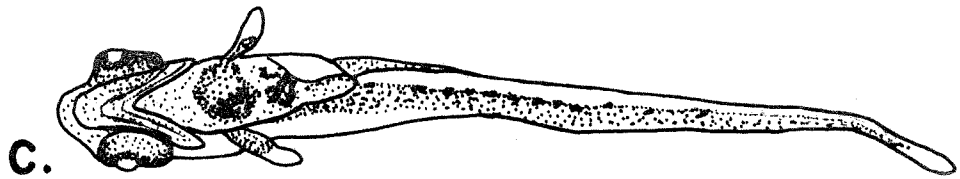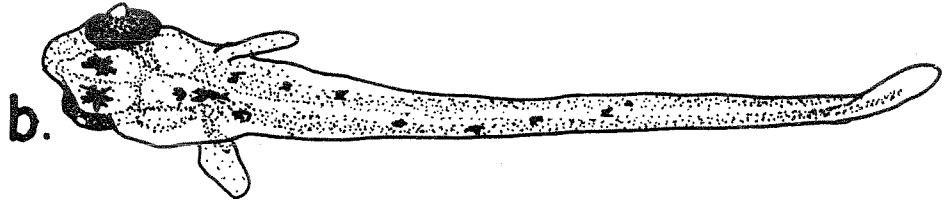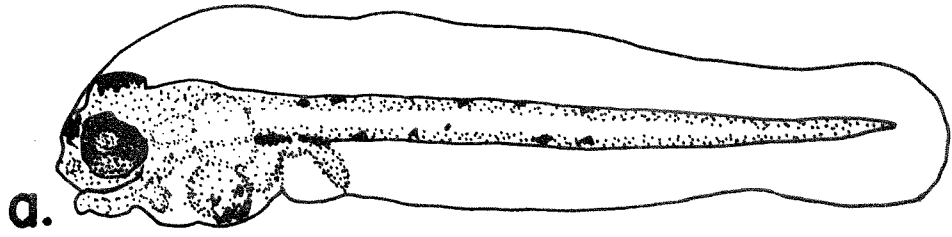
from a ventral to a terminal position. The eyes are pigmented and they range from lightly pigmented to completely covered by melanophores, but they are not dark black. The eye diameter is about 0.25 mm and the distance from the snout to the back of the eye is usually within the range 0.38 - 0.48 mm. The length of the lower jaw, from the tip to the isthmus, ranges from 0.15 - 0.20 mm. The optic lobes are most easily detected on top of the head while the slightly swelling hindbrain is distinguished behind the two auditory vesicles. The pectorals are differentiated into a fleshy base and a developing finfold, extending out vertically. The digestive tube is coiled and pushes the oil globule forward against the remaining yolk. There are usually two dendritic melanophores over the optic lobes, one over the hindbrain, and faint ones, if any, on the rest of the head. Over the trunk, the pigment cells are aligned in one widely spaced mid-dorsal row and in a denser, mid-ventral one. They are also dense along the frontal and antero-ventral parts of the visceral cavity.

15. *End of yolk sac* (Fig. 4d,e,f)

This is the last stage reached by larvae subsisting on yolk reserves only. It shows a better development of the jaws. The upper jaw points slightly upward while the lower one most often projects forward and reaches 0.25 mm and over from the tip to the isthmus. The elongate snout provides a clearer view of the whole brain with the forebrain close behind the nasal sacs, the midbrain with two

large optic lobes and the small hindbrain gradually taper-
ing into the spinal cord. The eyes are dark black and
their diameter is about 0.30 mm. The distance from the
back of the eye to the snout now exceeds 0.50 mm. The neck
is slightly arched over the visceral cavity. The pectoral
finfolds have enlarged, but no trace of rays is yet found.
The digestive tube is much coiled and takes up most of
the space within the visceral cavity. The yolk reserves
have practically disappeared and the remaining oil globule
is much reduced, if not absent. The pigmentation pattern
remains similar to what was observed in the previous stage.

In Davidson's solution, the developmental stages of
mackerel eggs and larvae appear identical to those describ-
ed above, except for stages 14 and 15. In these cases, the
mouth morphology is slightly different.

14. *Well formed mouth*

The mouth is always partially open and the tip of
the lower jaw curves downward slightly. The gill arches
are spread apart and, in the later part of stage 14 when
the lower jaw is more developed, this gives a globular
appearance to the jaw. In other respects, the larva is
identical to that described for stage 14 in formalin.

15. *End of yolk sac*

The major difference in this case is that the lower
jaw never protrudes forward but is always curved downward,
leading to a wide open mouth. The gill arches are wide

apart, giving a pronounced globular appearance to the lower jaw. The upper jaw usually shows a smooth, round snout and does not point upward. Otherwise, the larva is identical to the one described for stage 15 in formalin.

It is suggested that the difference in larval morphology in the two fixatives is due to the fact that live larvae react differently when dropped in these solutions. In formalin, there seems to be no reaction, the larvae simply sink slowly, whereas in Davidson's solution they show violent movements, jerking motions. It appears as if the mouth is widely opened on contact with the fixative, and this leads to separated gill arches and a distended lower jaw. An inanimate particle falling in this solution is set moving in a whirling motion indicating that Davidson's solution has characteristics not found in formalin[1]. No difference is noted in the earlier stages since the possibility for distention of the jaw or gill arches does not exist.

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[1] Additional evidence concerning the effect of the fixative on the morphology of the larvae came from the last sample from 13°C in the first series. At the time of collection, a mistake was made and larvae from incubator A were put in Davidson's solution instead of formalin and vice-versa. The two groups of larvae appeared quite different still, but each had taken the characteristics of the fixative they were in. Therefore, larvae from incubator A did not look like the previous sample from A, but like the previous one from B.

ANALYSIS OF DATA

Development rate

The observed relationship of developmental stage versus
time suggested an analogy with the second part of a fre-
quently observed form of fish growth (Figs. 5 and 6). The
growth curve of a fish (length against age) is often sigmoid.
The part before the inflection point represents the growth
of the early life phases whereas the second part applies to
the growth of older fish. Brody (1927, 1945) proposed the
following equation for this last part of the curve:

$$l_t = L_\infty - Ce^{-Kt} \tag{1}$$

or
$$L_\infty - l_t = Ce^{-Kt} \tag{2}$$

l_t being the length at time t, L_∞ the asymptotic length of
the fish, $L_\infty - C$ the hypothetical size that a fish would have
been at t = 0 if it had always grown according to equation
(1) and K is a constant determining the instantaneous rela-
tive decline in growth rate. K is often referred to as the
Brody growth coefficient (Ricker, 1975).

Von Bertalanffy (1934, 1938) rearranged equation (1)
into the form

$$l_t = L_\infty (1 - e^{-K(t-t_0)}) \tag{3}$$

replacing the parameter C by the new parameter t_0 which is
the hypothetical age at which the fish would have been zero
length if it had always grown in the manner described by
equation (3). The relation between these two parameters is

Figure 5. Mean stage of development of embryos and larvae from the first series plotted against time. The modified Brody-Bertalanffy equation was fitted to the data.

(●): specimens preserved in formalin.
(o): specimens preserved in Davidson's solution.
(1): value not included in the analysis (see text).

A. 8°C
$$S_t = 16 - 6.96e^{-0.00271t}$$
$r^2 = 0.613$
$P<0.001$

B. 13°C
$$S_t = 16 - 7.55e^{-0.00849t}$$
$r^2 = 0.954$
$P<0.001$

C. 18°C
$$S_t = 16 - 9.55e^{-0.01933t}$$
$r^2 = 0.951$
$P<0.005$

D. 23°C
$$S_t = 16 - 7.94e^{-0.02357t}$$
$r^2 = 0.897$
$P<0.05$

Figure showing four panels (A, B, C, D) plotting Stage of development against Time (hour).
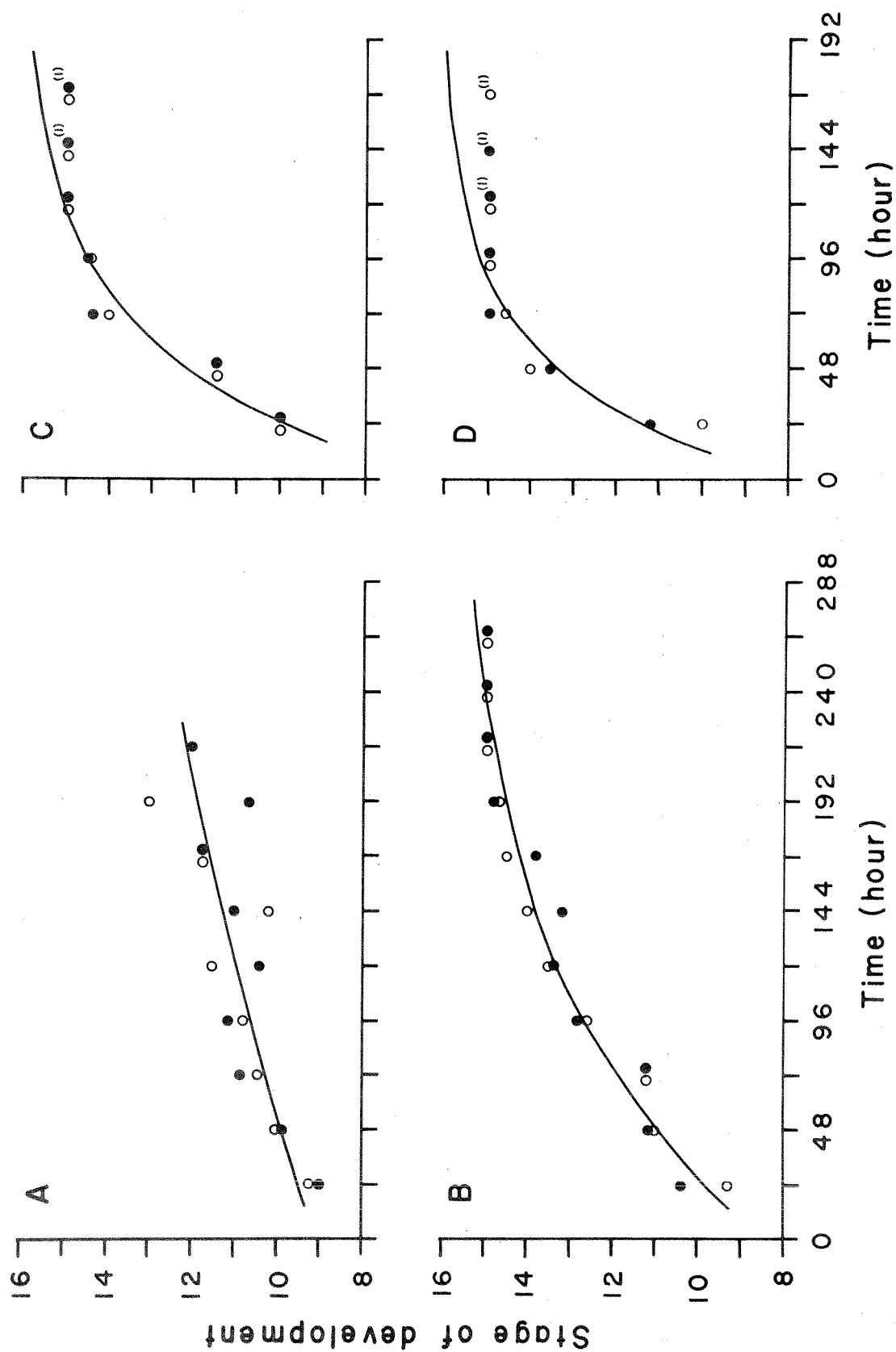
Figure 6. Mean stage of development of embryos and larvae
from the second series plotted against time. The
modified Brody-Bertalanffy equation was fitted to
the data.

Symbols as in Figure 5.
(2): value based on a single specimen and not in-
cluded in the analysis.

A. 13°C
$$S_t = 16 - 15.10e^{-0.00919t}$$
$$r^2 = 0.964$$
P<0.001

B. 18°C
$$S_t = 16 - 15.09e^{-0.01781t}$$
$$r^2 = 0.975$$
P<0.001
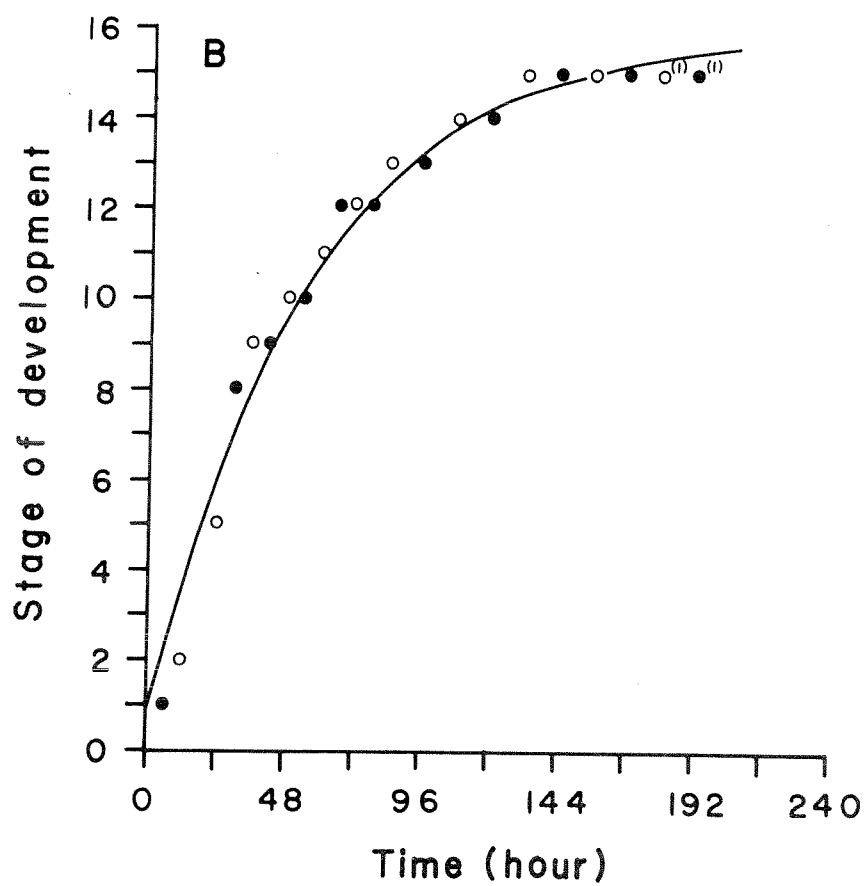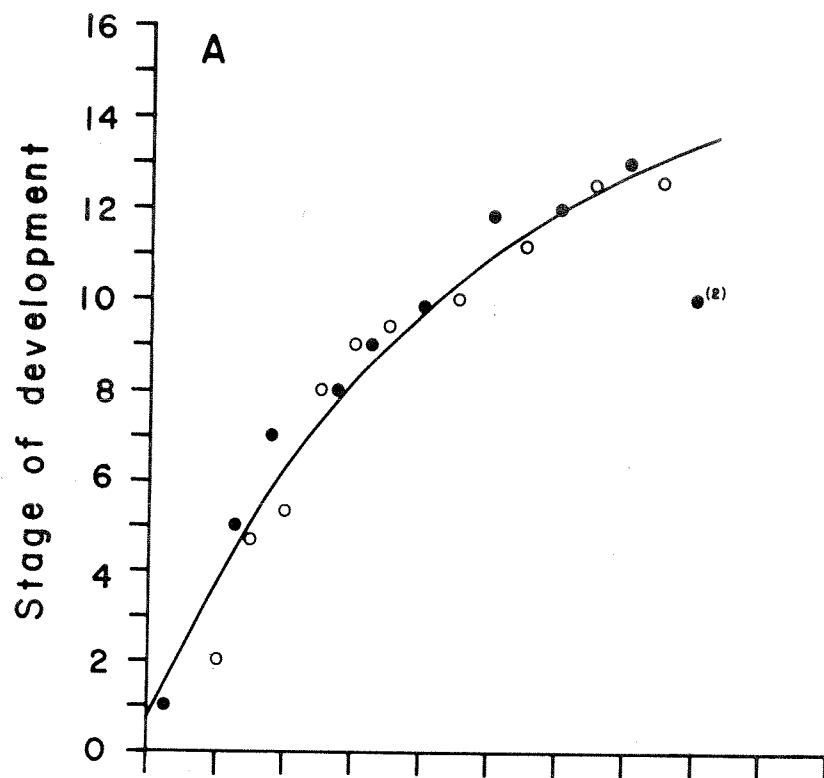
$$t_0 = \frac{\ln\ (\ C/L_\infty\ )}{K} \tag{4}$$

The Brody-Bertalanffy equation then calculates the rate of decrease of the difference between the asymptotic size and the actual size of a fish (Ricker,1975).

As development of the larva in the absence of food can only proceed until exhaustion of the yolk reserves, the idea of an asymptotic stage, one toward which the larva tends but which it does not reach, is applicable in this context. The Brody-Bertalanffy procedure can then be used to calculate the rate of decrease of the difference between the asymptotic stage and the actual developmental stage of the fish. This assumes that each stage represents an equal developmental increment.

There are fifteen stages described from fertilization until exhaustion of the yolk sac. Stage 16, as yet undefined, is considered the asymptotic stage. The general form of the modified Brody-Bertalanffy equation as used in this study is

$$S_\infty - S_t = C' - K't \tag{5}$$

where S_∞ is the asymptotic stage, S_t the stage at time t while $S_\infty - C'$ becomes the stage at which the embryo would have been at t = 0 if it had always grown according to equation (5), and K' is now the instantaneous relative decline in development rate. By taking the natural logarithms, I obtained an equa-

tion of form Y = a + bX:

$$\ln (S_{\infty} - S_t) = \ln C' - K' t \tag{6}$$

A least-squares regression analysis was performed for each temperature (after Sokal and Rohlf, 1969).

This approach has enabled me to estimate the time to hatching in cases where the time of fertilization was unknown. This was done by solving equation (6) for S_t = 12, the stage of the newly hatched larva, and for S_t = 0, the stage at fertilization. The time to hatching is then obtained by substracting the time at S_t = 0 from the time at S_t = 12.

$$\ln (16 - 12) = \ln C' - K' t \tag{7}$$

$$t_{12} = \frac{\ln C' - 1.386}{K'} \tag{8}$$

$$t_0 = \frac{\ln C' - 2.773}{K'} \tag{9}$$

$$\hat{I} = t_{12} - t_0 \tag{10}$$

where t_{12} is the time at S_t = 12, t_0 the time at S_t = 0, and $\hat{I}$ is the estimated hatching time. The values of $\ln C'$ and K', which will be referred to as the development coefficient, were available for each temperature used. Larvae defined as abnormal on the basis of body curvature (which affected swimming and orientation abilities) were used in this analysis if they were normal in all other respects, since larval descriptions were not based on length but on other characteristics.

In order to see if my method provided valid estimates
of time to hatching, I compared Worley's (1933) values of
hatching times at temperatures ranging from 10 to 21°C, as
measured directly from his Figure 5 of embryonic stages
against time, with estimates obtained from the same data by
the procedure described above. Table 1 shows that my esti-
mated hatching times are higher than Worley's data. However,
the difference is small and the trend is identical in both
cases. The modified Brody-Bertalanffy procedure therefore
appears to be a valid way of estimating the hatching time
when the time of fertilization is unknown. It also provides
another useful criterion for comparison, the development
coefficient.

Relationship between hatching time and temperature

Many models have been developed for describing the re-
lationship between hatching time and temperature, eg. the
thermal sums hypothesis of Reisbich (1902) and the more com-
plex models of Bĕlehrádek (1930, 1935), Colby and Brooke
(1973), Alderdice and Velsen (1978). One commonly used is
the Bĕlehrádek equation:

$$I = a(T - \alpha)^{b} \tag{11}$$

I being the time to hatching, T temperature in °C, and a, b
and α constants. Lockwood *et al.* (1977) in effect used this
equation as $I = aT^{b}$ to describe the development of mackerel
eggs at temperatures ranging from 7.4 to 17.8°C, but they did
not correct the Celsius temperature scale with the constant α.

The following Bĕlehrádek equation, obtained by succes-

Table 1. Comparison of the hatching times as obtained by Worley (1933) with those estimated by the modified Brody-Bertalanffy procedure described in the text and applied to Worley's data.

Temperature (°C)	Worley (1933)		modified Brody-Bertalanffy procedure		
	Hatching time (hr)	1/hatching time (hr^{-1})	Development coefficient	Hatching time (hr)	1/hatching time (hr^{-1})
10	207	0.00483	0.00614	225.8	0.00443
11	177	0.00565	0.00718	193.3	0.00517
12	151	0.00662	0.00864	160.5	0.00623
13	131	0.00763	0.00997	139.1	0.00719
14	110.5	0.00905	0.01167	118.8	0.00842
15	99	0.01010	0.01354	102.5	0.00976
16	88	0.01136	0.01481	93.6	0.01068
17	78	0.01282	0.01692	82.0	0.01220
18	70	0.01429	0.01927	71.9	0.01391
19	65.5	0.01527	0.02012	69.0	0.01449
20	57	0.01754	0.02208	62.9	0.01590
21	49.5	0.02020	0.02703	51.5	0.01942

sive approximations of α to maximize r^2, fits Worley's data very closely.

$$I = 182120.99 \; (\; T + 4.8 \;)^{-2.516} \qquad r^2 = 0.999 \qquad (12)$$

I attempted to describe the relationship between the estimated hatching times obtained in this study and temperature with a Bělehrádek equation, but the limited amount of data did not enable me to get an optimal least-squares value for α. Furthermore, the observed relationship appeared fairly linear and the simpler thermal sums hypothesis model was used:

$$1/I = a + bT \qquad (13)$$

where I is hatching time, T temperature in °C, a and b constants. It is to be noted here that this is formally equivalent to Bělehrádek's equation with the exponent = 1, i.e. rate = $a(\; T - \alpha)$.

Growth rate

The growth of embryos and larvae at different temperatures was analysed by the Brody-Bertalanffy procedure, since the absence of extraembryonic food led to an early asymptotic size. The parameters of the Brody equation were estimated by the Beverton method as described by Ricker (1975). A trial value of L_∞ was put in an expression derived from equation (2) by taking the logarithms:

$$\ln (\; L_\infty - l_t) = \ln C - Kt \qquad (14)$$

This line should be straight and the best L_∞ yields the minimal mean-square residuals. Different trial values of L_∞ were

used, and the one leading to the highest coefficient of determination (r^2) was chosen. The parameters ln C and K were then obtained directly from the equation. Larvae which appeared normal in other respects, but which had curved bodies, were not included in the analysis, because the length measurements were influenced by this deformity.

The growth curves obtained from eggs raised at the same temperature, but kept in different fixatives, did not coincide closely. Since their developmental stages corresponded, a two-way analysis of variance (after Sokal and Rohlf, 1969) was carried out, for each stage, in order to find out if temperature and fixative had any significant effect on the length of the larvae. Temperature and fixative were shown to have a significant effect on the length of the specimens in more than half of the cases (Tables 2 and 3). The data from each fixative were therefore treated separately for each temperature.

Table 2. Two-way analyses of variance of the effects of temperature and fixative on the egg diameter and on the length of the larvae from the first series (from partially developed eggs taken in nature). The length data were considered separately for each stage. The two fixatives used were formalin and Davidson's solution.

Source of variation	df	SS	MS	F
Egg diameter				
Temperature (8,13,18,23°C)	3	0.027	0.009	1.54 ns
Fixative	1	0.256	0.256	43.31 ***
Temperature-fixative interaction	3	0.003	0.001	0.19 ns
Stage 12				
Temperature (8,13,18°C)	2	0.176	0.088	1.09 ns
Fixative	1	0.097	0.097	1.20 ns
Temperature-fixative interaction	2	0.399	0.199	2.47 ns
Stage 14				
Temperature (13,18,23°C)	2	0.482	0.241	3.84 *
Fixative	1	1.257	1.257	20.03 ***
Temperature-fixative interaction	2	0.341	0.171	2.72 ns
Stage 15				
Temperature (13,18,23°C)	2	0.995	0.498	8.65 ***
Fixative	1	2.333	2.333	40.55 ***
Temperature-fixative	2	0.094	0.047	0.82 ns

ns $P>0.05$
* $P<0.05$
*** $P<0.001$

Table 3. Two-way analyses of variance of the effects of temperature and fixative on the egg diameter and on the length of the larvae from the second series (from laboratory-fertilized eggs). The length data were considered separately for each stage. The two fixatives used were formalin and Davidson's solution.

	Source of variation	df	SS	MS	F	
Egg diameter	Temperature (8,13,18,23°C)	3	0.011	0.004	1.68	ns
	Fixative	1	0.005	0.005	2.27	ns
	Temperature–fixative interaction	3	0.001	0.000	0.20	ns
Stage 12	Temperature (13,18°C)	1	0.019	0.019	0.22	ns
	Fixative	1	0.179	0.179	2.00	ns
	Temperature–fixative interaction[1]	–	–	–	–	
Stage 13	Temperature (13,18°C)	1	0.015	0.015	0.60	ns
	Fixative	1	0.373	0.373	15.47	**
	Temperature–fixative interaction	1	0.008	0.008	0.34	ns
Stage 14	Data were only available for 18°C and a Student–t test showed that the effect of the fixative was significant at the 0.01 level.					
Stage 15	A Student–t test carried out on data from 18°C showed that the effect of the fixative was significant at the 0.001 level.					

ns P>0.05
** P<0.01
[1] There was no data for the length of larvae preserved in Davidson's solution at 13 °C, so no interaction was calculated.

RESULTS

Hatching success and mortality

Hatching success and mortality varied with the incubation temperature and with the stage at which the embryos were subjected to that temperature (Tables 4 and 5). In the first series, where the majority of the embryos had already attained stage 9 when they were placed in the incubators, mortality was very low, ranging from 0 to 4.1% at the 4 temperatures. These percentages represent the mean for each temperature when data from both incubators are pooled. The only significant difference was found between 8 and 23°C (P<0.001, test for equality of 2 percentages after Sokal and Rohlf, 1969). The length of the incubation period influenced the number of embryos left for hatching, because of sampling removals, so at low temperatures fewer embryos were available for hatching than at high temperatures. The proportion of abnormalities over total hatching is a measure independent of this factor and it was used to reflect hatching success. The lowest values (22.0 and 26.8%) were found at the intermediate temperatures (13 and 18°C), whereas percentages of 36.7 and 74.6 occurred at 8 and 23°C respectively. There was no significant difference among the values from 8,13 and 18°C, but each of these differed significantly from the percentage at 23°C (P<0.001). Most of the abnormalities encountered at 23°C were body curvatures of the larvae.

In the second series, where the eggs were subjected to the incubation temperature from fertilization onward,

Table 4. Percentages of mortality, abnormalities and hatching success at different temperatures in the first series. A and B refer to separate incubators.

	8°C		13°C		18°C		23°C	
	A	B	A	B	A	B	A	B
Total number of eggs[1]	49	44	56	52	37	35	37	37
% mortality	0	0	1.8	0	0	2.9	0	8.1
% of specimens sampled before hatching	65.3	70.5	23.2	23.1	24.3	17.1	8.1	13.5
% normal hatching	16.3	25.0	66.1	51.9	56.8	57.1	32.4	10.8
% abnormalities	18.4	4.5	8.9	25.0	18.9	22.9	59.5	67.6
% total hatching	34.7	29.5	75.0	76.9	75.7	80.0	91.9	78.4
Proportion of abnormal hatching over total hatching	53.0	15.3	11.9	32.5	25.0	28.6	64.7	86.2

[1] The low numbers of eggs accounted for, as compared to about 100 put in the jars, are probably due to loss at time of transfer into the incubators.

Table 5. Percentages of mortality, abnormalities and hatching success at different tem-
peratures in the second series. A and B refer to separate incubators.

	8°C		13°C		18°C		23°C	
	A	B	A	B	A	B	A	B
Total number of eggs	136	150	102	161	106	117	104	58[1]
% mortality	99.3	85.3	65.7	63.4	59.4	61.5	95.2	81.0
% of specimens sampled before hatching	0.7	14.7	22.5	21.7	12.3	17.9	3.8	19.0
% normal hatching	0	0	11.8	6.2	22.6	14.5	0	0
% abnormalities	0	0	0	8.7[2]	5.7	6.0	1.0	0
% total hatching	0	0	11.8	14.9	28.3	20.5	1.0	0
Proportion of abnormal hatching over total hatching	–	–	0	60.0[2]	20.1	29.3	100	–

[1] This low figure is due to a missing bottle of preserved dead eggs.
[2] These high percentages are due to 12 eggs which failed to hatch: the tail was reaching
the nape rather than the eye, and it was growing past it. This abnormality was noticed
in this case only. There were two abnormal larvae.

mortality was quite high, ranging from 60.5 to 92% at the 4 temperatures (Table 5). It was significantly greater at the two temperature extremes than at 13 or 18°C (P<0.001). The difference between the two intermediate temperatures, or between 8 and 23°C was not significant. There was no hatching at 8 or 23°C, except for one abnormal larva which was found dead at 23°C. The proportion of abnormalities over total hatching was higher at 13 than at 18°C, 38.9 and 24.1% respectively (non-significant difference, P>0.05). However, this is mostly due to twelve abnormal embryos and 2 abnormal larvae in *one* incubator (see footnote 2, Table 5). These were not observed in the other incubator at this temperature.

Development rate versus temperature

The time from fertilization to hatching, in the second series, was determined directly from Fig. 6, as the time at which stage 12 was first attained. At 18°C, however, the sample at 67 hours was not considered because it is based on only 2 specimens. The time to hatching was therefore 145 hours at 13°C and 73 hours at 18°C. The development coefficients, which are another way of looking at development rate, are presented in Table 6 for different temperatures. In the analysis of data, the last two samples at 18°C in both series and the last three samples at 23°C were omitted in the calculations of the development coefficient. These values, which formed a plateau because the larvae were not categorized in fractional stages beyond stage 15 (see Figs. 5 and 6), imposed curvilinearity in the data plotted as $\ln (16-S_t)$ against

Table 6. Mean values, standard errors and 95% confidence
limits for the parameters of the development
equations, together with the estimated hatching
times at the different temperatures.

	8°C	13°C	18°C	23°C
First series				
Development coefficient	0.00271	0.00849	0.01933	0.02357
Standard error of the coefficient	0.00039	0.00050	0.00242	0.00482
95% confidence limits	±0.00092	±0.00113	±0.00770	±0.02074
n	17	22	10	8
ln C'	1.940	2.022	2.257	2.072
Standard error of ln C'	0.0507	0.0816	0.1923	0.3171
95% confidence limits	±0.1199	±0.1845	±0.6119	±1.3645
Estimated hatching time (hr)	511.9	163.4	71.8	58.8
Second series				
Development coefficient	–	0.00919	0.01781	–
Standard error of the coefficient	–	0.00043	0.00068	–
95% confidence limits	–	±0.00091	±0.00140	–
n	–	19	20	–
ln C'	–	2.715	2.714	–
Standard error of ln C'	–	0.0433	0.0616	
95% confidence limits	–	±0.0914	±0.1295	–
Estimated hatching time (hr)	–	150.9	77.9	–

time, and thus artificially decreased the calculated coeffi-
cient. As a consequence, a large 95% confidence interval is
attached to these development coefficients because of the
small number of data points. The results of both series
show the same trend: an increase in development coefficient
with an increase in temperature (Fig. 7). This means that
the development rate of mackerel embryos declines more rap-
idly at the higher temperatures. The values for 13 and 18°C
from the two series could not be compared by covariance anal-
ysis because of the heterogeneity of the variances (Snedecor,
1956). The relationship between the development coefficient
and temperature is based on limited data and it appears fairly
linear (Fig.7). A least-squares regression was carried out
after Sokal and Rohlf (1969) and the following equation was
obtained:

development coefficient = -0.00960 + 0.00149T

$$r^2 = 0.974 \qquad (15)$$

where T = temperature in °C.

The times to hatching for each temperature were esti-
mated from these development coefficients and the results
are presented in Table 6. The inverses of these calculated
hatching times are plotted against temperature (Fig. 8) and
the equation obtained is the following:

1/hatching time = -0.00694 + 0.00108T

$$r^2 = 0.974 \qquad (16)$$

The Bĕlehrádek equation fitted to Worley's (1933) re-
sults (equation 12) gives a better fit than the thermal sums

Figure 7. Development coefficient plotted against temperature.
Mean values and 95% confidence intervals.

(●): data from the first series
(■): data from the second series
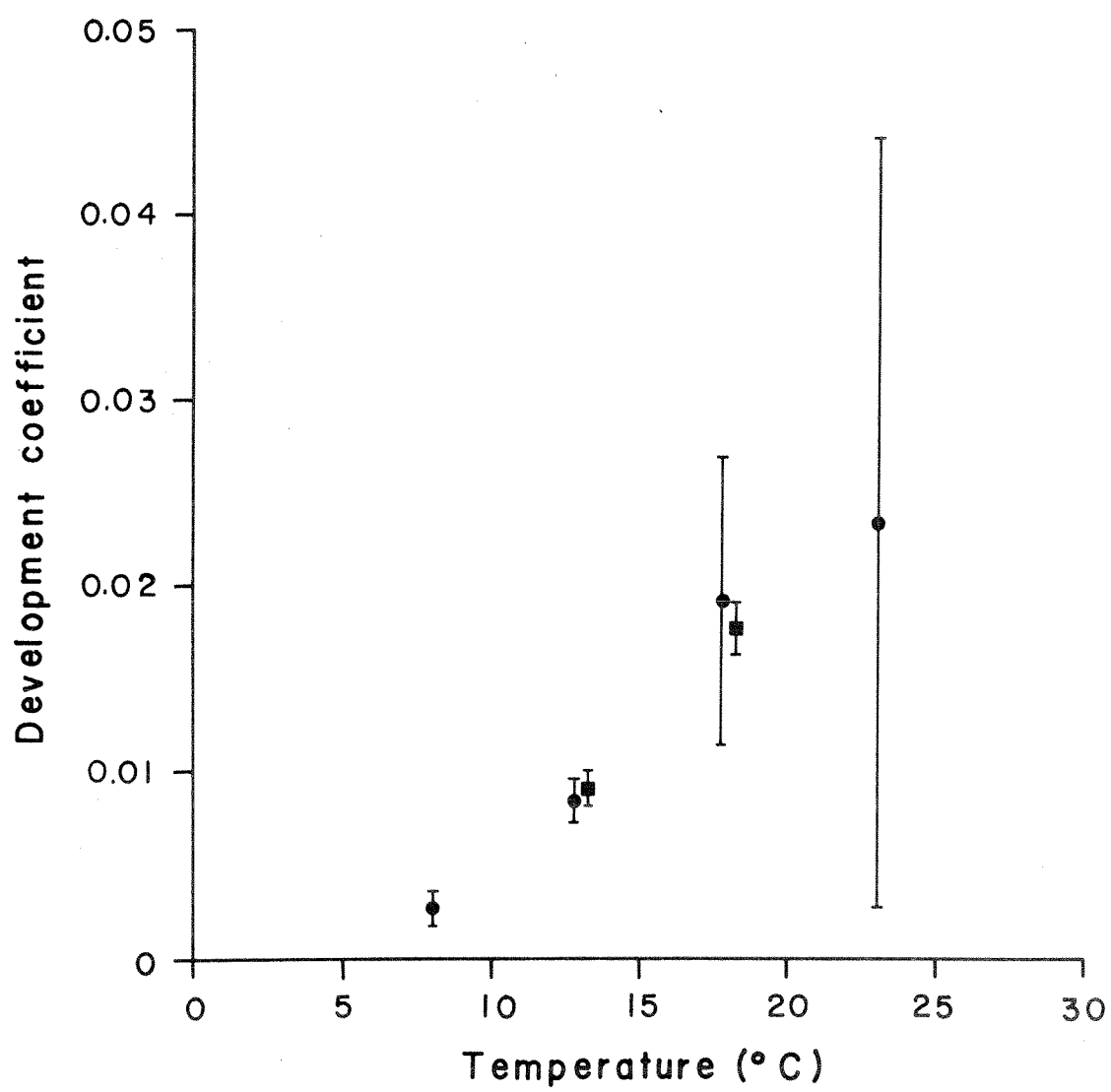
Figure 8. Inverse of hatching time plotted against tempera-
          ture. A comparison of different studies.

          Symbols as in Figure 7.

          (— · — · —): Worley (1933)
             1/hatching time = -0.00914 + 0.00128T
             r^2 = 0.978
             P<0.001

          (· · · · · · · · · · · ·): Lockwood *et al.* (1977)
             1/hatching time = -0.00495 + 0.00101T
             r^2 = 0.997
             P<0.001

          (——————): this study
             1/hatching time = -0.00694 + 0.00108T
             r^2 = 0.974
             P<0.001
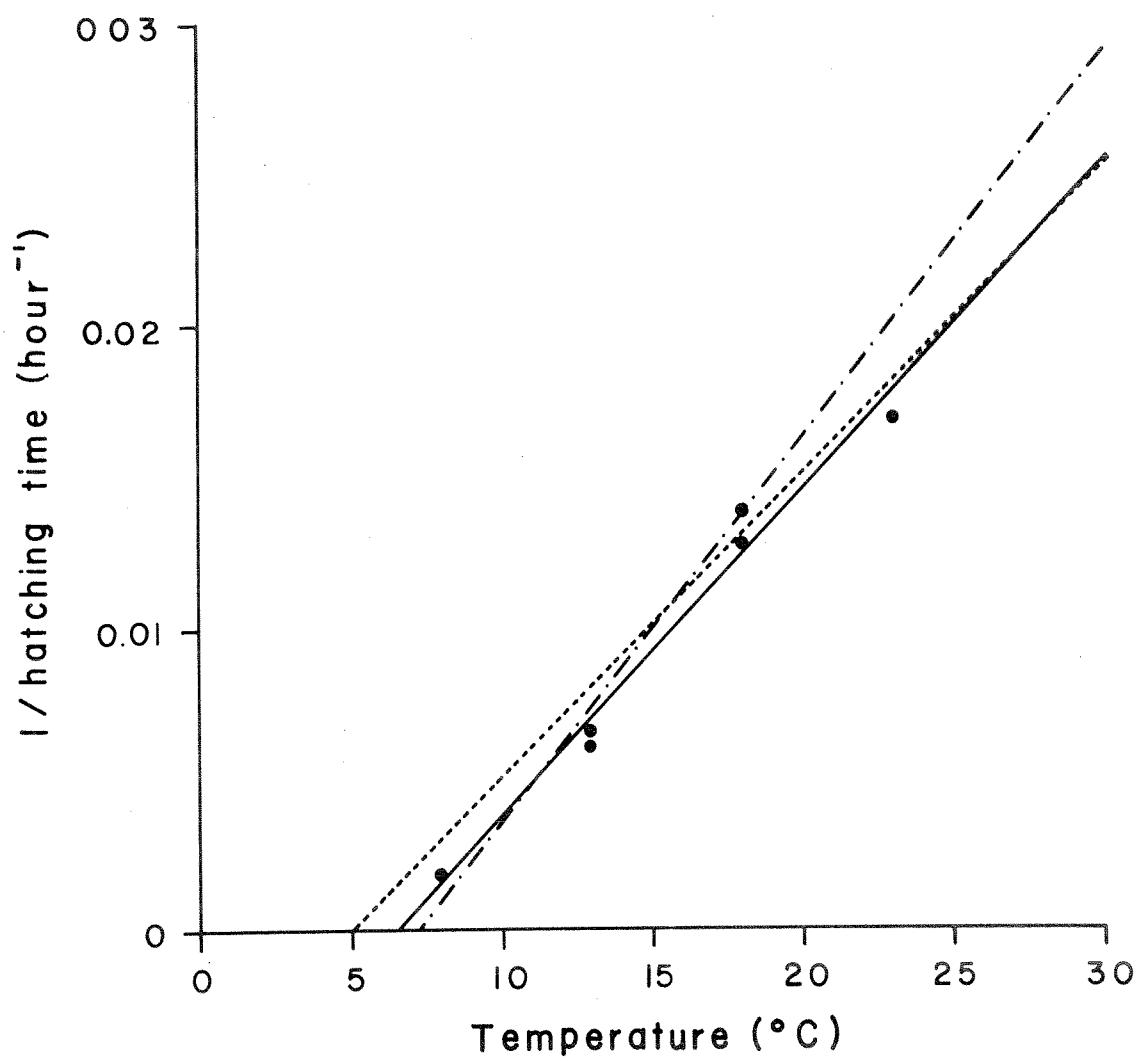
model, but the latter was used for comparing the results of this study with those already published (Worley, 1933). The estimated hatching times obtained from the modified Brody-Bertalanffy procedure applied to Worley's (1933) data were used in order to have the same method as the basis for comparison.

$$1/\text{hatching time} = -0.00914 + 0.00128T$$
$$r^2 = 0.978 \qquad (17)$$

An analysis of covariance was carried out after Snedecor (1956) and the two regression lines were not found to differ significantly at the 0.05 level[2]. The equation representing Lockwood et al.'s (1977) results is also included for comparison in Fig. 8, but covariance analysis was not possible due to variance heterogeneity.

Another comparison was done with the coefficients of development since these represent a more precise measure, not affected by extrapolation as the hatching times were. Equation (18) describes the relationship between the development coefficients and temperature as obtained from Worley's (1933) results using the modified Brody-Bertalanffy procedure.

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[2]This covariance analysis is based on the development coefficients which are in fact summarizing the data from each temperature, but they are not the actual data as such. The basis of covariance is therefore not rigorously respected, but this method nevertheless appeared a useful way of comparing the different studies. It is used in this context throughout this section. In the same way, the coefficient of determination (r^2) does not exactly reflect the variation of Y due to the regression, but it still is an indication of how well the equation describes the data.

$$\text{development coefficient} = -0.01274 + 0.00178T$$

$$r^2 = 0.978 \qquad (18)$$

This equation is presented in Fig. 9, together with equation (15), and no significant difference was detected between them when an analysis of covariance (Snedecor, 1956) was carried out.

Growth rate versus temperature

In order to obtain values for the Brody growth coefficient, the instantaneous relative decline in growth rate, asymptotic sizes had to be determined for each experimental situation (see Analysis of Data). The asymptotic values are presented in Table 7. Asymptotic sizes could not be obtained in the following cases, because of the limited data and of the associated variation: 8°C A (formalin-preserved specimens) and B (Davidson's-preserved ones), 18°C A and B and 23°C B in the first series and 13°C A and B in the second series. At 8°C, the eggs remained in the embryonic stages until a few hours before the end of the experiment and, by comparison with the other temperatures (Figs. 10 and 11), it appears that the size increase which usually occurs before hatching did not happen here, so that it is not possible to obtain a realistic value for the asymptotic size. At 23°C, for Davidson's-preserved specimens, there were too few data and no clear trend. For 13 and 18°C, the L_∞ determined for the corresponding case in the other series were used.

There appears to be an inverse relationship between asymptotic size and temperature: for formalin-preserved spec-

Figure 9. Development coefficient plotted against tempera-
ture. A comparison of Worley's (1933) study with
the present one.

Symbols as in Figure 7.

(— · — · —): Worley (1933)
development coefficient = -0.01274 + 0.00178T
r^2 = 0.978
P<0.001

(——————): this study
development coefficient = -0.00960 + 0.00149T
r^2 = 0.974
P<0.001
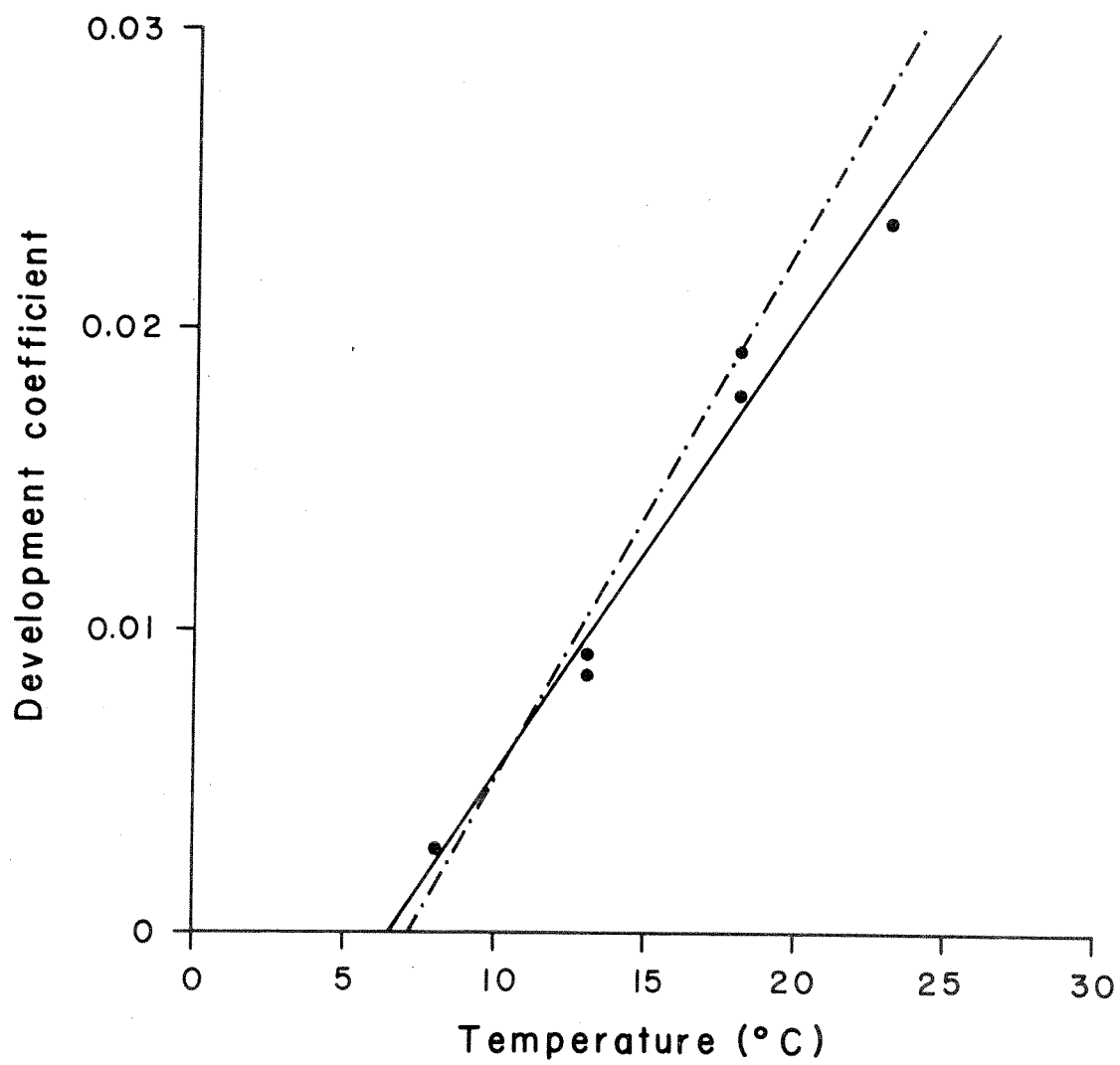
Table 7. Asymptotic sizes for the Brody-Bertalanffy equations at different temperatures. A and B refer to specimens preserved in formalin and in Davidson's solution respectively. The numbers in parentheses correspond to cases where no realistic asymptotic value could be obtained, and the value from the other series was used.

	8°C		13°C		18°C		23°C	
	A	B	A	B	A	B	A	B
First series	−	−	5.0	4.5	(4.6)	(4.1)	4.5	−
Second series	−	−	(5.0)	(4.5)	4.6	4.1	−	−

Figure 10. Size of embryos and larvae from the first series plotted against time. The Brody-Bertalanffy equation was fitted to the data from each fixative separately. The vertical arrow on the time axis represents hatching.

Symbols as in Figure 5.

A. 8°C
   no equation

B. 13°C
   In formalin,

   $$l_t = 5.0 - 2.79e^{-0.00816t}$$
   $r^2 = 0.694$
   P<0.001

   In Davidson's solution,

   $$l_t = 4.5 - 2.98e^{-0.01017t}$$
   $r^2 = 0.753$
   P<0.001

C. 18°C
   In formalin,

   $$l_t = 4.6 - 3.03e^{-0.02021t}$$
   $r^2 = 0.712$
   P<0.001

   In Davidson's solution,

   $$l_t = 4.1 - 1.24e^{-0.01255t}$$
   $r^2 = 0.457$
   P<0.001

D. 23°C
   In formalin,

   $$l_t = 4.5 - 3.81e^{-0.03516t}$$
   $r^2 = 0.796$
   P<0.001

   In Davidson's solution,

   no equation

Figure axes: Size of embryo or larva (mm) vs Time (hour). Panels A, B, C, D.
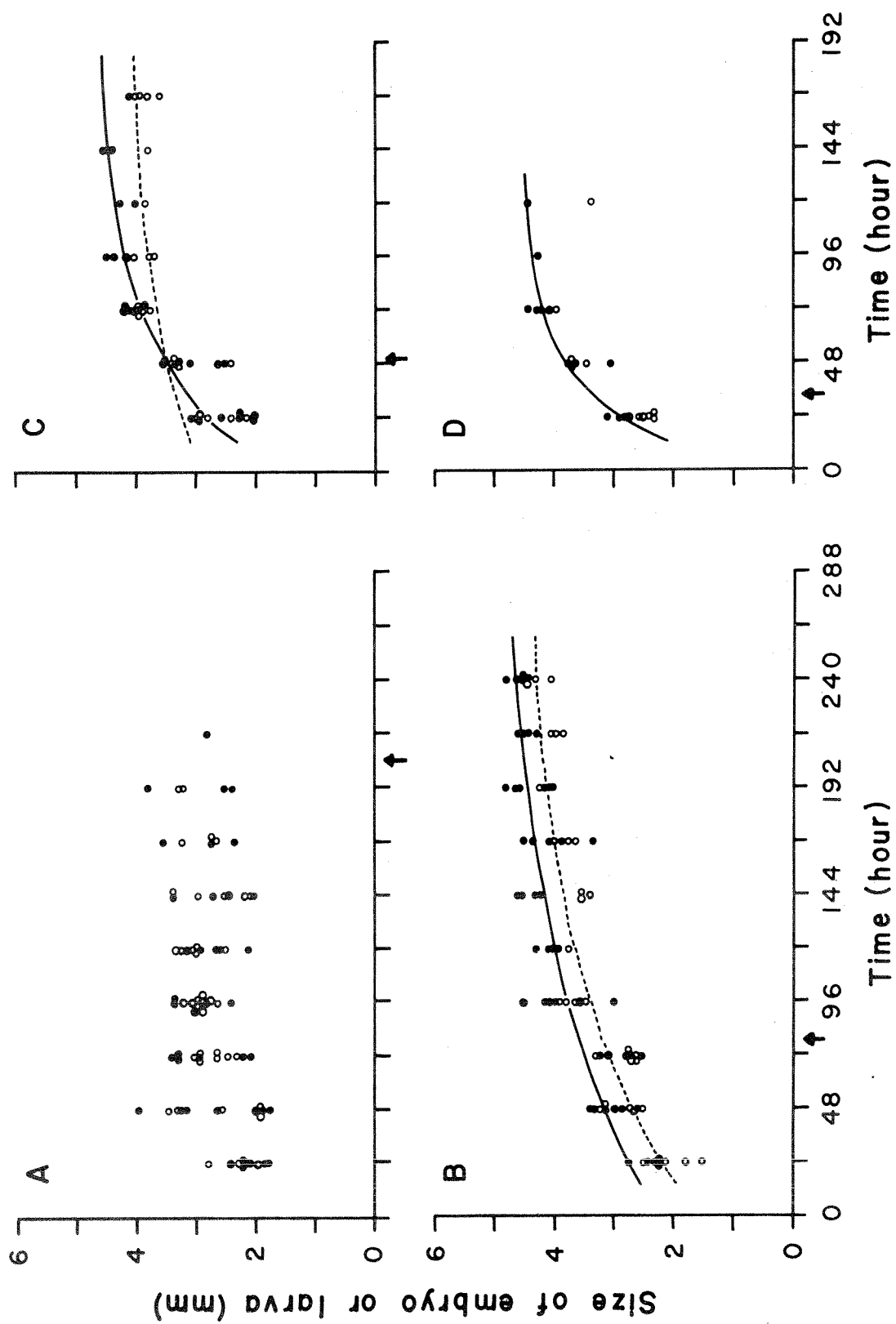
Figure 11. Size of embryos and larvae from the second series plotted against time. The Brody-Bertalanffy equation was fitted to the data from each fixative separately. The vertical arrow on the time axis represents hatching.

Symbols as in Figure 5.

A. 13°C
   In formalin,
   $$l_t = 5.0 - 8.72e^{-0.01373t}$$
   $$r^2 = 0.830$$
   $$P < 0.001$$

   In Davidson's solution,
   $$l_t = 4.5 - 5.27e^{-0.01014t}$$
   $$r^2 = 0.736$$
   $$P < 0.001$$

B. 18°C
   In formalin,
   $$l_t = 4.6 - 5.41e^{-0.02138t}$$
   $$r^2 = 0.720$$
   $$P < 0.001$$

   In Davidson's solution,
   $$l_t = 4.1 - 5.25e^{-0.02575t}$$
   $$r^2 = 0.606$$
   $$P < 0.001$$
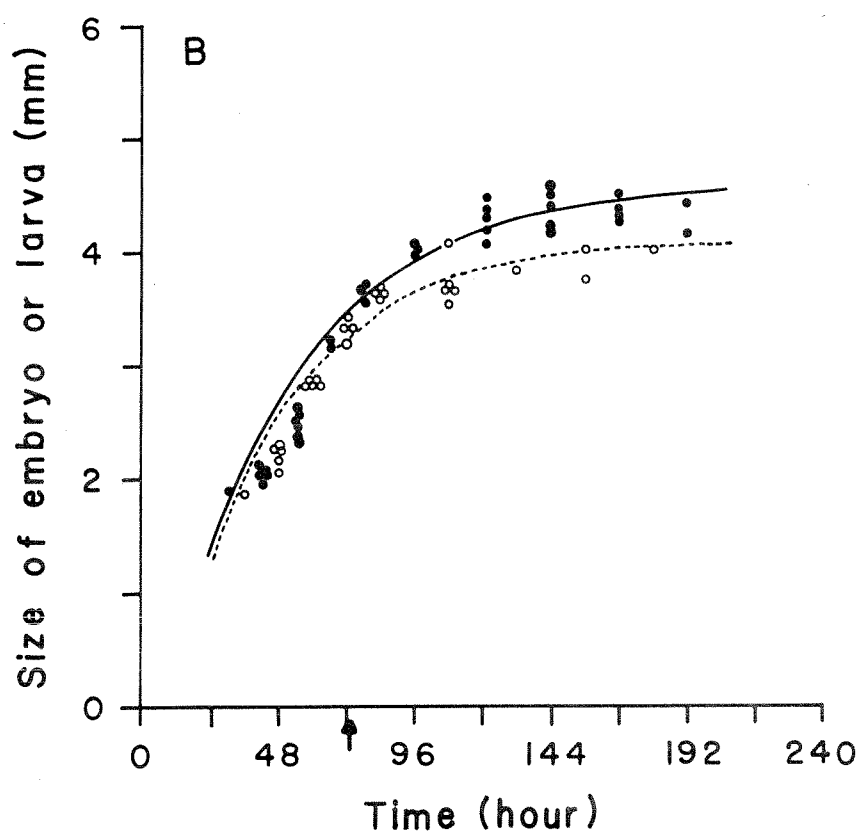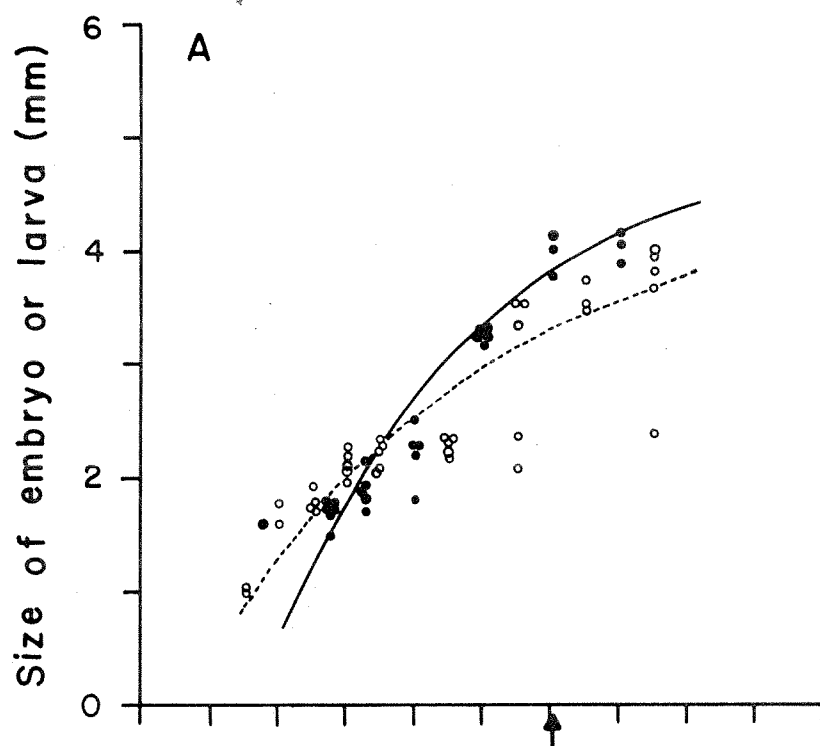
imens, L_∞ shows values of 5.0, 4.6 and 4.5 mm for 13, 18 and 23°C respectively. This cannot be tested statistically however.

The values for the Brody growth coefficient (Table 8) are positively correlated with temperature (Fig. 12). The relationship between the growth coefficient and temperature, for formalin-preserved specimens, is described by the following equation:

$$\text{growth coefficient} = -0.02034 + 0.00236T$$

$$r^2 = 0.946 \qquad (19)$$

No significant regression was found for data from the Davidson's fixative because of the very small sample size (n=4).

It is interesting to note that the growth coefficient becomes zero around 8.6°C (Fig. 12) so that this temperature would be the lower limit for growth. By comparison, the lower limit for development, in this study, would be around 6.4°C (Fig. 9). This suggests that growth and development may have different thermal requirements, growth necessitating higher temperatures.

Yolk utilization versus temperature

The change in yolk volume of embryos and larvae at each temperature shows a general pattern of yolk utilization with time (Figs. 13 and 14): not much drop in yolk volume up to hatching, a sudden decrease at hatching and then a very slow tapering off until exhaustion of all yolk reserves. This corresponds to the pattern of size increase (Figs. 10

Table 8. Mean values, standard errors and 95% confidence limits for the Brody-Bertalanffy growth coefficient at different temperatures. A and B refer to specimens pre-served in formalin and in Davidson's solution respectively.

	8°C		13°C		18°C		23°C	
	A	B	A	B	A	B	A	B
First series								
Brody-Bertalanffy growth coefficient	–	–	0.00816	0.01017	0.02021	0.01255	0.03516	–
Standard error of the coefficient	–	–	0.00076	0.00103	0.00252	0.00299	0.00514	–
95% confidence limits	–	–	±0.00152	±0.00210	±0.00518	±0.00622	±0.01120	–
n	–	–	53	34	28	23	14	–
Second series								
Brody-Bertalanffy growth coefficient	–	–	0.01373	0.01014	0.02138	0.02575	–	–
Standard error of the coefficient	–	–	0.00122	0.00104	0.00232	0.00407	–	–
95% confidence limits	–	–	±0.00251	±0.00211	±0.00472	±0.00837	–	–
n	–	–	28	36	35	28	–	–

Figure 12. Brody-Bertalanffy growth coefficient plotted
            against temperature. Mean values and 95% confi-
            dence intervals.

            (●): coefficient based on data from specimens
                 from the first series preserved in formalin
            (O): coefficient based on data from specimens
                 from the first series preserved in Davidson's
                 solution
            (■): coefficient based on data from specimens
                 from the second series preserved in formalin
            (□): coefficient based on data from specimens
                 from the second series preserved in Davidson's
                 solution

            Equation based on data from specimens preserved
            in formalin only:
                growth coefficient = -0.02034 + 0.00236T
                $r^2 = 0.946$
                $P < 0.01$
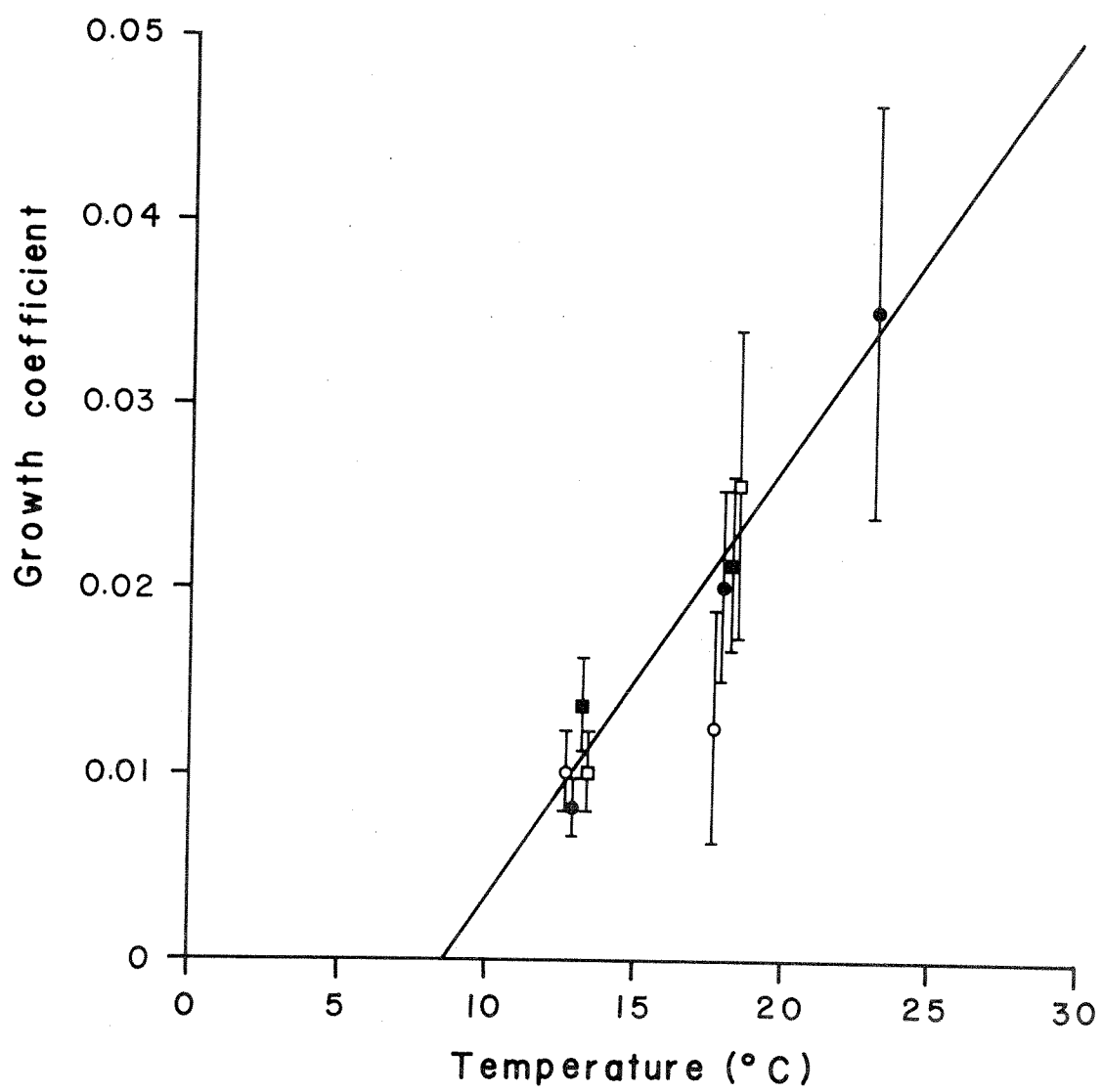
Figure 13.   Yolk volume of embryos and larvae from the first series plotted against time.
The vertical arrow on the time axis represents hatching.

Symbols as in Figure 5.

A. 8°C   C. 18°C

B. 13°C   D. 23°C
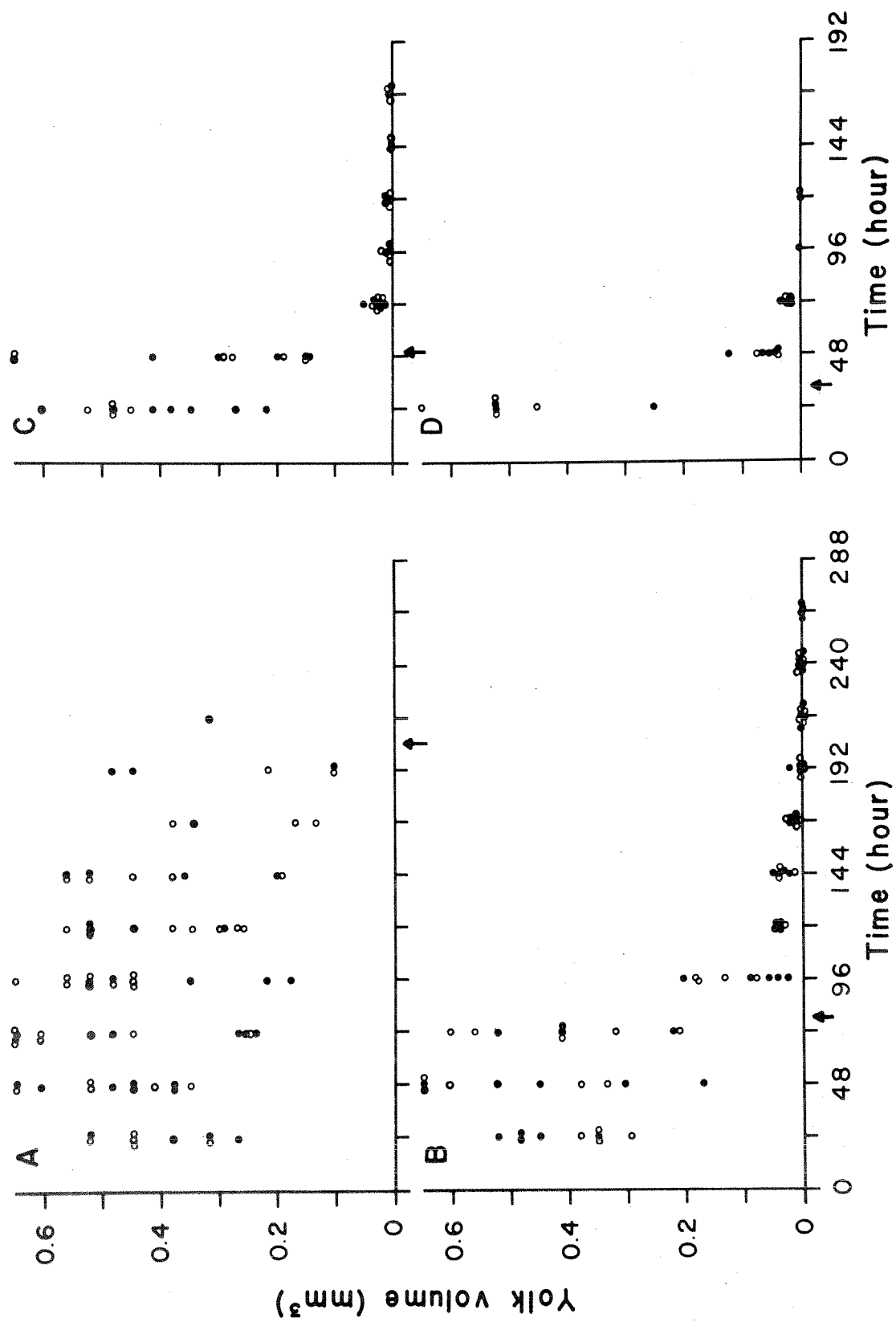
Figure 14.   Yolk volume of embryos and larvae from the second
             series plotted against time.   The vertical arrow
             on the time axis represents hatching.

             Symbols as in Figure 5.

             A. 13°C

             B. 18°C
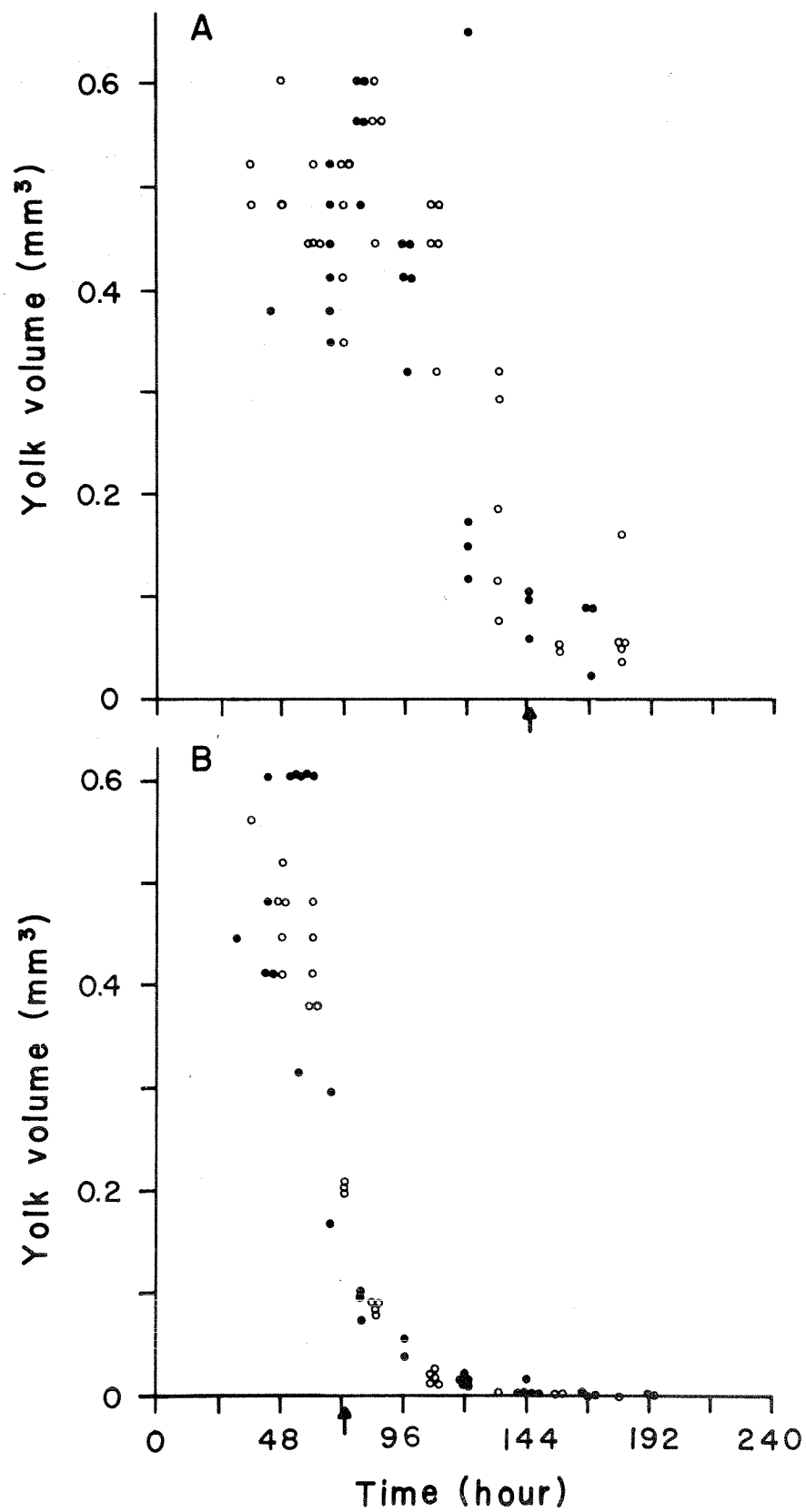
and 11), where there is a slow increase at the beginning,
a sudden increase before hatching and then the asymptote.

The yolk utilization rate increased with temperature
and the pronounced drop at hatching found at the other tem-
peratures is not apparent at 8°C. This is comparable with
the small increase in the size of the embryo during the first
100 hours and subsequent leveling off at 8°C (Fig. 10A).

DISCUSSION

The environmental temperature directly influences the development and growth of poikilotherms through its effect on rates of metabolic reactions. Temperature can thus be of great importance to the successful establishment of a year-class in fish populations. The results of the present study can therefore be considered in comparison with those obtained by previous workers on embryonic develop- ment of mackerel and other fishes, and also in the context of general theories concerning the early life history of fish.

Successful hatching

Many studies on the development of eggs from different fish species indicate that the early developmental stages, usually up to blastopore closure, are the least resistant to mechanical disturbance or thermal shock (McCauley, 1963; Swift, 1965; Pinus, 1974; Brewer, 1976; Guma'a, 1978). The time just before hatching is also reported to be a period of higher mortality in some embryos (Hayes, 1949; Swift, 1965; Forrester and Alderdice, 1966). In the present study, a large number of eggs hatched at 8 and 23°C when they were exposed to these temperatures after the 2/3 circle stage, but not if they were subjected to these conditions just after fertil- lization[3]. This agrees with the experimental findings cited

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[3] The experimental design did not account for eggs which were sampled in the embryological stages and which might have hatched if they had not been taken. It is possible that some of these eggs would have hatched at 8 and 23°C (one abnormal larva was found at 23°C), but this proportion would have been very small as mortality was already quite high.

above and also with the results of Hokanson and Kleiner (1974), who observed that yellow perch eggs exposed to extreme temperatures just after fertilization did not hatch, unlike those exposed after neural keel formation. McCormick (1978) reported a similar conclusion for white bass eggs exposed to a range of temperatures before or after gastrulation.

The range of temperatures over which hatching of mackerel eggs occurred was found to be 10-21°C by Worley (1933) and 7.4-17.8°C by Lockwood *et al.* (1977). Danielssen and Iversen (1977), using mackerel from the North Sea, report a range of 12-22°C for eggs from live fish and 12-18°C for eggs from fish which had been dead 3-4 hours (temperatures lower than 12°C were not used.) Lockwood *et al.* (1977) mention differences in "husbandry" (i.e. rearing techniques), as probable factor for discrepancies between their results and those of Worley (1933). Water temperature when their fish were caught in March was 12°C, whereas it was 16°C in June when Worley captured his fish. This shift of 3-4°C corresponds to the increase shown in the temperature range for successful hatching. Lockwood *et al.* (1977) dismissed the idea that acclimation was responsible for the difference in the range of temperature by reporting that the surface temperatures at Woods Hole from March to July do not differ much from those in the Bay of Biscay and Celtic Sea over the same period. However, the mean sea surface temperature is 8.9-11.1°C in March for the Bay of Biscay and Celtic Sea area and only 3.3-4.4°C around Woods Hole. It is only

in June and July that the means of the two regions corre-
spond closely (Anon, 1967). The parental thermal history will
therefore be different in the two stocks of fish and it ap-
pears that acclimation should not be ruled out so easily.
Furthermore, variations from year to year may occur in local
conditions and, as the fish become acclimated to colder or
warmer water, the eggs may show a corresponding change in
their temperature tolerance. Hubbs *et al.* (1971) found that
acclimation of adult *Menidia audens* influenced the thermal
tolerance of the zygotes obtained from these fish.

The difference in the survival of eggs from live or
dead fish when exposed to 20 and 22°C by Danielssen and
Iversen (1977) may be due to a poorer quality of gametes
from dead fish as the authors suggest, but it still points
out that mackerel embryos can develop in temperatures as
high as 22°C. Danielssen and Iversen mention that the dif-
ference in temperature tolerance between their results and
those of Worley (1933) could be because the American and Eu-
ropean mackerel are two separate races as concluded by
Garstang (1898). Hatching of partially developed eggs taken
from nature and exposed to 23°C was shown in the present
study, even though the proportion of abnormalities was high.
Furthermore, Danielssen and Iversen's (1977) results are
closer to those of Worley (1933) than to those of Lockwood
et al. (1977), who reported no hatching at temperatures above
17.8°C although their fish were also of the European race.
This suggests that differences in the experimental techniques,
and possibly in acclimation of fish, are more likely than

differences in thermal adaptation due to races as sources
of the reported difference in temperature tolerance. (Daniel-
ssen and Iversen [1977] did not state the temperature at
which adult fish were kept before spawning.) In addition,
Berrien (1978) reported that mackerel eggs are caught on
the east coast of the United States in waters with surface
temperature of 6.3-16.9°C, although 97% of them are in waters
of 8.7-13.8°C. These observations imply that mackerel eggs
can probably develop at lower temperatures than those re-
ported by Worley (1933) and this would agree with the findings
of Lockwood *et al.* (1977). The combined observations there-
fore indicate that mackerel development can take place at 7-
23°C, but it is most successful in the narrower range of 9-
18°C.

Mortality was more pronounced at the temperature ex-
tremes than in the intermediate range in the experiments
of Worley (1933), Lockwood *et al.* (1977) and in the present
study. Worley found a minimal mortality at 16°C, which
corresponds to the water temperature at the time of capture
of the fish that produced his eggs. This again suggests
that acclimation of adult fish might influence the thermal
tolerance of the embryos. Lockwood *et al.* obtained mortal-
ity percentages lower than 20% between 9.4 and 15.1°C, but
no definite minimum. The present study found approximately
62% mortality at the intermediate temperatures as opposed
to values around 90% for the temperature extremes. Daniel-
ssen and Iversen (1977) mentioned, on the other hand, that

mortality was between 75 and 90% at all temperatures when
hatching occurred, and presented no evidence for a minimum.
In spite of such variations in results, it seems that, in
general, mortality is lower at temperatures usually encoun-
tered by the developing mackerel embryos in nature. This
corresponds to the findings of Colby and Brooke (1970) for
lake herring, Hokanson and Kleiner (1974) for yellow perch,
Laurence and Rogers (1976) for haddock and Coombs and Hiby
(1979) for blue whiting. However, other studies have report-
ed an increase in mortality with temperature: Swift (1965)
for char, Koenst and Smith (1976) for walleye and Guma'a
(1978) for perch. It is possible that increased mortality
at lower temperatures was not noticed if these studies did
not use temperature much below the natural limits. For
example, Windermere char usually spawn in waters at 4-9°C
(Frost, 1951) and Swift(1965) studied the egg development
at temperatures from 4 to 14°C. The proportion of abnormali-
ties, on the other hand, generally increases with tempera-
ture, as the present study indicates along with Hubbs *et al.*
(1971), Saksena *et al.* (1972), and Koenst and Smith (1976).

Time to hatching

The relationship between temperature and embryonic
duration has been studied for a wide variety of organisms.
An inverse relationship is usually observed and many equa-
tions have been proposed to describe it. The temperature co-
efficients, Q_{10} and μ, developed for chemical reactions, have
lost their popularity among biologists, because they tend

to vary over the range of temperatures at which biological processes go on. The thermal sums relationship has practical features and was largely used by fish culturists on the development of trout embryos in hatchery (Wallich, 1901). Bĕlehrádek (1930, 1935) proposed an exponential expression which approximates the temperature-time curve over a wider range of temperatures than does a rectilinear hyperbola. He showed the thermal sums model to be a special case of his more general equation. Bĕlehrádek's equation has found wide applications among copepods (McLaren *et al.*, 1969; Corkett, 1972; Landry, 1975), frogs (McLaren and Cooley, 1972), fish (Lockwood *et al.*, 1977; Alderdice and Velsen, 1978; Coombs and Hiby, 1979). Davidson (1944), working on insects, developed a logistic equation to describe rate responses that slow down at high temperatures, but this equation is not encountered much in fisheries studies. Some workers, such as Colby and Brooke (1973), have derived complex polynomial equations for the fish species they study, but these formulas cannot be generalized to other species.

Worley (1933) used the temperature coefficient μ to describe the relationship between the rate of development of mackerel embryos and temperature. He had to postulate the existence of a critical temperature at 15°C at which he applied a change in the value of μ. Bĕlehrádek's equation has been found in the present study to describe his data very closely over the whole temperature range tested.

Lockwood *et al.* (1977) have also used this equation to summarize their results on the development of mackerel eggs at different temperatures although they did not include the temperature-scale correction factor, α. In the present study, the limited data did not enable me to get an optimal least-squares value for α. Furthermore, over the range of temperature studied, b was close to 1.0 and the thermal sums model adequately described the data.

The modified Brody-Bertalanffy procedure yields slight overestimates of hatching times. This is due to the fact that these estimates are based on the value of ln C', with a large standard error associated with it, and that they correspond to an extrapolation of the observed data. The values obtained nevertheless agree with Worley's (1933) results when these are analysed in the same way. A comparison carried out with the development coefficients based on the observed data only, and not on extrapolation, led to the same conclusion. This method proves quite useful in comparing data from partially developed eggs with the results of other studies. It is the only method that I know of which can estimate the time to hatching when the time of fertilization is unknown.

The Brody-Bertalanffy procedure, applied to the development of the embryos, is based on a stage classification where it is assumed that each stage represents an equal developmental increment. This is somewhat arbitrary, since there are no quantitative measures available for this

purpose, but the successful fit of the Brody-Bertalanffy
equation might be taken as a validation of the assumption.
The real value of such a classification resides in the fact
that it can be used to estimate hatching times when no other
method is available. It appears that this type of classi-
fication would be useful in any study of egg development,
and that it may very well be a criterion to look for when
making up keys to stages of development in future studies.

The development of mackerel eggs from St.George's
Bay, in the southern Gulf of St.Lawrence has been shown
to be very similar to that of the eggs from Woods Hole.
However, the temperature range over which this development
can take place is greater in the former locality, possibly
due to the previous thermal history of the eggs. Worley's
(1933) results, which cover more experiments than the pre-
sent study, can therefore be used with greater confidence in
studies on the population dynamics of the mackerel from
St.George's Bay, when the values of incubation times are
used to estimate the total number of eggs spawned. The
importance of the thermal history of the adult fish prior
to spawning in studies on egg development should be recog-
nized in order to make comparisons possible.

Growth

The influence of temperature on growth was investi-
gated through the use of the Brody-Bertalanffy equation.
This equation yields a growth coefficient which describes
the relative decline in growth rate with time. Hubbs (1926),

in an early account of such phenomenon, concluded that in accelerating conditions, such as high temperature, growth proceeds rapidly until the inhibitory processes are also hastened. This leads to a more abrupt decline in growth rate with age than found in retarding conditions where the inhibitory mechanisms are slowed down. In the context of larval development, this implies that larvae should reach their asymptotic size (asymptotic if no food is offered) more rapidly at high temperatures. The present study corroborates these ideas, since the growth coefficient increased from 0.00816 to 0.03516 between 13 and 23°C.

The size of newly hatched larvae has also been shown by others to be influenced by temperature, either negatively (Colby and Brooke, 1970; Tay and Garside, 1975; Brewer, 1976; Peterson *et al.*, 1977; Gunnes, 1979) or, alternatively, the lowest size values are found at extreme temperatures (Hokanson and Kleiner, 1974; Smith and Koenst, 1975; Koenst and Smith, 1976; Santerre and May, 1977). These two alternatives could represent the same phenomenon, if cold temperatures used by some experimenters were within the natural range of the fish. Exceptions to the occurrence of maximal sizes at low (or intermediate) temperature were found by Alderdice and Forrester (1971) who mentioned that the largest petrale sole larvae occur at high temperature and by Houde (1974) who reported the same conclusion for bay anchovy larvae.

The above observations are paralleled by studies showing that the rate and efficiency of yolk utilization are also affected by temperature. The rate increases with temperature but the efficiency (ratio of the final energy value of larval tissue to the initial value of yolk, or of the rate of larval growth to the rate of yolk utilization) is usually higher at low (Laurence, 1973) or intermediate temperatures (Marr, 1966; Ryland and Nichols, 1967). The salmonid embryo appears to differ in this respect as it exhibits an increase in efficiency with temperature (Hayes and Pelluet, 1945). In general, however, the observations on yolk imply that larvae should be able to reach a greater size at colder temperatures because more energy is directed into growth than into maintenance activity. At very low temperatures, however, the yolk utilization rate may be so low that, even though the maintenance requirements are small, there is not much energy available for growth. The size of the newly hatched larva will therefore be lower than that from specimens reared at intermediate temperatures.

Laurence (1973) reported that the size of the tautog larva at complete yolk absorption is also inversely related to temperature. This result is consistent with the above discussion of size at hatching, since the newly hatched larva is dependent on the same energy resources as the embryo and its development should be affected in a similar way. The asymptotic sizes of mackerel larvae, as determined

in this study also suggest an inverse relationship with temperature, since they were largest at 13°C. Since no asymptotic size could be estimated for 8°C, it is not possible to say whether the inverse relationship is maintained at colder temperatures. It is interesting to note that at 8°C, the embryos increased in size during the first 100 hours and then showed no pronounced increase. This suggests that for embryos near hatching, 8°C becomes suboptimal and it corresponds to the observation noted earlier on the difference between the lower thermal limits for development and for growth. This would agree with the conclusions of several workers, that the optimal temperature increases successively for fertilization, embryonic development and larval growth (Smith and Koenst, 1975; Sylvester and Nash, 1975; Koenst and Smith, 1976).

The mackerel egg in its environment

Temperature has been shown to influence the development of mackerel eggs in many ways: inhibiting development when extreme, and affecting the rate of development, hatching success and size of the resulting larvae. The success of a mackerel population could therefore be strongly affected by this environmental factor. However, when the results of the present study are compared with the situation in nature, it appears that mackerel eggs are well adapted to their typical thermal environment. The spawning

season for mackerel in the southern Gulf of St.Lawrence oc-
curs from mid-June to mid-August, during which period the
mean surface temperature increases from 10 to 21°C (Ware,
1977). This temperature range corresponds closely with that
shown for successful development of mackerel eggs. However,
the gradual seasonal increase in temperature merits further
discussion.

At the beginning of the spawning season, the low tem-
peratures lead to a slow growth and little energy goes into
maintenance. In this way, larvae are able to subsist on
their reserves for a longer time and reach a greater size.
They can then take advantage of food organisms from a wider
size range, perhaps compensating for the low level of food
supply early in the season (Ware, 1977). As temperature in-
creases, development and growth accelerate and larvae hatch
faster, but at a smaller size since more energy is used for
maintenance. However, as the growing season progresses, the
mean size of the zooplankton decreases while the abundance
shows the opposite trend (Ware, 1977). Therefore, even though
the larvae cannot exist on their reserves for a long period,
and may be more restricted in the size of their prey due to
their smaller size, the abundance of suitable food organisms
ensures that first feeding is not delayed too long under av-
erage conditions. Rising temperature regimes were shown by
Hokanson and Kleiner (1974) to favor shorter hatching period
and lower proportion of abnormalities in the eggs of the yel-
low perch. This corroborates the findings discussed earlier,

that the optimal temperature for successive developmental periods increases as development goes on. Rising temperature regimes were not investigated in the present study, but the results obtained suggest that mackerel eggs are also adapted to this situation, which is encountered in their environment.

Ware (1977) showed that the egg size of the Atlantic mackerel in St.George's Bay varied over the spawning season in ways that could be adapted to the changes in mean size and abundance of the plankton community. The gradual transition from large to small eggs is reported to lead to a corresponding change in the size of the larvae. However, for St.George's Bay mackerel, the decrease in egg size occurs simultaneously with the increase in temperature and these two factors then become hard to separate. Are the smaller larvae produced by smaller eggs or by higher temperatures, or by both? Blaxter and Hempel (1963) reported that longer herring larvae were produced by larger eggs and that they could survive starvation longer than smaller larvae. It appears reasonable to assume that mackerel larvae would be affected in a similar way. Experiments differentiating between the influence of egg size and temperature could be done by rearing at the same temperature eggs of different sizes, obtained at the same time, or by comparing the development and growth of eggs of similar sizes at different temperatures. However, if mackerel eggs do not show a wide range of sizes at any given time, it might be difficult to obtain

small eggs at the beginning of the spawning season, and vice versa. It would then be necessary to rely on a laboratory-reared brood stock. Although evidence points out that the variation in egg size is probably of parental as opposed to environmental origin (Ware, 1977), temperature may also influence the size of the spawned eggs by affecting the physiology of the maturing fish.

Sette's (1943) survival curve for mackerel eggs and larvae showed no increase in mortality after yolk-sac absorption. The adaptation exhibited by the mackerel larvae in their size at exhaustion of yolk supply in relation to the available food could explain the absence of a decrease in larval survival at this stage. A critical period, in Hjort's (1914) sense, then is not likely to be present and mortality is probably just as strong in the early, sensitive stages before blastopore closure. The mackerel population therefore appears to have adapted to its environment by regulating its spawning time, rates of development and early growth to the production cycle of the plankton community, thereby reducing the likelihood of mass mortality due to a poorly adapted stage of development.

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