When is year-class strength determined in western Baltic herring?

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Weekly surveys of larvae in the Strelasund and the Greifswalder Bodden were used to investigate when year-class strength is determined in western Baltic spring-spawning (WBSS) herring. An abundance metric of larvae reaching a length of 20 mm over the entire spawning season was constructed by accounting for increases in daily growth resulting from seasonal increases in temperature (5–20°C). The index was significantly correlated with the acoustic estimates of age-1 herring in the western Baltic Sea ($r = 0.88$) and with the estimates of year-class strength obtained from stock assessment ($r = 0.65$). Previous studies of herring elsewhere have reported that year-class strength is determined during the late larval stage, but we show that year-class strength can already be fixed at a larval length of only 20 mm. Although the index obtained may be used in stock assessment and predictions, the intriguing question remains, namely how can the signal of larval productivity from one single spawning component of WBSS herring reflect the year-class dynamics of the entire stock?

Keywords: Baltic Sea, herring larvae, year-class strength.

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Introduction

A greater understanding of the recruitment dynamics of fish has been a goal of fisheries science over the past 100 years (Rothschild, 1986; Houde, 2008). Our ability to provide advice on the sustainable management of fish stocks and to develop suitable recovery plans for depleted stocks depends on a process-based understanding of recruitment rather than on an empirical stock–recruitment relationship that merely reflects past observations. The assumption that the processes which control these dynamics are stationary is now considered inappropriate (Chaput *et al.*, 2005; Stige *et al.*, 2006; Walters *et al.*, 2008). Although it is unlikely that all variability in recruitment is related to the survival during one specific stage in the life cycle of fish, certain periods are more important than others in the determination of year-class strength (Leggett and Deblois, 1994). Year-class strength of Atlantic herring (*Clupea harengus*) appears to be mostly determined before metamorphosis of the larvae (Heath and Gallego, 1997; Nash and Dickey-Collas, 2005), and the variability in the production of larvae largely accounts for the major fluctuations in stock abundance (Nash *et al.*, 2009).

When a population is relatively small, the size of the spawning stock is the most important limiting factor in determining recruitment, as can be deduced from the almost linear relationship between the two parameters (e.g. North Sea herring, see Nash and Dickey-Collas, 2005). However, recruitment variability is mediated through the interaction of growth and survival of the individuals within a cohort (Houde, 1997), which is controlled by the biophysical environment of the fish (Brunel and Boucher, 2007). These processes become more important when the stock becomes larger, whereas the influence of stock size declines (Liermann and Hilborn, 2001). Therefore, in herring, the ratio of recruits to spawners commonly decreases with stock size (Anthony and Fogarty, 1985; Zheng, 1996; Fox, 2001; Nash *et al.*, 2009), but the size of the area inhabited by the stock may influence this density-dependent effect (Winters and Wheeler, 1987; Brunel and Boucher, 2007).

The strength of the recruiting year class is the sum of the survivors of the eggs produced by all reproductively active components in a stock. Within a stock, recruitment patterns among components may be different (Bjerkan, 1917; Cushing, 1992), which may dampen the overall variability. For this reason, recruitment variability is thought to be greater in Baltic herring than in North Sea herring (Cushing, 1996; Myers, 2001) because the latter comprises more spawning components.

We utilize data from herring larvae surveys conducted in the Strelasund and the Greifswalder Bodden in the western Baltic Sea (Oeberst *et al.*, 2009), in combination with information on temperature-dependent growth rates, to construct a time-series of larval indices of abundance. The western Baltic spring-spawning (WBSS) herring aggregate on several coastal spawning grounds, of which the Greifswalder Bodden is an important one (Biester 1989). Age groups 0 and 1 of WBSS are concentrated in the western Baltic Sea, and adults migrate between the North Sea for feeding and the shallow waters of the western Baltic Sea for spawning. In the North Sea, the abundance of small herring

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larvae is a good indicator of the spawning-stock biomass (SSB), whereas the abundance of large larvae is strongly correlated with recruitment at age 1 (ICES, 2007). Our principal objective was to determine whether an index of early larval abundance is correlated with independent estimates of recruitment in WBSS herring, and thereby to establish when the processes that determine year-class strength operate.

Material and methods

Surveys

Surveys of larval abundance in the Strelasund and the Greifswalder Bodden (Figure 1) have been conducted annually since 1992. During the spawning season, up to 14 surveys have been conducted weekly, using stepwise oblique hauls with a 60-cm Bongo net (mesh size 0.335 mm; Müller and Klenz, 1994). All samples were taken in daylight and preserved in 4% buffered formaldehyde-seawater solution immediately after collection.

In principle, each weekly survey covered 35 stations, but occasionally not all stations could be sampled. The area was subdivided into five strata for processing catch rates (Figure 1). The time taken to complete all stations within a cruise varied between 2 and 5 d because of bad weather or technical problems (cf. Table 1). The surveys initially started in week 14 but, from 1998 on, the first survey was delayed until week 17 because analyses had shown that the first weeks yielded low catches of the larger larvae that were considered more meaningful for estimating year-class strength.

Sample analysis

Herring larvae were identified, counted, and measured (total length to 1 mm below) in the laboratory. No corrections were made for shrinkage caused by fixation. For large samples (>1000 larvae), three subsamples of ~200 larvae were measured and the remaining larvae were counted. The size distributions of the subsamples were raised to the total number caught.

For each station i of week j and stratum h, the number of larvae by length group k per m^2 ($C_{i,h,j,k}$) was estimated, based on the volume of filtered water (measured by flowmeter) and the maximum sampled water depth of the tow (Müller and Klenz, 1994). The mean daily growth of the larvae (DG, mm d^{-1}) was estimated from a linear regression on surface temperature (T in °C; Oeberst *et al.*, 2009) as follows:

$$DG = 0.033 + 0.035\ T. \quad (1)$$

The N20 abundance index

The index calculated (N20) represents a summation of all the larvae that reached a length of 20 mm over the entire survey

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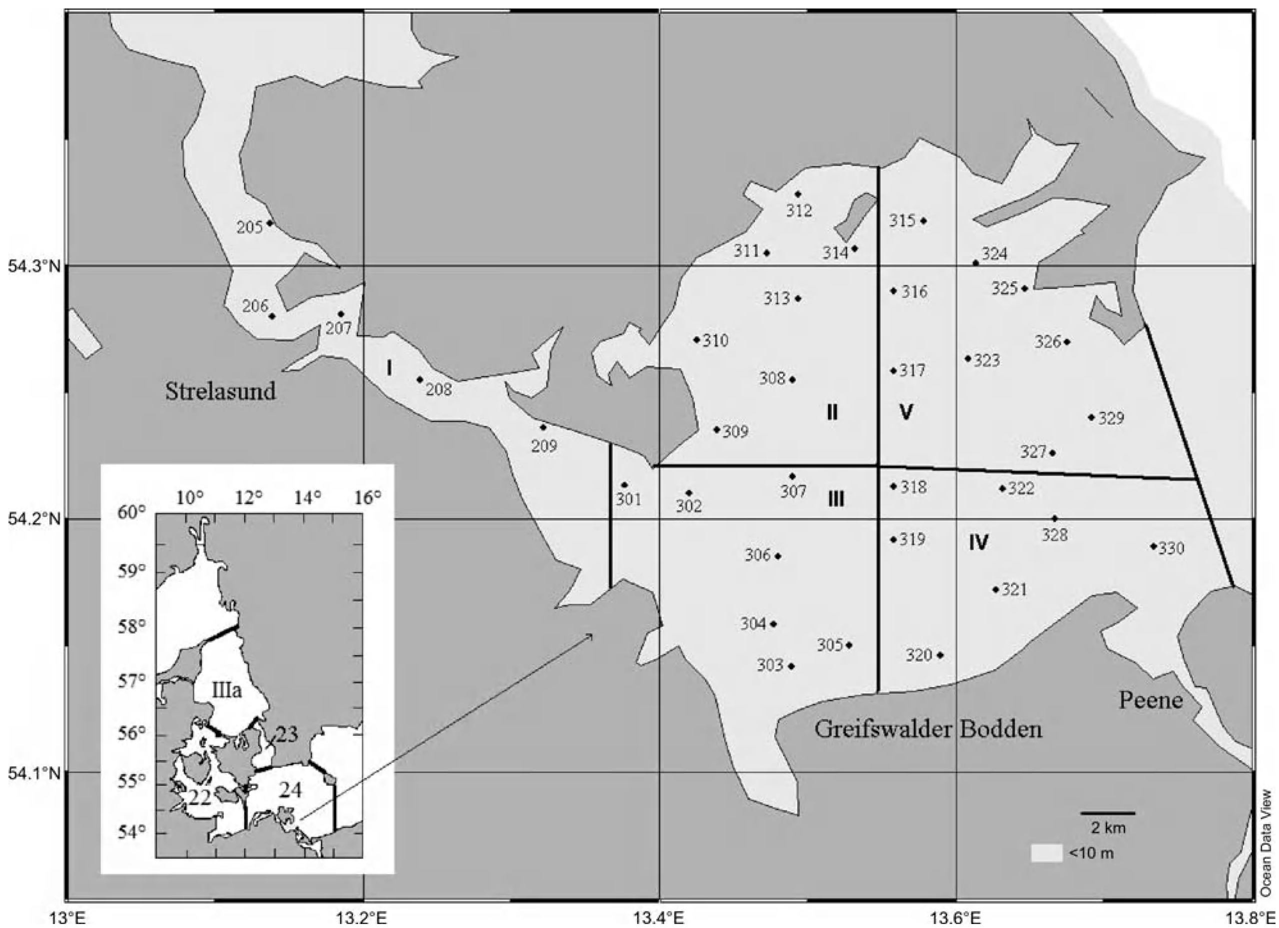

Figure 1. Map of Strelasund and the Greifswalder Bodden with the 35 sampling stations and the strata used in the analysis (I, 69 km^2, five stations; II, 100 km^2, seven stations; III, 95 km^2, seven stations; IV, 138 km^2, seven stations; V, 105 km^2, nine stations). Inset shows the area inhabited by WBSS and the ICES Subdivisions.

Table 1. Number of stations sampled by year and week number (numbers of days to complete each survey are given in parenthesis).

	Year														
Week	**1992**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
14	35 (3)	35 (3)	10 (3)	35 (4)	–	35 (3)	–	–	–	–	–	–	–	–	–
15	9 (3)	35 (2)	13 (3)	35 (3)	–	35 (4)	–	–	–	–	–	–	–	–	–
16	34 (2)	35 (2)	35 (3)	16 (3)	–	35 (3)	–	–	–	–	–	35 (4)	–	–	–
17	35 (2)	–	35 (3)	35 (5)	–	35 (2)	–	35 (3)	35 (3)	35 (3)	35 (3)	35 (2)	35 (3)	–	35 (3)
18	35 (3)	–	35 (3)	35 (2)	17 (3)	35 (2)	35 (3)	35 (3)	35 (3)	35 (3)	35 (2)	35 (3)	35 (3)	35 (2)	35 (3)
19	35 (4)	–	35 (3)	35 (3)	29 (2)	35 (2)	35 (4)	35 (2)	35 (3)	35 (3)	35 (3)	35 (3)	35 (3)	35 (3)	35 (3)
20	35 (2)	35 (2)	35 (3)	35 (4)	35 (2)	35 (3)	35 (3)	35 (3)	35 (3)	35 (3)	35 (3)	35 (3)	35 (2)	35 (3)	35 (3)
21	35 (3)	35 (2)	35 (2)	35 (2)	35 (2)	35 (3)	35 (3)	35 (3)	35 (3)	35 (3)	35 (3)	35 (2)	35 (3)	35 (3)	35 (3)
22	5	35 (2)	32 (4)	35 (3)	35 (2)	35 (3)	35 (2)	35 (3)	35 (3)	35 (3)	35 (3)	35 (3)	35 (3)	35 (3)	35 (3)
23	–	35 (2)	32 (3)	35 (2)	35 (2)	35 (3)	35 (2)	35 (3)	35 (3)	35 (3)	35 (3)	35 (3)	35 (3)	35 (3)	35 (3)
24	–	28 (4)	35 (2)	35 (2)	34 (2)	35 (3)	35 (4)	35 (3)	35 (3)	35 (3)	35 (3)	35 (3)	35 (4)	35 (3)	35 (3)
25	–	–	–	–	–	–	35 (3)	35 (3)	35 (3)	35 (3)	35 (3)	35 (4)	35 (3)	35 (3)	35 (3)
26	–	–	–	–	–	–	35 (3)	35 (3)	35 (4)	35 (2)	–	–	35 (3)	35 (3)	35 (3)

period. The length of 20 mm was chosen to minimize the effects of variable mortality during the transition from the yolk-sac stage to the active-feeding stage, and of gear avoidance by large larvae because of their increased swimming speed. A two-step algorithm was used to account for growth during each sampling cruise and to minimize the possibility of double-counting larvae:

(i) Larvae can grow >1 mm during the 2–5 d of a sampling cruise, depending on water temperature. Therefore, the length distribution of each station was corrected to represent the first day of each sampling week if the mean DG between the first day of the cruise ($D_{1,j}$) and the sampling day of the station ($D_{i,j}$) was ≥1 mm using

$$C'_{i,h,j,k} = C_{i,h,j,k-x}, \tag{2}$$

where x is estimated by

$$x = \mathrm{ROUND}[\mathrm{DG}_{i,j}(D_{i,j} - D_{1,j})]. \tag{3}$$

The arithmetic means by stratum ($C'_{h,j,k}$) were calculated from $C'_{i,h,j,k}$, then the overall stratified mean for the total area by week ($C'_{j,k}$) was calculated using the surface areas of the strata as weighting factors.

(ii) The number of larvae of cruise j contributing to the N20 index was defined as the number of larvae ($C'_{j,k}$) that reach a length of >21 mm by the first day of the next survey $j + 1$, using the average T data and the number of days multiplied by the total area of the Strelasund and the Greifswalder Bodden ($A = 514 \times 10^6$ m^2). A threshold of 21 mm was used because the length measurements were to the millimetre below. The contribution of the last cruise was estimated differently because information about subsequent development is lacking. In this case, all larvae ≤20 mm contributed to the index. The N20 index was calculated as:

$$\mathrm{N20} = A \sum_{j=1}^{n} \sum_{k=k(j)}^{20} C'_{j,k}, \tag{4}$$

where n denotes the number of cruises of the year, and k_j the minimum length of herring larvae during cruise j which was incorporated into the index of cruise k dependent on the mean surface temperature. The term k_j was estimated by

$$k_j = 21 - \mathrm{ROUND}[(0.033 + 0.035\ T_j)(D_{j+1} - D_j)]. \tag{5}$$

For the final cruise, k_j was defined as 5 mm. Mortality of larvae between cruise j and $j + 1$ was not taken into account.

Other time-series of year-class abundance

Year-class indices for age groups 0 (HA_0) and 1 (HA_1 and HA_NS_1) of WBSS and herring in Division IIIa are available from acoustic and bottom-trawl surveys, whereas the stock assessment provides annual recruitment estimates (ACFM_0) for the entire stock per year (ICES, 2007; Table 2). To analyse the data, a linear regression model was applied using the statistical software program Statgraphics (Statgraphics Centurion, Version XV, StatPoint, Inc.).

Results

The surface temperature increased from ~5°C in week 14 to ~20.5°C in week 26 (Figure 2). Surface and bottom temperatures are highly correlated (Oeberst *et al.*, 2009) because the area is generally shallow (mean depth 5.6 m). In most years, the temporal coverage appeared adequate for monitoring the larvae produced during the entire spawning season. This is important because the abundance of small larvae in the last survey may disproportionately affect the estimate if the production of larvae continues after sampling has stopped. From 1998 to 2006, during which time the cruises started and ended later in the year than in the initial years (Figure 3), the contribution to the N20 of larvae <11 mm in the final cruise was mostly negligible and always <6%, whereas their contribution in 1992–1997 was much larger and more variable. The larger proportions of newly hatched larvae during the earlier years indicate that spawning may have continued after the final cruise, although the water temperatures observed during these final cruises were probably too high for successful hatching (i.e. >14°C; Blaxter and Hempel, 1961; Klinkhardt 1986). Therefore, the probability that the index has been underestimated seems low for all years.

The year-class indices from the different surveys cover different components of the WBSS stock (Table 2). Therefore, the VPA-derived recruitment index from the stock assessment

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Table 2. Year-class indices compared for WBSS herring (ICES, 2007).

Index	Remarks
ACFM_0	VPA-derived age-0 recruitment in Division IIIa and Subdivisions SD22–24 (ICES, 2007)
N20	Larval index from the Greifswalder Bodden
HA_0	Age-0 abundance based on the acoustic survey in SD22–24 (year class 2001 uncertain[a])
HA_1	Age-1 abundance based on the acoustic survey in SD22–24 (year-class 2000 uncertain[a])
HA_NS_1	Age-1 in the North Sea based on the international acoustic survey in July[b]

[a]Uncertain because of interruption of the RV "Solea" time-series.

[b]Comprises only small proportions of spring spawners originating from the western Baltic Sea or Kattegat (Ruzzante *et al.*, 2006).

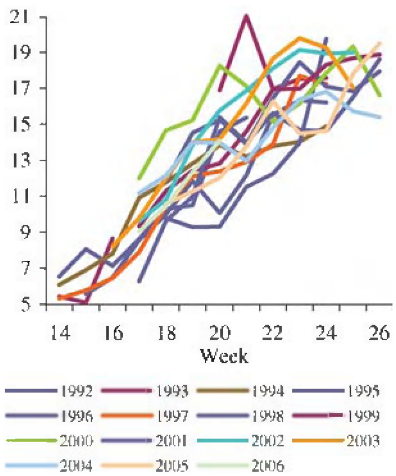

Figure 2. Trajectories of mean surface temperature by week number, 1992–2006.

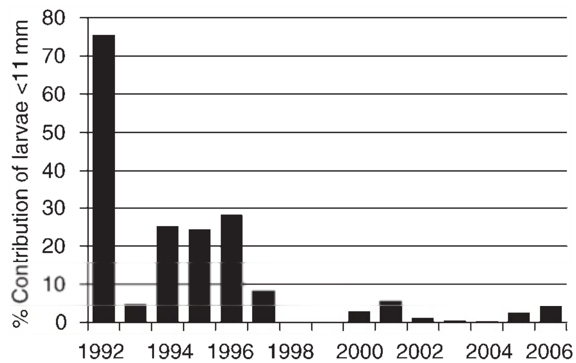

Figure 3. Percentage contribution of small larvae (<11 mm) caught in the final cruise to the N20 index.

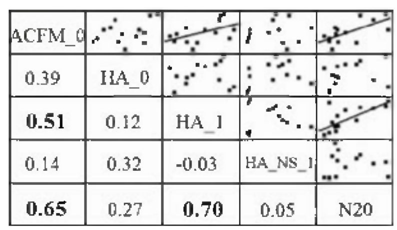

Figure 4. Correlation coefficients (bold, significant at $p < 0.05$) and $x-y$-plots (if significantly correlated, associated regression lines are plotted) for the various indices of year-class strength (for abbreviations see Table 2).

(ACFM_0) is used as the standard in comparing the year-class indices, including N20. ACFM_0 was significantly correlated ($p < 0.05$) with the acoustic estimates of age-1 WBSS (HA_1) and the N20 index (Figure 4). The other surveys, which contribute to HA_0 and HA_NS_1, probably sample a part of the year class that is not representative of the entire stock. In 2001, the series of acoustic surveys was disrupted because the ship used routinely was not available. Because of uncertainty about the estimate, correlations were repeated excluding the value for 2001. This yielded correlation coefficients of $r = 0.63$ and $r = 0.88$ for ACFM_0 and N20, respectively ($n = 13$ in both cases).

Discussion

The HA_1 index is based on the abundance of age-1 herring, whereas ACFM_0 is essentially a summation of all catches of each cohort over the exploited lifespan (allowing for a constant natural mortality). Their significant correlation with the N20 index indicates that the year-class strength of WBSS is determined early in the life of each cohort. Factors affecting the survival of larvae and juveniles beyond the small size of 20 mm appear to be almost constant between years, suggesting that the interannual variability of the mortality of the late larvae and juveniles is relatively small. The correlations also suggest that survival of early larvae from the Greifswalder Bodden spawning ground is representative of the conditions at the larger set of WBSS spawning grounds, so a consistent portion of each year class is produced at this particular location.

Evidence for early regulation of year-class strength has also been found for North Sea autumn-spawning herring (Nash and Dickey-Collas, 2005; Payne *et al.*, 2009) based on correlations between indices of abundance of larvae ~30 mm long, which may be up to 5 months old (Heath *et al.*, 1997). Our results indicate that year-class strength of WBSS herring is already determined when the larvae are 20 mm long and 20–40 days old, depending on temperature. Although this is earlier in life than has been found for North Sea herring, it may well be that the difference arises only because suitable survey data to test for year-class signals at smaller sizes are not available for the North Sea.

The high temperatures observed in the shallow water of the Greifswalder Bodden during spring appear to have no negative influence on larval growth (Oeberst *et al.*, 2009). Growth rates and mortality of larvae may also be influenced by biotic factors such as food supply, inter- and intraspecific competition for food, and predator abundance (Cushing, 1975; Fortier and Gagne, 1990; Busch, 1993; Houde, 2008). Variability in food availability does not appear to be a limiting factor for growth or survival of WBSS larvae after they have reached 20 mm. The production of copepod nauplii, the major food source, starts by the end of

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April (Fennel and Neumann, 2003), and the population soon reaches >15 000 ind. m^{-3}, higher than the minimum requirement of 6000 m^{-3} suggested for herring larvae (Rosenthal and Hempel, 1970; Kiørbe and Johansen, 1986).

Our method assumes that larvae <20 mm are not transported by wind-driven processes beyond the area surveyed, that larval mortality is low between consecutive weekly cruises, and that the area surveyed is representative of the wider range of spawning grounds. However, because the development of the N20 index was primarily driven by variability in the empirical observations of larval size distributions as well as by process understanding, rather than by model assumptions, the index is expected to be robust under current conditions. Larvae <20 mm are unlikely to be able to avoid the sampling gear, so are sampled representatively (Brander and Thompson, 1989).

It is somewhat surprising that an index derived from a single, though major, spawning ground carries the year-class signal for the whole WBSS stock in Division IIIa and Subdivisions 22–24. There are two possible explanations: either the vast majority of the recruits come from the Greifswalder Bodden spawning component or the factors affecting development and survival of eggs and early larvae operate at a region-wide scale. It seems probable that some spawning sites make a larger contribution to the stock than others because the survivors (recruits) come from non-random components of the reproductive output of a population (Heath and Gallego, 1997; Wright and Gibb, 2005). Although many studies suggest synchrony in recruitment across regions (Templeman, 1972; Koslow, 1984; Fox *et al.*, 2000), Myers *et al.* (1995) cautions that artefacts may be caused by the analytical methods used to test for synchrony. Also, the different North Sea spawning components show different recruitment patterns (Cushing and Bridger, 1966), thus arguing against synchrony.

The availability of reliable recruitment indices helps to improve stocks assessment and management of short-term catch. Given the significant correlation between N20 and ACFM_0 ($ACFM\_0 = 2.71 + 0.14\,N20$; $n = 15$; $r = 0.65$), the larval index from the Greifswalder Bodden serves as an early indication of year-class strength that may be used in predictions of recruitment of WBSS.

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