Laboratory Observations on the Influence of Temperature and Salinity on Development of the Eggs and Growth of the Larvae of *Solea solea* (Pisces)

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ABSTRACT: Eggs of the sole *Solea solea* (L.) were incubated at different constant temperatures (10 °, 13 °, 16 °, 19 °, 22 °C) and salinities (10, 20, 30, 40, 50 °/oo); the larvae were reared at the same temperatures but at one salinity (30 °/oo S). High survival and normal development to hatching were observed at temperatures from 10 ° to 16 °C and salinities from 20 °/oo to 40 °/oo S. The growth rate increased with increasing size of the larvae and also increased with the rearing temperature to a maximum at 22 °C. Some environmental factors which may influence the survival of sole eggs and larvae in the sea are discussed.

INTRODUCTION

In the eastern Atlantic Ocean the common sole *Solea solea* reaches its northern limit in the North Sea, where the adults occur at depths of about 10 to 60 m (Bückmann, 1934). North Sea soles migrate in winter offshore to greater depth thus avoiding low water temperatures (Woodhead, 1964a, b); they return in spring to the coastal areas for spawning (Christensen, 1960, Anonymous, 1965; De Veen, 1967, 1970). The pelagic eggs and larvae are transported by the residual currents along the coast (Flüchter, 1970; Riley, 1974), where the young soles start demersal life in shallow areas and in tidal estuaries. The Wadden Sea seems to act as an important nursery for North Sea sole (Zijlstra, 1972). Eggs and pelagic larvae are often found close to the shore but it is still unknown whether the soles actually spawn in the estuaries. It is therefore of interest to know whether estuarine conditions are favourable for the development and survival of eggs and larvae.

In 1976 some soles spawned in a tank in the seawater aquarium of our Institute and produced fertilized eggs. Experiments were carried out to estimate the influence of temperature and salinity on survival and development of the eggs. After hatching, the growth rate of the larvae was determined under various conditions. For a review on cultivation of marine fishes consult 'Marine Ecology' Volume III (Kinne, 1977, p. 968). Temperature and salinity effects on fishes have been reviewed in 'Marine Ecology' Volume I by Brett (1970), Garside (1970), and Holliday (1971).

MATERIAL AND METHODS

Spawning Stock

Adult soles *Solea solea* (L.) (7 males and 7 females) are kept in the laboratory in cylindrical tanks with a diameter of 160 cm and a depth of 70 cm, containing some 1400 l of seawater. The seawater supply is approximately 120 l h^{-1} (32 °/oo S); water temperatures are kept between 15 ° and 20 °C in summer and between 6 ° and 12 °C in winter. The fish are fed with fresh mussel meat *(Mytilus)* and lugworms *(Arenicola)*. The laboratory has a glass roof to ensure a normal day-night cycle.

From December to February each year females show a rapid development of the ovaries and spawning usually starts in April. After each spawning thousands of eggs, with a diameter of 1.2 mm, float at the surface where they are collected with fine mesh hand nets.

In 1976 spawning started on 2 April at 12 °C; the last spawning was recorded on 3 July. In 1977 spawning began on 1 April at 10 °C, in 1978 on 3 March at 11 °C; in both years spawning stopped by the end of June. In 1976 some 24 spawnings were recorded, but only in 9

cases did fertilization rate appear to reach 30 to 90 %.
In 1977 and 1978 all eggs remained unfertilized al-
though mature males were present in the tanks. Artifi-
cial fertilization of eggs stripped from ripe females,
employing chopped testes from freshly caught ripe
males from the fishmarket, were unsuccessful (see also
Cunningham, 1890). When stripped, a ripe female usu-
ally produces about 20 000 to 30 000 ripe eggs. How-
ever, the ovaries contain about ten times as many eggs,
which is sufficient for several spawnings with intervals
of about 3 to 10 days. The testes of the males are very
small (2–3 cm); this suggests a complicated spawning
behaviour and a close sychronization in the pairs to
ensure fertilization. Flüchter (1970) observed spawn-
ing in the laboratory and describes how male and
female swim together at the surface. Such behaviour is
frequently observed at night in the North Sea during
the spawning migration of soles in spring (De Veen,
1967.)

Incubation of Eggs

Fertilized eggs from natural spawnings were only
obtained in 1976. They were incubated in 14 light-
green coloured glassfibre-plastic incubation tanks
with a size of 60 × 40 × 50 cm depth, which contained
seawater with the following temperature-salinity com-
binations: 10 °C (20, 30 ‰ S), 13 °C (20, 30, 40 ‰ S),
16 °C (10, 20, 30, 40, 50 ‰ S), 19 °C (20, 30, 40 ‰ S)
and 22 °C (30 ‰ S). The constant temperatures varied
0.2 °C while salinities were kept constant within
2 S ‰. Subsamples of 200 eggs from the different
spawnings were incubated separately in small black
vulcathene cylinders (8 cm diameter × 10 cm height)
with a plankton gauze bottom (1 mm mesh size), floa-
ting by means of polystyrene-foam rings in the incuba-
ting tanks. The same incubators have been used suc-
cessfully in a similar set up for garfish eggs (Fonds et
al., 1974). The seawater in the incubation tanks was
only aerated, not changed or filtered, and antibiotics
were added once a month in concentrations of 25 000
I. U. Penicillin + 25 mg Streptomycine per litre.
Development of the eggs was recorded daily while
dead eggs were removed from the egg holders and
survival was roughly estimated.

Rearing of Larvae

After hatching, some batches of larvae were released
from the eggholders into the green incubation tanks at
30 ‰ S and reared at constant temperatures of 10 °,
13 °, 16 °, 19 °, and 22 °C. They were fed regularly with
sieved natural zooplankton, collected in large outdoor
seawater ponds. Samples of larvae were taken from
each tank at weekly intervals to estimate the growth
rate and to investigate their stomach contents.

Diseases and Parasites

Since the rearing tanks were not changed or filtered,
they became more or less polluted by the end of the
rearing experiments and many larvae died. Dying lar-
vae usually floated at the surface, showing a conspi-
cuously pale colour. They often had numerous blad-
ders on the body suggesting infection with fish tuber-
culosis. On one occasion, in the 13 °C tank, a larva of
5.6 mm length was attacked and lethally injured by a
very fast swimming pear-shaped ciliate (0.16 × 0.05
mm), probably introduced with the plankton.

Growth of Demersal Stages

At the end of the experiments all young soles were
collected in two asbestos concrete tanks (120 × 60 ×
30 cm high) and reared further for several months at
ambient seawater temperatures (19 °–22 °C) with
chopped mussel meat as the only food. In the 19 °C
rearing tank two albinos were found.

RESULTS

Egg Development and Survival

The embryonic and larval development of *Solea
solea* (L.) has been described by Fabre-Domergue and
Biétrix (1905), Rosenthal (1966), Flüchter and Pandian
(1968), Flüchter (1970), and Riley (1974). The embryos
hatch at an early stage of development when the eggs
are still transparent, the mouth and pectoral fins unde-
veloped. They float upside down at the surface; their
size is approximately 3–3.5 mm total length by
1–1.2 mm height including the larval fin. The passive
yolk-sac larvae develop in a few days into actively
swimming larvae of 4–4.5 mm total length with black
pigmented eyes, a well-developed mouth and pectoral
fins.

In Table 1 the estimated incubation times to different
stages of embryonic development are shown in rela-
tion to incubation temperatures. The effect of tempera-
ture (T, °C) on incubation time (D, 24 h) can be descri-
bed by an exponential relation $D = A.T^B$, where A
refers to the different development stages, while the
exponent B is a constant ($B = 1.334$, Table 1) descri-
bing the temperature effect.

At 22 °C no viable larvae hatched; at 19 ° at least

Table 1. *Solea solea* eggs. Estimates of incubation time in days (D, 24 h) from fertilization to various developmental stages. Eggs were incubated at the different constant temperatures listed

Stage	Incubation temperature T				Expon. corr. D with T	Corr. coeff. r (n = 4)	Calculated D	
	10 °C	13 °C	16 °C	19 °C			10 °	16 °
1	1.75	1.25	1.0	0.75	$D = 34.4\ T^{-1.290}$	0.997	1.76	0.96
2	3.0	2.25	1.75	1.25	$D = 66.6\ T^{-1.332}$	0.991	3.10	1.66
3	5.25	3.75	2.75	2.25	$D = 114.6\ T^{-1.338}$	0.999	5.26	2.80
4	6.50	4.50	3.50	2.75	$D = 137.8\ T^{-1.329}$	0.999	6.46	3.46
5	11.0	8.0	6.0	4.5	$D = 270.9\ T^{-1.383}$	0.997	11.22	5.85

Developmental stages: 1 = End of gastrular overgrowth (epibolie), blastopore closed; 2 = Development of tailbud, blood circulation (heart beats); 3 = Complete embryo bent in U-shape, prior to hatching; 4 = Hatched, transparent embryos floating upside down; 5 = Black-eyed swimming larvae, start of feeding.

10 ‰ of the embryos hatched but many were abnormal. At 13 ° and 16 °C survival to hatch was high, at 10 °C near 100 ‰.

The effect of salinity on egg development is less obvious than of temperature. The eggs and larvae floated in salinities higher than 30 ‰ S, at salinities below 30 ‰ S they sank to the bottom of the incubators and often showed mortality due to crowding and probably respiratory stress. Apart from this mortality, survival at 20, 30 and 40 ‰ S was approximately the same;

at 10 ‰ and 50 ‰ S survival was clearly reduced and the majority of the larvae produced were abnormal. At 10 ‰ S the hatched larvae failed to swim up to the surface to fill their swimbladders and finally died on the bottom of the incubators.

The rate of development was clearly lower at the lower salinities (10 ‰ and 20 ‰ S); at the highest salinity (50 ‰ S) many larvae failed to hatch (approx. 30 ‰). These larvae continued development inside the egg until they suffocated.

Table 2. *Solea solea* larvae. Length distribution at the end of growth experiments. Dotted lines: beginning of metamorphosis; solid lines: end of metamorphosis

Total length (mm)	End date: / Temp. (°C):	Started 31 May					Started 18 June			
		8/VII 13	5/VII 16	29/VI 19	29/VI 22	9/VII 10	9/VII 13	9/VII 16	8/VII 19	8/VII 22
4–5						5			2	
5–6						7	8	3	9	
6–7						2	11	2	6	
7–8			4				8	9	9	1
8–9		1	2	1			6	5	7	3
−10		5	4	4			1		11	1
−11		8	7	8	3		1	1	18	3
−12		2	9	9	6			1	5	3
−13		13	14	6	5			3	6	4
−14		13	13	7	7			1	9	6
−15		12	8	8	8			1	5	1
−16		9	6	11	5			1	3	2
−17		10	7		8				4	3
−18		6	5		5				1	2
−19		5	2	3	3				1	2
−20		3	2	4	3					2
−21			4		3					1
−22		3	1		2					1
−23			1							
−24			1							
−25			3	1	1					
−26			1	1						
Mean length (mm):		14.9	14.9	14.1	16.0	5.6	7.2	9.1	10.8	14.5
Standard deviation:		2.9	4.1	3.4	3.2	0.6	1.3	1.2	3.3	3.9
Total numbers reared:		195	230	184	82	14	35	28	152	35
Variance (% of mean):		56	113	82	64	6	23	16	101	105

Development of Larvae

Two groups of larvae were reared in the green incubating tanks, a first series from 31 May to 5 July, a second series from 18 June to 9 July (Table 2).

After yolk-sac absorption, the active swimming first-feeding larvae were 4–4.5 mm long and 1.5 mm high including the larval fin. Between 6 to 7 mm length the development of the finrays started, particularly at the tail, while small orange spots appeared on the body. At 7 mm length the larvae showed a conspicuously brown colour and were still symmetric; metamorphosis started at 8 to 9 mm length. At high temperatures (19 °C), metamorphosis started earlier and the larvae were already fully metamorphosed at 9 mm length, as compared to 10 mm for complete metamorphosis at lower temperatures (Table 2). During metamorphosis the 9-mm larvae already spent long periods on the bottom of the tanks, the full change-over from pelagic to demersal life occurred gradually at a size of 9 to 10 mm. After metamorphosis the young soles changed gradually in colour from dark brown to yellowish grey at a size of 11–12 mm.

Food

Zooplankton was fished with a 200-μm meshsize net and sieved over 500 μm or 1000 μm meshsize to remove unwanted plankters like crab zoeas and jellyfish. Balanoid nauplii were always predominant, followed by copepods, cladocerans (*Podon*, in spring) and polychaete larvae.

The stomach contents of the sole larvae examined during the rearing experiments are summarized in Table 3. It appears that the larvae preferred polychaete larvae, copepods and cladocerans. Balanoid nauplii were underrepresented in the stomachs considering

Table 3. *Solea solea* larvae. Stomach contents of individuals reared in the laboratory on natural zooplankton. Balanoid nauplii and copepods dominated in the plankton

Contents	Numbers of stomachs examined
Worm larvae (polychaetes)	37
Copepods	24
Cladocerans (*Podon*)	19
Balanoid nauplii	15
Balanoid cyprids	8
Mollusc veligers	7
Sand grains	6
No contents (empty stomachs)	6
Total number of stomachs examined:	85

their abundance in the plankton. According to Last (1978) sole larvae in the sea eat predominantly lamellibranch larvae and dinoflagellates; only larger larvae feed mainly on polychaete larvae.

The dimensions of the open mouth of small (4–5 mm) sole larvae was approximately 0.20–0.35 mm, the size of the prey in their stomachs measured 0.15–0.25 mm width by 0.40–0.70 mm length. Larger larvae (5–7 mm) had a mouth opening of approximately 0.35–0.70 mm; the prey dimensions were 0.15–0.50 mm by 0.50–0.70 mm. These dimensions are difficult to compare with the measurements reported by Last (1978), who estimated mouth openings and stomach contents of *Solea solea* larvae of 1.5–3 mm length, well below the length at hatching (3.5 mm). Although shrinkage of the larvae examined by Last, due to formalin fixation, may have been considerable, the question arises whether Last's material might have contained the smaller larvae of a related sole species, for example of the solenette *Buglossidium luteum*, a smaller-sized species with very similar larvae and high abundance in the southern North Sea. If from Last's Table 4 only larvae larger than 4 mm are considered, we may conclude that *Solea solea* larvae eat mainly dinoflagellates, polychaete larvae, copepods and lamellibranch larvae. This is confirmed by our observations on larvae reared in the laboratory.

Feeding Behaviour

The feeding behaviour of sole larvae was often closely observed. They usually swam actively about and examined every little particle encountered. When confronted with a potential prey they stopped swimming and floated with the particle – their body bent in an S-shape and ready for attack. The 'picking-on-the-bottom' behaviour described by Rosenthal (1966) was not observed in the green rearing tanks, although the larvae tended to stay close to the green walls. Only in a small perspex tank with a sand bottom were some larvae seen picking on the bottom. However, in spite of the zooplankton available their stomachs contained only sandgrains (see Table 3).

Growth Rate

The mean total length of the larvae, from measurements of subsamples taken from the rearing tanks at regular intervals, are plotted against time in Figure 1. Growth rate increased with increasing size of the larvae; a linear fit was obtained when the logarithm of the length (log L, mm) was plotted against the larval age in days (t, 24 h). Hence the length of the larvae can be
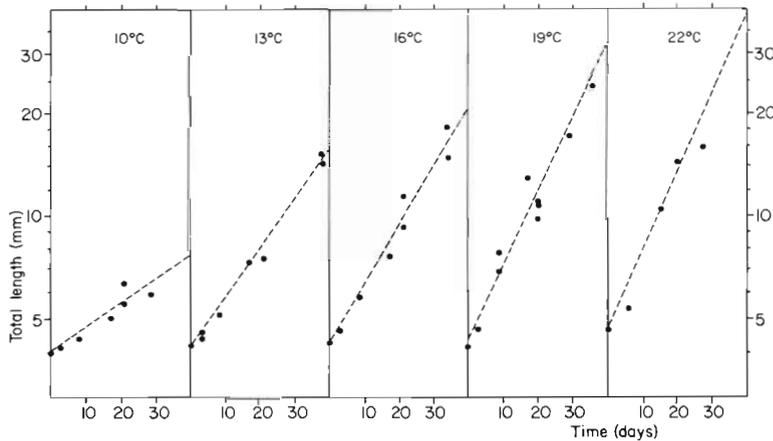
Fig. 1. *Solea solea* larvae. Growth in length at different temperatures; measurements of subsamples taken at regular intervals. Total length plotted on a log scale against age in days. Dots: mean length

described as a function of time as $L = A. e.^{Bt}$, where A is the length of the larvae at the start (L_o at $t = o$ was usually about 4–4.5 mm in the experiments) and B is a growth-rate coefficient measuring time t in days. How-
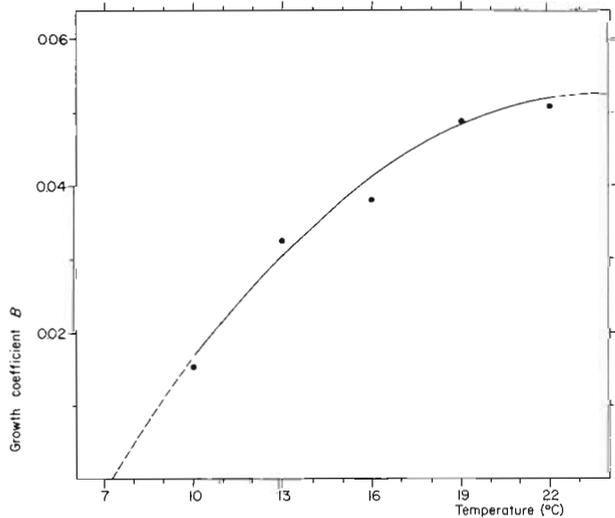

Fig. 2. *Solea solea* larvae. Relation between rearing temperature and growth coefficient B for growth in length (L) according to $L = A.e^B$

ever, B increases non-linearly with the rearing temperature (Fig. 2), reaching a maximum value of 0.052 at 22 °C. The relation of B with T (°C) can be fitted to a second degree polynomial as follows: $B = 0.0092T - 0.00019T^2 - 0.056$. Extrapolation predicts a maximum growth rate at about 23 °–24 °C while B, and hence growth, is zero at 7 °C. Actually, growth of the larvae at 10 °C was already very poor and none of these larvae reached metamorphosis which would have taken two months according to our equation.

The increase in growth rate at rearing temperatures from 10 ° to 19 °C is considerable. In Table 4 the mean length for a given age is calculated and Figure 3 illustrates the effect of temperature on the average growth rate and time to metamorphosis. At 22 °C metamorphosis was completed on average two weeks after the first feeding at a size of 9 mm; at 13 °C the larvae metamorphosed on average at 10 mm length after four weeks. The length distribution of the larvae in the tanks at the end of the growth measurements is shown in Table 2. Growth of young soles after metamorphosis (19 °–22 °C, chopped mussel) is summarized in Table 5. The mortality rate of these fish was about 14% per month, mainly due to bacterial diseases. Such a mortality probably occurs only during the

Table 4. *Solea solea* larvae. Linear correlation between mean log length (L, mm) and age (t, days, 24 h) of subsamples reared at different constant temperatures. Parameters are given of the semi-exponential relation $L = A.e.^{Bt}$, where A is body length at start ($t = o$), e the base of the natural logarithm, and B a temperature-dependent growth coefficient

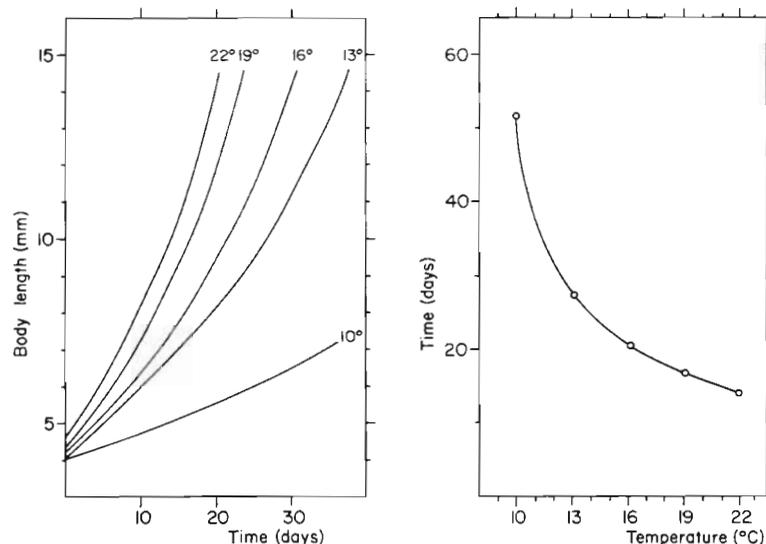| Rearing temperature (°C)	Correlation coefficient (r)	Number of subsamples (n)	Length at start (L_o) (A, mm)	Growth coefficient B	Calculated length (mm) at the age of		
					10	20	30 days
10	0.96	7	4.00	0.0152	4.6	5.4	6.3
13	0.99	10	4.10	0.0325	5.7	7.9	10.9
16	0.99	8	4.15	0.0382	6.1	8.9	13.1
19	0.98	9	4.40	0.0493	7.2	11.8	19.3
22	0.98	6	4.51	0.0510	7.5	12.6	21.1

Fig. 3. *Solea solea* larvae. Calculated growth rate in relation to rearing temperature. Left: Estimated increase in total length. Right: Estimated time from start measurements (feeding larvae) to metamorphosis

juvenile stage, larger soles usually show little mortality in the laboratory.

DISCUSSION

Spawning

In the North Sea soles usually start reproduction at water temperatures of 7 °–8 °C. They may start in March along the Belgian coast (Van de Velde, 1975) and late April along the Dutch coast; where spawning continues through May and Junge (Anonymous, 1965; De Veen, 1970). In the laboratory the soles spawned early (1–2 April 1976, 1977, 1 March 1978). This indicates that in the North Sea low water temperatures (below 7 °C) may delay spawning.

Egg Development

The rate of egg development is strongly dependent on water temperature, particularly between 10 ° and 16 °C, the actual temperature range in the North Sea in late spring. The temperature limits for development of sole eggs have been estimated by Flüchter (1970): 7 °–19 °C, Riley (1974): 7 °–15 °C (after gastrulation 6 °–20 °C), and Irvin (1974): 7 °–17 °C. All authors agree on a lower limit at 7 °C. Survival of the eggs at the higher temperature limit probably depends also on other factors like the thermal history of the parent fish, the developmental stage of the eggs, the oxygen supply etc., which may explain the different values obtained.

Riley (1974) calculated the exponential relation between incubation temperature (T, °C) and the incubation time in days (D) for the development of sole eggs to various stages. In the relation $D = AT^B$ the exponent B varied between −1.2852 and −1.588 for the different stages, with a mean value of −1.3965 (S. E. = 0.1046). Our estimates of B, shown in Table 1 (on average 1.334) agree reasonably well with those of Riley.

The eggs of *Solea solea* can develop successfully to feeding larvae at salinities between 20 and 40 ‰ S.

Table 5. *Solea solea*. Growth after metamorphosis; 19 °–22 °C, mussel meat as food

Date		Number of fish	Length range (cm)	Mean length (cm ± S. D.)	Relation of length (L) to height (H) or to weight (W)
1976	9/VII	513	0.5–2.5	1.3 ± 0.4	
	21/IX	444	2–10	5.3 ± 1.5	$L/H = 2.347 ± 0.026$
			Larger fish selected, smaller fish discarded		
	21/IX	63	7–10	7.9 ± 0.8	selected fast growers
	14/XII	44	8–12	10.6 ± 1.1	$W = 0.0033\ L^{3.457}$ ($r = 0.98$)
1977	2/III	37	12–18	15.0 ± 1.4	
	17/IV	29	15–21	17.2 ± 1.7	$W = 0.0027\ L^{3\ 492}$ ($r = 0.98$)

Higher salinities interfere with the hatching process and lower salinities slow down the rate of development. Although the eggs still develop to hatching at 10 ‰ S, the larvae cannot survive at this salinity. This may explain why soles reach a limit in their eastward distribution in the Belt area (Johansen, 1916; Lindquist, 1970). Moreover, the eggs tend to sink at salinities below 30 ‰ S, which does not appear to be particularly favourable for survival.

Growth of Larvae

The growth rate of the pelagic larvae shows a strong positive correlation with water temperatures from 10 ° to 16 °C, the normal temperature range in North Sea coastal areas in late spring. The temperature range for successful development of the eggs (7 ° to 19 °C) is lower than that for growth of the larvae (10 ° to 23 °C). Hence, during development the operational temperature range seems to shift to higher values, in agreement with conditions in nature for a spring spawner (cf. Irvin, 1974).

Environmental Factors

The main factors which may influence the survival of sole larvae in the sea are probably temperature, food, predation, and transport to the nurseries.

T e m p e r a t u r e influences the beginning of the spawning season and therefore also the growth season for the juveniles. Besides, the rate of development of the eggs and the growth rate of the larvae increase with the temperature. Hence, high- or rapidly increasing temperatures in spring shorten the duration of the pelagic stage. This is probably favourable considering the high mortality rate at that stage (Riley, 1974).

F o o d . The spring phytoplankton bloom in the southern North Sea usually starts in March and continues until the end of May (Gieskes and Kraay, 1975, 1977), while zooplankton is most abundant in April to July (Fransz, personal communication). Pelagic sole larvae are usually found from April–May until June (Last, 1978) during a period of abundance of zooplankton, hence food shortage is unlikely. However, the availability of zooplankton for the larvae is probably strongly dependent on weather conditions, particularly wind and cloud cover. The behaviour of the sole larvae in rearing tanks indicate that they catch their prey by sight (Rosenthal, 1966). This confirms the observation by Last (1978) that sole larvae in the sea only feed during day time (see also Fuchs, 1978). It is evident that they need a minimum amount of light to find their food in a way similar to plaice larvae (Blaxter, 1969,

1972). Cloud cover diminishes underwater visibility in the sea, while strong winds bring silt and detritus in suspension in the coastal areas which reduces visibility even more. Under such conditions it will become difficult for the sole larvae to select their plankton prey from the thousands of silt particles.

P r e d a t i o n . The slow-swimming sole larvae are conspicuously brown-coloured and probably an easy prey for active predators. However, the most abundant pelagic predators are jellyfishes like species of *Phialidium, Pleurobrachia, Beroë, Aurelia* and *Cyanea* (Fransz et al., 1978), which are quite capable of catching fish larvae (Lebour, 1922, 1923). When underwater visibility is low and turbidity high, due to cloud cover and strong wind, the sole larvae will have less chance to avoid such passive predators.

T r a n s p o r t . The transport of the nearly metamorphosed larvae to the nurseries might be influenced by the wind direction affecting the currents in shallow coastal areas. However, according to Rauck (1974), the time of arrival and subsequent yearclass strength of 0-group plaice in spring in the German Wadden Sea is mainly correlated with the water temperature, not with the wind vector. The immigration and settling of sole larvae in the coastal nurseries probably takes place in the same way as has been described for plaice larvae by Creutzberg et al. (1978).

Table 6. *Solea solea*. Possible effects of abiotic environmental factors on growth and survival of larvae in sea

Climatic factors	Effects on environment	Effects on larvae
Air temperature →	Water temperature →	Growth rate
↗		↑
Cloud cover or sunshine →	Underwater visibility →	Availability of plankton
	↑ ↘	
Wind vector →	Turbulence and water currents →	Predation
	↘	
		Transport to nursery

Finally, some possible relations between climatic factors, biological factors, and survival of sole larvae are summarized in Table 6. This simplistic scheme suggests that warm sunny springs, such as those in 1975 and 1976, are more favourable for the survival of sole larvae than cold windy springs such as prevailed in 1977 and 1978. However, the success of a yearclass depends also, if not mainly, on the survival of demersal

young during their first year in the nursery (Bergman et al., 1976; Rauck and Zijlstra, 1978). A severe winter may wipe out a whole yearclass of 0-group soles.

Solea solea is a southern species which thrives best at temperatures between 16 ° and 22 °C (Fonds, 1975; Fonds and Saksena, 1977). Its reproduction in spring in coastal areas provides for optimum conditions for growth and survival of the juveniles: (1) higher and rapidly increasing temperatures in spring; (2) rich food supply for pelagic larvae (particularly polychaete larvae); (3) vicinity of nurseries with a rich food supply for demersal young.

For marine fish species which spawn in lagoons and estuaries, low salinities are, in general, not particularly favourable (Fonds et al.,1974; Fonds and van Buurt, 1974). Salinity probably acts mainly as limiting factor, particularly in the range of 5 to 10 $^o/_{oo}$ S.

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