Western Indian Ocean J. Mar. Sci. Vol. 9, No. 2, pp. 175-183, 2010

Vertical Migration of Gold-spot Herring (*Herklotsichthys quadrimaculatus*) Larvae on Sofala Bank, Mozambique

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Keywords: fish larvae, diel vertical migration, ontogeny, net avoidance.

Abstract—Vertical larval fish movement influences their survival and dispersal, hence recruitment variability. This study presents the vertical behaviour of gold-spot herring (*Herklotsichthys quadrimaculatus*) larvae observed on the Sofala Bank (Mozambique) throughout a 48-hour period when depth-stratified samples were taken every 2 h, together with CTD profiles, at a fixed station. Their ontogenetic variation was also investigated. Larval catches were greater at dusk and night, probably due to net avoidance during dawn and day periods. Generally, larvae were concentrated in the first 20 m of the water column, though larger larvae were most abundant in the neuston at dusk and night, and smaller larvae frequented the deeper strata up to 20 m. The results are discussed in terms of vertical migration, ontogenic changes, and net avoidance.

INTRODUCTION

Vertical larval fish movement is a key process that determines recruitment success (Fiksen *et al.,* 2007). An understanding of larval behaviour and hydrological circulation patterns is crucial to elucidate fish larval growth, survival and dispersion. Furthermore, information on their vertical distribution is needed to properly sample the larvae (Yamashita *et al.,* 1985), elucidate their dispersal processes (Hare & Govoni, 2005; Voss *et al.,* 2007) and is used in fish stock estimations (Reid, 2001).

Depth selection by fish larvae has been shown to be advantageous in avoiding adverse physical conditions, optimizing their horizontal distribution and escaping high predator densities and predation (Olla & Davis, 1990; Hare & Govoni, 2005). These features

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have been widely studied in a number of fish larvae, particularly clupeids. For example, *Clupea harengus* larvae tend to aggregate close to the surface at night (Blaxter, 1973), as do sprat (*Sprattus sprattus*; Voss *et al.,* 2007) and European sardine (*Sardina plichardus*) larvae (Santos *et al.,* 2006). These latter studies also investigated ontogenetic changes in diel vertical movement and observed that surface samples were dominated at night by larger larvae, while smaller larvae were spread throughout the water column. Reasons given for this were predator avoidance, feeding activity and preference for certain water conditions. Other studies on clupeid larvae have reported the reverse; larger larvae were found in deeper water at night with little vertical movement in response to light (Heath *et al.,* 1988; Olivar *et al.,* 2001; Stenevik *et al.,* 2001). The previous factors were again used to explain this pattern. Vertical behaviour thus seems to vary according to species and local hydrographic conditions, since light response, prey selectivity, reproductive period and sinking rates differ amongst the species, as do the hydrographic conditions that affect larval behaviour (Heath *et al.,* 1988; Hare & Govoni, 2005; Santos *et al.,* 2006; Fiksen *et al.,* 2007; Voss *et al.,* 2007). However, vertical larval fish distribution studies are often biased by catch probabilities that are influenced by net avoidance and escape (Grioche *et al.,* 2000). Eggs and small larvae escape sampling gear by slipping through the mesh while larger larvae avoid the gear by swimming away from it. Avoidance rates vary according to species, larval ontogeny, diel vertical movement, water properties and sampling methodology (e.g. gear type, tow speed, and mesh and mouth size) (Davis *et al.,* 1990; McGurk, 1992; Grioche *et al.,* 2000).

Despite the numerous studies on clupeid larvae, none have focused on the tropical herring, *Herklotsichthys quadrimaculatus* (Rüppell, 1837), also known as gold-spot herring. It is a major prey of tuna bait (Lewis, 1990) and is also consumed by coastal communities in East Africa (KMFRI, 1981). The post-larvae are fast growing, feed selectively on zooplankton and spawn continuously after maturing until death (Milton *et al.,* 1994). In Mozambique, *H. quadrimaculatus* is widely distributed in the coastal zone, particularly on the Sofala Bank (INIPM, unpublished data), a wide, shallow shelf off the Zambezi River mouth (Figure 1) where the most important East African fisheries are found. Information on *Herklotsichthys* spp. larvae is scarce (Thorrold & Williams, 1989) and, in the case of *H. quadrimaculatus*, their presence has only been recorded near Durban (South Africa) in the Western Indian Ocean (Harris & Cyrus, 1999). The vertical distribution and behaviour of *H. quadrimaculatus* is unknown, as are ontogenic changes in its diel depth distribution. Furthermore, hydrological conditions on the

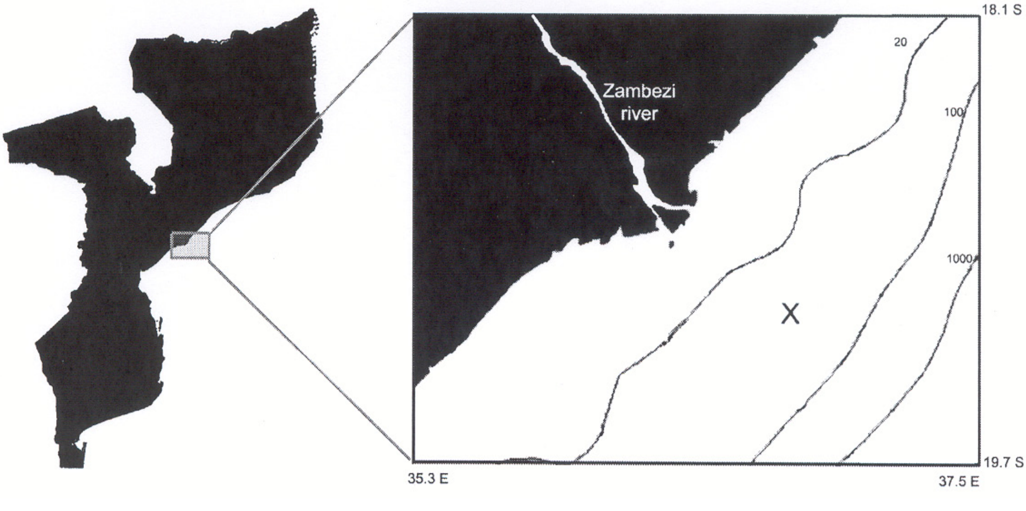

Fig. 1. Location of the sampling station.

Sofala Bank, such as strong tidal currents and the effects of estuarine discharge (Lutjeharms, 2006; Leal *et al.,* 2009), may influence the normal regulating factors that affect its vertical larval dynamics. Tidal energy and vertical mixing, as well as other local oceanographic phenomena, may play a major role in determining vertical *H. quadrimaculatus* larval distribution and diel movement.

The objectives of this study were to establish whether (1) vertical *H. quadrimaculatus* larval distribution varies during diel or tidal cycles and (2) and with larval ontogeny. An Eulerian approach was employed, based on a fixed station sampling.

MATERIAL AND METHODS

Sampling was undertaken from the R/V "Dr. Fridtjof Nansen" during 7-9 December 2007 on the Sofala Bank near the Zambezi River mouth where river runoff and tidal currents strongly influence ecological processes (Lutjeharms, 2006; Leal *et al.,* 2009). Sampling was carried out every 2 h for 48 h at a fixed station in 50 m of water (Figure 1). CTD profiles were recorded at 1 m depth intervals. Detailed analyses of currents, physico-chemical (salinity, temperature, nutrients) and biological (phytoplankton pigments, zooplankton) data are provided by Leal *et al.* (2009). Depth-stratified zooplankton samples were collected using a multinet (Midi model, 0.5 x 0.5 m mouth size, Hydro-bios) with 405 µm mesh, towed at ~2 knots in oblique hauls for 2 min in each stratum (0-5, 5-10, 10-20, 20-30 and 30-40 m), and a neuston net (0.2 x 1.0 m mouth size) of the similar mesh towed horizontally at the same speed and duration, sampling the upper 20 cm of the water column. All nets had flowmeters to measure flow. Samples were preserved in ~4% borax-buffered formaldehyde, prepared using seawater. *H. quadrimaculatus* larvae were subsequently sorted, counted, measured (standard length) to the nearest 0.1 mm, and grouped in four diel time periods: day, dusk, night and dawn. The larvae were identified and grouped according to larval stage (pre- and postflexion) (Leis & Rennis, 1983; Leis & Carson-Ewart, 2004).

As an index of vertical location of zooplankton, weighted mean depths (WMDs) of the diel groups were calculated according to Worthington (1931):

$$WMD = (\Sigma n_i d_i)/(\Sigma n_i)$$

where n_i is the zooplankton biovolume at mean depth d_i of each stratum.

Autocorrelation analysis was performed to test periodicities in the hydrological and biological data. Significant autocorrelations in each 2 h period were assessed, and the Spearman's rank correlation, Student's t-test, ANOVA and Tukey's HSD test were applied to the data. All the statistical analyses were performed using the software R (R Development Core Team, 2008).

RESULTS

The water column was vertically stratified in its physico-chemical properties and clinal depths varied between 10 and 30 m (Figure 2). While the upper 10-20 m of water was well-mixed, with low salinity and higher temperatures, near the bottom, higher salinity and lower temperatures were encountered. These conditions occurred throughout the sampling period with little variation. Towards the end of the 48-hour sampling period, a deepening of the mixing layer (up to 30 m) was observed (Figure 2).

Larval abundance in the water column varied significantly ($P < 0.1$), corresponding to a 24 h (diel) cycle with higher abundances at night (t test = 5.01, $P < 0.01$) (Figure 2d, e). Preflexion larvae were recorded in greatest abundance, on average, at 10-20 m at night (22012 larvae 100 m^{-3}), while postflexion larvae were, on average, most abundant in the neuston layer at dusk (200711 larvae 100 m^{-3}). Preflexion larvae were more abundant at night between 5 and 30 m, while most postflexion larvae were collected at dusk and night in the shallowest strata, the neuston and at 0-5 m (Figure 2d, e). Both pre- and postflexion larvae were more abundant at dusk and night than at dawn and in the day (Figure 3). Greater differences were observed between both larval stages at dusk, when postflexion larvae

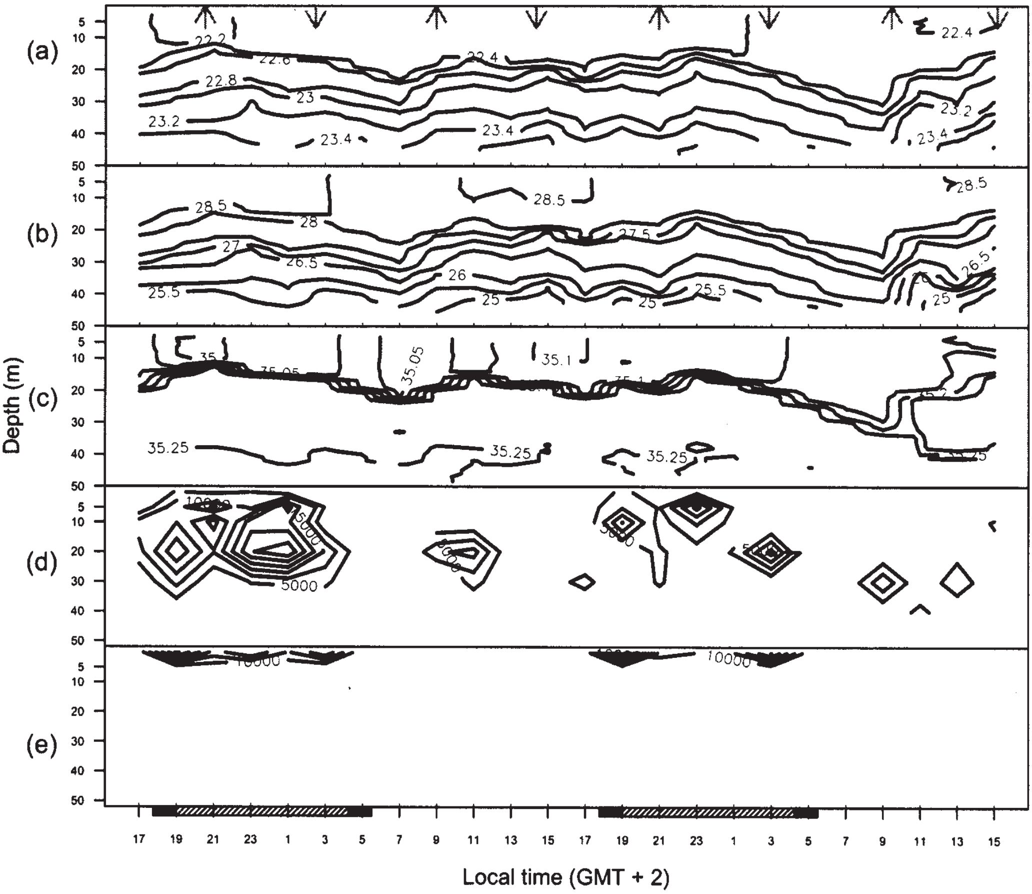

Fig. 2. Water column (a) density σ_t (kg m^{-3}), (b) temperature (°C) and (c) salinity variation during the 48-hour sampling period. Vertical densities of pre- (d) and postflexion (e) larvae (larvae.100 m^{-3}) are also presented. Dashed rectangles indicate night periods, black rectangles crepuscular periods, and upward and downward pointing arrows indicate high and low tides, respectively.

were clearly dominant, and in the day when only low numbers of preflexion larvae were collected (Figure 3). Zooplankton WMDs (data not shown) manifested significant 12-hour periodicity ($P < 0.001$) and were significantly correlated with total larval abundance ($r = -0.65$, $P < 0.001$), with shallower zooplankton mean depths being associated with higher larval concentrations.

The larval fish length distribution varied between 2.99 and 22.89 mm and differences between sampling periods were significant (ANOVA, $F = 130.71$, $P < 0.001$), as well as throughout the water column (ANOVA, $F = 189.25$, $P < 0.001$). However, these differences were mostly noticeable in the neuston and at 0-5 m in dusk and night samples (Tukey's HSD, $P < 0.05$). Larger larvae dominated dusk and night samples in the neuston, while smaller larvae dominated the mid-water strata (5-30 m) during the same periods (Figure 4). Although preflexion larvae were not abundant, they were collected in all strata at dawn and during the day. Length composition analysis revealed that small larvae were displaced to increasing depths at night.

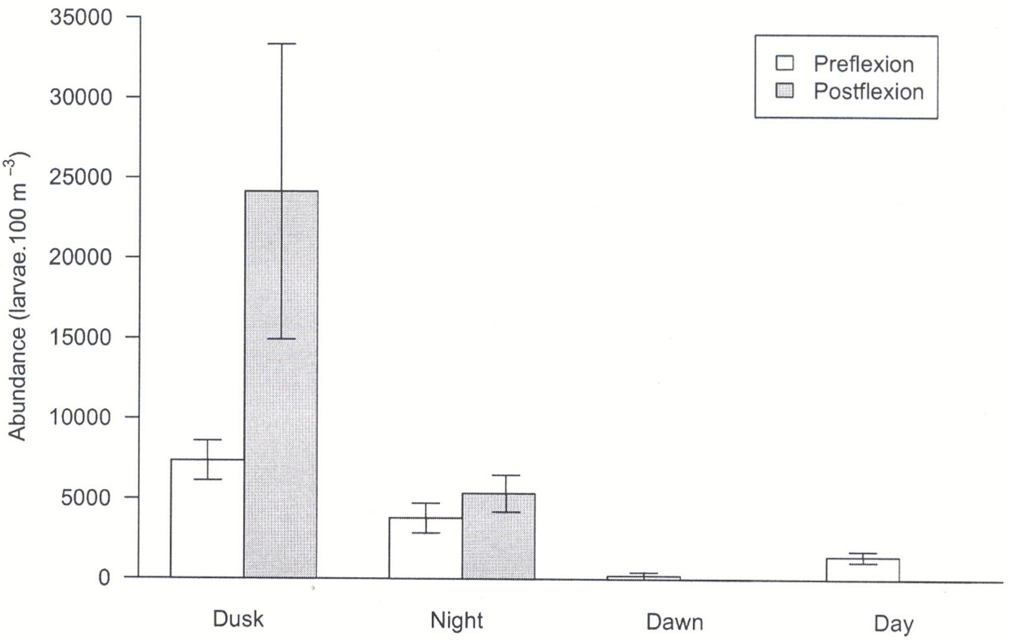

Fig. 3. Mean total abundance of *H. quadrimaculatus* pre- and postflexion larvae in the water column at dusk, night, dawn and in the day, with standard errors.

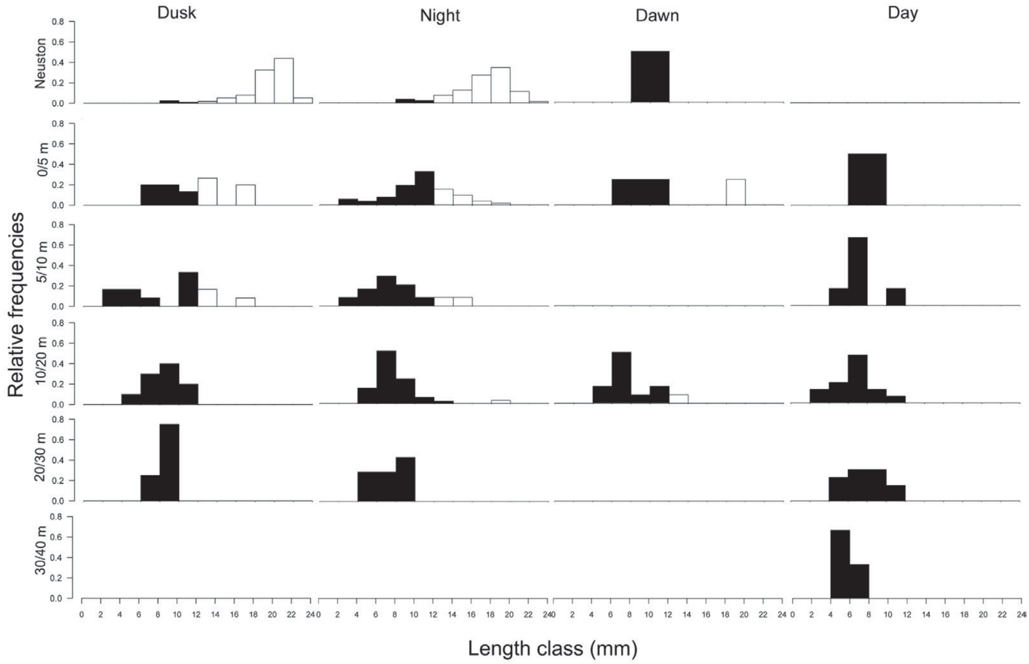

Fig. 4. Larval *H. quadrimaculatus* length composition in the water strata at dusk, night, dawn and in the day. Black and white columns represent pre- and postflexion larvae, respectively.

DISCUSSION

Sofala Bank is a shallow, expansive shelf in Mozambique characterized by strong tidal currents and estuarine runoff that determine hydrological features in the region (Lutjeharms, 2006). Variation in both tides and estuarine runoff was previously shown to be an important factor that determines the physico-chemical properties of water masses that influence the vertical dynamics of the plankton (Leal *et al.,* 2009). Vertical stratification in the water column has been shown to affect larval fish behaviour by blocking their vertical migration (Olivar *et al.,* 2001; Stenevik *et al.,* 2007). Both upward and downward movements of larvae to avoid turbulence and clines have been studied (Heath *et al.,* 1988; Olla & Davis, 1990; Coombs *et al.,* 2001). Santos *et al.* (2006) observed that European sardine larvae occur within 0-30 m during the day and mainly in the neuston at the night. Furthermore, they found the distribution of larger larvae was shallower and smaller larvae tended to be deeper. While this corroborates the results presented here (Figure 2d-e), other studies have reported the opposite. Stenevik *et al.* (2001) observed a tendency for bigger *Sardinops sagax* larvae to be found deeper, as was the case with *Engraulis encrasicolus* and *Sardina plichardus* (Olivar *et al.,* 2001). These studies concluded that, while larval distribution was mostly determined by light and food availability, it was also influenced by vertical stratification/mixing of the water column. However, as observed by Gray & Kingsford (2003), no correlation was found in the present study between vertical larval distribution and water stratification.

Diel differences observed in vertical pre- and postflexion larval distribution between the dusk/night and dawn/day samples could be related to net avoidance (during the day at shallower depths), vertical migration (movement to shallower depths at dusk/night and to deeper strata during dawn/day), or both factors. Several studies have identified net avoidance as the major factor contributing to reduced catch rates in shallower strata during the day (Brander & Thompson, 1989; Davis *et al.,* 1990; McGurk, 1992, Sakuma *et al.,* 1999; Grioche *et al.,* 2000), particularly by larger (postflexion) larvae, which are better able to swim away from the net than small larvae. In consequence, results presented here for vertical larval distribution during the day could be biased.

Vertical distribution of preflexion larvae was generally limited to a depth of 5-20 m and, apparently, there was no vertical movement. As no migratory behaviour has been observed in smaller larvae (see Coombs *et al.,* 2001 and references cited therein), the greater abundance of these larvae recorded at dusk and night (Figure 3) might be further evidence of net avoidance during the day, something the larvae cannot accomplish at night. Despite net avoidance probably occurring during the day, length composition analysis of dusk and night samples indicated that the largest larvae occupy the neuston, and smaller larvae occur at increasing depths. This trend is probably related to several factors, such as preferences by different larval stages for particular physico-chemical conditions, as well as intra-specific competition for certain environmental conditions, amongst others (Santos *et al.,* 2006; Fiksen *et al.,* 2007).

Leal *et al.* (2009) recorded maximum zooplankton densities on the Sofala Bank near the bottom during the day and near the surface at night, and there was a significant correlation between zooplankton WMD and total larval fish abundance. Bearing in mind that *H. quadrimaculatus* larvae are visual predators that feed during the day, if vertical larval distribution was associated with food availability, one would expect the larvae in the lower strata during the day, which was not observed. Our results thus corroborate other studies that emphasize the importance of hydrographic conditions in the regulation of vertical larval fish distribution (Perry & Neilson, 1988; Davis *et al.,* 1990)

In conclusion, despite the fact that diel vertical movements of *H. quadrimaculatus* larvae were probably biased by net avoidance in this study, there was evidence that they preferred the upper 20 m of the water column at dusk and night. Furthermore, ontogenetic vertical displacement was observed during the night in the shallowest layers (< 20m). These results contribute to knowledge on their vertical distribution and movement, which will be valuable in studies on their dispersal and survival. Apart from gaps in knowledge on the basic ecology of gold-spot herring, such as its distribution, growth, feeding and reproduction, further studies are needed on its larval movement and dependence on coastal processes that modulate larval survival and recruitment. Improved gear and methods are needed to overcome net avoidance in the estimation of its larval abundance.

Acknowledgments–This Special Study was part of the "Ecosystem Survey Mozambique 2007" research cruise conducted during the Nansen Programme, an EAF Project funded by the Norwegian government through NORAD, the Institute of Marine Research (Bergen, Norway) and the United Nations through FAO. We thank Instituto Nacional de Investigação Pesqueira (IIP) and its current director, Dr. D. Gove, as well as P. Afonso and E. André for their support, and J. Mwaluma of the Kenya Marine Fisheries Research Institute (KMFRI) for help in identifying the fish larvae. We are grateful for assistance provided by the crew of the R/V "Dr. Fridtjof Nansen", J-O. Karkstad, C. Bento and fellow IIP scientists. We would also like to thank the anonymous reviewers for helpful comments on the manuscript.

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