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REPRODUCTIVE SUCCESS OF SPRAT (*SPRATTUS SPRATTUS*) IN GERMAN BIGHT DURING 1987

by

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ABSTRACT

The SARP "within year" experiment was carried out on sprat by Alshuth (1988a) in the German Bight in 1987 when production of small larvae was determined over the entire spawning season from April to August and, subsequently, the birth-date distribution of the juveniles which were surviving until November was established.

These data were now analysed in relation to wind speed, stability of the water column and tidal impact. The ratios of the birth-date frequencies, found by counting daily otolith marks, to the within-season variations of larval production indicate only modest survival during late May and early June even though substantial larval production was indicated. However, a period of consistently low wind conditions occurred from June 9 to June 27. Correspondingly, the apparent survival rate during the final two weeks of June increased several fold over that of the preceeding four weeks. However, during the first half of July following a period of higher winds from 29 June to 4 July the apparent survival rate declined somewhat. In late July and early August the apparent survival rate again increased to the highest values found during the operation, even though some wind events of lesser intensity than the early July event occurred during the period.

INTRODUCTION

Methot (1983) introduced an elegant method when studying recruitment variability of the northern anchovy, ***Engraulis ringens***, in the California Current, a species with a protracted spawning season of about seven months. He recorded the production of young anchovy larvae over the entire spawning period from December to June of the following year. Subsequently, he collected the juveniles several months after spawning season and determined their birthdate distribution by counting daily rings on their otoliths. The birthdate distribution curve of the juveniles was then compared to the larval production curve to identify periods of heavy mortality or of exceptional survival of different cohorts of larvae. These "exceptional" periods can then be matched with environmental data sets to determine the causes of heavy mortality or good survival.

So, by analyzing larval production, birthdate distribution of juveniles and oceanographic, meteorological observations one can record intra-seasonal changes in larval survival, pinpoint critical periods of survival and identify the causal mechanisms.

This high temporal resolution experiment was refined by the Southwest Fisheries Center under the leadership of Reuben Lasker (Lasker 1985) and became known as the "within-year exercise" in SARP studies (Bakun et al. 1991). It has been identified as a uniquely promising process-oriented approach for analyzing the causal mechanisms and consequences of short-term larval survival (Anon. 1983, 1984, 1987). The particular advantage of this approach is that it addresses the problem on the population level, rather than addressing the fate of typical or "average" larvae which may be irrelevant to net reproductive success (Bakun et al. 1991).

As larval production can vary on small temporal scales, frequent surveys are required to establish a valid larval production curve. Because of the high demand of ship time and other operational resources required, no fully elaborated SARP "within-year" exercise , incorporating a full suite of environmental and biological data, has been completed to date (Bakun et al. 1991).

A first attempt to apply the "within-year" experiment to North Sea sprat, ***Sprattus sprattus***, was made in the German Bight in 1987 (Alshuth 1988a, 1988b). Larval production of sprat in the German Bight was monitored and the birthdate distribution of the juveniles was established subsequently. However, no analysis of causal mechanims of the differential "within-season" larval mortality was done. The objective of this study is to relate the results of Alshuth's studies (1988a) to wind speed, tidal impact and stability of the water column.

LARVAL PRODUCTION AND BIRTHDATE DISTRIBUTION OF JUVENILES

Larval production was determined by eight fortnightly cruises over the entire spawning season from the second half of April to the first half of August on a grid of 14 sampling stations spread evenly over the German Bight (Fig. 1). The larvae were collected by oblique bongo tows and only larvae up to 5 mm length were considered for the production estimate (Alshuth 1988a). Juveniles were collected in October and November with a RMT and their age was determined subsequently by counting daily rings on the otoliths (Alshuth 1988a). A comparison of the birthdate distribution of the juveniles and the larval production curve clearly indicates differential "within-season" mortality of the different larval cohorts (Fig. 2). The almost identical birthdate distribution of juveniles caught in mid-October and those caught four weeks after that shows that there was no differential mortality during this juvenile phase.

DISCUSSION

This initial SARP field study of sprat in the German Bight was more a "proof of concept" for the development of a short-time scale "survival index" than a complete SARP "within-year" exercise. That is, it did not include a comprehensive suite of equally high frequency measurements of the physical and biological environment, histological measures of starvation (Theilacker 1986), immunoassays of predator stomach contents (Theilacker et al. 1986), etc. Thus, the data available for interpretation of the indicated short time-scale variations is minimal. Stability of the water column, tidal impact and local wind conditions were analyzed in relation to the survival index of the juveniles.

Analysis of the tidal regime and the stability of the water column did not indicate any relationship with the survival index. However, variability in local wind conditions showed interesting relationships to the differential survival index of sprat juveniles in the German Bight.

Wind effects are involved in many of the currently popular hypotheses concerning regulation of recruitment variability. Nutrient enrichment of the illuminated upper zone of the ocean by wind-driven upwelling or mixing may be important in maintaining the trophic base for production of larval food. A wind-based index of coastal upwelling (Bakun 1973) has been empirically related to population dynamics of a number of commercial fish stocks of the California Current and other eastern ocean upwelling systems (Bakun and Parrish 1981, Shepard et al. 1984, Bakun 1985, Bakun in press). The hypothesis of Lasker (1975, 1978, 1988), which addresses detrimental effects of dispersion of fine scale food particle strata by wind-induced turbulent mixing, has been very influential in the development of SARP. Lasker's hypothesis is supported by the analysis of Peterman and Bradford (1987), who empirically related interyear variability in larval anchovy mortality rate off California to frequency of calm periods of sufficient duration for fine scale strata of food organisms to form. Rothchild and Osborn (1988) have suggested that certain levels of turbulence could actually enhance feeding efficiency of small marine organisms. Parrish et al. (1981) surveyed reproductive habits of fishes of the California Current and found a pattern of avoidance of detrimental effects of wind-induced offshore Ekman transport , which would carry eggs and larvae away from the favourable coastal habitat. Identification of similar patterns in other types of fish stocks and regional settings, indicating wide-spread importance of "physical retention areas", have lead to Sinclair's (1988) formulation of the "member/vagrant" hypothesis. Parrish et al. (1983) show a pervasive tendency, in reproductive habits of eastern ocean coastal pelagic fishes, for simultaneous minimization of exposure of larvae to both offshore transport and turbulence. Cury and Roy (1989) have used new non-linear methods (Mendelssohn and Cury 1987), to empirically demonstrate a consistent "optimal environmental window", where reproductive success is favoured at an intermediate range of wind speed, neither too low for adequate upwelling-based enrichment nor so high that excessive offshore transport and turbulent mixing occurs. Roy (1990) showed the same pattern of apparent selection for an intermediate ideal characteristic wind speed in a survey of the reproductive habits of West African coastal pelagic fishes.

Indices of wind-related processes

Several series of wind-related indices (Fig. 3 A, B, C) related to the various hypotheses enumerated above, have been prepared. The basic data source is the file of 6-hourly northern hemisphere synoptic atmospheric pressure/wind analyses produced at the U.S.Navy's Fleet Numerical Oceanography Center in Monterey, California. From these a series of estimates of the local surface wind in the German Bight was produced according to the method of Bakun (1973). The "wind mixing index" (Fig. 3A) is an estimate of the rate of transfer of wind-derived turbulent mixing energy through the sea surface; it is formed as the bi-weekly average of the third power (cube) of the wind speed (Bakun and Parrish 1980).

In addressing Lasker's hypothesis, it is probably not the average mixing intensity that is crucial, but the existence of adequate temporal "windows" (Bakun and Parrish 1980) during which the production of turbulent mixing energy remains low for a long enough period for concentrated food particle strata to accumulate and for larvae to accomplish successful "first-feeding". These calm periods have been called variously "Lasker events", "Lasker gates", etc. Here we specify a "Lasker (x,y) window" as being a full day in which the wind speed did not exceed "x" m s $^{s-1}$, which directly follows an unbroken sequence of at least "y" preceeding days with wind speeds not exceeding the same "x" m^{-1} limit. Peterman and Bradford (1987) chose 10 m s^{-1} for the wind speed limit for their study of California anchovy. Mendelssohn and Mendo (1987) chose 5 m s^{-1} for their study of Peruvian anchovy. We show both (5,4) and (10,4) Lasker windows for the period and location of the 1987 German Bight "Sprat-SARP" operation in Fig. 3 .

The stress exerted by the wind on the sea surface was computed from the synoptic surface wind estimates using the standard quadratic drag law and assuming a constant drag coefficient of 0.0013. The resulting stress estimates where then averaged by component for each bi-weekly increment of the study (e.g., Fig. 3C).

The survival index (Fig. 3D) was defined as the ratio of the percentage of the sampled larval birthdates (Fig. 2A) in each bi-weekly increment to the corresponding larval production estimates (Fig. 2A and Fig. 3E). The survival index (Fig. 3D) was defined as the ratio of the percentage of the sampled larval birthdates (Fig. 2) in each biweekly increment to the corresponding larval production estimates (Fig. 2 and Fig. 3E).

We can examine these series for apparent conformities to the hypothetical linkages. However, lacking corroborating data on sub-surface processes and effects, the analysis is at this point merely correlative and subject to all well-known limitations of a correlative approach (e.g. Bakun 1985). Note also that the period of substantial larval production contains only five bi-weekly increments (Fig. 3E) with perhaps two other data points (first half of May and first half of August) having very uncertain relative magnitude of survival because of very low indicated larval production but at least an indication that survival may have been rather good. Accordingly, the degrees of freedom available for any sort of empirical analysis are extremely limited. Thus the brief analysis that follows should be properly regarded as merely an exercise in hypothesis generation. No implication that this dis-cussion in any way constitutes a valid hypothesis test is intended.

Larval retention hypothesis

The most evident visual correlation appears to be with eastwards wind stress (Fig. 3C). The orthogonal northward component showed no perceptabel degree of correlation. Eastwards stress would produce southward surface Ekman transport (Ekman 1905) in a deep ocean situation. However, in a shallow area such as the coastward portions of the German Bight, frictional effects would probably cause the transport to be angled somewhat more directly downwind than the "90° to the right" specified by the "pure" Ekman transport derivation. Thus, the near surface transport from an eastward wind stress would, in all likelihood, be directed from the North Sea at large, directly into the German Bight. This would tend to hold drifting larvae within the shallow portions of the German Bight, retarding their dispersion into the open North Sea, and helping to keep them as "members" rather than becoming "vagrants", according to the terminology of Sinclair (1988). In the shallower parts of the German Bight, larvae may find improved feeding conditions within the frontal systems produced by the fresh water inflows and perhaps find some refuge from predation, etc. In addition, since the birthdate distributions which deter-mine the survival index are collected locally, the variation of the proportion of "members" to "vagrants" may be of comparable significance to variations in actual survival in determining the variability of the survival index.

Stable ocean hypothesis (Lasker's hypothesis)

The most notable deviation from a direct visual proportionality of survival index (Fig. 3D) to eastward wind stress (Fig. 3C) is a period of relatively enhanced apparent survival during the second half of June. This period corresponds to a period of consistently low winds yielding eleven Lasker (5,4) windows within the 15-day period (dark shading Fig. 3B). We note that the spawning period of sprat (Fig. 3E) is confined to the seasonal period of low turbulent mixing energy production by the wind (Fig. 3A). The one two-week period where an indication of substantial survival (Fig. 3D) corresponds to a period of relatively high mixing index (Fig. 3A) is during the first half of May where presence of four "Lasker (4,5) windows" indicates an extended period of calm conditions even although the mean turbulence generation, for the period as a whole, was high.

SUMMARY

Thus, looking only at potential wind effects, the results of the 1987 German Bight Sprat-SARP exercise appear to be consistent with a combination of favourable effects of (i) larval retention (Parrish et al. 1981; Sinclair 1988) and of (ii) water column stability during early larval life (Lasker 1975, 1978). There is little evidence here for any substantial favourable effect of increased turbulence generation, acting either to stimulate food particle production by mixing nutrients from the pycnocline into the upper mixed layer or to increase contact rates (Rothchild and Osborn 1988) between feeding larvae and appropriate food particles.

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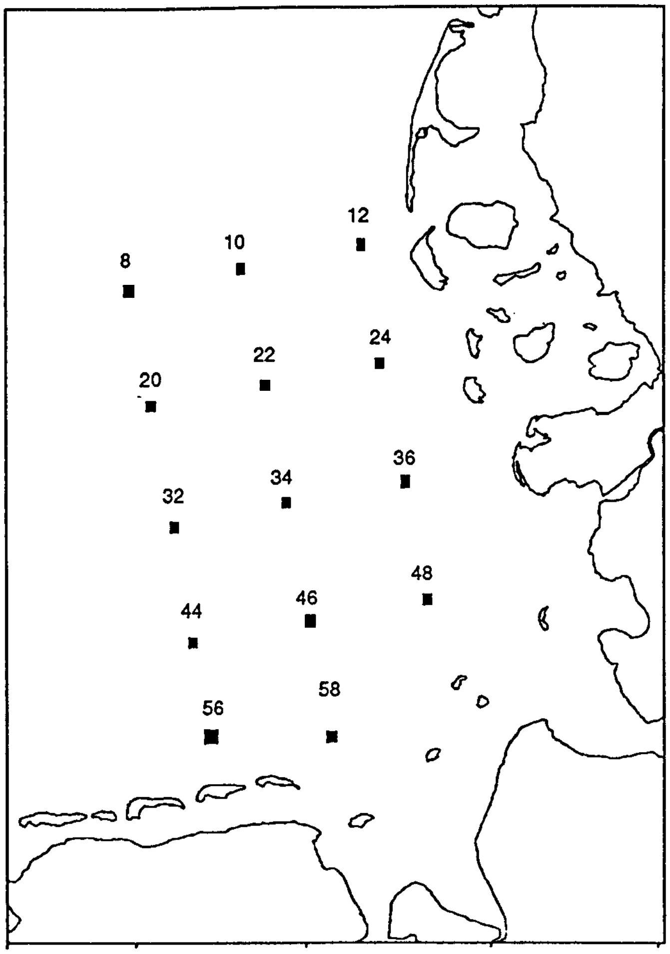

Fig. 1: Study area in German Bight with location of sampling stations.

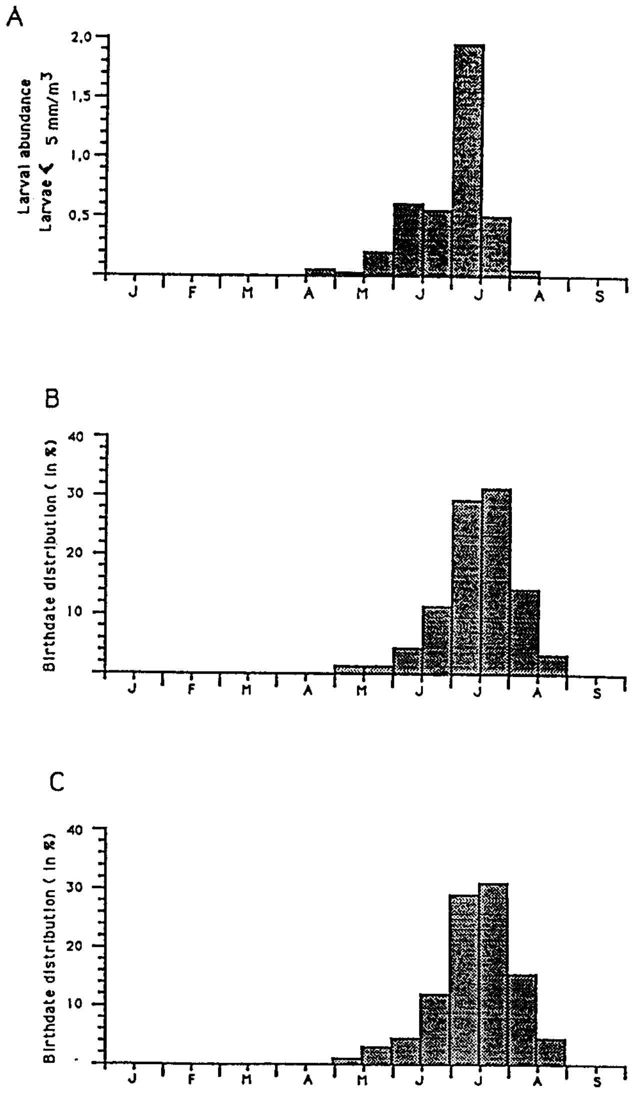

Fig. 2: A - Seasonal distribution of abundance of larval sprat in German Bight in 1987.

B - Seasonal distribution of birthdates of juvenile sprat collected 13/14 October 1987 in German Bight

C - Seasonal distribution of birthdates of juvenile sprat collected 11 November in German Bight

(modified after Alshuth 1988 a,b)

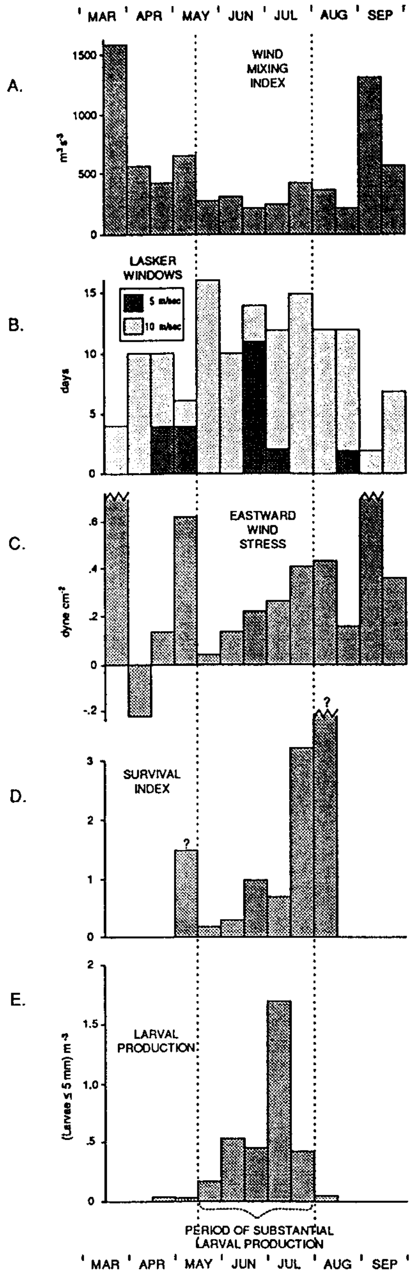

Fig. 3: A, B, C - Series of wind-related indices.

D - Survival Index of juvenile sprat.

E - Larval production of sprat (as Fig. 2 A).