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Fish larvae at fronts: Horizontal and vertical distributions of gadoid fish larvae across a frontal zone at the Norwegian Trench

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ABSTRACT

The reproduction and early life history of many fish species are linked to the physical and biological characteristics of fronts. In order to ascertain linkages between frontal physics and fish larvae, we investigated distributional differences among gadoid fish larvae comparing these to both horizontal and vertical variability in hydrography and abundances of potential copepod prey The investigation was carried out at a frontal zone along the Norwegian Trench in the northern North Sea, and was based on a series of cross-bathymetric sampling transects. Tows with a large ring net and an opening–closing net were used for describing fish larval horizontal and vertical distributions, while a submersible pump was used for describing vertical distributions of copepods. Hydrographic profiles and current velocity measurements were used to outline variability in temperature, salinity and current structure. Measurements demonstrated a distinct bottom front at the southern slope of the Trench with deepening isopycnals and high chlorphyll *a* concentrations. Abundances of both gadoid fish larvae and copepods peaked in vicinity of the front around mid-depth, and findings points to an inter-connection between the vertical and horizontal distributions of each species. However, the three-dimensional pattern of distribution differed significantly among species of larvae and species of copepods. The study underlines the complexity of bio-physical interrelationships in the frontal zone, and indicates that the zone encompasses specific ecological niches to which each species of fish larvae is adapted.

1. Introduction

Fish larvae and other planktonic organisms often show aggregated distributions both in horizontal and vertical directions (Sabatés and Olivar, 1996; Lough and Manning, 2001; Lee et al., 2005). The aggregation is linked to the suitability of the immediate environment for the larvae, physical processes, and active behavior of the organism (Franks, 1992; Genin et al., 2005). A wide range of factors have been proposed to influence the vertical distribution of fish larvae, including light, prey density, turbulence, up- or downwelling, tide, buoyancy, temperature and salinity (Munk et al., 1989; Neilson and Perry, 1990; Sclafani et al., 1993; Jenkins et al., 1998). The relative importance of each factor has been intensely debated. Some of the factors change larval behavior, leading to upward- or downward migration, while others such as turbulence and buoyancy exert a direct influence on larval distribution. Larval horizontal swimming is negligible compared to the passive drift caused by currents. However, due to the vertically stratified current field, vertical position of larvae will affect the subsequent horizontal dispersion and drift (Hernandez et al., 2009). This is apparent at hydrographic fronts, where plankton behavior, converging currents, and frontal jet formation, play an important role in the aggregation and advection of plankton organisms (Le Fèvre, 1986; Bakun, 2006; Genin et al., 2005).

Physical characteristics are interrelated vertically and horizontally. For example, when vertically stratified water masses interface with mixed waters, the vertically oriented pycnocline and the horizontally oriented frontal zone would be connected. Likewise, the distributions of fish larvae should be considered in three dimensions, i.e. the spatial distribution of fish larvae along the vertical axis cannot be fully understood without considering the horizontal variability, and vice versa. There is an increasing focus on the three-dimensional aspects of the bio-physical relationships, and several recent studies of larval fish assemblages used an extensive three-dimensional approach when examining larval distribution (e.g. Sanvicente-Añorve et al., 2000; Danell-Jiménez et al., 2009).

In studies of gadoid fish larvae in frontal areas of the northeastern North Sea, Munk et al. (1995, 1999) found larvae aggregated in the vicinity of a frontal zone. Species included Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*), saithe (*Pollachius virens*), and Norway pout (*Trisopterus esmarki*). Concentrations of larvae were seen along the entire path of the front, and the pattern was evident during several years of investigation. However, there were also consistent differences among

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the studied species: some species prevailed in the offshore part of the frontal zone while others were distributed more inshore. The authors suggested that these patterns of horizontal distribution were related to the variable physical characteristics across the frontal zone, that a given species would be associated with a specific physical environment. The strong linkage of cod larvae to characteristics of the front was emphasized during a subsequent study of larval growth rates in the area which showed highest growth rates of this species in central parts of the front coinciding peaking abundances of these larvae (Munk, 2007).

In order to develop the understanding of bio-physical interactions associated with the vertical distribution of gadoid fish larvae, we revisited the area during a separate survey and carried out both horizontally and vertically stratified sampling. In this investigation, we focused on a restricted area of the observed front, and emphasis was given to larval fish and zooplankton distributions relative to the relatively narrow frontal zone. We here provide a three-dimensional description of the cross-frontal variability in physics, phytolankton, zooplankton, and fish larvae to improve understanding of the species-specific vertical and horizontal distribution patterns in the frontal zone.

2. Material and methods

The study was carried out from the ship R/V Dana in the northeastern North Sea and the Skagerrak during May 3–10, 1997. Weather conditions during the cruise were moderately cloudy and wind speeds were primarily in the range 5–8 m s^{-1}, except for 2 days of 10–12 m s^{-1} wind speeds. Five north-south sampling transects were sampled during the first 4 days (May 3–7), covering a section of the southern slope of the Norwegian Trench from about 40–300 m bottom depth (Fig. 1). Distances between stations were 5, 10 or 15 nm. Sampling at each station was initiated with a hydrographic cast using a Seabird SBE 9/11 conductivity–temperature–depth (CTD) profiler that also carried a mounted fluorometer and a Niskin bottle rosette sampler. Temperature and salinity measurements were averaged at 0.5 m depth intervals. Two bottle samples were taken at each station, one sample 5 m below the surface and another where the fluorescence profile showed maximal fluorescence. Later these samples were analyzed for chlorophyll *a* content as described by Riemann (1978) and used for conversion of fluorescence to chlorophyll *a*. While traveling along transects, we measured water current speed and direction in 2 m depth intervals to a maximum depth of 90 m, using a 600 kHz Acoustic Doppler Current Profiler (ADCP, RD Instruments®). We also estimated the volume backscattering strength (Sv) in 1 m depth intervals to the sea-bottom, using a ship-mounted 120 kHz echo sounder (SIMRAD®) and the analysis package 'Ekkoanna'.

Depth-stratified sampling of zooplankton was carried out along 6° 40' E (Transect V) during the night of May 6–7 using a submersible pump equipped with a 30 μm mesh conical net and a calibrated flowmeter measuring the volume of water entering the net (pump capacity 1.2 m^3 min^{-1}). The pump was let down to the upper level of the target stratum, started, and then moved to the lower level of the strata within approximately one minute. It was then turned off and taken to deck, where the net was washed down and the plankton transferred to 4% buffered formaldehyde. Stratum widths were 10, 12.5, 15 or 20 m. In the laboratory, the planktons were subsampled and copepods were identified to species and size. Based on flowmeter readings and numbers caught, the copepod density (no/vol. filtered; in no m^{-3}) of each species and stage was calculated.

Two gear types were used for sampling fish larvae. First, we used oblique hauls to resolve the horizontal distribution of fish larvae in the survey area. An oblique haul was made at each station from surface to 5 m above bottom using a 2 m diameter ring-net equipped with 14 m long black netting of 1.3 mm mesh size. This sampling was carried out around the clock at a frequency of one sample every 2–3 h. The oblique net was deployed and retrieved at wire speeds of 25 and 15 m min^{-1}, respectively, while ship's speed was kept at 1.5 ms^{-1}. The volume of water filtered was estimated using a calibrated flowmeter in the opening of the net.

Second, we used depth-stratified sampling along 7° 40' E (Transect III) to resolve the vertical distribution of larvae using an opening–closing net system with a 1 m^2 opening (Bioness®, see Sameoto et al., 1980). This sampling was initiated during early afternoon on May 7 at a central station of the transect (57° 25'N), followed by sequences along the entire transect during dark hours on the night of May 7–8. The frame was equipped with 5 black

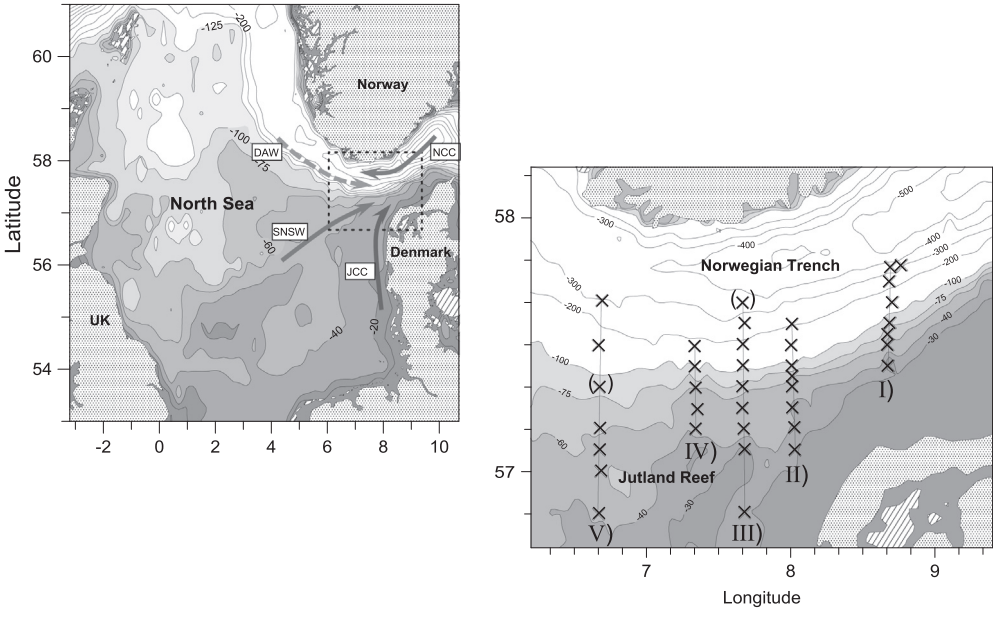

Fig. 1. Study area in the northeastern North Sea and Skagerrak. Gray arrows and labels indicate major currents and water masses, respectively. Crosses show sampling stations along five transects (I–V) across the slope towards the Norwegian trench; Parentheses around cross indicate that no oblique haul was made. Contours illustrate bottom depth in meters.