

Recruitment variability in Norwegian spring-spawning herring (*Clupea harengus* L.): the effect of temperature in larval drift trajectories

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Abstract

During late winter, the Norwegian spring-spawning (NSS) herring migrate southward along the Norwegian coast to spawn in March-April. The larvae drift northwards in the Norwegian coastal current during their first months and eventually most of the larvae and juveniles end up in the Barents Sea. Here, we have compiled measurements of temperature along the coast back to 1936 and analyse these data for correlation with recruitment success (recruits/SSB) of the herring. We find that although the average temperature in the larval drift trajectory may vary with as much as 2°C between years, the effect on recruitment success is minor. A model using temperature-dependent growth and size-dependent mortality predicted a strong relationship between recruitment and the annual temperature variations, but no strong support of this was evident in the data. Nor did we find a relation between recruitment success and the condition of the spawning stock, while a strong stock-recruitment relationship and density-dependent recruitment prevails.

Introduction

Environmental factors affecting growth and survival of fish larvae are expected to affect the variability of recruitment success for a given Spawning Stock Biomass (SSB). Among the most important variables is temperature, which has a major influence on growth rate in most fish larvae, including Norwegian spring spawning (NSS) herring (Fiksen & Folkvord 1999). There are several studies relating averaged temperatures to recruitment (see e.g. Ottersen & Loeng 2000, Toresen & Østvedt in press). Naturally, it is difficult to find measures of temperature that overlaps the spatial distribution of the larvae over time, and consequently these relations are typically made by correlating large-scale average temperatures with recruitment. In the analysis presented here, we search for patterns of recruitment success in NSS herring originating from both the condition of the SSB, and the ambient temperature at the time and location where the larvae hatch and their subsequent drift trajectories. Toresen & Østvedt (in press) describe the stock structure of NSS herring back to 1907, and we applied these data for this study. Sea temperatures from surface to a few hundred meters have been measured at lighthouses along the Norwegian coast since 1936. Most of these observations have been compiled by Aure & Østensen (1993), and will be available from Institute of Marine Research (Bergen, Norway). NSS herring spawn along the Norwegian coast from Lista near the southern tip of Norway to Eggum in Lofoten (Fig. 1). After hatching, the larvae drift northwards in the Norwegian Coastal Current and eventually they end up in the Barents Sea where they stay until 2-3 years old when they join the adult population in the Norwegian Sea. The measurements from the lighthouses thus cover the relevant area for the larvae.

Data analysis and modelling

spatio-temporal interpolation of temperature data

The Norwegian Coastal Current transports the larvae northwards from their hatching site along the coast (Fig. 1). At Møre, some of the larvae may be mixed into the North-East Atlantic Current, and the most fortunate individuals will end up in Norwegian fjords or in the Barents Sea by the end of the year. Temperature measurements from the lighthouses are made at opportunity, therefore the intervals between each measure vary from several times each week to only a few per year. A few years there is no data available from some of the lighthouses. We have interpolated the data from Lista, Utsira (Western side), Sognesjøen, Bud, Eggum and Ingøy in time and space, such that each day there is a temperature accessible for each 25th kilometre along the coast from Lista to Ingøy (Fig. 1). We assume that the temperature at 10 m depth is the most relevant to herring larvae. The interpolation was linear between each measured point. In Fig. 2, the time-interpolated temperatures at each station are displayed for day 91-140 for all 65 years from 1936-2000.

Missing data were treated as follows. First, when the missing data were at **Lista** or **Ingøy** (at the bounds of the dataset), the data were extrapolated from the nearest station using the long-term monthly average between the two locations (**from Aure & Østensen 1993**). This was necessary for 1954-57 at **Lista**, 1936-41 at **Lista** and **Utsira**, and for 1945-68 and 1977-78 at **Ingøy**. Second, when data **from** the other stations were **missing**, data could be interpolated between stations to the north and south, balanced by the distance between them. **This** was done for Bud during 1936-46, 1955-71 and 1994-95, and for Eggum in 1972. Third, during some periods (not very many) the intervals between measures were so long that the linear **interpolation** would cause to high or low temperatures. This was remedied by inserting the long-term monthly average at these points.

A size- and temperature-dependent model of larval growth and survival

We make the assumption that the larvae grow at temperature-limited rates, i.e. they are not limited by food. As in an earlier application of this model (Slotte & Fiksen 2000), the temperature-dependent growth is based on recent rearing experiments conducted at 4, 6, 8, 10 and 12 °C (Folkvord & al. 2000). The growth rate $g(T)$ as a function of temperature T in mm day⁻¹ were:

$$g(T) = 0.419(1 + 20.6\exp(-0.57T))^{-1}$$

From hatching, the larvae spawned at any given spawning ground will drift along the coastline **with** a predetermined velocity of 12.5 km day and are exposed to the interpolated temperature field outlined above. The larvae are followed for 50 days after hatching with daily increments of length L (mm) and weight W (from a length-weight regression):

$$L(D, d, t+1) = L(D, d, t) + g(T_{d,t}) \tag{2}$$

where D is the original spawning or hatching site, d is the spatial location at time t , and t is the Julian day of the year starting from time of hatching (day 91). The temperature $T_{d,t}$ is the interpolated value at location d at day t . At the final day, the size $W(D, d, t=50)$ of the larvae originating from **all** hatching sites is assessed. The hatching day is assumed to be fixed and similar for all years and spawning locations. As in Slotte & Fiksen (2000), the mortality rate $\mu(W)$ is assumed to be dependent on size (ii g dry weight W). We applied the equations in McGurk (1986), where a number of estimated mortality rates from fish larvae of various sizes were compiled. Fish larvae generally experience higher mortality rates than other marine organisms:

$$\mu = 2.2 \times 10^{-4} W^{-0.85}, n = 74, r = 0.58, \text{ (McGurk 1986)} \tag{3}$$

while all other marine organisms seemed to obey the following size-dependence:

$$\mu = 5.26 \times 10^{-3} W^{-0.25}, \text{ (McGurk 1986).} \tag{4}$$

We used the largest μ from eqs. 4 and 5, i.e. we switched from equation 4 to 5 at the intercept of about 5.04×10^{-3} g dry weight (McGurk 1986). The accrued survival probability of the larvae after 50 days (from hatching at day 91) is

$$Ps(D) = \prod_{i=91,91+50} \exp(-\mu_i) \tag{5}$$

The population data

The population data are based on the WA used in stock assessment (**Toresen & Østvedt** in press). There seems to be a relatively strong S-R relationship in NSS herring (Fig. 3A), but as in all S-R plots the variance is considerable. The relationship may be impeded by the fact that the years with low SSB were concentrated in time and coincided with low a cold **climatic** period. This may cause some autocorrelation in the data. The positive S-R link persists even though there is a clear density-dependent effect on recruitment success (Fig. 3B). From the wintering areas in **Vestfjorden** (in earlier periods east of Iceland), NSS herring migrate to different spawning **locations** along the Norwegian coast. The **fraction** of total SSB at each spawning site varies between years, and we expect that this variation will influence on the growth and survival of the larvae (Slotte & Fiksen 2000). We have not yet included **the detailed** annual distribution of **spawning** biomass in the analysis. However, the major shift in spawning area that took place a about 1950 are accounted for by letting the **SSB** be normally

distributed around a mean site $S=12$ (Karmøy) before 1950 and $S=25$ (Møre) after 1950. The spatial coefficient of variance σ is assumed to be 10 in both cases. Then, the number of larvae $F(D)$ hatching at any spawning site D along the coast is

$$F(D) = SSB \times N(S, \sigma) \times \epsilon \quad 6$$

where SSB is the spawning stock biomass (in 1000 tonnes) of any particular year, N is the relative distribution of spawning biomass along the coast, and ϵ is the number of eggs laid per SSB (10^6). The distribution is restricted to occur between Lista and Ingøy, i. e. $S \in [1, 72]$. The SSB that falls to the south or north of these limits is placed in site 1 or 72, respectively.

An index of recruitment and calculation of the average temperature

Finally, an index of recruitment I_y was calculated for each year y to evaluate the effect on recruitment success from the SSB and the temperature experienced by the larvae during their early life history:

$$I_y = \sum_{D=1,72} F(D) \times P_s(D) \times W(D, d, 50) \quad 7$$

This index accounts for the accrued size-dependent survival probability of the larvae during its first seven weeks. In addition, by including the body mass of the larvae, an extra reward is given to the larger larvae at the end of the larval stage. This seems reasonable, as larger larvae are more likely to survive and recruit to the stock. To evaluate the effect of temperature on the survival and growth of larvae, we calculated the average temperature T^* to which the larval stock is exposed to during its drift in the coastal current. This index is calculated each year by assessing the temperature in the drift trajectory of larvae hatched at each of the 72 possible sites. The weight of each larval trajectory in the index is balanced to account for the number of eggs laid at each site (i. e. multiplied by $N(S, \sigma)$).

Results

1) The temperature in the larval drift route does not explain much of the variance in recruits R per spawning stock biomass SSB (Fig. 4A). The effect is considerably stronger when the recruitment is not corrected for SSB (Fig. 4B).

2) The model predicts a much stronger dependence on temperature than what is evident in the data. This is apparent when comparing Figs. 4a and 5. While the measured dependent variable $\log_{10}(R/SSB)$ increase by about one order of magnitude from cold to warm years, the index I_y increase by nearly five orders of magnitude over the same temperature range.

3) Holst (1996) developed an index of the condition of the spawning stock back to 1936. In Fig. 6. we plotted this index with recruitment per SSB in NSS herring, and it is clear that no correlation between the two variables is evident in the data.

Discussion

The temperature in the average larval drift route varies by as much as 2 °C (Fig. 4), a difference that will have major effects in terms of growth of herring larvae (Fiksen & Folkvord 1999). This is also reflected in the predictions from the model of larval growth and survival as a function of temperature (Fig. 5). The index I_y (Eq. 7) spans over several orders of magnitude more than what is evident in the data. This suggests that the model only including temperature during the larval stage is not sufficient to explain the recruitment process in NSS herring. However, other potentially important factors affecting recruitment success not treated here are prey (Fossum 1996) and predator abundance. Some deviation between the model and the index is expected since the index only evaluates the larval stage, and the mortality is likely to vary considerably between metamorphosis and the age of 1 year when recruitment is assessed. Still, we found a weak, but significant ($p = 0.035$) effect of temperature in the coastal water on the recruitment success of NSS herring (Fig. 4A). The correct measure of environmental influence on recruitment variability should be corrected for SSB as in Fig. 4A. However, since this is frequently not the case in studies like this, we have also presented the correlation between the number of recruits and temperature (Fig. 4B). Surprisingly, the environmental effect is much stronger ($p < 0.0001$) in this plot. This may relate to the fact that there is a strong decline in R/SSB as SSB increase (Fig. 3B); this may limit recruitment per biomass in warm years and change the picture in the SSB-corrected plot.

Contrary to our expectations, there was no effect **from** the condition of the spawning stock on the recruitment success (Fig. 6). In other stocks (Marshall & al. 2000), the condition of the maternal stock **has** improved the S-R relationship, but this does not seem to apply to herring.

The study by Fossum (1996) indicated that the match between first feeding of the larvae and the abundance of food (nauplii) were decisive for growth and survival of the early herring larvae. There is no strong reason to believe that there is a connection between temperature and the match between larvae and the peak abundance of nauplia, although warmer water may generally stimulate the zooplankton production. An important factor not included in the **model** is the timing and temporal spread of the spawning. The analysis will be extended to include this.

References

- Aure J, Østensen Ø 1993. Hydrographic normals and long-term variations in Norwegian coastal waters. *Fisken og Havet* 6, '75 pp.
- Fiksen Ø, Folkvord A 1999. **Modelling** growth and ingestion processes in herring *Clupea harengus* larvae. *Mar. Ecol. Prog. Ser.* 184: 273-289.
- Fossum P 1996. A study of first feeding herring (*Clupea harengus* L.) larvae during the period 1985-1993. *ICES J mar Sci* 53: 51-59.
- Holst JC 1996. Long term trends in the growth and recruitment pattern of the Norwegian spring-spawning herring (*Clupea harengus* Linnaeus 1758). Ph. D. Thesis, University of Bergen, Bergen, Norway.
- McGurk MD 1986. Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. *Mar Ecol Prog Ser* 34, 227-242.
- Ottersen G, Loeng H 2000. Covariability in early growth and year-class strength of Barents Sea cod, haddock, and herring: the environmental link. *ICES J mar Sci* 57:339-348.
- Slotte A, Fiksen Ø 2000. State-dependent spawning migration in Norwegian spring-spawning herring. *J Fish Biol* 56: 138-162.
- Toresen, R. & O. J. Østvedt 2000. Variation in abundance of Norwegian spring spawning herring throughout the 20th century and the influence of climatic fluctuations. Fish and Fisheries (in press).

Figures:

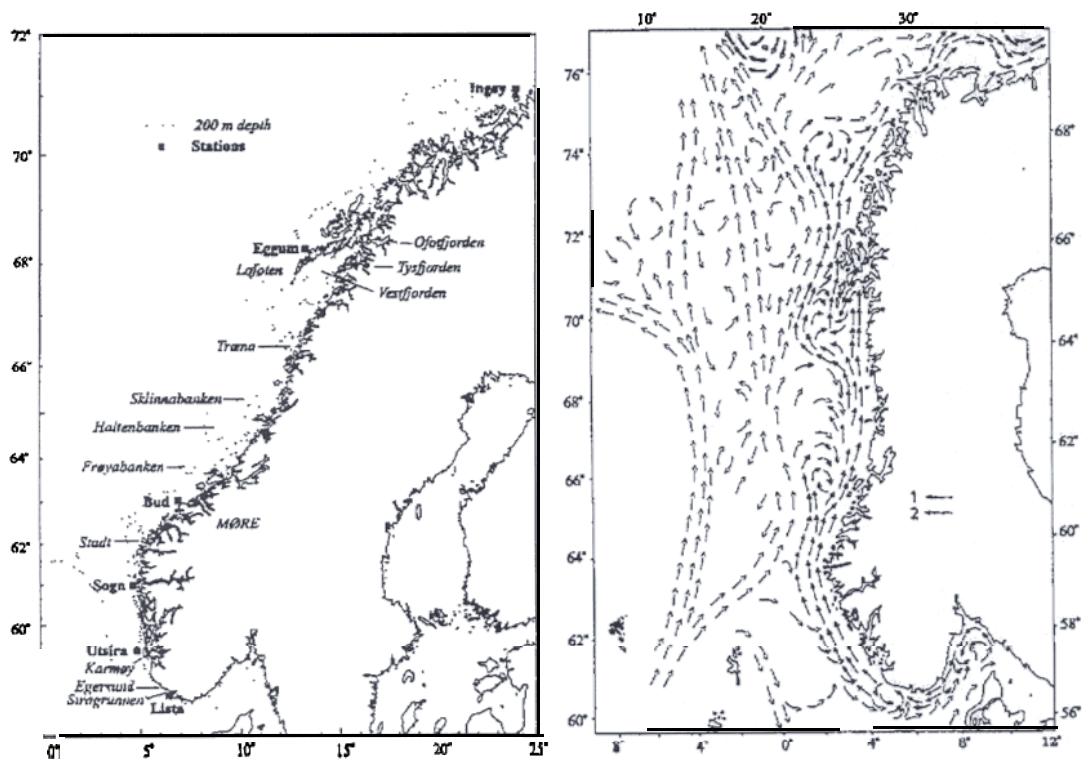


Fig. 1. Left panel: The coast of Norway with the spawning grounds of **herring** and the lighthouses supplying the temperature data. Right panel: The coastal current flows northwards along the coast.

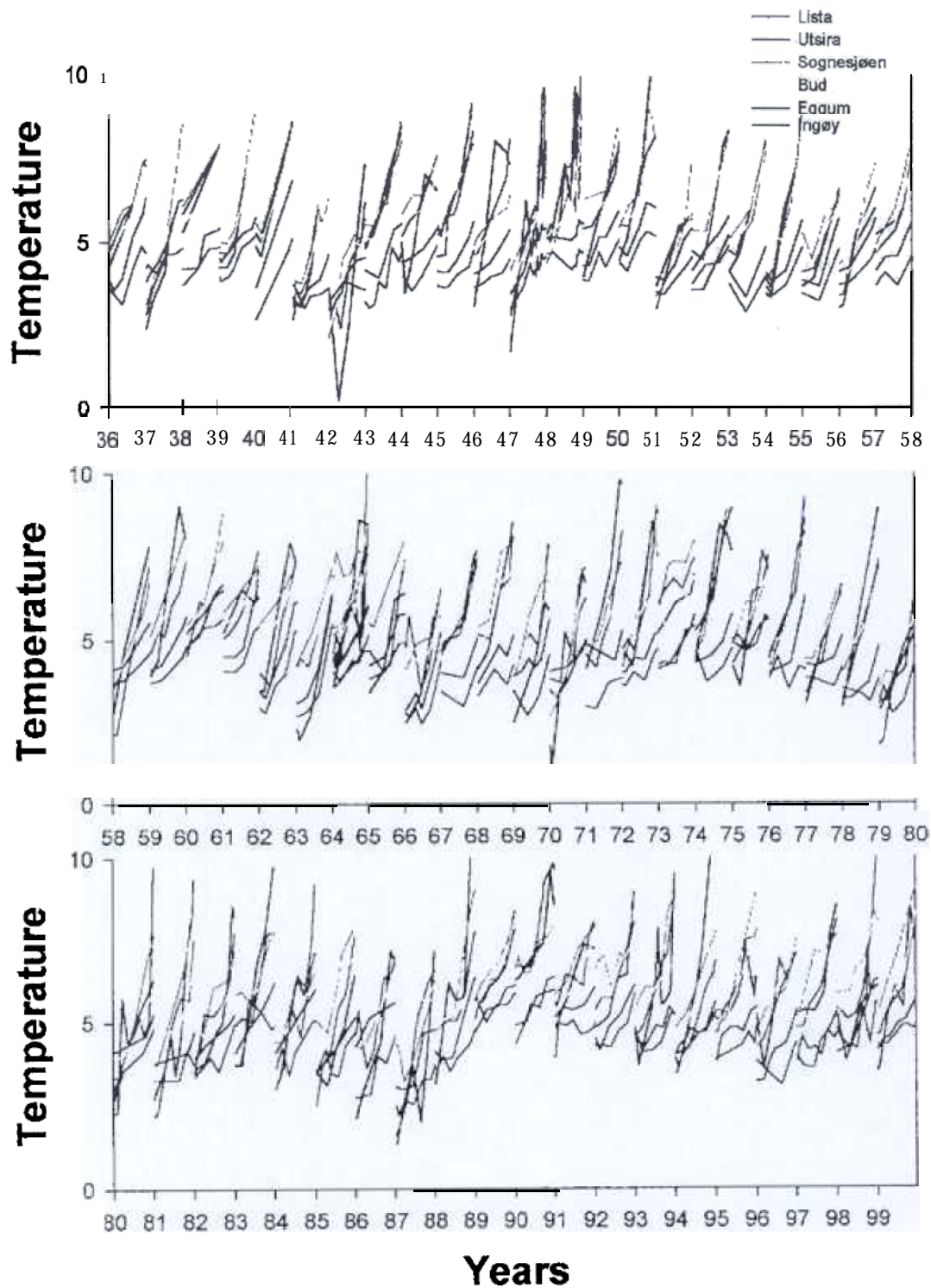


Fig. 2. The **time-interpolated** temperature **from** the 6 lighthouses during 1936-2000. Each year is here limited to seven weeks during April and May (**Julian day** $91 + 140$), which is the most **important** period for the larvae. **In** the model including **larval** growth and drift trajectory, the temperatures are interpolated in space as well.

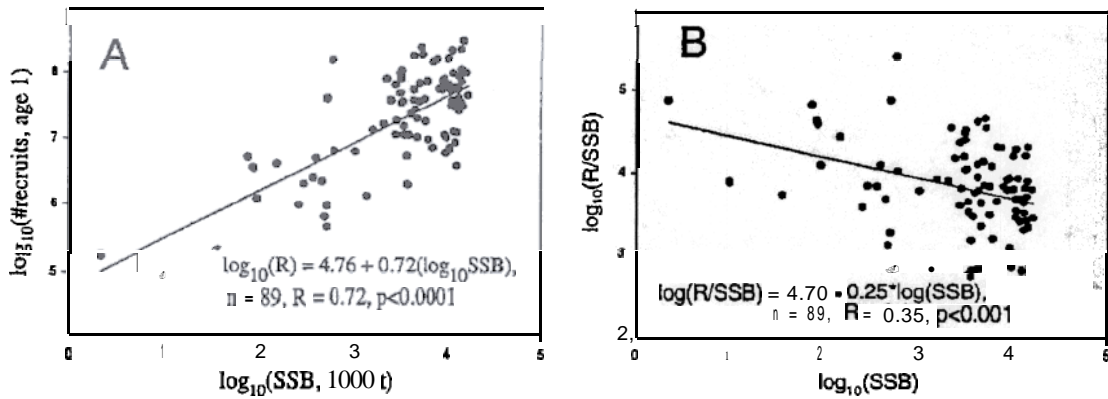


Fig. 3. A) The stock-recruitment relationship in NSS herring from VPA data 1907-1997 (Toreisen & Østvedt in press). B) There is some density-dependence in the recruitment success.

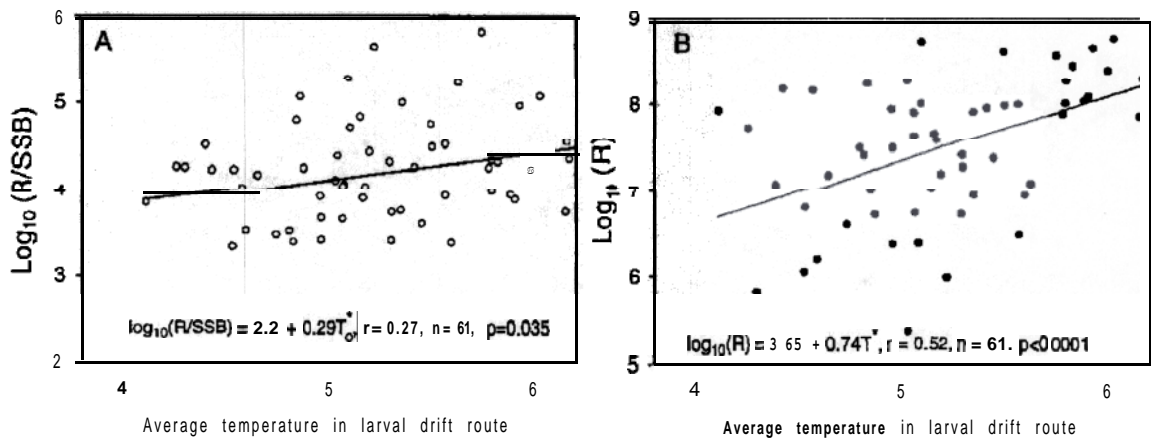


Fig. 4. This plot shows the average temperature in the drifting route of the larvae versus the recruitment (number of individuals 0 years old this year) for the period 1936-97. A: Recruits per spawner biomass. B: Total number of recruits.

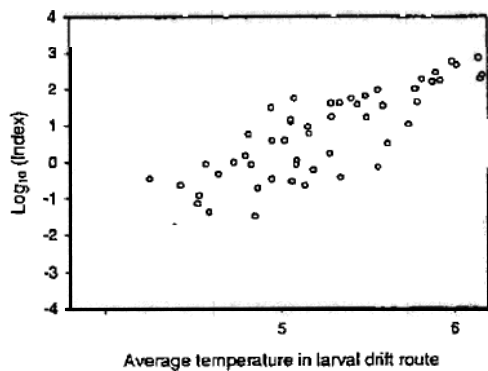


Fig. 5. The dependency of the predicted index I_p (eq. 7) on the average temperature in the larval path.

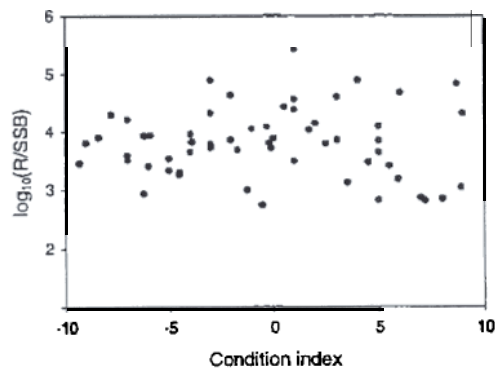


Fig. 6. The recruitment success ($R = \#$ individuals at age 0) per spawner biomass versus the condition index of the stock the previous year (Holst 1996) in the period 1934-1995. There is no correlation between the variables.