

The effect of local wind on the distribution of Norwegian spring spawning herring (*Clupea harengus* L.) larvae

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Abstract. Distribution of newly hatched larvae of Norwegian spring spawning herring (*Clupea harengus* L.) and prey availability are described in relation to wind and hydrophysical events. Larvae were collected in April 1993 off Karmøy and in the Boknafjord. Samples of zooplankton and nutrients as well as data on hydrophysical processes were obtained. During prevailing southerly winds herring larvae were distributed more nearshore, whereas after only 2 days of northerly winds larvae were distributed up to 30 km offshore. Microzooplankton concentrations decreased and nutrient concentrations increased off western Karmøy with the shift from southerly to northerly winds. Relatively high proportions of postyolk-sac larvae (stage 2a) and macrozooplankton were observed in the inner Boknafjord. The significance of short-term environmental events are discussed in relation to larval herring advection.

Key words: advection, current, southwestern Norway.

Introduction

Spawning products in the pelagic phase are subject to physical forces during the drift period. For fish with demersal eggs, such as herring (*Clupea harengus* L.), only the larval stages are affected during this period. This can be through advection [1,2] or retention in local areas [3–5].

Meteorological factors prevailing during early life stages of herring are believed to have great impact on the relative amount of time spent in inshore or open sea environments. For Norwegian spring spawning herring, the likelihood of being lost from the main current system flowing northwards is higher when the proportion of larvae transported offshore is high. But if the larvae are not dispersed further offshore and are still entrained in the main current system, the likeliness of growing up in the Norwegian Sea or the Barents Sea may be increased compared with an early advection towards inshore regions. Strong year-classes of Norwegian spring spawning herring spend a relatively high proportion of their juvenile period in the Barents Sea, and this mechanism is to be considered advantageous for the recruitment to the stock [6].

The area off western Karmøy is a coastal bank, nearly 30 km wide and with

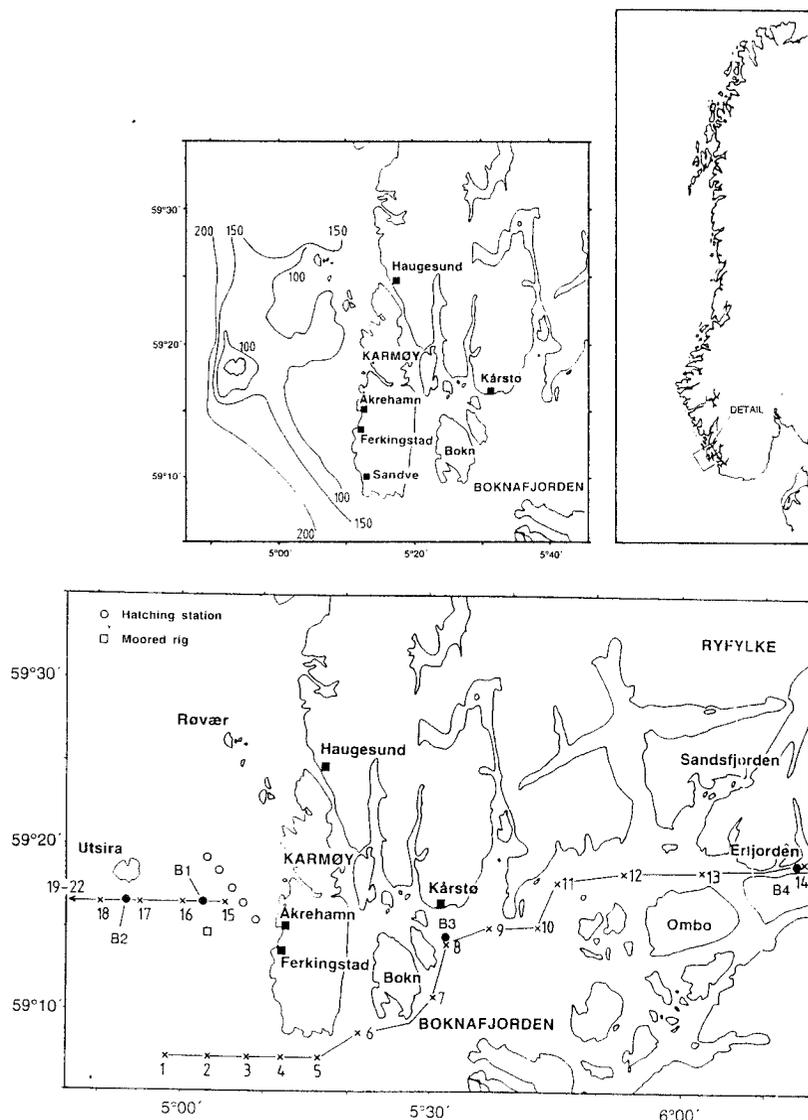


Fig. 1. The study area at Karmøy with depth contours (upper). Transect (solid line) with CTD-stations (x) conducted from western Karmøy to and including the Boknafjord during 20–23 April (stations 1–14) and off western Karmøy during 15–17 April (stations 15–22). Stations B1–B4 for sampling of nutrients, zooplankton and herring larvae (lower). The position for the location of a moored rig with current meters is also given. Stations for regular sampling of herring larvae at a hatching ground off Ferkingstad (o) during 29 March–15 May are also given. Location of stations (T80 net) for sampling herring larvae during the survey are given in Figs. 7, 8 and 10.

depths of 30–100 m (Fig. 1), bordering to the Norwegian Trench and the North Sea. Spawning grounds of herring have historically been important in this area [7] and after 1989 spawning has again been observed off Ferkingstad, and at Bokn and Kårstø [8,9]. The bank is regularly flushed by coastal or Atlantic water masses. The direction of the currents vary largely between southwards and northwards according to the tidal cycle. The hydrography of the region is also regularly modified by freshwater runoff from the surrounding fjords. The Norwegian coastal current flowing northwards off the coastal region of Karmøy is characterized by a strong and variable residual current caused by fluctuating local winds and windfields from the North Sea, outbreaks of brackish water in the Skagerrak, mesoscale frontal waves and associated eddies. The residual current in the area is the major transportation system of fish larvae to more northern nursery areas.

During blocking of outflow of brackish water in the Boknafjord due to winds from south-southwest, a frontal area between coastal and fjord water appears from where the upper layer water penetrate into intermediate depths in the inner fjords with a compensating outflow below [10–12]. Larvae may be entrained in specific water masses and advection of larvae to inshore coastal areas shortly after spawning has been reported for herring larvae off Helsinki in the Baltic [13] and in the coastal Gulf of Maine [14,15]. Also at the west coast of Scotland herring larvae may be retained in the vicinity of hatching grounds, depending on their exact location in relation to the coastal current [16,17]. Concentrations of copepod food items may also be retained together with herring larvae [18,19]. It is likely that variable wind stress is the triggering factor of frontal waves and that the wave motion probably is governed by baroclinicity and bottom topography [20]. In periods with stratification of the water column and northerly winds, eddies may be shed 150–200 km off the coast at Karmøy.

This investigation was carried out at a herring spawning ground off Karmøy and in the Boknafjord area during the hatching period in April 1993. The aim of the study was to examine the effects of local wind stress and hydrophysical events on the distribution of young herring larvae and their potential food organisms. The water layers may respond differently to variations in wind stress and tidal currents, and this may have implications for the larval distribution and their feeding and growth conditions. During the survey in April 1993 southerly winds predominated during the hatching season, interrupted by northerly winds in shorter periods only. The immediate effects on biological particles (e.g., herring larvae and their prey items) following such periods were examined in the hatching area and its vicinity. A null hypothesis suggests that different wind regimes have no immediate effects on the dispersal of larvae and their prey. Alternatively, different wind regimes can have significant impact on the dispersal of larvae and prey. Such a variable occurrence of inshore or offshore environments as nursery areas for the larvae may have great impact for the stock structure and also for management of the herring fisheries.

Material and Methods

Survey period and area

The RV "Håkon Mosby" conducted surveys, primarily off the western coastline of Karmøy during 14–23 April, 1993. Due to periodical strong winds, particularly in the western offshore area, the survey was frequently interrupted and redirected to more sheltered areas where sampling could be carried out, i.e., in the surrounding fjords. Figure 1 shows the area and stations at which sampling were conducted.

Physical data

Temperature and conductivity (converted to salinity) were measured at selected stations, using a Neil Brown Mark III CTD-sonde, operated from the vessel. The CTD-data were averaged over one meter depth intervals.

Currents were measured at a moored rig, located northwest of Ferkingstadøyene on the west coast of Karmøy (59°16.8'N 05°01.5'E) (Fig. 1). The rig carried three Aanderaa current meters (25, 55 and 80 m depths). The measuring interval was 10 mins. In order to eliminate the tidal signal, the data were filtered using 40 h smoothed average means.

The wind conditions, measured at Utsira lighthouse (see Fig. 1), are assumed to be representative for the area of investigation. Individual measurements of wind data were performed every 6 h. Wind data were provided by the Norwegian Meteorological Institute.

Almost no precipitation occurred during the survey period and data from the only power plant outlet in the area indicated that freshwater runoff would make no significant influence on the stratification of the fjord water in this period.

Data on mean water level variations at Stavanger in April were provided by Norwegian Hydrographic Service. Tidal signals were removed from the observations.

Biological data

A rosette sampler (attached to the CTD), equipped with four 5 l Niskin bottles was used at stations B1–B4 to collect water samples at depths of 2, 10, 30 and 50 m for analyses of nutrients and micro- and macrozooplankton. Also a Juday net (180 µm) was applied for sampling zooplankton. The net was hauled vertically (150–0 m), or from close to the seabed to the surface in shallow areas, at a speed of about 0.5 m s⁻¹. Nutrient samples (100 ml) were added 2–3 drops of chloroform, and later analysed for nitrate, phosphate and silicate with an automatic analyser.

Sampling of herring larvae were conducted at 117 stations, using a 0.5 m² 375 µm net (T80). The net was hauled vertically (75–0 m), or from close to the seabed to the surface in shallow areas, at a speed of about 0.5 m s⁻¹. In catches of ≤20 herring larvae, all were measured fresh and staged according to Doyle [24]. For catches of >20 larvae, a subsample of 20 specimens were analysed for size and stage. All

specimens were counted and preserved in 96% ethanol. All herring larvae beyond stage 1c were examined for gut contents, but all guts were empty.

Zooplankton (sample volume: 10 or 15 l) retained on 30 µm mesh sieves was preserved in 96% ethanol, and later enumerated and identified to the lowest taxon possible. Microzooplankton was arbitrarily defined as zooplankters with body lengths ≤600 µm, which include the most appropriate prey size spectra [21–23] and macrozooplankton was defined as zooplankters with body lengths >600 µm. Copepod nauplii were further classified into two size fractions: ≤250 µm and 250–600 µm. The average depth integrated nutrient concentrations and zooplankton densities in µM and number l⁻¹ respectively, were calculated according to the depth interval represented by each sample.

At five predetermined stations close to the Ferkingstad spawning ground (Fig. 1), sampling of herring larvae was conducted regularly twice a week from 29 March to 15 May with a T80-net hauled from the bottom to the surface. All samples were preserved in 96% ethanol for further analyses.

Herring eggs hatch as stage 1a larvae [24]. The mean duration of this stage is 1–3 days [24,25], and the larvae continue the development through the subsequent yolk sac stages 1b and 1c and pass a transitional stage 1d (without yolk remains) [26] prior to developing into the post yolk sac stages 2a, 2b and further [24]. The rate of development is temperature dependent, but the majority of 2-week-old larvae have attained stage 2a [24,25]. Sampling of postyolk-sac larvae was carried out at night only, to minimize problems with net avoidance [27].

Results

General description

South-southeasterly (S-SE) winds dominated off Karmøy in April 1993 and were interrupted by two periods with northerly winds, 18–19 April and 25–28 April (Fig. 2). The impact of the winds could be observed as variations in water level (Fig. 2) and on the relative horizontal distribution of different stages of herring larvae. A prerequisite is, however, that the geographic location of spawning grounds is rather accurately known. Hatching intensity of larvae should also be known in order to calculate expected rates of larval production and thus also rates of larval advection.

From the spawning grounds off western Karmøy [8,9] only few larvae had hatched before 15 April. After this date, the rate of larval production increased, with a peak about 25 April (Fig. 3), followed by a sharp decline during the subsequent days. Hatching of larvae from western Karmøy continued until the beginning of May. The mean advection rate of early yolk-sac larvae could be assessed in a relatively accurate way due to the young age and easily identifiable age criterion of these young stages [24], whereas older larvae had experienced a longer history of environmental events and were thus subject to integrated environmental processes which were difficult to trace back to selective short-term physical events. Higher sampling effort per unit

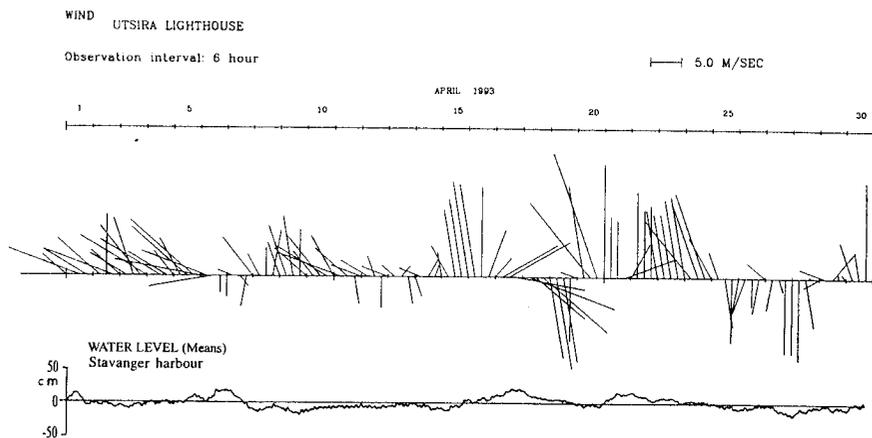


Fig. 2. Wind vectors from measurements at Utsira lighthouse (upper), and water level measurements at Stavanger in April 1993 (lower).

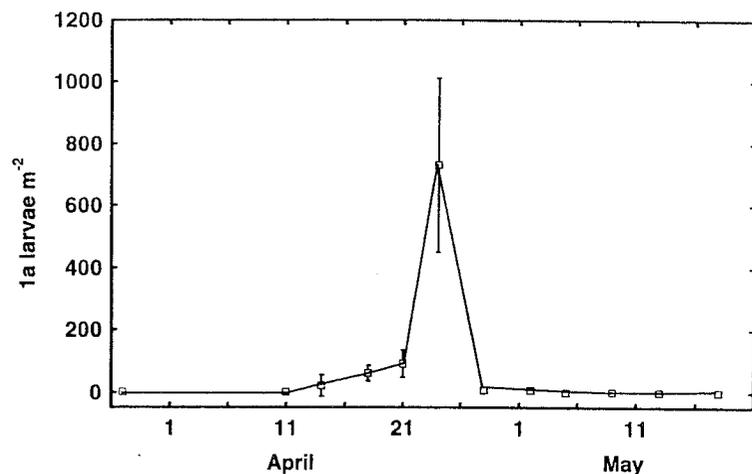


Fig. 3. Hatching intensity curve. Newly hatched herring larvae ($N \times m^{-2}$) (stage 1a) (Mean \pm SD), at five fixed sampling stations off western Karmøy (see Fig. 1).

time (i.e., more vessels) to obtain more sampling units and better area coverage during the relatively brief period of those events would, however, improve the information collected about larval distribution.

During southerly winds the mean water level increased gradually towards an upper level of about 15–20 cm, and declined abruptly during northerly winds. The mean water level was above the “zero level” for about 10 days of April, including the

survey periods 16–19 and 21–24 April. During the rest of the month, including 20 April, the mean water level was either at the zero level or below (Fig. 2).

There was a pronounced tidal signal in the current. The total flow oscillated “backwards and forwards” along the coast in periods when the mean flow was weak, 19 and 22 April. A distinct tidal signal also appeared in the measurements during the period with strong mean flow northwards, 17–18 April, but only as a modulation. The mean flow in the three observation depths was mainly directed northwards (Fig. 4), except for 16 and 19 April.

Both temperature and salinity off Karmøy had their lowest values in the upper 30 m near the coast, about 5°C and 32 psu respectively (Fig. 5). The values increased seawards and with increasing depth, and reached about 7°C and 35.5 psu at 120 m depth.

The vertical distribution of temperature and salinity varied with time indicating

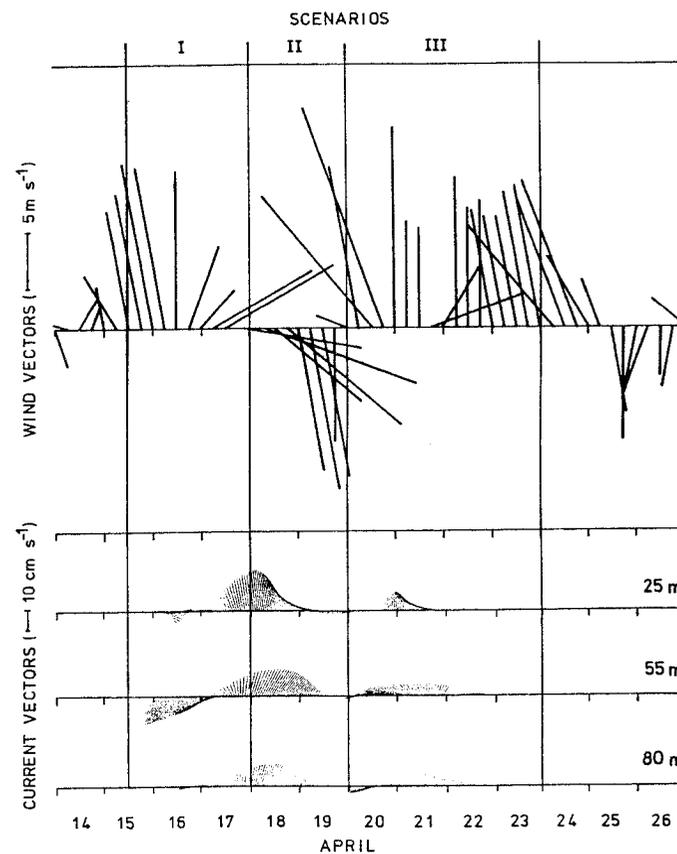


Fig. 4. Wind vectors from measurements at Utsira lighthouse (upper), and (lower) current velocity (40 h average mean) from measurements at a moored rig (see Fig. 1).

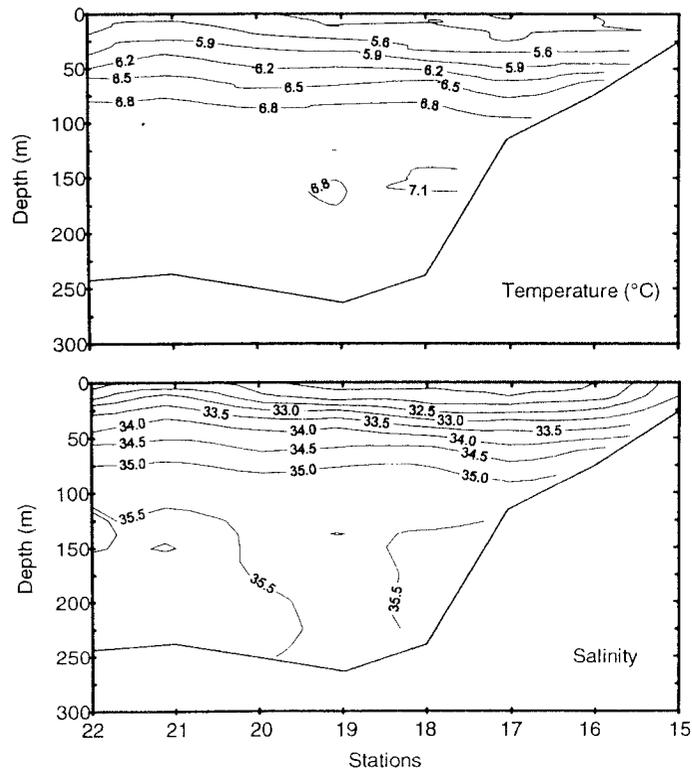


Fig. 5. Temperature (upper) and salinity (lower) from CTD-measurements off western Karmøy (stations 15–22, see Fig. 1).

lateral water movements. The wavy pattern of the isopycnals may be related to internal waves and/or eddies, in the Boknafjord area (Fig. 6).

During the survey 15–23 April, three periods of relatively persistent wind direction and speed were selected; I) southerly winds during 15–17 April, II) northerly winds during 18–19 April, and III) again southerly winds 20–23 April (Fig. 4). These periods were therefore analysed as separate scenarios (I–III).

Scenario I (15–17 April)

Southerly winds predominated during 15–17 April (wind speed up to 15 m s^{-1}) and the same wind direction had also predominated for most of April with an average wind speed of about 10 m s^{-1} (Fig. 4). Relatively few herring larvae were observed west of Karmøy and in the Boknafjord area (Fig. 7). The majority of 1a-larvae were caught in the vicinity of the hatching grounds, and maximum 10 km offshore. Some

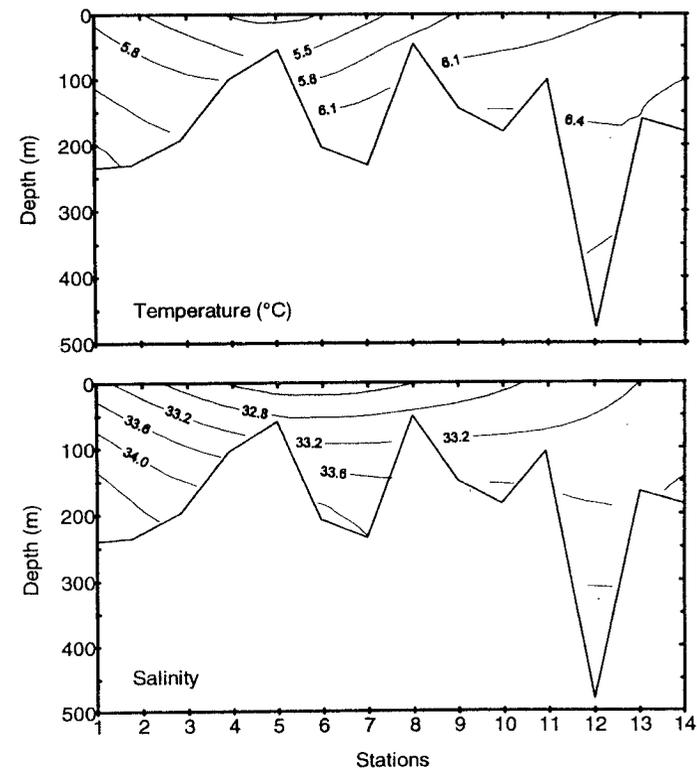


Fig. 6. Temperature (upper) and salinity (lower) measurements from west of Karmøy through Boknafjorden (stations 1–14, see Fig. 1). Bottom topography as indicated refers to sampling locations. Actual bottom depths in the Boknafjord exceed 500 m.

were also advected into the Boknafjord area. The larvae in the inner part of the fjord probably originated from the observed hatching grounds, most likely from the ones at Kårstø/Bokn and off Ferkingstad. A relatively low proportion of 1a-larvae compared with older stages was observed in the samples, although increasing hatching intensity took part throughout the study period (Fig. 3). Postyolk-sac herring larvae in developmental stage 2a were recorded at several locations in the Boknafjord, at densities only up to 4 m^{-2} , and no records were made off western Karmøy (Fig. 7). The offshore sampling effort was low due to adverse weather conditions in this period, but there is no reason to assume severe underestimation of postyolk-sac larvae.

Scenario II (18–19 April)

The predominating southerly windfields in April were interrupted by a brief period

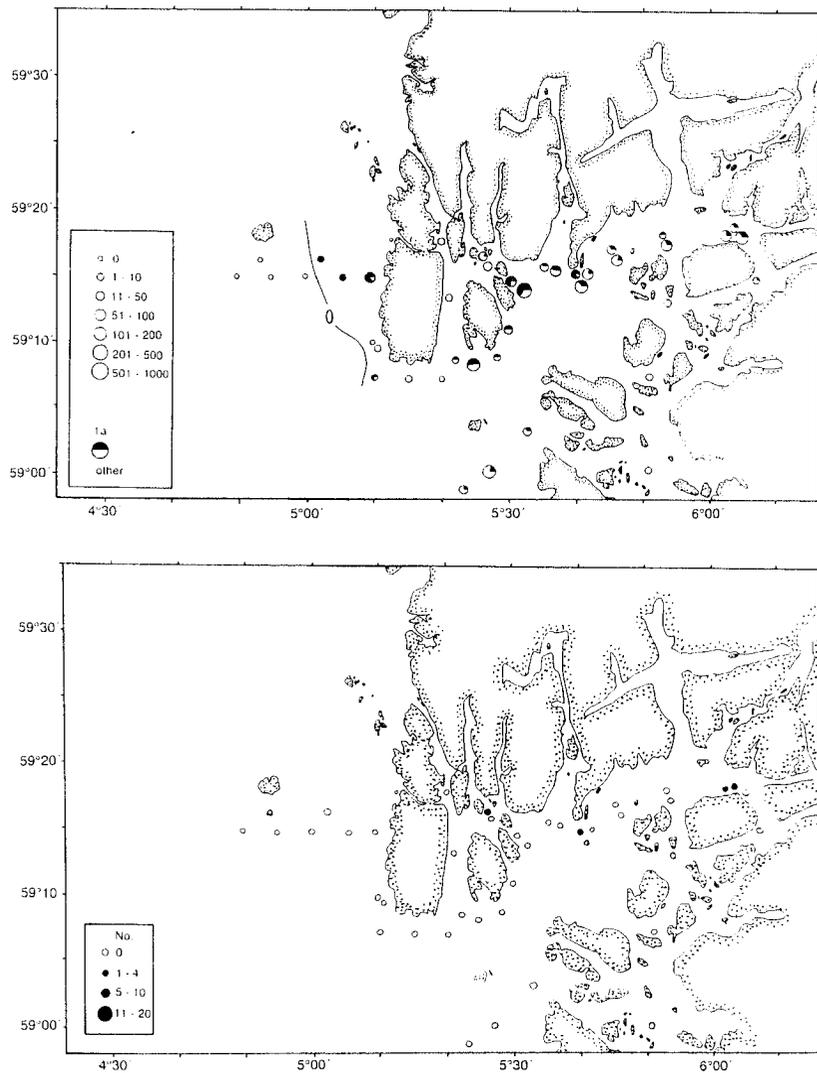


Fig. 7. Distribution of herring larvae ($N \times m^{-2}$) during sampling at 15–17 April off Karmøy and in Boknafjorden. (Scenario I). Relative proportion of stage 1a and other stages (upper). Relative proportion of stage 2a (lower).

of about 2 days (18–19 April) with northerly winds, wind speed up to 14 m s^{-1} . Figure 8 indicates that some 1a-larvae (10 m^{-2}) had been transported far offshore (about 30 km) and a simultaneous reduction in larval density over the spawning ground was also observed, from 38 m^{-2} to 24 m^{-2} . Although few, 2a-larvae were

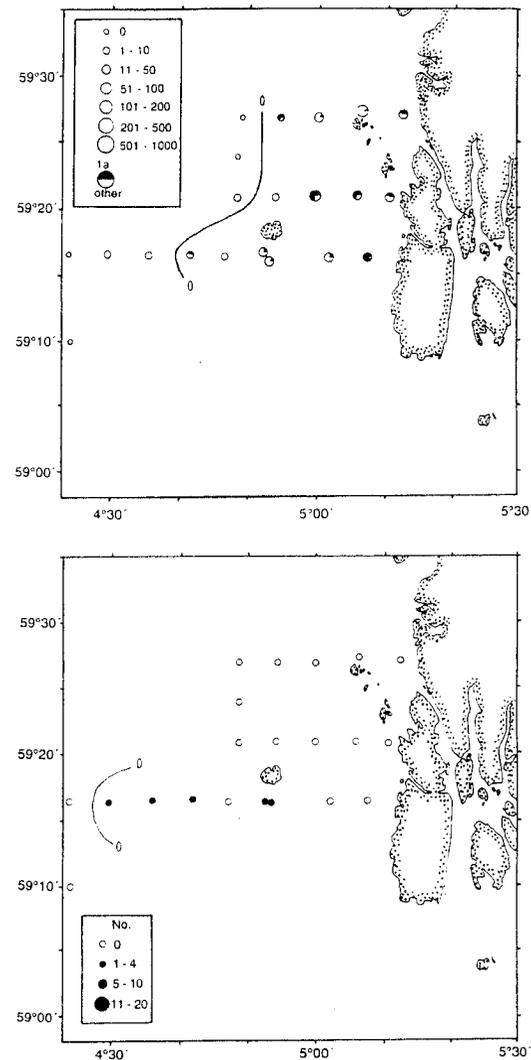


Fig. 8. Distribution of herring larvae ($N \times m^{-2}$) during sampling at 19 April off Karmøy. (Scenario II). Relative proportion of stage 1a and other stages (upper). Relative proportion of stage 2a-larvae (lower).

observed about 38 km offshore (Fig. 8). The weather conditions did not permit more than 1 day of sampling during this 2-day scenario, and the limited sampling effort was allocated to the offshore area only.

The concentrations of nutrients at stations B1 and B2 (Fig. 1) increased markedly

with the change from southerly to northerly winds. From 17 (scenario I) to 19 April concentrations of nitrate, phosphate and silicate increased from less than 1.6 to more than 4.0 μM , from 0.3 to 0.5 μM and from about 0.9 to more than 1.2 μM , respectively.

Total microzooplankton occurred at similar magnitudes at the two offshore stations on 17 and 19 April, 2.8–7.5 l^{-1} , although a decline in microzooplankton densities was discernible with the change from southerly to northerly winds (Fig. 9). Copepod nauplii were the most abundant microzooplankters, comprising 70–95% of total microzooplankton, and copepod nauplii of the smaller fraction ($\leq 250 \mu\text{m}$) were most numerous at all stations observed.

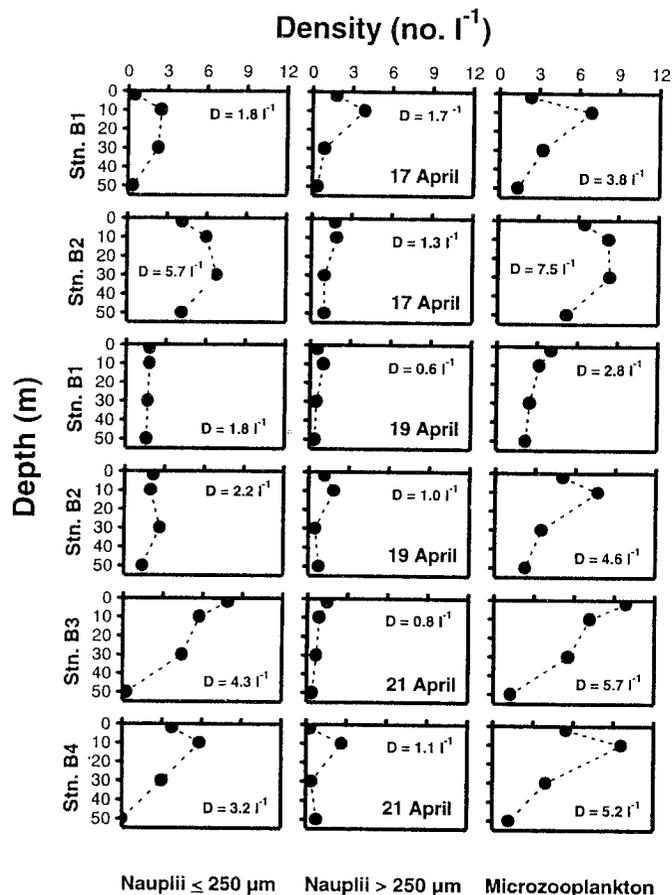


Fig. 9. Two size fractions of copepod nauplii ($\leq 250 \mu\text{m}$; 250–600 μm) and total microzooplankton ($\text{N} \times \text{l}^{-1}$) from stations B1 and B2 (off western Karmøy) (see Fig. 1) during 17 and 19 April 1993, and from station B3, east of Bokn (see Fig. 1) on 21 April 1993 and from station B4 on 21 April 1993. D = depth integrated mean density.

Scenario III (20–23 April)

The larvae were distributed closer to the coastline and at higher densities off western Karmøy during 20–23 April compared to under the previous scenario II with reversed windfield. The densities of 1a-larvae over the spawning grounds off Ferkingstad and Åkrehamn amounted to more than 700 larvae m^{-2} (Fig. 10). Some young larvae (stages 1a-1b) were recorded far offshore (28 km) in the northwestern part of the surveyed area. These were most likely advected northwards by the residual current under the period with southerly winds. In the Bokn/Kårstø area some 1a-larvae were observed, however, at relatively low densities ($\leq 16 \text{m}^{-2}$). Occurrence of postyolk-sac herring larvae in developmental stages up to 2b were recorded in a few major areas: the inner parts of the Boknafjord (Erfjorden) and around the island Bokn (Fig. 10). The high number of post yolk-sac herring larvae ($< 22 \text{m}^{-2}$) at the inner fjord stations suggests that some kind of retention mechanisms had operated to keep high densities of larvae in this area.

The nutrient concentrations generally increased with increasing depth. At station B3 off Bokn/Kårstø the mean concentrations of nitrate, phosphate and silicate increased from 2.5 to 5.0 μM , from 0.4 to 1.0 μM and from 1.6 to 2.0 μM from 21 April to 22 April, respectively. Corresponding mean concentrations at station B4 on 21 April were 4.3, 0.6 and 1.7 μM , respectively.

Mean densities of microzooplankton were observed to be at the same levels at the two inshore stations (B3 and B4), i.e., in the range 5.2–5.7 l^{-1} (Fig. 9). The density of calanoid copepodites, which dominated the macrozooplankton, was very high on station B4, with an average density of 39.3 l^{-1} . Similar densities were observed with the Juday net samples. Higher densities of macrozooplankton, mainly *C. finmarchicus*, *Pseudocalanus* sp., *Temora longicornis* and *Oithona similis*, were observed at the inner station B4 (39.3 l^{-1}) compared with those off the coast (5–9 l^{-1}). The only carnivorous zooplankton observed were cnidarians, at densities up to 25 m^{-3} and these densities were similar at the offshore and inshore stations.

Discussion

Shortly after hatching, herring larvae seek the upper sea levels [28], where their destiny is strongly determined by properties of the water masses in which the larvae are entrained. Variations of mean current velocity were strongly related to variations in the wind field (Fig. 4). In addition to the wind, freshwater supply may be an important driving force and it may also influence on stratification. In this study, however, precipitation and freshwater runoff were almost nil and would therefore have negligible influence on stratification of the water masses. The effect of the wind was, however, strongly dependent on the stratification. The phase lag downward in the water column increases with increasing stratification [12]. It was therefore expected that the mean current is quasi-geostrophic due to stacking up of water along the coast, and that the wind has a direct influence on the current in the upper layer

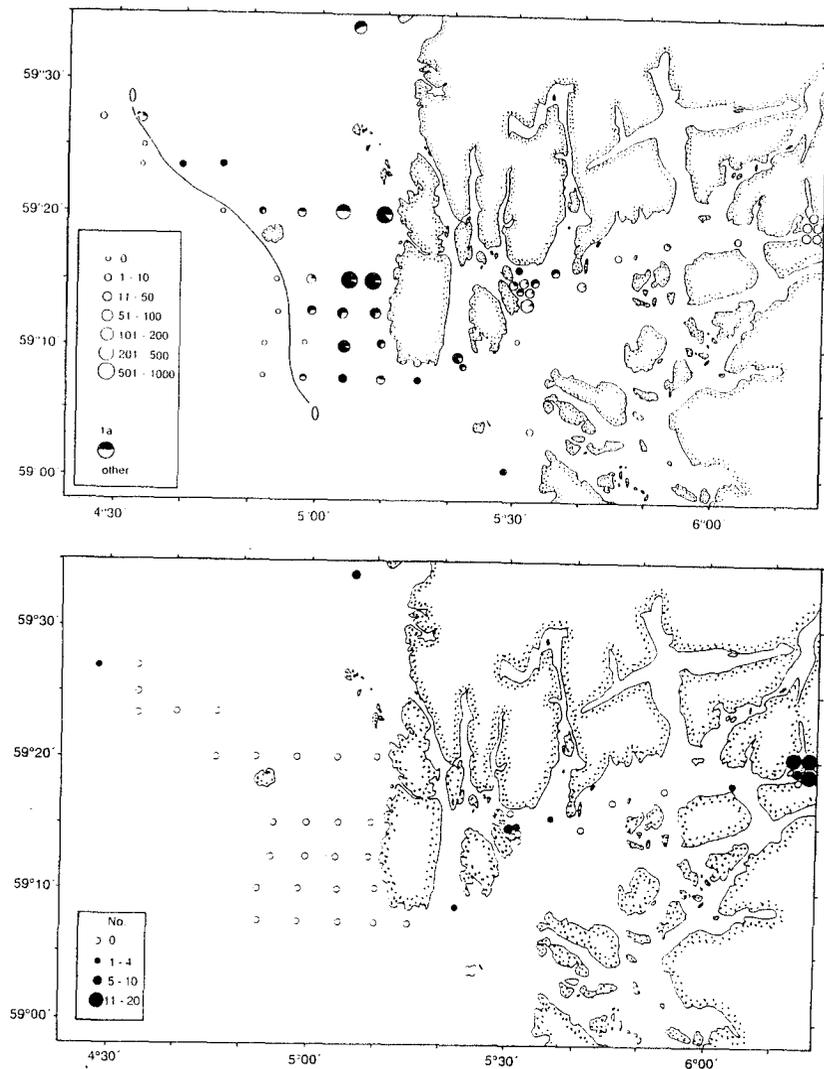


Fig. 10. Herring larvae ($N \times m^{-2}$) during sampling 20–23 April 1993 off Karmøy and in Boknafjorden (Scenario III). Relative proportion of stage 1a and other stages (upper). Relative proportion of stages 2a–2b larvae (lower).

only. The fact that the mean current directions were the same in all measured depths support this assumption.

It takes some time to “build up” the water level along the coast and with that also the quasi-geostrophic current. As a consequence there was a time lag between the

wind and the water level (Fig. 2) and the current (Fig. 4). Variations due to the wind were also reflected in the lateral (on- and offshore) movements of the water masses as well as in the water level variations. Stacking up of water masses along the coast, Ekman transport, is related to periods with wind components directed northwards and onshore. Offshore transport is related to reversal of the wind field. A strong offshore wind component during the 1st 5 days of April moved the upper layer water offshore. When the wind slackened and turned to a weak southerly wind, the water level increased as a consequence of onshore return flow (Fig. 2). The inclination of the isopycnals are usually larger in periods with onshore transport compared to the period with offshore Ekman transport when the isopycnals are almost level (Fig. 6).

It is expected that water masses from the coast and the outer part of the Boknafjord penetrate below the upper layer into the Boknafjord with a compensating outflow below during the periods with north-northeastward flow along the coast. With persisting winds from the south, coastal seawater may intrude into the fjord under the less saline fjord water in the upper stratified part of the water column. Such a physical situation occurred during the southerly wind periods which persisted for most of the study period, as documented from water level measurements and lighthouse wind vectors. During similar conditions in March–April 1979 the water penetrated through the Boknafjord and into the Sandsfjord system and probably into all the other inner Ryfylke fjords [29]. The time for the water to cover the distance from the coast to the Sandsfjord in the inner Boknafjord was calculated to be 25–40 h [12].

The consequences of vertical distribution variability may be very significant for advection of the larvae. Little consistent information on the vertical distribution of herring larvae is, however, available under different environmental conditions [30,31]. Bjørke et al. [32] stated that 60% of the herring larvae were above the pycnocline at all times of the day. Also Johannessen [28] found that the majority of yolk-sac herring larvae stayed at or above the pycnocline throughout day and night. Heath et al. [30] demonstrated, however, that wind mixing events could modify the vertical distribution of larvae (6–18 mm), and that high wind velocities may cause dispersion of the population and downward displacement of the centre of density. In the case of herring larvae, vertical distribution has been documented as a behavioural adaptation for position maintenance in rapidly flushing estuarine situations [14,33]. However, the significance of this for larvae in the open sea is unclear. Iles and Sinclair [3] indicated that herring larvae are retained by the circulation on Georges Bank, and vertical migration could be a mechanism for achieving this. But off the north of Scotland larvae are clearly advected very rapidly through the area and indeed, are widely distributed in the North Sea some months later [1,34].

Fortier and Gagné [35] stated that herring larvae could be considered as passive particles up to a size of about 10 mm. It is therefore likely that herring larvae from the upper 50 m of the water column in the outer fjord region may intrude into the inner part of the fjord, and this distance may be covered within only a few days. This means that the larvae may have drifted along with the current at a speed of about $0.5\text{--}1 \text{ km h}^{-1}$ from the hatching grounds at Bokn/Kårstø and Ferkingstad. This also

agreed with the observed current speeds at the moored rig, at 0.2–0.5 m s⁻¹. Our drift rates were substantially greater than the average drift rates of 2–4.4 km day⁻¹ and about 6 km day⁻¹ observed for larval herring in the North Sea [36,37] and outer Hebrides [2] respectively, and the drift rates observed for larval capelin of 5.2 km day⁻¹ in a small embayment in eastern New Foundland [38]. The 1a-larvae observed in the inner part of the fjord were probably not hatched there. Support for this assumption comes from interpretation of the larval density estimates in successive yolk sac stages. High daily mortality rates as well as rates of development to succeeding stages suggest that 1a-larvae were more likely to be found near hatching grounds briefly after hatching than the subsequent stages, and particularly during a period which coincided with the ascending section of the hatching curve. Also reports from fishermen indicated that no spawning was observed that far into the fjord. In the Gulf of Maine, shoreward transportation of recently hatched herring larvae in deep water is rather common in spring [33].

High density estimates of stage 2a-larvae (more than 2 weeks old) and macrozooplankton distributed in the inner fjord system (station B4 in Erfjorden) suggested that this area was important for retention of fish larvae and macrozooplankton. Advection of oceanic plankton from off the coast is well known for other Norwegian fjords, such as Masfjorden, where substantially higher standing stocks of i.e., cod juveniles, could be raised with extra supplies of advected zooplankton, rather than only from indigenous plankton production [39]. But advective processes may also affect distribution of microzooplankton, which was difficult to confirm in this study. Onshore winds have been shown to induce increasing densities of zooplankton in the edible size fraction for fish larvae coupled with reduced predator densities in the hatching areas of capelin at Newfoundland [40]. Briefly after hatching, onshore winds, i.e., southerly winds on the continents of the NE Atlantic, therefore seem to have a general favourable effect on the aggregation of young fish larvae and their prey in inshore coastal areas. Overwintering in deep fjords of calanoid copepods of oceanic origin is not uncommon [41]. High abundance of adult copepods may lead to increased production of potential prey for young fish larvae, although the observed microzooplankton densities during the survey were not too high (about 5 l⁻¹). Increased predation on young herring larvae by carnivorous zooplankton seems less likely in inshore compared with offshore areas due to similar densities in the two areas.

Feeding of herring larvae was not possible to assess due to the findings of empty stomachs only. Partial or total defecation is not uncommon in herring larvae and is mainly due to capture and preservation [21,22]. Coincidence in time between the availability of suitable food and hatching of herring larvae is, however, a prerequisite for successful feeding [42]. In the present study, appropriate stages of prey were found at stations located offshore and in the Boknafjord, at densities of about 5 l⁻¹. These densities were in agreement with densities of copepod nauplii and microzooplankton on the west coast of Norway, averaging 2.1 and 6.3 l⁻¹, respectively [23]. Similarly, Fossum and Moksness [43] observed prey densities of herring of 1–4 l⁻¹ at the spawning grounds off Møre in the middle of April 1990. We found also that

nutrient concentrations increased after a period with northerly winds. Wroblewski and Richman [44] modelled that if there was a net nutrient flux into the euphotic zone, local concentrations of prey after a wind event might be higher than before the event. Wroblewski et al. [45] found that if initial prey concentrations were insufficient for optimal growth of larval northern anchovy (*Engraulis mordax*), then a wind event which increases primary and secondary production may be beneficial to larvae emerging from the yolk-sac stage after a storm. The conclusion was that optimal wind conditions for larval survival occur when a wind event strong enough to deepen the mixed layer into the nutricline is followed by a calm period. With the observed wind speeds off southwestern Norway in April, feeding conditions of larvae were assumed to be beneficial. Observed wind speed was ≤5 m s⁻¹ for only 3 days in April, and for more than 10 days wind speed was ≥12 m s⁻¹. This means that contact rates between larvae and food items may have been high, even if ambient food densities were relatively low [46,47]. MacKenzie et al. [48] found a dome-shaped relation between probability of feeding and wind speed, and their model indicated a peak in ingestion rate at a wind speed of about 15 m s⁻¹.

The distinct peak of the hatching curve about 25 April 1993 suggested that the herring larval production must have been intense during a brief period, which corresponded with high spawning activity in the area in late March and early April [8]. The shape of the hatching curve may, however, be biased, because strong northerly winds prevailed during the declining part of the curve, and the location of sampling stations were predetermined at the northern flank of the hatching ground close to the shore. The latter suggestion seems to be likely because strong northerly winds occurred during a period after 25 April. Unless sampling strategy and location of stations for sampling herring larvae are adjusted according to the prevailing wind patterns, horizontal distribution and estimates of hatching intensity and thus larval production estimates may be seriously biased. Underestimation of larval production due to insufficient coverage of larval distribution area was most likely during northerly winds due to offshore dispersal of larvae. During periods of southerly winds, the residual current will carry the larvae northwards alongshore and inshore. Also Rowe and Epifanio [49] emphasized that studies of larval dispersal demands sampling on temporal scales which are well matched to relevant physical processes, and this advice could also be extended to relevant spatial scales.

In conclusion, the investigation has shown that wind and subsequent hydrophysical events may have significant effects on the short-term distribution of herring larvae shortly after hatching. It is therefore reasonable to assume that prevailing onshore winds after hatching may enhance the relative proportion of coastal (or fjord) stock components, which is consistent with the lack of conclusive evidence of genetic stock separation in many herring stocks [50].

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References

- Corten A. On the causes of recruitment failure of herring in the central North Sea in the years 1972–1978. *J Cons Int Explor Mer* 1986;42:281–294.
- Heath MR, MacLachlan P. Dispersion and mortality of yolk-sac herring (*Clupea harengus* L.) larvae from a spawning ground to the west of the Outer Hebrides. *J Plankton Res* 1987;9:613–630.
- Iles TD, Sinclair M. Atlantic herring: stock discreteness and abundance. *Science* 1982;215:627–633.
- Sinclair M, Iles TD. Atlantic herring (*Clupea harengus* L.) distributions in the Gulf of Maine-Scotian Shelf area in relation to oceanographic features. *Can J Fish Aquat Sci* 1985;42:880–887.
- Townsend DW. Ecology of larval herring in relation to the oceanography of the Gulf of Maine. *J Plankton Res* 1992;14(4):467–493.
- Dragesund O, Hamre J, Ulltang Ø. Biology and population dynamics of the Norwegian spring spawning herring. Rapp. P.-v. Réun. Cons Int Explor Mer 1980;177:43–71.
- Runnstrøm S. Quantitative investigations on herring spawning and its yearly fluctuations at the west coast of Norway. *FiskDir Skr Ser Havunders* 1941;6(8):5–71.
- Johannessen A, Bergstad OA, Dragesund O, Røttingen I, Slotte A. Reappearance of Norwegian spring spawning herring (*Clupea harengus* L.) at spawning grounds off southwestern Norway. This publication.
- Nøttestad L, Aksland M, Beltestad A, Fernø A, Johannessen A, Misund OA. Schooling dynamics of Norwegian spring spawning herring (*Clupea harengus* L.) at a coastal spawning area. *Mare Nor Symposium on the Ecology of Fjords and Coastal Waters, Tromsø, Norway* 1994.
- Svendsen H. A study of the circulation in a sill fjord on the west coast of Norway. *Mar Sci Comm* 1977;3(2):151–209.
- Svendsen H. Wind-induced variations of circulation and water level in coupled fjord-coast systems. In: Sætre R, Mork M (eds) *Proc The Norwegian Coastal Current I*. 1980;229–261.
- Klinck, JM, O'Brian JJ, Svendsen H. A simple model of fjord and coastal circulation interaction. *J Phys Oceanogr* 1981;11:1612–1626.
- Urho L, Hilden M. Distribution patterns of Baltic herring larvae, *Clupea harengus* L., in the coastal waters off Helsinki, Finland. *J Plankton Res* 1990;12:41–54.
- Graham JJ. Retention of larval herring within the Sheepscot estuary of Maine. *Fish Bull US* 1972;70:299–305.
- Graham JJ. Production of larval herring, *Clupea harengus* L., along the Maine coast, 1964–1978. *J Northw Atl Fish Sci* 1982;3:63–85.
- Heath M, Rankine P. Growth and advection of larval herring (*Clupea harengus* L.) in the vicinity of the Orkney Isles. *Est Coast Shelf Sci* 1988;27:547–565.
- Heath MR, MacLachlan P, Martin JHA. Inshore circulation and transport of herring larvae off the north coast of Scotland. *Mar Ecol Prog Ser*. 1987;40:11–23.
- Heath MR, Leaver M, Matthews A, Nicoll N. Dispersion and feeding of larval herring 1989 (*Clupea harengus* L.) in the Moray Firth during September 1985. *Est Coast Shelf Sci* 1989;28:549–566.
- Townsend DW, Graham JJ, Stevenson DK. Dynamics of larval herring (*Clupea harengus* L.) production in tidally mixed waters of the eastern coastal Gulf of Maine. In: Bowman MJ, Yentsch CM, Peterson WT (eds) *Tidal Mixing and Plankton Dynamics*. Berlin: Springer-Verlag, 1986;253–277.
- Mork M. Circulation phenomena and frontal dynamics of the Norwegian coastal current. *Phil Trans R Soc Lond* 1981;A302:635–647.
- Cohen RE, Lough RG. Prey field of larval herring, *Clupea harengus* on a continental shelf spawning area. *Mar Ecol Prog Ser* 1983;10:211–222.
- Blaxter JHS. The feeding of herring larvae and their ecology in relation to feeding. *Rep Calif Coop Ocean Fish Invest* 1965;10:79–88.
- Bjørke H. Food and feeding of young herring larvae of Norwegian spring spawners. *FiskDir Skr Ser Havunders* 1978;16:405–421.
- Doyle MJ. A morphological staging system for the larval development of the herring, *Clupea harengus* L. *J Mar Biol Assoc UK* 1977;57:859–867.
- Fossum P. Laboratorieeksperimenter med sildelarver (*Clupea harengus* L.) fra den lokale sildestammen Lindåspollene (Hordaland). Cand. real. thesis, University of Bergen, 1980;62(mimeo).
- Øiestad V. Growth and survival of herring larvae and fry (*Clupea harengus* L.) exposed to different feeding regimes in experimental ecosystems: Outdoor basin and plastic bags. Dr. philos. thesis 1983;299.
- Mc Gurk MD. Avoidance of towed plankton nets by herring larvae: a model of night-day catch ratios based on larval length, net speed and mesh width. *J Plankton Res* 1992;14:173–182.
- Johannessen A. Recruitment studies of herring (*Clupea harengus* L.) in Lindaaspollene, western Norway, 2. *FiskDir Skr Ser Havunders* 1986;18:139–240.
- Svendsen H. A study of circulation and exchange processes in the Ryfylke fjords. Dr.philos. thesis 1981; Rep. 55, Geophysical Institute, University of Bergen.
- Heath MR, Henderson EW, Baird DL. Vertical distribution of herring larvae in relation to physical mixing and illumination. *Mar Ecol Prog Ser* 1988;47:211–228.
- Brander K, Nichols J, Thompson A. A study of avoidance of sampling gear by herring larvae. *CM. ICES*. 1987; L:18.
- Bjørke H, Fossum P, Sætre R. Distribution, drift and condition of herring larvae off western Norway in 1985. *CM. ICES* 1986;H:39.
- Fortier L, Leggett WC. Fickian transport and the dispersal of fish larvae in estuaries. *Can J Fish Aquat Sci* 1982;39:1150–1163.
- Heath MR, Walker J. A preliminary study of the drift of larval herring (*Clupea harengus* L.) using gene-frequency data. *J Cons Int Explor Mer* 1987;43:139–145.
- Fortier L, Gagné JA. Larval herring (*Clupea harengus* L.) dispersion, growth, and survival in the St. Lawrence estuary: Match/mismatch or membership/vagrancy. *Can J Fish Aquat Sci* 1990;47:1898–1912.
- Munk P, Christensen V, Paulsen H. Studies of a larval herring (*Clupea harengus* L.) patch in the Buchan area. II. Growth, mortality and drift of larvae. *Dana* 1986;6:25–36.
- Kjørboe T, Munk P, Richardson K, Christensen V, Paulsen H. Plankton dynamics and larval herring growth, drift and survival in a frontal area. *Mar Ecol Prog Ser* 1988;44:205–219.
- Taggart CT, Leggett WC. Short-term mortality in postemergent larval capelin, *Mallotus villosus*. I. Analysis of multiple in situ estimates. *Mar Ecol Prog Ser* 1987;41:205–217.
- Aksnes D, Aure J, Kaartvedt S, Magnesen T, Richards J. Significance of advection for the carrying capacity of fjord populations. *Mar Ecol Prog Ser* 1989;50:263–274.
- Frank KT, Leggett WC. Coastal water mass replacement: its effect on zooplankton dynamics and the predator-prey complex associated with larval capelin (*Mallotus villosus*). *Can J Fish Aquat Sci* 1982;39:991–1003.
- Hirche HJ. Overwintering of *Calanus finmarchicus* and *Calanus helgolandicus*. *Mar Ecol Prog Ser* 1983;11:281–290.
- Dragesund O. Factors influencing year-class strength of Norwegian spring spawning herring. *FiskDir Skr Ser Havunders* 1970;15:381–450.
- Fossum P, Moksness E. A study of spring- and autumn-spawned herring (*Clupea harengus*) larvae in the Norwegian coastal current during spring 1990. *Fish Oceanogr* 1993;2(2):73–81.
- Wroblewski JS, Richman JG. The nonlinear response of plankton to wind mixing events – implications for survival of larval northern anchovy. *J Plankton Res* 1987;9(1):103–123.
- Wroblewski JS, Richman JG, Mellor GL. Optimal wind conditions for the survival of larval northern

- anchovy, *Engraulis mordax*: a modelling investigation. Fish Bull US 1989;87:387–395.
46. Sundby S, Fossum P. Feeding conditions of Arcto-Norwegian cod larvae compared with the Rothschild-Osborn theory on small-scale turbulence and plankton contact rates. J Plankton Res 1990;12:1153–1162.
 47. Muelbert JH, Lewis MR, Kelley DE. The importance of small-scale turbulence in the feeding of herring larvae. J Plankton Res 1994;16(8):927–944.
 48. MacKenzie BR, Miller T, Cyr S, Leggett WC. Evidence for a dome-shaped relationship between turbulence and larval fish ingestion rates. Limnol Oceanogr 1994;39(8):1790–1799.
 49. Rowe PM, Epifanio CE. Tidal stream transport of weakfish larvae in Delaware Bay, USA. Mar Ecol Prog Ser 1994;110:105–114.
 50. King DPF, Ferguson A, Mofett IJJ. Aspects of the population genetics of herring, around the British Isles and in the Baltic Sea. Fish Res 1987;6:35–52.