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Diet composition and feeding activity of larval spring-spawning herring: Importance of environmental variability

T. Arula [a,*], J. Kotta [b], A. Lankov [a], M. Simm [b], S. Põlme [c]

[a] Estonian Marine Institute, University of Tartu, Lootsi 2a, 80012 Pärnu, Estonia
[b] Estonian Marine Institute, University of Tartu, Mäealuse 14, 12618 Tallinn, Estonia
[c] Natural History Museum, University of Tartu, Vanemuise 46, 51014, Tartu, Estonia

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ABSTRACT

Availability of suitable prey in sufficient quantities during the shift to exogenous feeding is an important factor determining survival and growth of larval fish. The question of what factors regulate prey consumption in larval fish has remained a focus of fisheries oceanography. In this paper feeding ecology of the larval spring-spawning herring *Clupea harengus membras* was studied in relation to selected environmental abiotic and biotic parameters in the shallow sheltered Pärnu Bay during the 1970s and 2000s. The copepod *Eurytemora affinis* was the strongly dominating dietary item during all the years while other prey items were ingested only sporadically. Feeding activity of herring larvae was governed by different environmental variables and the relationships varied amongst the size classes of herring larvae. The studied abiotic (i.e., wind speed, water temperature, water transparency) or biotic variables (i.e., density of copepod *nauplii*, copepodite stages I–V and adults of *E. affinis*, mean developmental stage of copepods and density of fish larvae) had no significant effects on the feeding activity of small larvae. The feeding activity of medium larvae was only affected by water transparency and that of large larvae by a combination of water temperature, wind speed and the structure of local copepod community, respectively. On the other hand, the diet composition of all herring larvae was best described by the density of copepod *nauplii*. In addition, the density of fish larvae improved the model of small larvae and the density of adult copepods that of medium larvae, respectively. Time was significant for the feeding activity of medium larvae indicating some unexplained variability that was not taken into account by the studied abiotic and biotic variables.

1. Introduction

The question of what factors regulate patterns of feeding in larval fish has remained a focus of fisheries oceanography for several decades (Dower et al., 2002). The majority of marine fishes possess a pelagic phase, and a complex interaction of physical, chemical and biological variables likely results in the observed spatio-temporal distribution of larval fishes (e.g., Pepin et al., 1995). Thus, it becomes crucial to describe how e.g., water temperature, wind strength, light climate, turbidity and prey field interactively affect prey ingestion (Fox et al., 1999; MacKenzie and Kiørboe, 2000).

Recent studies on RNA:DNA analysis of larval herring proved that sheltered coastal areas are high quality nursery habitats in the Baltic Sea (Höök et al., 2008). Feeding conditions of fish larvae likely explain the fluctuations in the recruitment of fish populations in such habitats, either directly by inducing mortality or indirectly by lengthening the duration of the larval stage and thus exposure to predators. For instance, the year-class strength of the Atlantic herring in the North Sea appears to be mostly determined by the abundance of larvae that have not yet metamorphosed (Nash and Dickey-Collas, 2005). Similarly, the abundance of large herring larvae determines their year-class strength in the Baltic Sea (Oeberst et al., 2009, Ojaveer et al., 2011). In addition, the variability in the production of larvae largely accounts for the major fluctuations in herring stock abundance (Nash et al., 2009).

Several recent studies have focused on explaining how environment affects the feeding dynamics of fish larvae (e.g., Bergeron, 2000) without considering a wide range of environmental factors (Dower et al., 2002). Other larval fish feeding investigations have been carried out under laboratory conditions (e.g., MacKenzie et al., 1990) or have used modelling approaches (Fiksen et al., 1998). Thus, although various approaches are currently used in order to better link environmental variability and feeding ecology of larval fish, important advances still need to be made in many areas of feeding ecology of fish larvae.

Prey characteristics, such as size, pigmentation and motion, play an important role in the detection of prey for visual foraging by fish (O'Keefe et al., 1998). During the larval stage, most species feed on

* Corresponding author. Tel.: +372 4394755; fax: +372 6718900.
E-mail address: timo.arula@ut.ee (T. Arula).

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similar prey (*nauplii* and early life-history stages of copepods) (Pepin and Penney, 1997), but why larval fish prefer more advanced developmental stage of prey remains often inconclusive. However, it is known that most fish use vision for orientation towards prey (Guthrie and Muntz, 1993) and therefore it is expected that predators can sight larger prey more efficiently. To complicate it further, the detection of prey may be influenced by the reduced water transparency (Utne-Palm, 2002), as well as several other ecological factors, amongst them wind-induced turbulence (MacKenzie, 2000) that may reduce the encounter rate between prey and predator.

Herring is the principal commercial fish in the Gulf of Riga (GoR). Its local populations have been relatively well studied as well as the mechanisms that are behind its dynamics are well understood (Raid et al., 2010). While herring spawners abundance and recruitment have been at relatively high levels for two decades (Raid et al., 2010), larval herring abundance has significantly dropped recently and remained low (Ojaveer et al., 2011). Pärnu Bay (GoR) with its adjacent areas is an important nursery ground for herring larvae. Growth conditions in the nursery ground are expected to be crucial for year-class formation (Ojaveer et al., 2011). In the present paper, we focus on selected biotic and abiotic factors (such as water transparency, water temperature, wind speed and prey density and structure) to study changes in feeding activity and diet composition of herring larvae in the main spawning and larval nursery areas in the GoR. We evaluate the importance of several ecological factors on the observed feeding ecology. We hypothesize that, amongst others, larval herring food intake might be affected by decreased water transparency (HELCOM, 2009), and shift in copepods seasonality. It has been shown recently, that *Eurytemora affinis*, the main food item for fish larvae, had significant earlier seasonal development in the 1990s and 2000s than in the 1970s and 1980s (Kotta et al., 2009).

2. Material and methods

2.1. Sampling

Herring larvae were obtained from six larval fish monitoring stations in Pärnu Bay (the NE part of the GoR) at depths of 5–9 m (Table 1). Sampling of fish larvae was performed weekly from May to July during daytime in 1973–1974 and 2004–2005. Samples were taken with a Hensen larval fish trawl (mouth opening d = 80 cm, mesh size 500 μm) in the surface layer (0–1 m) by 10-minute hauls at a boat speed of ca 2 knots. The collected larvae were immediately preserved in a 4% formaldehyde solution. Altogether the guts of 2748 herring larvae were analysed from 97 hauls; thus, seasonal and spatial variability was covered in the all studied years. As guts of larval fish contained very few (mainly one) dietary items, the percentage of larvae containing food in their guts were used as a measure of the feeding activity of larval herring. This was calculated on haul basis using the following formula:

$$\text{Feeding activity} = (N_{\text{fedlarvae}}/N_{\text{alllarvae}}) \times 100,$$

where $N_{\text{fed larvae}}$ is the number of herring larvae with the prey in the guts and $N_{\text{all larvae}}$ is the total number of analysed individuals.

For analysis of feeding activity and diet composition, herring larvae were divided into three size groups: small (8.1–10.0 mm), medium (10.1–16.0 mm) and large (16.1–20.0 mm). Larvae were separated into length classes so as to be able to evaluate variations in diet and selectivity in prey size. Several research papers dealing with larval herring feeding have used similar length discrimination (e.g., Munk et al., 1989). The size group of the smallest larvae contains first-feeding larvae (Munk et al., 1989). Individuals smaller than 8 mm were excluded from gut analyses due to the presence of yolk-sac larvae. The medium size group contains larvae that have already grown but are still dependent on a relatively narrow prey spectrum and are also restricted in their swimming ability. The morphological development of the largest larvae, in particular the formation of fins, is considerably progressed. The spectrum of prey has become broader than for the other size groups, and the food availability is in general not as critical as in case of smaller larvae (Haslob et al., 2009). We limited the size span of the largest length group to 20 mm to avoid potential misinterpretation due to relatively sporadic occurrence of over 20 mm long herring larvae in samples.

Mesozooplankton were collected from two stations (at 7 m and 11 m depths) which are considered spatially representative to characterize zooplankton dynamics in Pärnu Bay. The sampling was performed simultaneously to larval fish collection from May to July with weekly resolution and was done by vertical hauls with a Juday net (opening area 0.1 m^2, mesh size 100 μm) through the whole water column from bottom to surface. Samples were preserved in a 4% formaldehyde solution and analysed by a routine method suggested by the Baltic Monitoring Programme (HELCOM, 1988). Adults and copepodite stages of copepods were identified to a species levels. *Nauplii* were involved as a separate group. The major larval prey (i.e., copepods) was identified and counted by the following different developmental stages: *nauplii*, copepodites by stages from I to V and adults. Mean developmental stage of copepods was calculated for each haul. The following developmental stages of copepods were applied: 1—copepod *nauplii* (*nauplii*); 2–6—copepodite stages I–V of *E. affinis* (EI-V); 7—adult *E. affinis* (Ead).

In addition, sea surface water temperature (SST) (°C) and water transparency (Secchi depth, precision 0.1 m) were measured throughout all larval herring sampling events. Water temperature was measured with thermometer in near-surface water layer. Secchi measurements were obtained by lowering a circular white disc slowly down in the water. The depth at which the pattern on the disc is no longer visible was taken as a measure of the transparency of the water. Data on the strength of daily wind speed were obtained from the Estonian Meteorological and Hydrological Institute for all sampling events.

The length of herring larvae was measured under binocular microscope (type MBC 10, magnification of 8 × 1) from the tip of the snout to the end of the neurochord. Larval digestive tracts were inspected with the same microscope at magnifications of 8 × 4 to 12.5 × 7. Diet items were identified to the lowest taxonomic level.

Table 1
Sampling stations for zooplankton (1–2) and fish larvae (3–8) in Pärnu Bay (Gulf of Riga, Baltic Sea).

Station	Coordinates	
	N	E
1.	58° 13′	24° 18′
2.	58° 20′	24° 25′
3.	58° 22′	24° 22′
4.	58° 20′	24° 26′
5.	58° 19′	24° 31′
6.	58° 15′	24° 27′
7.	58° 13′	24° 13′
8.	58° 16′	24° 19′

2.2. Statistical analyses

The monthly aggregated data were analysed by the statistical software SPSS PASW (Predictive Analytics SoftWare) Statistics version 18 and R version 2.10.1. Repeated measures analysis of covariance (RMA) was used to analyse the time-effect (levels: months in respective years) on the feeding activity of herring larvae. Sampling time was considered as repeated measures. Wind speed, water temperature, transparency, copepods density (by developmental stages, i.e. *nauplii*, EI-V and Ead), mean developmental stage of copepod and density of fish larvae were included into analysis as time-varying covariates. The unit of measurement to analyse the feeding activity of herring larvae was one haul. RMA tests whether time factor has an