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AN EVALUATION AND REVIEW OF THE ICES HERRING LARVAL SURVEYS IN THE NORTH SEA AND ADJACENT WATERS

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ABSTRACT

Surveys of larval herring began in the North Sea in 1946 and have continued with few interruptions until the present day. In 1967, coordination of the international survey effort was assumed by a Working Group of the International Council for the Exploration of the Sea (ICES), and from 1972 onwards the data have been archived in a data base at the Marine Laboratory in Aberdeen. Until 1986, Larval Abundance Indices (LAIs) were calculated for each assessment unit from catches of larvae smaller than 10 mm, and spawning-stock biomass estimated by reference to historical regressions of LAIs against spawning biomass derived from Virtual Population Analysis (VPA). The regressions were updated each year. From 1986 onwards, a Larval Production Estimate (LPE) was calculated for each assessment unit in addition to an LAI. The LPE was determined by back-calculating the abundance at hatching date and size, from abundance at capture date and size using estimates of growth and mortality rates, and integrating over the spawning area and period. The LPE method utilised data on all size classes of larvae captured, rather than solely larvae smaller than 10 mm. The LPE method performed better than the LAI when compared to other assessment data for the North Sea over the period from 1972 to 1989. A comparison of spawning-biomass estimates calculated directly from LPEs by reference to fecundity data, with those derived from acoustic surveys, revealed similar trends but an inconsistency in the absolute levels which could not be readily explained.

North Sea stocks of Atlantic herring (*Clupea harengus harengus* L.) suffered a major collapse during the 1970s, resulting in the first widespread ban on herring fishing in the North Sea which was enforced from mid-1977 to mid-1983. Preceding the collapse, fishing pressure peaked in the late 1960s following the replacement of the drift net fisheries of the early 1900s by trawling and ultimately purse seine netting. However, environmental factors, as well as fishing pressure, may have been responsible for the collapse. North Sea stocks staged a recovery in the mid-1980s and thereafter increased steadily in size, supporting a substantial fishery.

Scientific research to assess the biomass of stocks of commercially important species, advice on their management, and understand the reasons for their decline and resurgence, began in the late 19th century. Research on Atlantic herring populations increased markedly during the 1950s and 1960s, partly as a result of concerns about the state of the North Sea stocks. However, the assessment procedures available at the time were inadequate to diagnose unequivocally the signals of imminent stock collapse. Partly in response to this failing, internationally coordinated larval herring surveys were instigated to aid stock assessment and have continued ever since. This review follows the course of herring larval survey development and evaluates its utility as a stock assessment tool.

Spawning Distribution of Herring in the Northeast Atlantic

There is a strong latitudinal effect on herring spawning times in the northeast Atlantic. In general, spawning occurs in mid-summer (June) at the northerly extent of the geographical range around Iceland and northern Norway (70°N) and in mid-winter (December and January) at the southerly extent in the English Channel

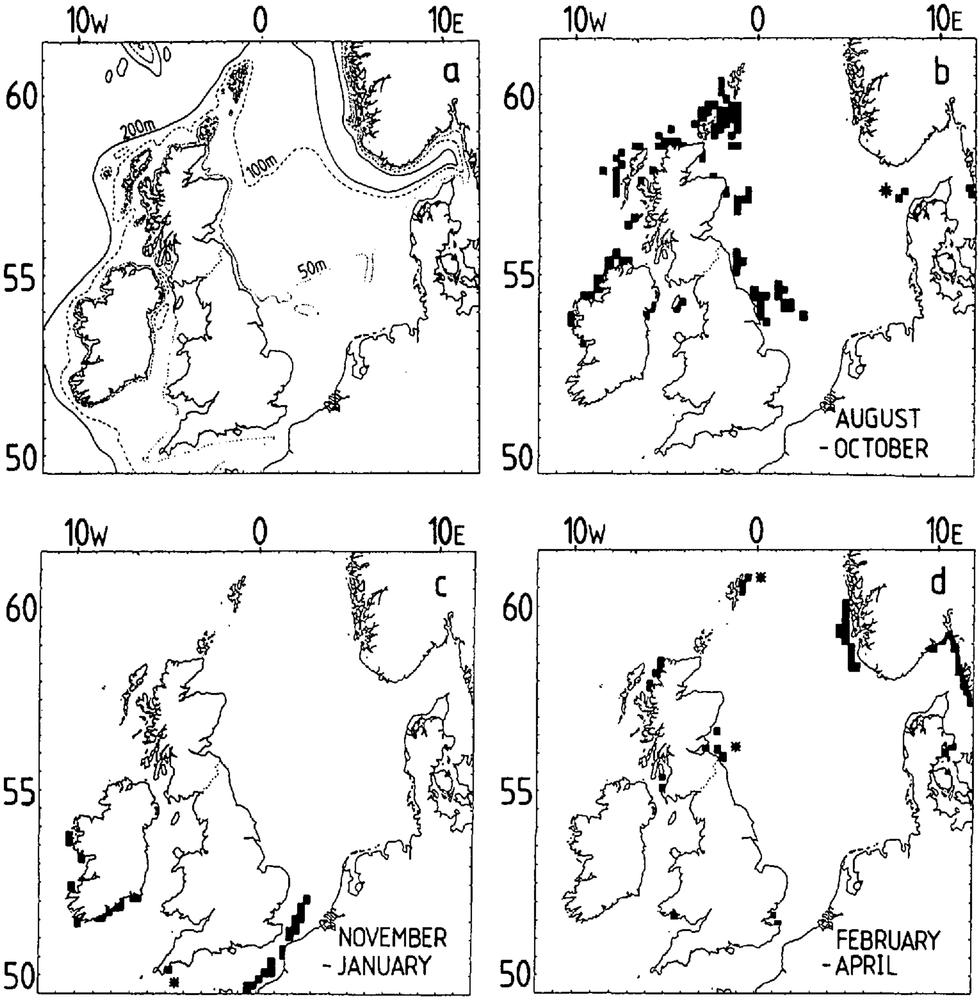

Figure 1. a) Sea bed topography of the North Sea region. b, c, d) Distribution of herring spawning areas determined from catches of yolk-sac herring larvae, ripe fish, and haddock with herring eggs in the stomach. Asterisks indicate spawning sites thought to be no longer in use. (Redrawn from Heath and Richardson, 1989).

(50°N). At mid-latitudes, spawning may occur during either the spring or autumn, but in the North Sea and to the west of the UK the majority of fish spawn in the autumn (Parrish and Saville, 1965). Spawning takes place in August around the Orkney and Shetland Isles and becomes progressively later with distance south, finishing off the south coast of England in January (Fig. 1). The main spring spawning occurs during March and April in the Baltic Sea, off southwestern Norway and at Faroe. Isolated spring spawning groups are also found at locations around the UK coast (Thames Estuary, Milford Haven, Clyde Sea) and along the Continental European coast but have been of minor significance in recent times. The Norwegian-Icelandic spring/summer spawning fish are referred to as the Atlanto-Scandian herring and considered to be a distinct group, as are the Baltic herring (Parrish and Saville, 1965). The ICES larval surveys concentrate exclusively on the autumn/winter spawning fish in the North Sea and to the west of the British Isles.

History of Herring Larval Surveys

Sporadic surveys of larval herring distribution in northern European waters were carried out between the late 1880s and 1940 (Bowman, 1922; Clark, 1933; Wood, 1930), but UK laboratories began regular annual surveying in 1946 in the southern North Sea (Bridger, 1960, 1961), and 1951 in the northern North Sea (Saville, 1971). Other European nations began sampling during the following years and standardised sampling procedures have been followed since 1967 when coordination of most of the international survey effort was assumed by a Working Group of the International Council for the Exploration of the Sea (ICES) and the surveys became known as the International Herring Larval Surveys (IHLS) south of 62°N (Saville, 1968).

The original IHLS covered the North Sea from Shetland in the north to the English Channel in the south, and also a historical spawning area off the Danish coast in the Skagerrak and Kattegat. Hardly any larvae were ever caught in the Danish area, and these surveys were discontinued after 1973. In 1971, the annual survey coverage was expanded to encompass the west of Scotland and northwest Ireland. Surveys off the west of Scotland have continued to the present day, but those off northwest Ireland suffered from poor sampling coverage and were discontinued after 1988.

Only the UK (Scotland) and the Netherlands have participated in all the surveys carried out since 1967, but Denmark, the then Federal Republic of Germany, and UK (England) have participated in the most of the surveys. A number of other nations have contributed from time to time (Table 1). All survey data collected since 1972 are archived in Aberdeen, Scotland, for use by the IHLS Working Group which supervises the collection and analysis of data. Survey reports have been published annually as ICES Committee Meeting documents and sometimes also as ICES Cooperative Research Reports (Table 2). The application of IHLS data in the stock assessment procedure has been carried out by another ICES Working Group—the Herring Assessment Working Group—for the area south of 62°N (HAWG) which convenes annually at the beginning of April.

Not all nations engaged in larval herring surveys in the northeast Atlantic have subscribed to the ICES coordinated programme. For example, surveys in the Celtic Sea, off the southern coast of Ireland, were carried out between 1959 and 1962, and from 1978 to 1985 (Grainger et al., 1982), but the data have not been included in the IHLS Working Group database. Similarly, Poland, USSR, and the then German Democratic Republic conducted independent surveys in the North Sea from 1962 to 1975 (Siudzinski, 1975; Hahlbeck, 1976).

Sampling Methods in North Sea Larval Surveys

Sampling Net.—The earliest surveys were carried out with oblique tows of a 1-m diameter conical net, Hensen net or Heligoland net (Bridger, 1961; Saville, 1971). During 1955 to 1957, these were replaced by a modified version of the Gulf high speed sampler (Gehringer, 1952, 1961; Bridger, 1958) fitted with at 450-μm mesh aperture metal gauze filtering cone. This was considered to have better facilities for measuring the volume of water filtered, and to minimise evasion of the sampler by larger sizes (> 10 mm) of larvae by use of a higher towing speed (5 knots).

By 1967, when ICES assumed a coordinating role, a variety of different versions of the Gulf sampler were in use by the participating nations. Following exhaustive comparative fishing trials with different versions of the sampler (Nellen and Hempel, 1969; Saville and McKay, 1969, 1970; Wood, 1973), a Dutch modification of the Gulf III (Zijlstra, 1970) was adopted as the "standard sampler" for the

Table 1. Participants in the ICES International Herring Larval Surveys, 1967 to 1990 (In addition, Poland, the former German Democratic Republic and Soviet Union carried out independent surveys of larval herring in the North Sea during the period 1967 to 1975)

	Denmark	Federal Republic Germany	France	German Demo-cratic Republic	Iceland	Ireland	Nether-lands	Norway	Poland	Sweden	UK (England)	UK (Scotland)
1967	*	*					*	*			*	*
1968	*	*					*	*			*	*
1969	*	*					*	*		*	*	*
1970	*	*					*	*		*	*	*
1971		*					*			*	*	*
1972	*	*			*		*			*	*	*
1973	*	*					*			*	*	*
1974	*	*					*				*	*
1975	*	*					*				*	*
1976		*		*			*	*	*		*	*
1977		*		*			*	*	*		*	*
1978							*	*			*	*
1979		*					*	*			*	*
1980		*					*	*			*	*
1981	*	*	*			*	*	*			*	*
1982	*	*	*			*	*				*	*
1983	*	*				*	*				*	*
1984	*	*				*	*				*	*
1985	*	*				*	*				*	*
1986	*	*				*	*				*	*
1987	*	*				*	*				*	*
1988	*	*				*	*				*	*
1989	*	*					*				*	*
1990		*					*					*

Herring Larval Surveys (Anon, 1971, 1976, 1979). The main modifications were the substitution of 250- to 275-μm aperture nylon mesh for the metal gauze in the filtering cone and the location of the flowmeter in the nose cone, which had a mouth aperture of 20 cm. This decision was in marked divergence to herring larval survey strategies in the northwest Atlantic regions where the Bongo net was adopted as the standard gear. It was recommended that the sampler should be lowered to within 5 m of the sea bed at the deepest point of the tow. This was considered particularly important for the capture of larvae recently hatched from eggs on the sea bed. Originally, the depth of the sampler was determined from calibration tables of wire length against sampler depth, but by the late 1970s acoustic and conducting cable systems for real-time measurement of the sampler depth and altitude were in widespread use.

Flowmeter Calibration.—Impeller type flowmeters were installed in the Gulf samplers used to capture larval herring during the earliest ICES surveys. The importance of accurate flow measurement was demonstrated by consistent differences in catch per unit volume between vessels conducting comparative fishing exercises (Wood, 1982), and the calibration of flowmeters was identified as being a significant source of variation. The key feature was the acceptance efficiency of the sampler nose cone. With the filtering net removed from a Gulf sampler, the mean water speed through the mouth opening differs from that of the sampler through the water. Flume tank studies reported by Harding and Arnold (1971) and Wood and Nichols (1983) indicated that the flow rate was accelerated in the centre of the mouth, and decelerated towards the edges, relative to the speed of the sampler through the water. The mean flow over the mouth area was estimated to be approximately 0.9 of the sampler speed (referred to as an "efficiency" of 0.9). The IHLS Working Group (Anon, 1985a) recommended that flowmeters should be calibrated in situ by towing the sampler at a fixed depth over a known distance with the filtering net removed, to determine the "free-flow" impeller revolutions per minute (c, in the following equation). The volume filtered during sampling tows (V, in m^3) should then be determined from the relationship $V = f \cdot A \cdot E/c$, where A is sampler mouth area (in m^2), f is flowmeter revolutions during the sampling tow, and E is efficiency determined from the flume measurements.

Harding and Arnold's (1971) measurements of efficiency were made with mini-impeller type flow-

Table 2. Annual Survey Reports of the International Herring Larval Surveys. Annual reports have been published as documents of the ICES Pelagic Fish Committee cited in the typical form ICES CM 1972/H:28, and typically entitled "Report on the International Herring Larval Surveys in the North Sea and adjacent waters in 1971/72." Surveys off the west of Scotland from 1971 to 1978 were published separately as ICES Committee Meeting documents under the typical title "The distribution and abundance of herring larvae to the west of Scotland in 1978." From 1967 to 1977 the annual reports from all surveys, including those west of Scotland, were combined into an ICES Cooperative Research Report under the typical title "Herring Larvae Surveys in the North Sea and adjacent waters, 1977/78"

Survey year	Report author(s)	ICES CM citation	Cooperative Research Report number and year of publication
1967/1968	Saville	1968/H:20	19 (1970)
1969/1969	Boetius	1969/H:34	19 (1970)
1969/1970	Wood	1970/H:4	22 (1971)
1970/1971	Zijlstra	1971/H:15	28 (1972)
1971/1972	Schnack	1972/H:28	34 (1973)
1972/1973	Saville and McKay	1973/H:13	41 (1974)
1973/1974	Wood	1974/H:13	48 (1975)
1974/1975	Pommeranz	1975/H:29	61 (1977)
1975/1976	Jacobsen and Hansen	1976/H:26	88 (1979)
1976/1977	Saville and McKay	1977/H:30	88 (1979)
1977/1978	Wood	1978/H:10	90 (1980)
1978/1979	McKay	1979/H:38	
1979/1980	McKay	1980/H:45	
1980/1981	McKay	1981/H:52	
1981/1982	Wood	1982/H:2	
1982/1983	Schofer	1983/H:57	
1983/1984	Saville and Rankine	1984/H:59	
1984/1985	Saville and Rankine	1985/H:33	
1985/1986	Rankine	1986/H:14	
1986/1987	Rankine and Bailey	1987/H:10	
1987/1988	Rankine	1988/H:62	
1988/1989	Rankine	1989/H:5	
1989/1990	Hopkins	1990/H:40	
1971	Wood	1972/H:6	
1973	McKay	1974/H:28	
1974	McKay	1975/H:44	
1975	McKay	1976/H:30	
1976	McKay	1977/H:31	
1977	McKay	1978/H:50	
1978	McKay	1979/H:37	

meters at various radial distances across the mouth of a sampler. However, other studies in wind tunnels could not confirm their results, and in particular, an unencased German version of the Gulf sampler was found to have an efficiency of approximately 1.0. More recently, Pitot tube measurements of flow gradients across the mouth of a Gulf sampler have indicated an efficiency of approximately 1.1 (Anon, 1990), confirming in situ observations using dye streamers that the water flow is accelerated into the mouth. The problem of accurate flow determination remains unresolved and is the subject of investigation by an ICES Study Group.

Sample Treatment.—Plankton catches from the sampling tows are preserved at sea in 4% buffered formaldehyde solution. Larvae are sorted from the samples either at sea or at a later date in the laboratory. Total length measurements (tip of snout to end of tail) are performed on all or a subsample of the larvae from each sample, and the data recorded in 1-mm length classes. Total length measurements are not corrected for the effects of shrinkage during capture and preservation.

The catches of larvae in each sampling tow are converted to densities below 1 m^2 sea surface ($D_L \cdot m^{-2}$ in each length class (L) using the flowmeter data: $D_L = (N_L \cdot d \cdot c)/(f \cdot A \cdot E)$, where N_L is the number of larvae in length class L caught during the tow, and d is the echo sounding at the midpoint of the tow (in m). This relationship assumes that the unsampled zone between the sea bed and the maximum

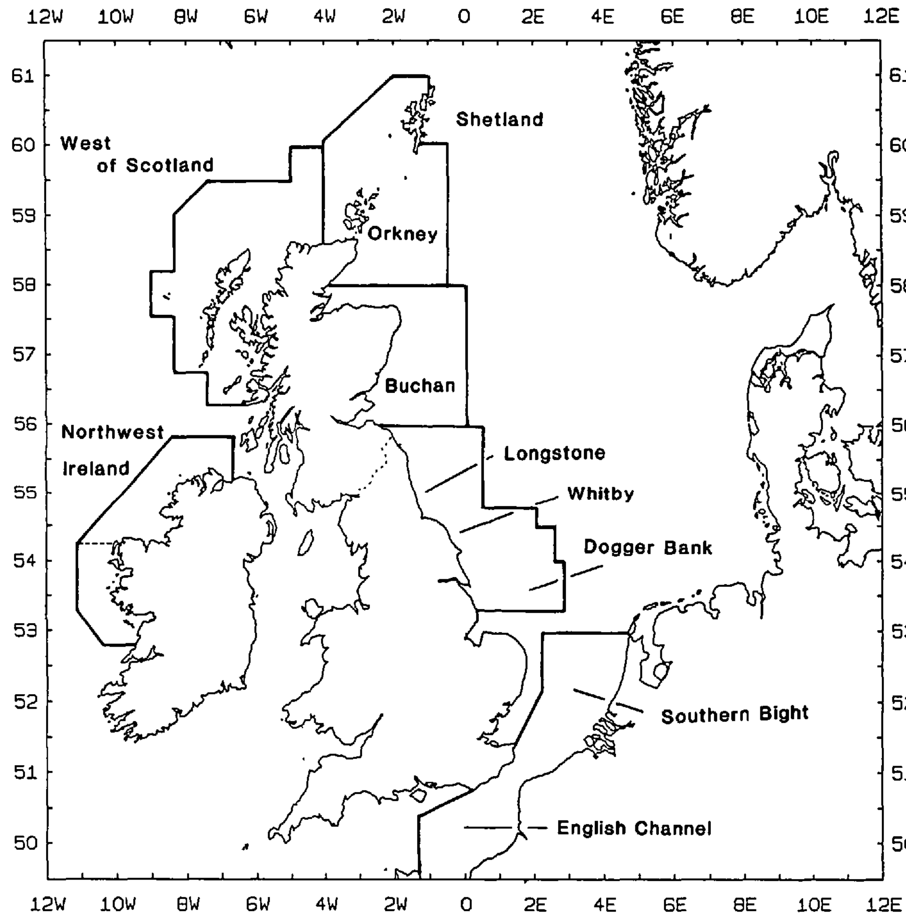

Figure 2. Sampling areas covered by the ICES International Herring Larval Surveys. The area sampled in the Skagerrak between 1967 and 1973 is not shown. The full area off northwest Ireland was covered only between 1981 and 1988. Prior to 1981 only the northern part was surveyed. All sampling off northwest Ireland was discontinued after 1988.

sampler depth (5 m above the sea bed) contains larvae at a density equivalent to the mean over the sampled part of the water column. No corrections are carried out for losses due to extrusion of larvae through meshes of the collecting nets, as field trials have indicated such loss to be insignificant for the recommended mesh size (Harding et al., 1969; Wood, 1972).

Larval Survey Design

The total area covered by the larval herring surveys is divided into subareas corresponding to the main spawning groups (Fig. 2). Sampling in each subarea is timed to coincide with the historical peak hatching periods (Table 3).

Sampling locations were first formally specified by the IHLS Working Group in 1971 (Anon, 1971), and are located at the centres of rectangles 10′ of latitude × 20′ of longitude (1/6 of an ICES statistical rectangle, approximately 18 km × 18 km grid). Prior to 1971, the pattern of sampling was somewhat variable. The number of sampling stations has changed from time to time to accommodate changes in the distributions of spawning activity and constraints imposed by changes in the available sampling effort. However, the LAI from 1972 onwards has been based on a constant subset of core stations constituting a standard area.

The spawning season in each area was divided into successive 14-d sampling periods, this being approximately the time required to complete a coverage of the sampling stations in an area.

Table 3. International Herring Larval Survey sampling periods

Area	Annual sampling period
Northern North Sea: (Orkney/Shetland/Buchan)	1–30 September
Central North Sea: (Longstone/Whitby/Dogger Bank)	1 September–31 October
Southern North Sea: (Southern Bight/English Channel)	16 December–31 January
West of Scotland	1 September–31 October
Northwest Ireland	1 October–31 November

Calculation of the Larval Abundance Index

Early IHLS Working Groups considered that any correlation between annual larval abundance and spawning biomass would become weaker with increasing age of the larvae, due to interannual variation in mortality and dispersal. An annual Larval Abundance Index (LAI) was therefore calculated on the basis of catches of only the most recently hatched larvae, and in particular larvae <10 mm in length. The mean hatching length of larvae is approximately 6.5 mm, and growth rates estimated from field investigations have been approximately 0.2 to 0.3 $mm \cdot d^{-1}$. Hence, the LAI included all larvae up to approximately 10 to 15 d old. The only exception to this rule was for the surveys in the Southern Bight of the North Sea and English Channel, where the hatching length of larvae was significantly larger and few larvae <10 mm were caught. For this reason, and for continuity with the very long time series of earlier data (from 1946), all sizes of larvae were included in analyses up to 1984. After 1984, the historical data from the Southern Bight and English Channel for 1946 to 1971 were disregarded, due to inconsistencies with more recent survey dates and sampling methods, and the LAIs for 1972 onwards were recalculated. Data on larvae ≥17 mm long were excluded from the calculations due to doubts concerning the effectiveness of the Gulf III for sampling the larger larvae (Anon, 1984).

For each 14-d sampling period, replicate estimates of the density (per m^2) of larvae <10 mm from individual 10′-latitude-×-20′-longitude sampling rectangles are first averaged (arithmetic mean). The mean density in each rectangle is then raised to the sea surface area of the rectangle, and the resulting abundances summed over a group of rectangles representing a "standard area" for the sampling period.

$$I_T = \sum_{r=1}^{R} \bar{D}_{rT} \cdot a_r$$

where I_T = standard area abundance index during the 14-d sampling period T, R = total number of sampling rectangles, r, in the standard survey area, $\bar{D}_{rT}$ = mean density of larvae in rectangle r during time period T and a = sea surface area of rectangle r.

The annual LAI for an area is then the sum of the standard area abundances for successive 14-d periods (Fig. 3).

The main difficulties in constructing the LAI accrue from three sources. First, the distribution of larvae is extremely patchy in space and time, leading to high variability in density between samples. In some cases, single samples of exceptionally high numbers of larvae (e.g., $>30{,}000 \cdot m^{-2}$ compared to an average of typically $<100 \cdot m^{-2}$) have dominated the annual LAI. Secondly, in some years the abundance of 10 to 15-mm and >15-mm larvae in the later time periods has been higher than can be accounted for by the abundance of <10-mm larvae, suggesting that the sampling programme had missed the peak production, or that there had been significant immigration. Finally, spatial coverage of the standard areas has been incomplete in some years, especially the pre-1979 surveys. The LAI requires data from every sampling rectangle in the standard area. Missing values must either be assumed to be zero, or filled by interpolation from neighbouring rectangles. Successive IHLS Working Groups up to 1985 attempted to devise rules for filling in missing values. However, there was no solution to this problem in the most extreme cases where >50% of the abundance index for a time period is based on interpolated values (Anon, 1985b). No detailed analyses of the precision or confidence intervals for the LAI has so far been carried out.

Calculation of Larval Production

Because of the difficulties in constructing a comparable LAI for each year, an alternative method of analysing larval survey data was developed by the IHLS Working Group (Anon, 1986, 1987) based

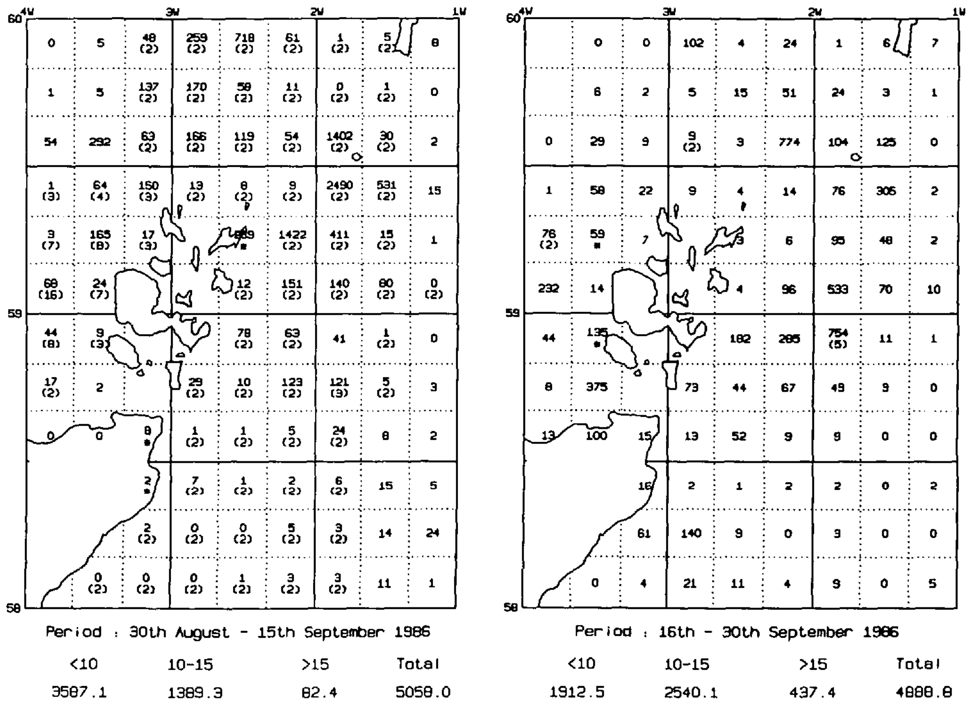

Figure 3. An example of data used to construct the Larval Abundance Indices for the 1986 surveys. The value shown in each rectangle is the mean number of larvae <10 mm per m^2 in each sampling period during the 1986 surveys in the Orkney-Shetland region. Data refer to results from a single tow unless indicated by a number in brackets representing the number of samples collected. Rectangles containing an asterisk were not sampled, but the density of larvae was estimated by interpolation from neighbouring samples. Total abundance indices ($\times 10^{-9}$) ([number$\cdot m^{-2}$]$\cdot$sea area, summed over the survey area) are shown for each of three size categories of larvae, and for all larvae.

on methods proposed by Christensen (1985), Lassen and Pedersen (1985) and Lough et al. (1985). The new method, referred to as the Larval Production Method, utilised data on each 1-mm length class of larvae (Fig. 4), rather than the summed abundance of larvae smaller than 10 mm.

The method estimated the production rate (i.e., hatching rate) of larvae (larvae$\cdot m^{-2}\cdot d^{-1}$) on successive days throughout the spawning season, averaged over the survey area. This was achieved by back-calculating the abundance at hatching length on the estimated hatching date, of each 1-mm length class in the daily mean length frequency distribution of larvae. The assumptions of the method were that: 1) Growth in length is linear over time, i.e., $L_t = L_0 + k(t - i)$, where L_t is the length on day t; L_0 is the length at hatching on day i, and k is the daily mean growth rate. 2) Mortality and emigration are constant over time and independent of length, i.e., $N_t = N_{(t-1)}\cdot e^{-Z} + P_t$, where N_t is the abundance of larvae on day t, Z is the daily mortality rate including emigration, and P_t is the production of newly hatched larvae on day t. 3) There is no immigration.

Combining the growth and mortality relationships given above, the production of newly hatched larvae on day i is given by:

$$P_i = N_{L,t}\cdot \exp[(L_t - L_0)\cdot(Z/k)]$$

where $i = (t - (L_t - L_0)/k)$ and $N_{L,t}$ = the mean abundance of larvae length L on day t determined from the daily average length frequency distribution (Lassen and Pedersen, 1985).

The larval production rate on any day may be estimated by back-calculating abundances from several sampling dates using different length classes of larvae in each case. For example, production of 6-mm larvae on 5 September could be estimated from sampling of 9-mm larvae on 17 September and also from 11-mm larvae on 25 September (growth rate 0.25 mm$\cdot d^{-1}$) (Fig. 5). The estimated production of a particular length class depends only on the ratio Z/k. However, an independent estimate of growth rate (k) alone is still required to determine the production day (i). During the development of the method, no relationship was found between estimates of production on any particular day and

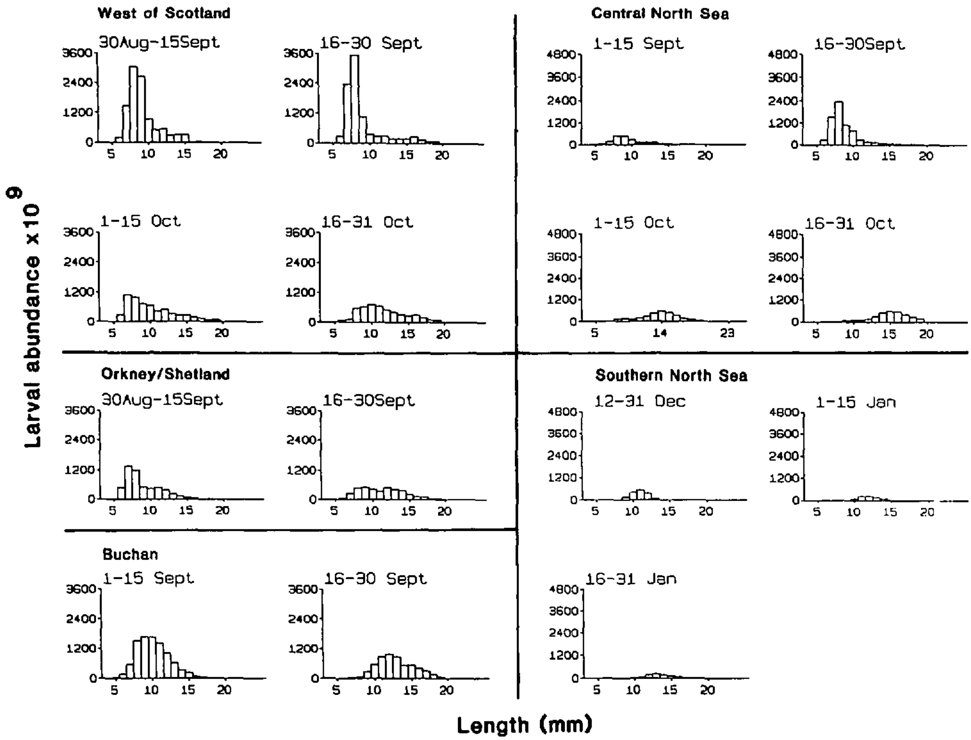

Figure 4. Abundance of larvae in 1-mm length categories by sampling period for west of Scotland and North Sea survey areas sampled during 1986/87.

the sampling date of the source data, indicating that the timing of surveys relative to the spawning period should not be a significant source of bias in the estimate of production for a particular day (Anon, 1986).

In practice, mean production rates (larvae $\cdot m^{-2} \cdot d^{-1}$) are estimated for successive 10-d periods covering the annual production period. All daily estimates of production rate falling within each 10-d period are averaged, and then raised by the sea area (m^2) of the survey region, to give an estimate of the total production of larvae (Fig. 6). The total annual production, referred to as the Larval Production Estimate (LPE), is then the sum of the productions in each 10-d period. There is a particular problem with estimating annual production in the southern North Sea due to the systematic lack of sampling covering the period approximately 20 December to 2 January in every year.

The critical parameter in the method is the length specific mortality rate (i.e., the ratio of daily mortality and growth rates, (Z/k, per mm) which is assumed to be constant. Z/k is estimated from the log mean abundance of each 1-mm length class over the whole spawning season (Fig. 7). A critical assumption of this approach is that the average production rate over the time period when all individuals in the largest length class included in the analysis were hatched, equals the mean production rate when all individuals in the smallest class were hatched. Investigation of the data has shown that this is probably valid only for the middle part of the total sampled length range of larvae (Anon, 1986). An examination of estimates of Z/k for six survey areas over the period 1980 to 1986 (Anon, 1987), indicated that a complete time series could not be produced for any of the areas, but that in general, between-area variation in mortality was greater than the interannual variation within an area (Table 4). Consequently, the mortality rate applied to each annual survey has been the average over preceding years in the same area, thereby ignoring any annual variations. Once a value for Z/k has been determined for a survey area, then the choice of daily growth rate (k, mm $\cdot d^{-1}$) has only minor consequences for the estimated production and mainly affects the estimated timing of peak production (Anon, 1987). The hatching length (L_0) is taken to be 6 mm in all areas except the southern North Sea and English Channel where 8 mm is used.

A second assumption in the estimation of Z/k is that all sizes of larvae are sampled with equal efficiency by the Gulf III. All larvae 6 to 16 mm in length (8 to 16 mm in the southern North Sea/

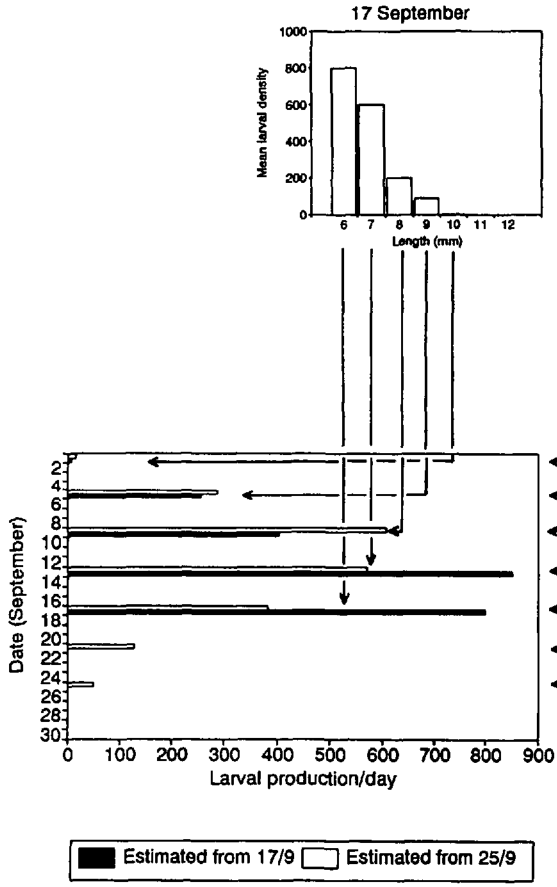

Figure 5. Diagram illustrating the operation of the Larval Production Method. Growth rate of larvae has been assumed to be 0.25 mm·d,$^{-1}$, and the mortality rate (Z/k) to be 0.35·mm^{-1}. Production (number of 6-mm larvae hatching·m^{-2}·d^{-1}) on 5 September can be estimated from both the mean density (m^2) of 9-mm larvae sampled on 17 and 11 mm larvae on 25 September.

English Channel) are included in the LPE calculations, and no distinction is made between samples collected at night and those collected during the day. However, differences in the day and night catch rates have been shown to increase with length for larvae >12 mm (Brander and Thompson, 1989). Length dependent diurnal avoidance of the sampler will lead to over-estimation of Z/k, although this may be compensated to some extent by under-representation of the larger length classes in the LPE calculations.

Close examination of the LPE method has highlighted inconsistencies which are difficult to explain. In particular, realistic timing of peak larval production can only be reproduced by assuming a growth rate of 0.35 mm·d^{-1}, which is approximately 50% higher than rates measured in the field (Anon, 1987). The crucial assumption of no immigration to the sampling areas is also hard to defend, since studies of larval dispersal have clearly demonstrated large scale advection, especially from the west of Scotland into the northern North Sea areas (Health, 1989, 1990).

No procedures for estimating the precision or confidence intervals of the LPE have yet been established.

Calculation of Spawning Biomass from Larval Production

Since the LPE should be an absolute estimate of annual larval production, then, with knowledge of egg mortality and mean annual fecundity, it should be possible to estimate directly the spawning biomass (Anon, 1986, 1987).

$$\text{Spawning biomass (Kg)} = (\text{LPE})/F \cdot S$$

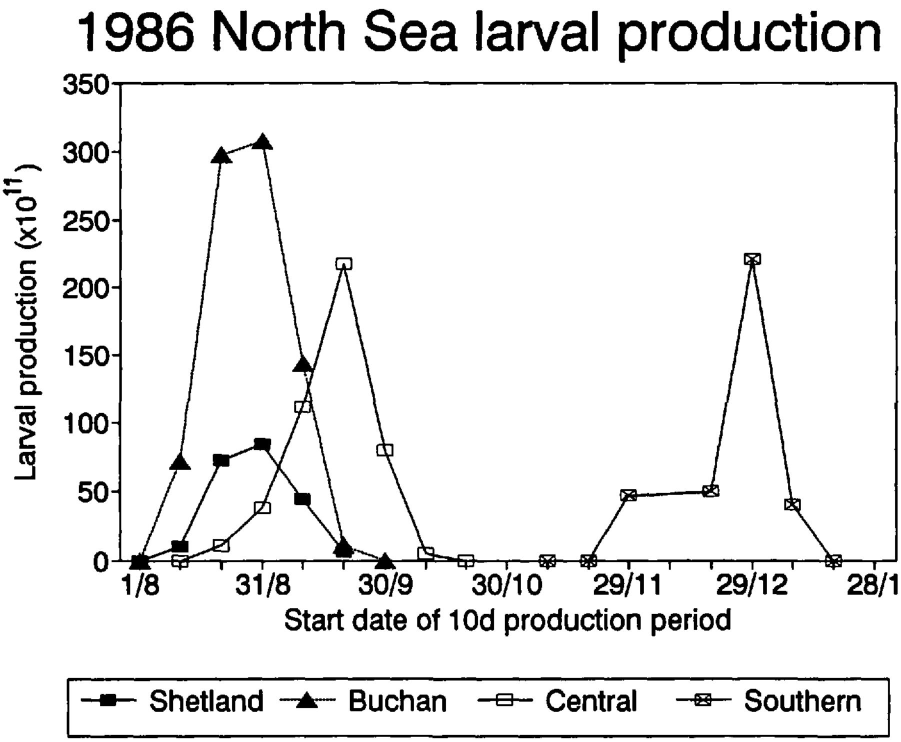

Figure 6. Production of larvae in the North Sea in 10-d periods between 1 August 1986 and 6 February 1987, back-calculated from daily mean length distributions by the Larval Production Method. The annual LPE is the sum of productions in successive 10-d periods in each survey area.

where F = annual mean fecundity (eggs/kg) including males. S = proportion of spawned eggs surviving to hatching.

The annual fecundity of herring varies with fish length and between stocks, depending on the spawning period. In general, summer or autumn spawning fish are more fecund and produce smaller eggs than winter or spring spawning fish of equivalent length. Fecundity data have not been collected regularly in all areas of the North Sea. However, in each area and year for which data are available, fecundity/length and weight/length relationships have been assembled and applied to the mean length distribution of fish sampled from commercial or research vessel catches taken during the spawning period, to estimate the mean fecundity$\cdot$kg^{-1} of females. Mean fecundity$\cdot$kg^{-1} stock (including males) was taken to be half of the female value, assuming a sex ratio of 0.5 and that the mean weights of males and females were identical (Table 5).

Losses from herring spawning beds due to oxygen depletion, physical disturbance, and predation have been reported to account for between 10 and 90% of the eggs laid (Aneer, 1985; Morrison et al., 1990; Tibbo et al., 1963; Toresen, 1985). However no data could be found on the mortality rate of eggs in the North Sea, although circumstantial evidence (e.g., from records of eggs in stomachs of demersal fishes) suggested that it might be considerable. As a consequence, no absolute estimates of spawning biomass can be calculated from the larval production results. However, ICES Working Groups have calculated conservative, minimum estimates of spawning biomass by assuming 100% egg survival (i.e., spawning biomass = (LPE)/F), using the fecundity data shown in Table 5 (Anon, 1986, 1987). At the very least, this procedure permits inter-regional differences in larval production to be interpreted in terms of spawning biomass, by accounting for the geographical variation in fecundity.

Comparative Merits of the LAI and LPE

Both the LAI and LPE methods have advantages and disadvantages. In general, the main advantages of the LAI are that it is simple to understand and has few inherent assumptions, and also provides incidental information on the distribu-

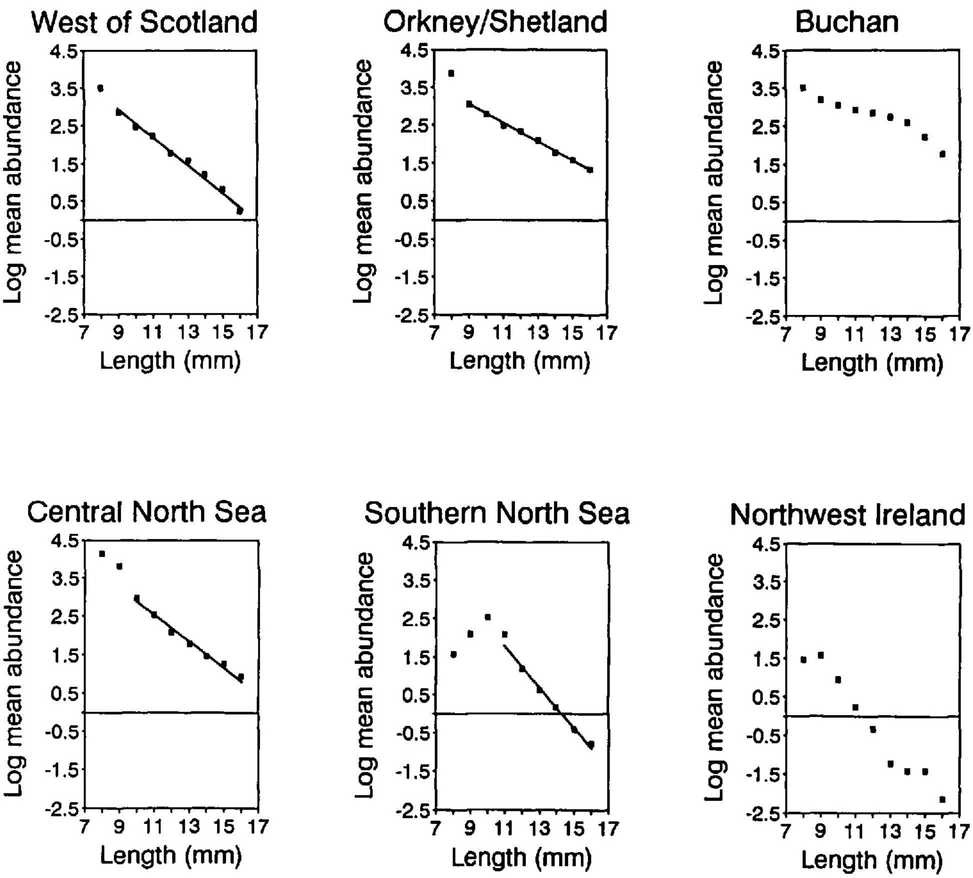

Figure 7. Data on log mean abundance of length groups of larvae during 1985/86 surveys. The mortality rate ($Z \cdot k^{-1} \cdot mm^{-1}$) was estimated by linear regression. Data from Buchan and northwest Ireland were considered unsuitable for analysis. Mortality was estimated from length groups 11 to 16 mm in the southern North Sea, 10 to 16 mm in the central North Sea, and 8 to 16 mm in the remaining areas.

tion of spawning activity within the survey region. On the other hand, the LAI utilises only a fraction of the data collected, ignoring the abundances of larvae >10 mm (except in the Southern Bight/Channel area), and requires a high sampling effort to achieve the necessary temporal and spatial coverage of the <10-mm larvae.

The main advantage of the LPE is that it makes use of data on a wide range of larva sizes, reducing the risk of missing the peak hatching period, and is therefore potentially less demanding of survey effort than the LAI. The method provides an absolute estimate of annual larval production whereas the LAI is merely an index. Hence, the LPE also has, in principle, the potential to estimate spawning biomass directly, which the LAI does not. The main disadvantage is that it requires a number of crucial assumptions concerning growth, mortality, and immigration that are often difficult to support. The use of size classes of larvae >10 mm is also contentious on account of evidence of increasing diurnal avoidance of the Gulf sampler with increasing length of larvae.

Table 4. Mortality rate estimates ($Z \cdot k^{-1} \cdot mm^{-1}$) of larval herring in each survey area, estimated from the log-mean larval abundance over the survey period. (*) indicates that the mortality rate could not be estimated from the data (from Anon, 1987, 1991)

	Survey area				
Year	West Scotland	Shetland	Buchan	Central North Sea	Southern North Sea
1972	0.49	0.57	*	0.42	*
1973	0.62	0.38	*	0.34	*
1974	0.36	*	0.27	0.49	*
1975	0.46	*	*	0.39	*
1976	0.32	0.42	*	0.45	*
1977	*	0.11	*	*	*
1978	*	*	0.70	*	*
1979	*	0.29	*	0.40	*
1980	0.39	*	*	*	0.33
1981	0.34	0.29	*	*	*
1982	0.39	0.25	*	0.40	0.80
1983	*	0.27	0.43	0.33	*
1984	0.57	0.20	0.42	*	0.54
1985	0.37	0.25	*	0.33	0.56
1986	0.24	0.28	0.27	*	0.48
1987	0.53	0.37	0.37	0.35	0.64
1988	0.47	0.53	0.38	0.31	0.71
1989	0.40	0.39	0.22	0.46	
1990	0.64	0.36	0.40	0.38	1.07
Mean 1980–1990	0.43	0.32	0.36	0.37	0.64

Long-term Changes in Larval Distribution and Abundance

Early applications of larval distribution data by Wood (1930) and Clark (1933) successfully delineated the general distribution of the major spawning areas. However, Cushing (1964) and Cushing and Bridger (1966) were the first to use larval survey data to document long-term trends in spawning activity in the English Channel. Saville (1971) showed that trends in the abundance of larvae in the northern North Sea reflected geographical shifts in the distribution of spawning activity.

It is difficult to combine the time series of larval distribution and abundance prior to 1972 with the data currently available in the IHLS database, partly because the survey methods used in the earlier years were somewhat different from those adopted more recently, and partly because the raw data from the pre-1972 surveys are no longer readily accessible. Nevertheless, an attempt has been made to compile a complete time series from 1946 to 1990, using the abundances of larvae published by Saville (1971) and Saville and McKay (1973) for the northern North Sea areas (Shetland and Buchan), van de Kamp (1976) and Zijlstra (1966) for the central North Sea, and Wood (1978) for the southern North Sea in the period 1946 to 1971. For the period 1972 to 1990, LAI data calculated for reduced sampling areas corresponding approximately to the areas covered during the 1946 to 1971 period, were available from Anon (1990). Early data collected with Hensen, Heligoland, or other conical nets were corrected to conform with Gulf III catch rates by intercalibration of the sampling gears (Saville, 1971).

The recent, reduced area LAIs (Anon, 1990) were calculated on the basis of 30-d time periods in each survey region. The total North Sea LAI was the sum

Table 5. Mean fecundity (eggs·kg^{-1} [$\times 10^5$], including males) for each IHLS sampling area. (*) indicates values estimated from nearest years and/or areas for which data were available. (From Almatar, 1987; Anon, 1986; P. Hopkins, pers. comm. and unpubl. data)

	Survey area			
Year	West Scotland	Shetland and Buchan	Central North Sea	Southern North Sea
1972	1.39*	1.56*	1.79*	0.94
1973	1.39*	1.56*	1.79*	0.93
1974	1.39*	1.56*	1.79*	0.87
1975	1.46	1.59	1.79*	1.01
1976	1.23	1.52	1.79*	0.74
1977	1.49	1.57	1.79*	1.02
1978	1.37	1.57	1.79*	1.18
1979	1.49	1.64	1.79*	1.07
1980	2.04	1.69	1.79*	1.14
1981	2.12	1.51	1.79*	1.06
1982	1.95	1.60	1.83*	1.11
1983	1.88	1.53	1.82*	1.10
1984	1.75	1.67	1.67	1.04
1985	1.86*	1.60*	1.88	1.08
1986	1.85*	1.60*	1.76*	1.08*
1987	1.86*	1.60*	1.76*	1.08*
1988	1.86*	1.60*	1.76*	1.08*
1989	1.86*	1.60*	1.76*	1.08*
1990	1.86*	1.60*	1.76*	1.08*

of values in each area. In the main, data from the pre-1972 period were presented as abundance indices for successive 15-d periods. Where possible, data were therefore adjusted to achieve consistency between areas and with the more recent LAI data. In years when all sampling areas had been covered, the data were summed to provide an abundance index for the total North Sea. The main difficulty arose with data for the central North Sea from 1960 to 1965, when only the Dogger Bank area was surveyed. Data from 1969 to 1974 (van de Kamp, 1976) indicated that on average the Dogger Bank/Dowsing region contributed 14% of the total central North Sea larvae. Hence, the data from 1960 to 1965 raised accordingly.

Despite the high degree of uncertainty concerning the pre-1972 data, the long time series shows the decline and resurgence of the North Sea herring (Fig. 8a). The trend is consistent with spawning biomass estimates from a Virtual Population Analysis (VPA) of fishery catch data from 1947 to 1990 (Anon, 1989, 1991) although, not surprisingly, the specific relationship between abundance of larvae and spawning biomass is clearly different for the pre- and post-1972 data. It could be argued that the larval data and VPA are not truly independent of each other since LAI values are used to "tune" the VPA. However, the tuning affects only the fishing mortality estimates for the final year of the VPA, and these in turn only have a major influence on spawning biomass estimates for the final 2 to 4 years of the analysis. Estimates for earlier years are comparatively insensitive to the tuning procedure.

Larval distribution data (Fig. 9) and calculated LAIs for each survey area (Fig. 8b) show that the changes indicated by the larval surveys have not occurred uniformly throughout the North Sea. The central North Sea area took the longest to recover following the collapse in abundance of larvae in the late 1960s. Fishery catch data cannot readily be assigned to each spawning group since the fish intermingle relatively freely, except during spawning periods. Consequently, there

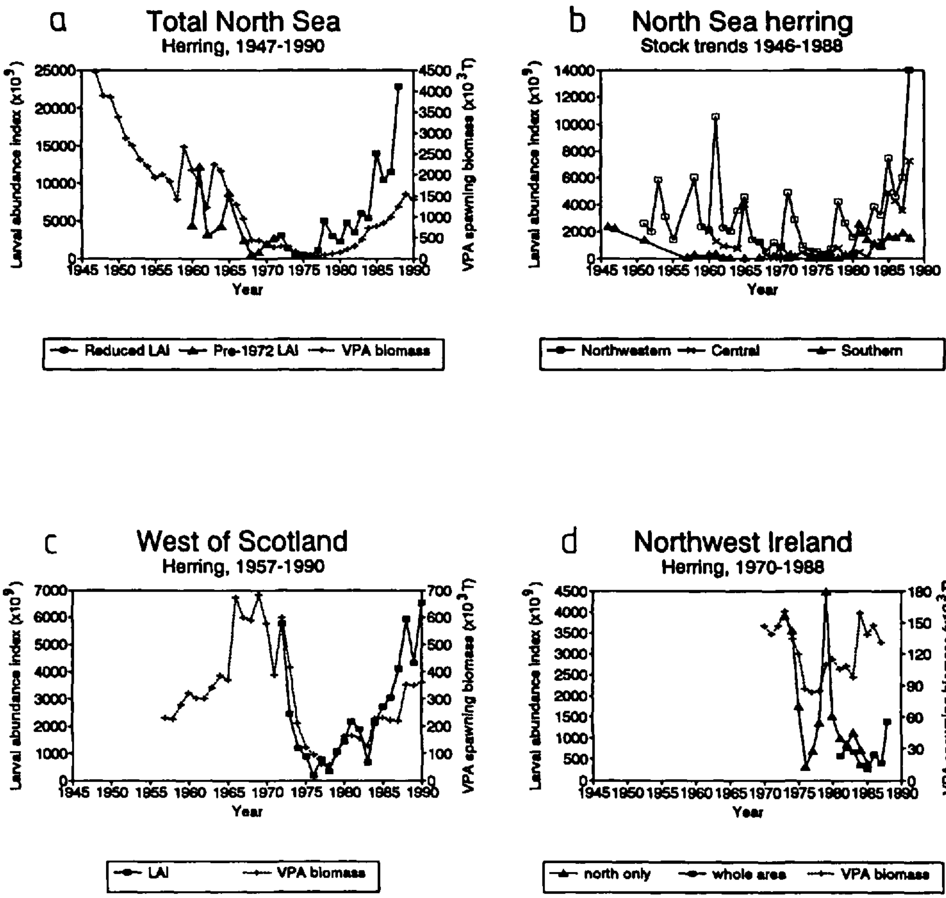

Figure 8. Long term (1947 to 1990) trends in annual Larval Abundance Indices and spawning biomass estimated from Virtual Population Analysis for a) the whole North Sea, b) the northwestern central, and southern subregions of the North Sea, c) the west coast of Scotland, and d) northwest Ireland. North Sea data for 1946 to 1971 derived from a variety of sources; data for 1972 to 1988 are for reduced sampling areas (Anon, 1990). 1973 to 1985 series for northwest Ireland refer to the northern part of the area only; 1981 to 1988 data refer to a different index for the full survey area.

are no absolute estimates of spawning biomass attributable to the individual spawning-stocks, only for the North Sea as a whole.

No LAI data are available for the area west of Scotland prior to 1972. However, the post-1972 data series show a strong and consistent relationship to spawning biomass derived from VPA (Fig. 8c). The maximum biomass of the stock west of Scotland has been substantially smaller than that in the North Sea, but the stock apparently both collapsed and recovered more quickly than in the North Sea.

VPA data for herring stocks off northwest Ireland indicate that the population has been comparatively stable over the period from 1970 to 1988, although the data may be misleading since the catch statistics forming the basis of the VPA may not refer to an isolated population. The data have not shown a consistent relationship with larval survey results (Fig. 8d). Two indices for larvae have been calculated, the first referring to only the northern part of the region, surveyed from 1971 to 1988, and the second to the full area, surveyed from 1981 to 1988.

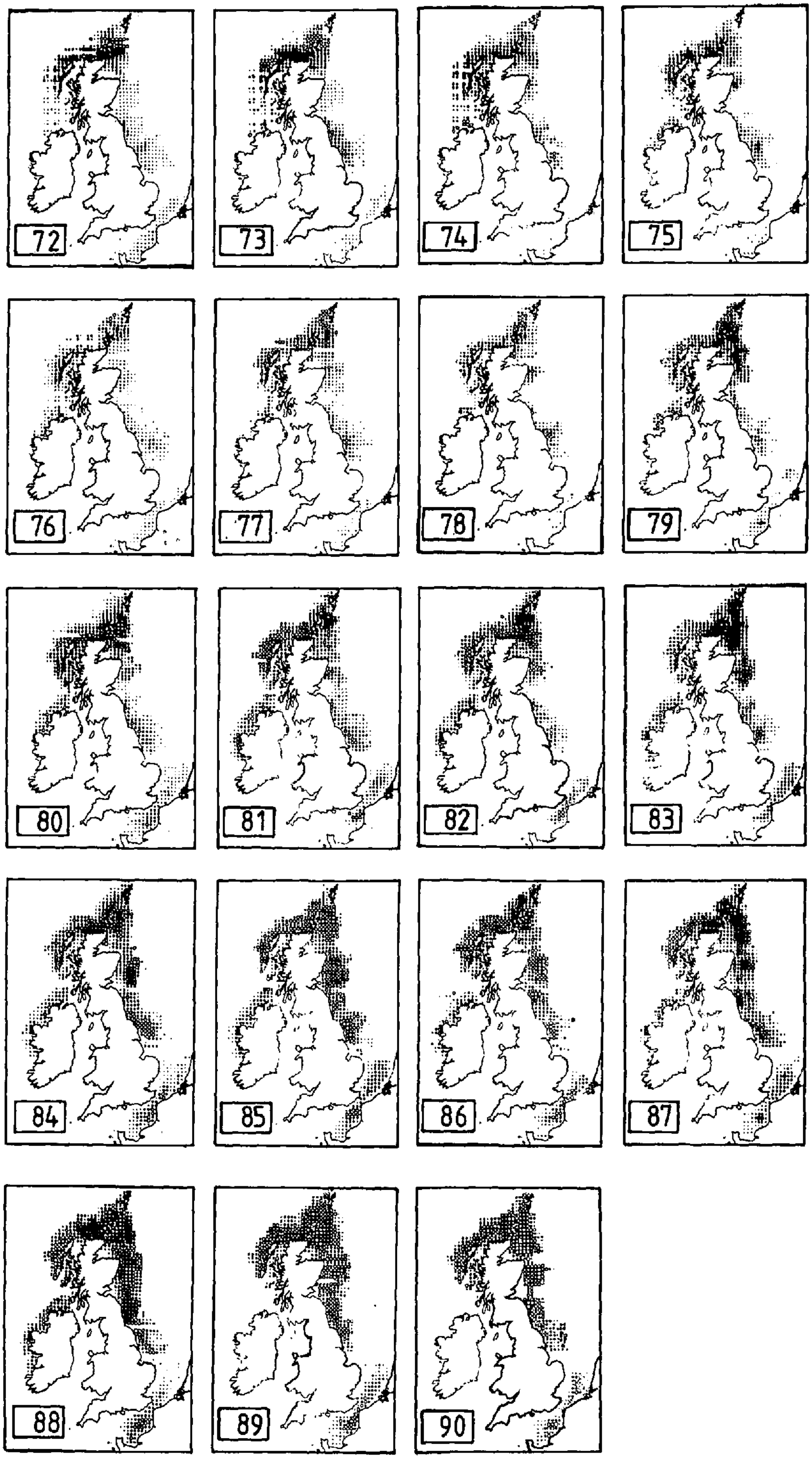

Figure 9. Distributions of the herring larvae sampled during the International Herring Larval Surveys between 1972 and 1990. The largest symbols represent an annual average density of larvae > 1,000 · m^{-2} at a particular sampling location. Smaller symbols denote lesser densities.

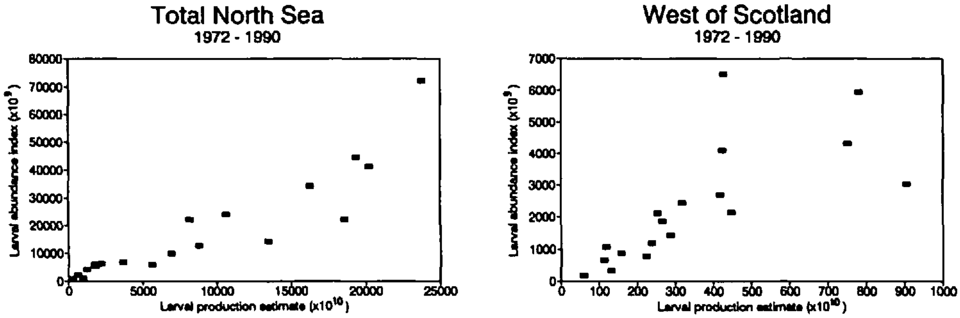

Figure 10. Relationships between larval production estimates (LPE) and larval abundance indices (LAI) for the periods from 1972 to 1990 in the North Sea and to the west of Scotland. North Sea: $r^2 = 0.824$; west Scotland: $r^2 = 0.544$.

LPE data for the North Sea in the period 1972 to 1990 show a similar trend to the LAI values (Fig. 10). However, off the west coast of Scotland, the correlation between the LPE and LAI has been poor, possibly due to high variability in the rate of emigration from the area as a result of advection by water currents (Heath and Richardson, 1989). No reliable LPE data are available for the northwest Ireland area, due to inconsistencies in the survey coverage from year to year.

Over the long term, the relationships between LAIs and VPA estimates of herring spawning biomass have been reasonably good. Cushing and Bridger (1966), Postuma and Zijlstra (1974), Burd and Wood (1976), Anon (1976, 1981) and Saville (1978, 1981) have advocated the use of linear regression relationships calculated from such data for stock assessment purposes. However, this practice has been criticised on statistical grounds. In particular, most North Sea LAIs during the 1980s were outside the range of previously encountered values, thereby requiring extrapolation rather than interpolation from historical data in order to estimate spawning biomass. The relationship for the west of Scotland has had a high positive intercept with the y axis (spawning biomass) at zero larval abundance, suggesting their either the relationship is nonlinear, or that the indices are biased (Fig. 11). There were no significant relationships for the northwest of Ireland area over the period from 1981 to 1988 (Anon, 1988), and the surveys were abandoned thereafter.

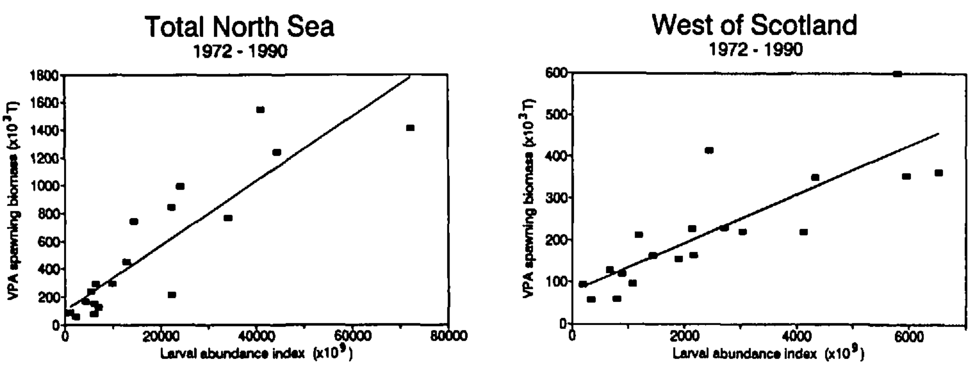

Figure 11. Relationships between Larval Abundance Indices and spawning biomass from Virtual Population Analysis in the North Sea and to the west of Scotland for the periods from 1972 to 1990. North Sea: Biomass = 103.0 + 0.023·(LAI), $r^2 = 0.791$; west of Scotland: Biomass = 76.4 + 0.058·(LAI), $r^2 = 0.676$.

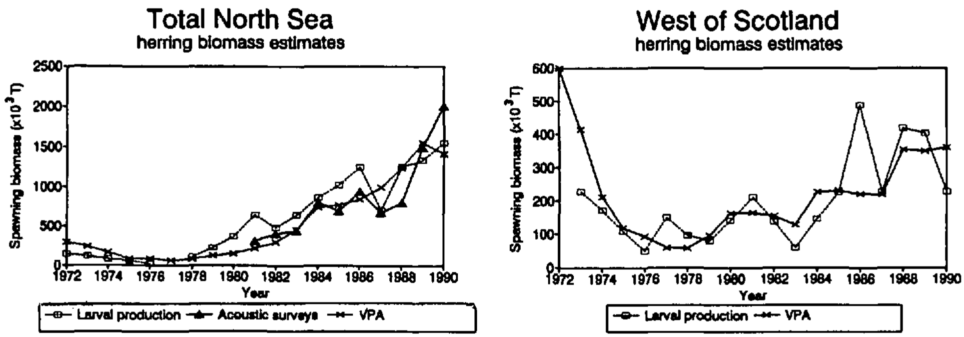

Figure 12. Herring spawning biomass for 1972 to 1990 for the North Sea and west of Scotland, estimated directly from Larval Production Estimates (LPE/[fecundity·kg^{-1}]), acoustic surveys (North Sea only), and Virtual Population Analysis (VPA).

Minimum estimates of spawning biomass calculated directly from LPE and fecundity data are of the same order as, or slightly higher than, the biomass estimates calculated from fishery statistics by VPA, and from acoustic surveys (Fig. 12). This result is extremely surprising since the biomass estimates derived from LPE data take no account of egg mortality and should therefore be substantially lower than the VPA or acoustic estimates. The anomaly cannot be accounted for by VPA tuning procedures since these affect only the relative levels within the analysis, not the absolute levels. The acoustic survey results are truly independent of the data for larvae. Hence, the results must indicate either remarkably low mortality of North Sea herring eggs, or some unknown systematic bias in one or more of the methods. A possible source of bias may be over-estimation of the mortality rate Z/k used in the calculation of the LPE, caused by avoidance of the Gulf III Sampler by the large sizes of larvae. Over-estimation of mortality rates would inflate the LPE, although this should be compensated to some extent by the under-representation of large larvae in the sampled length distributions. Because of these concerns, biomass estimates calculated directly from LPE data have been regarded merely as improved versions of the LAI for stock assessment purposes.

Use of Larval Survey Data in Stock Assessment

Prior to the closure of North Sea herring fisheries in 1977, the Herring Assessment Working Group (HAWG) relied mainly on Virtual Population Analysis of commercial catch statistics to estimate the biomass of herring stocks. During the early 1970s, LAI data were used primarily as confirmation of changes in stock size. However, with the collapse of stocks and closure of fisheries, larval survey data became the only method for assessing the mature stock.

Data from larval and acoustic surveys were the basis for the decision to allow a resumption of herring fisheries in the North Sea in 1983. With the acquisition of new fishery catch statistics, a Virtual Population Analysis could once again be performed on the herring stocks. However, the lack of catch data during the closure years meant that convergence of the VPA was slow, and fishery independent estimates for stock biomass were required for estimating fishing mortality during the last year of each analysis. There had been little experience of the reliability of acoustic surveys at that time, so LAI data played a vital role in the re-establishment of the VPA series during the years following re-opening of the fisheries.

As experience of acoustic survey methods increased, so the arguments for their use in the stock assessments became stronger. Between 1983 and 1988, the Assessment Working Group chose to use either acoustic survey or larval survey data as the basis for their assessment, the justification for selecting one or the other varying from year to year. In 1989, a more objective approach was introduced, whereby time series of annual data from acoustic, larval, and annual trawl surveys were compared with converged VPA data in a regression type analysis designed to assign weighting factors to each fishery independent method (Anon, 1989). In 1989, the North Sea spawning biomass estimates for the unconverged years of the VPA (1986 to 1988) were based mainly on the acoustic surveys (71%) rather than the larval surveys (10%).

The results of surveys in 1989 and 1990 suggested that the high confidence previously placed in acoustic survey data may have been misplaced. Both the 1989 and 1990 acoustic surveys indicated a trend of rapidly increasing stock size in the North Sea, which could not be sustained by either the catch statistics or the larval survey data (Fig. 12). The analyses performed by the Assessment Working Groups in 1990 and 1991 increased the weighting of larval survey data at the expense of acoustic survey data. In 1991 the LAI for the North Sea was disregarded completely in favour of the LPE, whilst for the west coast of Scotland the LAI was used as the basis for the assessment, and the LPE ignored (Anon, 1991).

Viability of Larval Surveys for Stock Assessment

Larval survey data have been subjected to rigorous evaluation since the early 1980s, and their value in relation to alternative assessment methods has been questioned on the account of their cost. However, their performance invariably has been evaluated by comparison to the fishery-dependent VPA, which has not been subjected to the same critical examination, despite the acknowledged variable quality of the international catch statistics. Under-reporting of fishery catches as a consequence of discarding practices may be a significant factor in North Sea fisheries, and is only now beginning to be taken into account in the assessments. Discarding would lead to underestimation of biomass by the VPA, providing a possible explanation for the inconsistency between minimum spawning biomass estimates derived directly from LPE, and the VPA biomass values.

Despite the continuing reliance of the ICES herring assessment procedure on larval survey data, there has been a steady decline in international support for the surveys since 1984, with an all-time minimum number of ship days available for the 1990 surveys (Fig. 13).

The progressive contraction of the surveys since 1986 has forced a critical re-examination of the survey methods by the IHLS Working Group (Anon, 1990) to determine whether the viability of the surveys has been compromised by the reduction in sampling effort.

The basic assumption of no immigration to the population required for calculation of the LPE imposes constraints on the coverage of the larval distribution. With reducing spatial coverage, larval dispersal makes an increasing contribution to the changes in larval abundance within the survey area. Reduced temporal coverage does not invalidate the analysis of survey data, but restricts the ability to estimate the mortality rate (Z/k), since the assumption of constant average production may be violated. Nevertheless, accepting that estimation of the mortality rate would be impossible, the LPE could be calculated for a single annual survey coverage performed at a suitable time and covering an adequate area. Analysis of historical data on a survey-by-survey basis indicated that the timing of surveys would be critical for the success of such an approach. Early or late

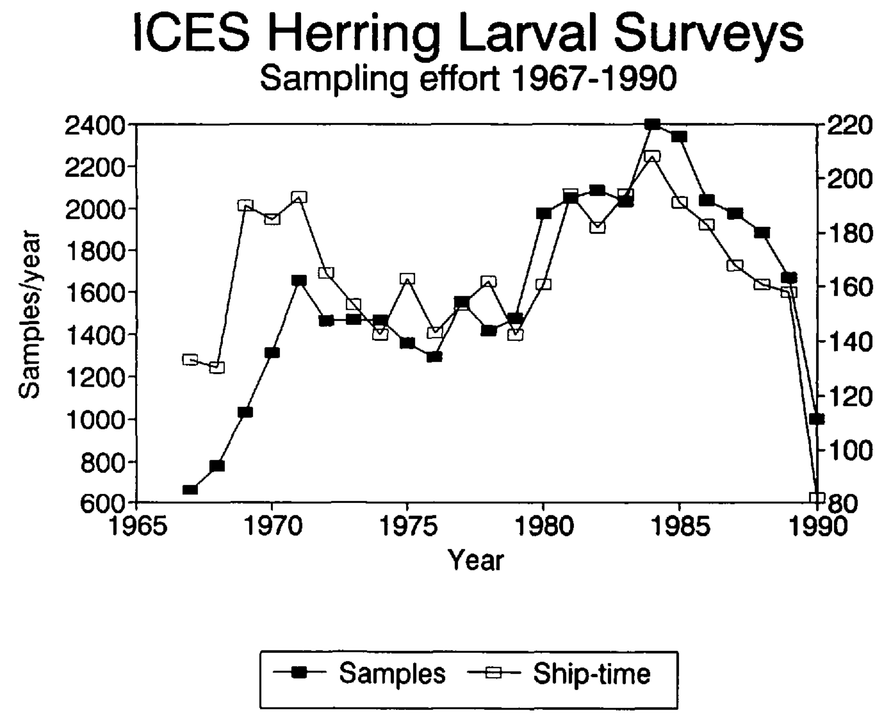

Figure 13. Trends in sampling effort (samples·year^{-1} and days of ship time·year^{-1}) for the International Herring Larval Surveys, 1967 to 1990.

coverages gave poor estimates of the total production, whilst single surveys at the critical time yielded estimates of between 80 and 120% of those generated by the full data set. The conclusion of the analysis was that the single survey approach could be used to sustain the LPE method, but with reduced precision, provided that there were no shifts in peak spawning time and that historical average mortality rates could be used in each survey area.

The reduction in resources for North Sea herring assessments has also focused attention on the relative merits of larval and acoustic surveys as sources of fishery-independent data. The main arguments in favour of acoustic methods are that they have considerable potential for improvement and should give absolute estimates of biomass, whereas the larval surveys seem to have achieved almost their full potential and can only give minimum estimates of biomass. On the other hand, the long time series of data for larvae is a valuable asset which will be compromised if the surveys are interrupted. Acoustic surveys have a more recent history and there is still considerable doubt as to the reliability of their results due, in part, to the uncertainty of target strength values. In addition, acoustic surveys, in their present form, have no capacity to provide data relating to individual spawning areas, whereas this information is available from larval surveys. Such data are used increasingly to assess the depletion of individual spawning populations and the potential impact of offshore oil exploration and gravel extraction activities. Taking all factors into account, in the event of having to choose between larval and acoustic surveys as the provider of fishery-independent data for stock assessment, the larval surveys would at present appear to be the preferable option.

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