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Underwater Marine Environment

Annica Långnabba, Juha Hyvönen, Sanna Kuningas, Antti  
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Natural Resources Institute Finland, Helsinki 2019

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## Summary

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Along the Finnish coast, the Gulf Olympia paired ichthyoplankton samplers have been widely used for collecting early life stages of pelagic fish, e.g. within the Finnish Inventory Programme for Marine Underwater Environment (VELMU), aiming to localize larval habitats. The aim of this study was to examine how prevailing conditions during the sampling period impact the sampling efficiency and the data obtained with the Gulf Olympia samplers.

The study was conducted in the Skinnarfjärden-Köklotfjärden Bay on the west coast of Finland, within the northern Kvarken Archipelago in the northern Baltic Sea. Sampling was carried out along 10 randomly pre-allocated transects during 5 days between the 6th and 12th of June 2017. Effect of sampling depth (0.5 m and 1.0 m), wave height, light availability and sampling time (morning / afternoon) on larval density of perch (*Perca fluviatilis*) and smelt (*Osmerus eperlanus*) was studied using linear mixed model analysis.

Sampling depth affected the results, as sampling at 0.5 m yielded 6 times more perch and 1.3 times more smelt larvae than at 1.0 m depth. Wave height was also found to correlate positively with larval abundance of both perch and smelt at depth of 0.5 m, with a 16-fold and 8-fold increase in perch and smelt density respectively, following a change in wave height from 0 m to 0.3 m. Both perch and smelt larval density correlated positively with increasing levels of light, while no significant effect of sampling time was found. Finally, we give recommendations for future sampling settings.

This study was carried out as a part of the VELMU 2 programme, funded by the Ministry of the Environment and the Ministry of Agriculture and Forestry of Finland.

Keywords: Gulf Olympia, ichthyoplankton sampler, sampling, method, fish, perch, smelt, coastal area, environmental variables

## Yhteenveto

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Vastakuoriutuneiden kalanpoikasten esiintymisalueita on Suomen rannikolla kartoitettu veneen keulaan kiinnitetyillä Gulf Olympia-noutimilla. Parittaiset noutimet on kiinnitetty molemmin puolin veneen keulaa, toinen 0.5 m ja toinen 1.0 m syvyyteen. Noutimet keräävät haavipussin perällä olevaan näyteastiaan pelagiset kalojen pienpoikaset. Tämän tutkimuksen tarkoituksena oli selvittää, miten Gulf-näytteenoton aikana vallitsevat ympäristöolosuhteet vaikuttavat poikasten pyydettyvyyteen ja näytteenoton tehokkuuteen.

Tutkimus toteutettiin Skinnarfjärden-Köklotfjärdenin lahdessa Merenkurkussa. Näytteenotto tehtiin kymmenellä satunnaisesti valikoidulla näytteenottolinjalla viiden päivän aikana, 6.-12.6.2017. Näytteenottosyvyyden (0.5 m ja 1.0 m), aallonkorkeuden, valoisuuden ja näytteenottoajan (aamupäivä / iltapäivä) vaikutusta ahvenen (*Perca fluviatilis*) ja kuoreen (*Osmerus eperlanus*) poikasten runsauteen tutkittiin käyttäen lineaarista sekamallianalyysiä.

Näytteenottosyvyys vaikutti tuloksiin, sillä 0.5 metrin syvyydestä saatiin saaliiksi kuusi kertaa enemmän ahvenen ja 1.3 kertaa enemmän kuoreen poikasia kuin 1.0 metrin syvyydestä. Aallonkorkeuden havaittiin korreloivan positiivisesti sekä ahvenen että kuoreen poikasten runsauden kanssa 0.5 m syvyydestä kerätyissä näytteissä. Ahvenen poikasten määrä kasvoi 16-kertaiseksi ja kuoreen 8-kertaiseksi aallonkorkeuden kasvaessa nolasta metristä 0.3 metriin. Sekä ahvenen että kuoreen poikasten runsaus korreloi myös positiivisesti kasvavan valoisuuden kanssa. Näytteenottoajalla ei osoitautunut olevan merkittävää vaikutusta poikasmääriin. Raportin lopussa annamme vielä suosituksia tuleviin näytteenottoihin.

Tutkimus toteutettiin osana VELMU 2 -inventointiohjelmaa ja sen rahoittivat Ympäristöministeriö ja Maa- ja metsätalousministeriö.

Asiasanat: Gulf Olympia-näytteenotin, näytteenotto, kala, ahven, kuore, rannikko, ympäristöolosuhteet

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# 1. Introduction and main aims of the work

Along the Finnish coast, the Gulf Olympia paired ichthyoplankton samplers have been widely used for collecting early life stages of pelagic fish, e.g. within the Finnish Inventory Programme for Marine Underwater Environment (VELMU), aiming to localize larval habitats. The method provides quantitative measures on abundance and density, and is therefore advantageous for mapping and modelling availability and extent of habitats essential for fish reproduction, as well as for predicting larval survival and recruitment (Kraufvelin et al. 2018; Kallasvuo et al. 2016; Veneranta et al. 2011; Aneer et al. 1992; Urho & Hildén 1990; Hudd et al. 1984).

As the spatial extent of important reproductive habitats is commonly highly disproportionate to the distribution of adult fish, and for many commercially important species smaller still than the extent of the nursery areas, the availability of suitable habitats for early larval stages may act as a bottleneck for fish stock recruitment (Kallasvuo et al. 2016; Sundblad et al. 2014). As such, knowledge on early life stage habitat availability, as well as temporal and spatial changes or patterns in larval abundance, may be useful for estimating population size variations of exploited adult fish (Sundblad et al. 2014; Kjellman et al. 2003; Urho & Hildén 1990).

With more information on larval habitats available, maps, species distribution models and other GIS based applications have also gained in accuracy. Such visual aids have become fundamental for coastal and marine spatial planning, management and conservation efforts, as a majority of essential fish habitats are located in areas exploited by humans, and thus, affected by constant and often cumulative anthropogenic pressures in combination with broader threats such as climate change (Kraufvelin et al. 2018; Kallasvuo et al. 2016; Seitz et al. 2014; Sundblad & Bergström 2014; Backer & Frias 2013; Veneranta et al. 2013; HELCOM 2010; Snickars et al. 2010).

As local conditions can deteriorate fast in anthropogenically affected environments, there is a need for developing ways to reliably identify and evaluate the importance of individual reproductive habitats. Gulf sampling and similar methods, that provide quantitative measures of larval fish habitats, have an advantage over more commonly used occurrence models, when examining fish production potential and identifying the most favorable localities amongst the total pooled areas used for reproduction (Kraufvelin et al. 2018; Kallasvuo et al. 2016).

However, with the increasing investment of effort into studies and surveys aimed at gathering quantitative data on early life stages of fish, there has also been a growing realization that encountered larval abundances fluctuate due to both well-known and lesser studied factors of both biotic and abiotic origin (Kallasvuo et al. 2016). As an example, larvae are known to actively perform vertical migrations in the water column as a response to temperature, light, and prey availability (Voss et al. 2007; Wang & Appenzeller 1998; Wanzenböck et al. 1997; Munk et al. 1989). Larvae will also migrate horizontally, in order to avoid being preyed upon, in search of more favorable conditions, or in response to changing habitat requirement (Veneranta et al. 2011; Urho 1996; Urho et al. 1990). In addition to active dispersal, environmental gradients, weather conditions and fluctuations in water quality are also likely drivers of temporal and spatial variations, as differences in abundance over relatively small areas and intervals of sampling depth have been observed in several studies (Härmä & Lappalainen 2009; Snickars et al. 2009; Žiliukiene 2002; Margoński 2000; Wanzenböck et al. 1997; Urho & Hildén 1990; Hudd & Urho 1985).

It is not known to what degree these factors, separately or combined, impact the sampling efficiency and the data obtained with Gulf Olympia samplers, but it is likely that e.g. notable differences in weather conditions will affect larval abundances in surface waters. In order to facilitate comparison and utilization of abundance data between studies of different areas or years, there is a need for

increased knowledge on how to account for such potential impacting factors. Furthermore, if the effects of varying weather and environmental conditions become known, the knowledge can be used to improve future sampling set-ups, so that timing and extent of larval sampling and abiotic parameter measurements are chosen according to the area being studied, while also taking into account the transferability of data to other contexts.

The aim of this study was to examine whether variations in larval fish density can be explained by measures of prevailing conditions during sampling, and if so, which variable(s) would have the strongest determining effect on larval abundance. Hence, this study was designed and conducted in order to evaluate which, if any, measurable environmental parameter is likely associated with determining vertical and horizontal variations in spatial and temporal distribution of newly hatched pelagic larvae of coastal fish species in the surface water layer. The sampling therefore had to be carried out within a narrow time span, in order for the fish larval assemblage to remain comparable regarding species composition and length distribution, and within a relatively homogenous nursing area to avoid results being confounded by larger gradients.

This study was carried out as a part of the VELMU 2 programme, funded by the Ministry of the Environment and the Ministry of Agriculture and Forestry of Finland.



## 2. Description of the method

### 2.1. Gulf sampling method

The Gulf Olympia paired ichthyoplankton samplers were developed in the 1980s by Hudd et al. (1984), for sampling in shallow estuarine and coastal waters. The first Gulf samplers had been introduced in the 1950s and 1960s, most models encased in a sturdy frame, designed to be towed at relatively high speed and, therefore, their use limited by both depth and the need of a sizable vessel to tow the weight. As the Gulf Olympia was intended for sampling in shallow areas, it was designed to be lightweight and operable by a small crew of two persons for use in smaller boats (Borg et al. 2012; Aneer et al. 1992; Hudd et al. 1984).

The design of the sampling unit is similar to previous Gulf models, consisting of a conical steel nosecone (widening from the mouth) with an attached conical, narrowing plankton net ending in a plastic fitting to which a collecting jar with a filtering mesh window is affixed. The key difference from previous Gulf samplers was the shift from tow- to push-net sampling – this was achieved by attaching the samplers on adjustable levers perpendicular to a steel frame, horizontally mounted across the front-end of the boat (Figure 1). As a result, the nosecones are set facing forwards approximately 2 m apart at either side of the bow of the boat. The lever bars can be adjusted to sample depths between 0.25 and 2.0 m, meaning fine-scale vertical distribution differences can be examined. At completion of sampling, the bars are heaved up parallel to the side of the boat, lifting the mouth of the nosecone face-up out of the water, effectively trapping the sample in the net for collection (Borg et al. 2012; Veneranta et al. 2011; Aneer et al. 1992).

Further advantages of the pushed Gulf Olympia design over towed nets include having no forward obstruction in front of the nosecone mouths, as well as a lowered risk of net avoidance amongst larvae, as perturbations from the movement of the boat does not impact the surface water at the bow (Borg et al. 2012; Wanzenböck et al. 1997). A disadvantage common to most Gulf samplers, is the relatively small diameter of the nosecone mouth, meaning that it will only sample larvae up to a certain size reliably, after which active avoidance likely will increase (Borg et al. 2012; Urho & Hildén 1990). Despite this, Gulf samplers are among the best suited methods for collecting quantitative data on pelagic larvae of fish, and the use of the Gulf Olympia paired sampler is well-established in the northern Baltic Sea, where coastal shallow areas make up the bulk of essential fish habitats for reproduction of commercially fished species (Kraufvelin et al. 2018; Kallasvuo et al. 2016; Borg et al. 2012; Veneranta et al. 2011; Ljunggren et al. 2010; Žiliukienė & Žiliukas 2009; Nilsson et al. 2004).



**Figure 1.** Gulf Olympia paired ichthyoplankton samplers are mounted parallel to each other at the bow of the boat, allowing for simultaneous sampling of different depths (0.25 – 2 m). The nosecones are lifted out of the water for collection of the samples and during transport between sampling sites (photo: Lari Veneranta, Luke)

## 2.2. Experimental set up

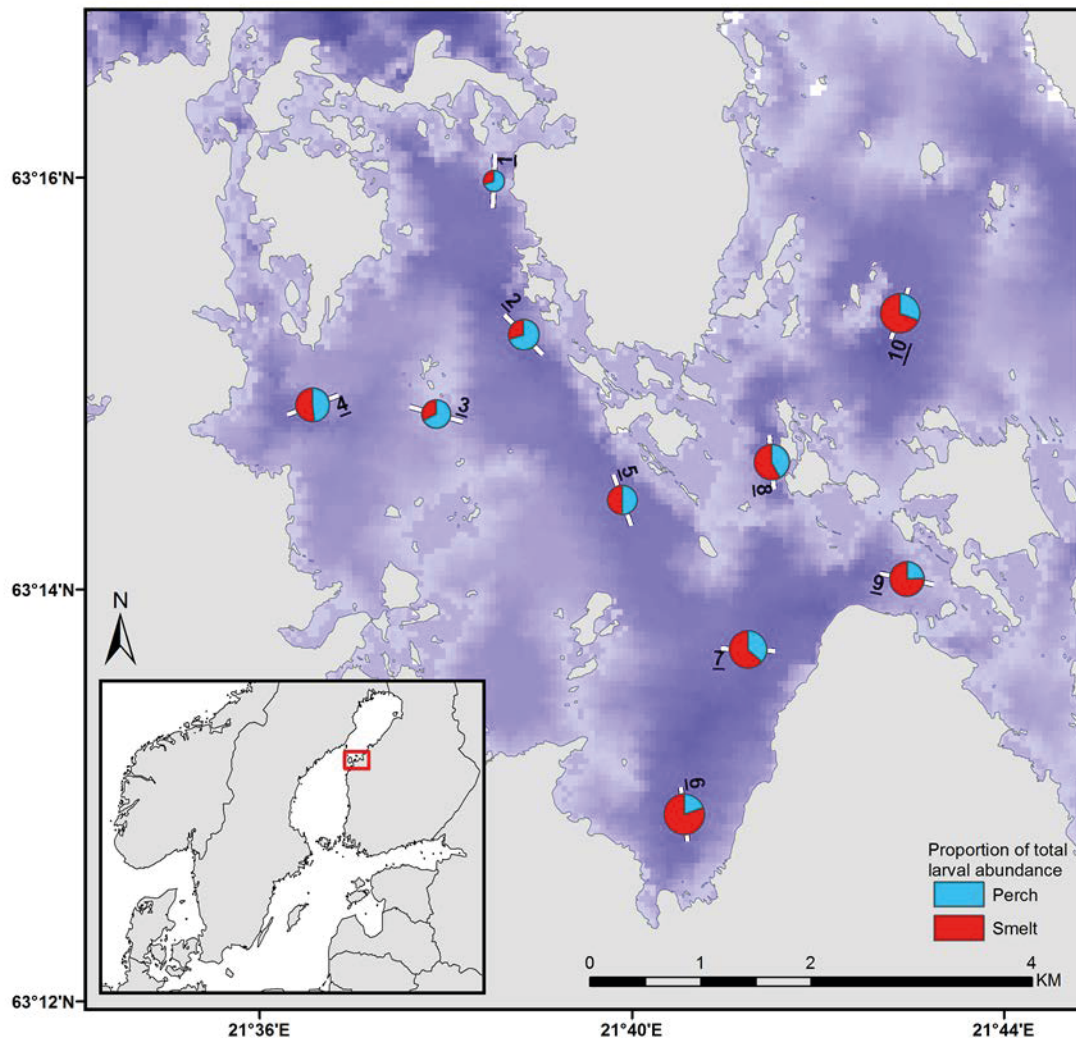
### 2.2.1. Study area

The study area was located in the Skinnarfjärden-Köklotfjärden Bay on the west coast of Finland, within the northern Kvarken Archipelago in the northern Baltic Sea (Figure 2). Northern Kvarken forms a sill between Finland and Sweden, connecting the Gulf of Bothnia with the Bothnian Bay.

Glacial events of the last ice-age resulted in its present-day geomorphology, the most prominent features being the archipelago landscape, moraine ridges, shallow depths (the majority within 0-25 m; maximum depth 30 m) and underwater reefs, all continuously affected by post-glacial isostatic land uplift (Voipio 1981; Breilin et al. 2004). Strong environmental gradients from north to south, as well as between the inner and outer archipelago zones, result in a multitude of biotopes and hydrological conditions where a mix of saline and freshwater species co-occurs (Voipio 1981; Snickars et al. 2009; Kallasvuori 2010). The coastal morphology in combination with land-uplift further facilitates diversity through creating a succession of shallow flads and lagoons characteristic of the Kvarken Archipelago, before they eventually become freshwater ponds only occasionally linked to the sea. Such flads and lagoons often exhibit ideal conditions regarding temperature and vegetation cover for egg development and as nursery grounds of spring spawning fish (Snickars et al. 2009, Snickars et al. 2010).

The shallow Skinnarfjärden-Köklotfjärden Bay has a maximum depth of 9 m and is located in the inner archipelago zone, covering 34 km<sup>2</sup> interspersed with small islands, eskers and underwater reefs (Westberg et al. 2009; Westberg & Lax 2016), and within it are many flads, lagoons and estuaries known to be spawning grounds for e.g. perch (*Perca fluviatilis*) and smelt (*Osmerus eperlanus*) (Hudd

et al. 1984; Hudd 1983). Results from water quality and zoobenthos surveys in the area indicate strong anthropogenic impact, due to nutrient rich and occasional acidic discharge from nearby rivers, and the ecological status of Skinnarfjärden-Köklotfjärden Bay has been classified as poor, as per EU Water Framework Directive guidelines (Westberg et al. 2009; Westberg & Lax 2016). Despite this, Kallasvuo et al. (2016) identified the bay as an important reproduction habitat for perch and smelt, in a modelling study of high-resolution abundance prediction maps. The suitability as a nursery ground is best explained by its shallowness, low wave exposure, and relatively high cumulative spring temperature, as it's encased by mainland, larger islands, and built causeways, having only limited water exchange with the surrounding sea through natural narrow and shallow straits. Hence, the bay's geographical homogeneity and likely importance as a nursery ground made it a suitable sampling area for this study, allowing for measurements of fine-scale weather changes and hydrological gradients for identifying patterns in fish larvae distribution. As the ecological status of the area is expected to improve long-term (Westberg & Lax 2016), the data collected for this study may also be of value for future surveys.



**Figure 2.** Map displaying allocation and orientation of Gulf-transects numbered 1 to 10 within the study area, and geographical location of Skinnarfjärden-Köklotfjärden Bay (inset). Pie charts display respective proportions of total abundance of perch and smelt larvae for each transect.

### 2.2.2. Sampling

Sampling was carried out along 10 randomly pre-allocated transects in the Skinnarfjärden-Köklotfjärden Bay during 5 days between the 6<sup>th</sup> and 12<sup>th</sup> of June 2017 (Figure 2). The timing of the study was chosen to coincide with the early life stages of newly-hatched perch larvae, as these exhibit highest abundances and disperse in open water shortly after hatching, making the use of pelagic zooplankton nets the most advantageous method for quantitative sampling (Urho 1999; Kjellman et al. 2003; Veneranta et al. 2011; Kallasvuo et al. 2016). In order to evaluate the importance of diurnal variation, sampling was repeated twice daily, with one set of samples collected during morning hours (AM), followed by a second set during the afternoon (PM).

Pelagic larvae were collected using a set of paired Gulf Olympia samplers (Hudd et al. 1984; Aneer et al. 1992), with a net mesh size of 300  $\mu\text{m}$ , sampling at fixed depths of 0.5 and 1.0 m. Sampling depths were chosen based on newly-hatched larvae generally tending to prefer warmer surface waters (Kallasvuo et al. 2016). Sampling effort for each transect comprised moving along a 500 m straight line at a near constant speed of 2  $\text{ms}^{-1}$ , with sampling time per transect averaging 4.2 minutes. A handheld Garmin 76CSx GPS was used to adjust speed and measure the distance travelled. Both Gulf Olympia nosecones had a mouth diameter of 0.19 m, each sampling a water volume of  $\sim 14.2 \text{ m}^3$  per transect.

At the starting point of each transect, before deploying the paired samplers, prevailing weather conditions (air temperature ( $^{\circ}\text{C}$ ), wind speed ( $\text{ms}^{-1}$ ) and direction, relative cloud cover (0-8), mean wave height (m), and presence/absence of rain) were noted and parameters for water quality measured using a Hanna Instruments HI-98194 multiparameter meter and a Eutech TN-100 turbidimeter. Parameters for salinity, pH, dissolved oxygen and water temperature ( $^{\circ}\text{C}$ ) were measured at 0.5 m depth, followed by additional water temperature measurements at depths 1.0, 2.0, and 3.0 m. Surface water was used for measuring turbidity, the noted value being a mean of three readings of the same vial sample. After noting environmental descriptors, the course was set and the paired samplers lowered simultaneously as sampling speed was adjusted. On the completion of a transect speed was let up, the samplers lifted, and the net bags rinsed to assure larvae were trapped in the collecting bottles. The respective samples were transferred to glass jars and labelled, and preserved in 4 % formaldehyde solution.

Samples were viewed at a later date in a laboratory setting, firstly rinsed clean of formaldehyde and fixed in 94 % ethanol before examined under stereomicroscope. Fish larvae were separated from the plankton, identified to species (gobies to family Gobiidae), counted and measured to the nearest millimeter. In the case of large samples, larvae were separated according to species and a subset of visually estimated proportion was taken for counting and measuring, after which the counts were multiplied to represent the sample total for analysis.

Additional weather and atmospheric data were further accessed via the Finnish Meteorological Institute's (FMI) open data services (<https://en.ilmatieteenlaitos.fi/download-observations#!/>) for the time of the sampling. The nearest observational stations to the study area were Vaasa Klemetilä (Weather data; 63°10 N, 21°64 E), Vaasa Vaskiluoto (Mareograph; 63°08 N, 21°57 E), and Mustasaari Valassaaret (Weather data; 63°44 N, 21°07 E). Estimated relative cloud cover was exchanged with illuminance readings (lux) measured with an Onset HOBO UA-002-64 Pendant, located at ca. 1.8 m depth in a shallow flad within the Skinnarfjärden-Köklotfjärden Bay (63°13'21 N, 21°37'54 E). Illuminance was measured with two hour intervals, and the reading closest to the respective sampling time of each transect was used in the analysis.

### 2.3. Study species

The spring-spawning perch and smelt commonly occur and reproduce along the Finnish coast (Kallasvuo et al. 2016), and thus, the timing of the study was chosen to overlap with the pelagic larval stages of the two species (Figure 3). Perch spawns in shallow, sheltered coastal areas and estuaries, commonly between April and May in response to warming of waters, laying the egg strands commonly onto perennial macrophytes. Embryonal development and hatching is closely dependent on ambient water temperature, with 8 °C the minimum, and 13 °C being the optimum for development and survival. Perch larvae are relatively well-developed at hatching, and capable of active horizontal and vertical movement early-on. Shortly after hatching, larvae will disperse evenly in the pelagic waters of the larval habitat, but will move towards the littoral vegetation after the first few weeks of growth, as active habitat selection starts soon after reaching a length of 8 mm (Snickars et al. 2010; Urho 1999; Sandström et al. 1997; Urho 1996; Hudd et al. 1984).

Smelt spawns in rivers, estuaries, or sheltered bays between March and May, at the first onset of spring warming of water. Spawning sites are located where hard bottom substrates dominate and water flow is continuous. Eggs attach to the substrate, and hatch from the end of May to late June, after water temperature has reached 12 °C. Newly-hatched larvae measure 5 mm, and initially increase in length at a rate of 0.3 mm per day. Shortly after hatching, larvae are dispersed throughout the nursery area through water circulation. (Žiliukiene 2002; Margoński 2000; Urho et al. 1990; Hudd & Urho 1985; Hudd et al. 1984).



**Figure 3.** Newly-hatched larvae of perch (left) and smelt (right). Both species hatch at a length of ca. 5 mm (Photos: Lari Veneranta, Luke).

## 2.4. Statistical analysis

Larval density (number of larvae per cubic meter) of perch and smelt were modelled separately using the linear mixed model, including the following fixed and random effects (levels:  $i$  = sampling transect,  $j$  = sampling date,  $k$  = sampling time,  $l$  = sampling depth):

$$\begin{aligned} \ln(\text{Density}_{ijkl}) = & \beta_0 + \beta_1 (\text{Depth}_{ijkl}) + \beta_2 (\text{Time}_{ijk}) + \beta_3 (\text{Depth}_{ijkl} \text{Time}_{ijk}) + \beta_4 (\text{Wave}_{ijk}) \\ & + \beta_5 (\text{Depth}_{ijkl} \text{Wave}_{ijk}) + \beta_6 (\text{Illum}_{ijk}) + \beta_7 (\text{Depth}_{ijkl} \text{Illum}_{ijk}) \\ & + \text{Transect}_i + \text{Date}_{ij} + \text{Timecat}_{ijk} + e_{ijkl} \end{aligned}$$

Logarithmic transformation (ln) of larval density (Density) was used to normalize and homogenize the model residuals. The explanatory variables for the fixed effects (with parameters  $\beta_0, \dots, \beta_7$  to be estimated) were: **Depth** = indicator variable (1/0) of sampling depth (0.5 m/1 m), **Time** = sampling time (in hours, minutes converted to decimals), **Wave** = wave height (m) and **Illum** = illuminance (lux).

Three random effects were added in the model with four level hierarchy: Transect = sampling transect, Date = sampling date within sampling transect, Timecat = time (AM/PM) within sampling date, and  $e$  = random error (sampling depth within time (AM/PM)). All random terms were assumed to be normally distributed and independent of each other. Autoregressive covariance structure for sampling date within sampling transect and heterogeneous variance structure for random errors by sampling depths were used with random effects to take account of correlation and variance (estimated covariance parameters) of larval density values.

The used model was based on experimental design, interesting and reasonable fixed effects, statistical tests (in logarithmic scale), and diagnostic model statistics and plots. After estimation of the model parameters, the mean larval densities in the original scale – approximately median values – were predicted using only the fixed effects in exponential back-transformation (exp):

$$\begin{aligned} \text{Density}_{ijkl} = & \exp[\beta_0 + \beta_1 (\text{Depth}_{ijkl}) + \beta_2 (\text{Time}_{ijk}) + \beta_3 (\text{Depth}_{ijkl} \text{Time}_{ijk}) + \beta_4 (\text{Wave}_{ijk}) \\ & + \beta_5 (\text{Depth}_{ijkl} \text{Wave}_{ijk}) + \beta_6 (\text{Illum}_{ijk}) + \beta_7 (\text{Depth}_{ijkl} \text{Illum}_{ijk})] \end{aligned}$$

When mean larval densities were predicted by values of one explanatory variable, other variables were adjusted to their means effects.

Mixed modelling was also done separately for both sampling depths to clarify the effects and significance of sampling time, wave height and illuminance on larval density.

Modelling was carried out by the MIXED procedure of the SAS statistical software, version 9.4.

## 3. Results

### 3.1. Occurrence of larvae

Overall abundance was dominated by perch and smelt, accounting for over 41 % and 58 %, respectively, of all collected larvae (Table 1). The remaining portion was made up by Eurasian ruffe (*Gymnocephalus cernua*) and larvae within the Gobiidae family; they were however excluded from further analysis due to their low abundance.

Regarding the size distribution of perch and smelt, both species showed a small daily growth over the sampling period, but the dominating size classes were well within the range commonly represented during the pelagic life stages (Figure 4). This was expected, and a prerequisite for the direct comparison of samples when testing for effects of varied environmental conditions.

Overall density for both perch and smelt was highest during the first two days of sampling, and decreased notably thereafter (Figure 5). Perch exhibited a sharper decline, indicating that the sampling probably caught at least part of the occurrence peak, but also the cohort tail, as larval numbers began to decrease. At closer inspection of daily differences in density by sampling time (AM/PM) and depth (0.5/1.0 m) both perch (Figure 6) and smelt (Figure 7) were caught in higher numbers in the near-surface (0.5 m) samples during morning (AM). Perch also demonstrated higher densities in the near-surface samples during afternoon (PM), especially during the three first days of sampling. During the last two days, with low overall abundance, the pattern was less obvious or reversed, and larvae more evenly distributed over the two depths and sampling times. Perch larvae were seemingly evenly distributed across the study area, as the decrease in density over the course of the study was apparent at each sampling location, and no spatially tied pattern for abundance was visible.

Contrary to perch, smelt abundance varied between transects, showing consistently higher densities in the South-Eastern part of the study area (transects KO6 – KO10; Figures 2 & 7). The pattern of higher density in near-surface AM samples was present during the three first days of sampling, after which smelt, similarly to perch, was more evenly distributed both over depth and sampling time. The decrease in total abundance during the sampling dates was also reflected within each transect. Thus, smelt was proportionately evenly distributed across the study area, despite higher abundance overall exhibited by transects KO6 – KO10.

Sampling order of transects was kept constant during sampling, but hourly sampling time differed notably between dates, with 82 % of AM samples collected within 2 hours (9:30-11:30), compared to only 74 % of PM samples collected over the span of 4 hours (14:30-18:30). In effect, the time that passed between morning and afternoon sampling varied between 3.5 – 8 hours during the five sampling dates, rendering straight-forward comparisons between AM and PM data difficult.

**Table 1.** Summarised data on larval assemblage (all samples pooled).

Species	Number of larvae		Mean length mm	Mean density larvae m <sup>-3</sup>	Sample occurrence n (total) = 200
	Count	% of grand total			
Smelt	10 875	58.75 %	8.4	3.84	197
Perch	7 602	41.07 %	6.8	2.68	181
Ruffe	29	0.16 %	4.4	0.01	26
Gobiidae	4	0.02 %	3.3	0.001	4

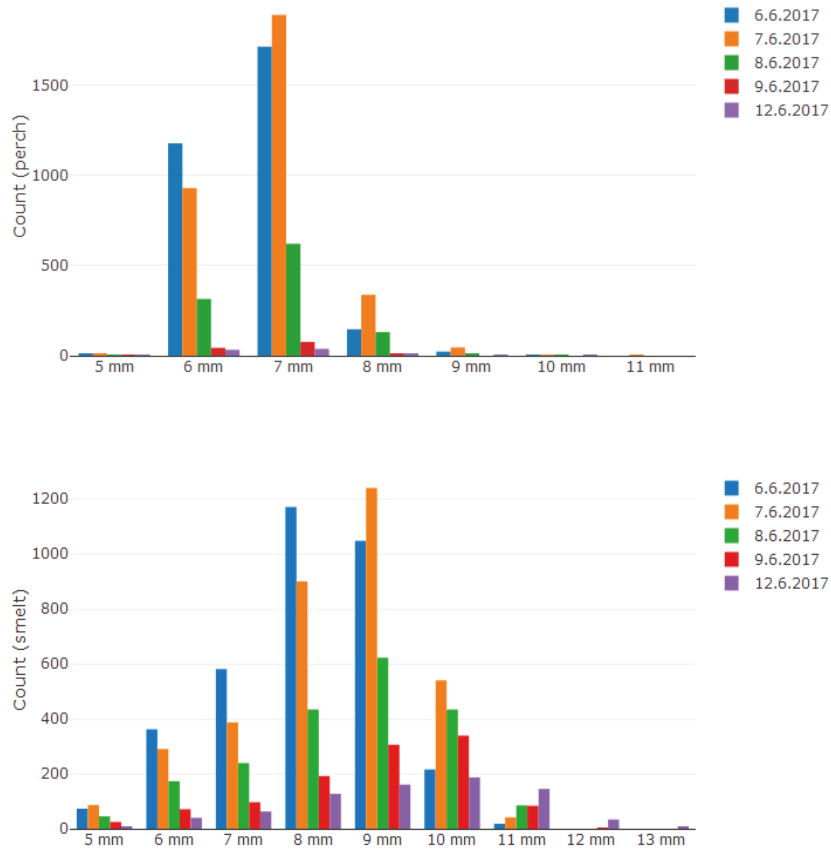


Figure 1. Size distribution for perch and smelt per sampling date.

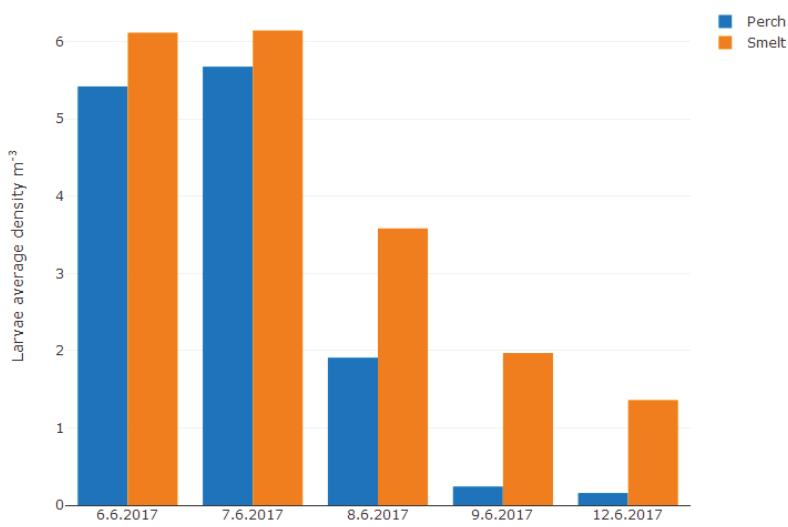
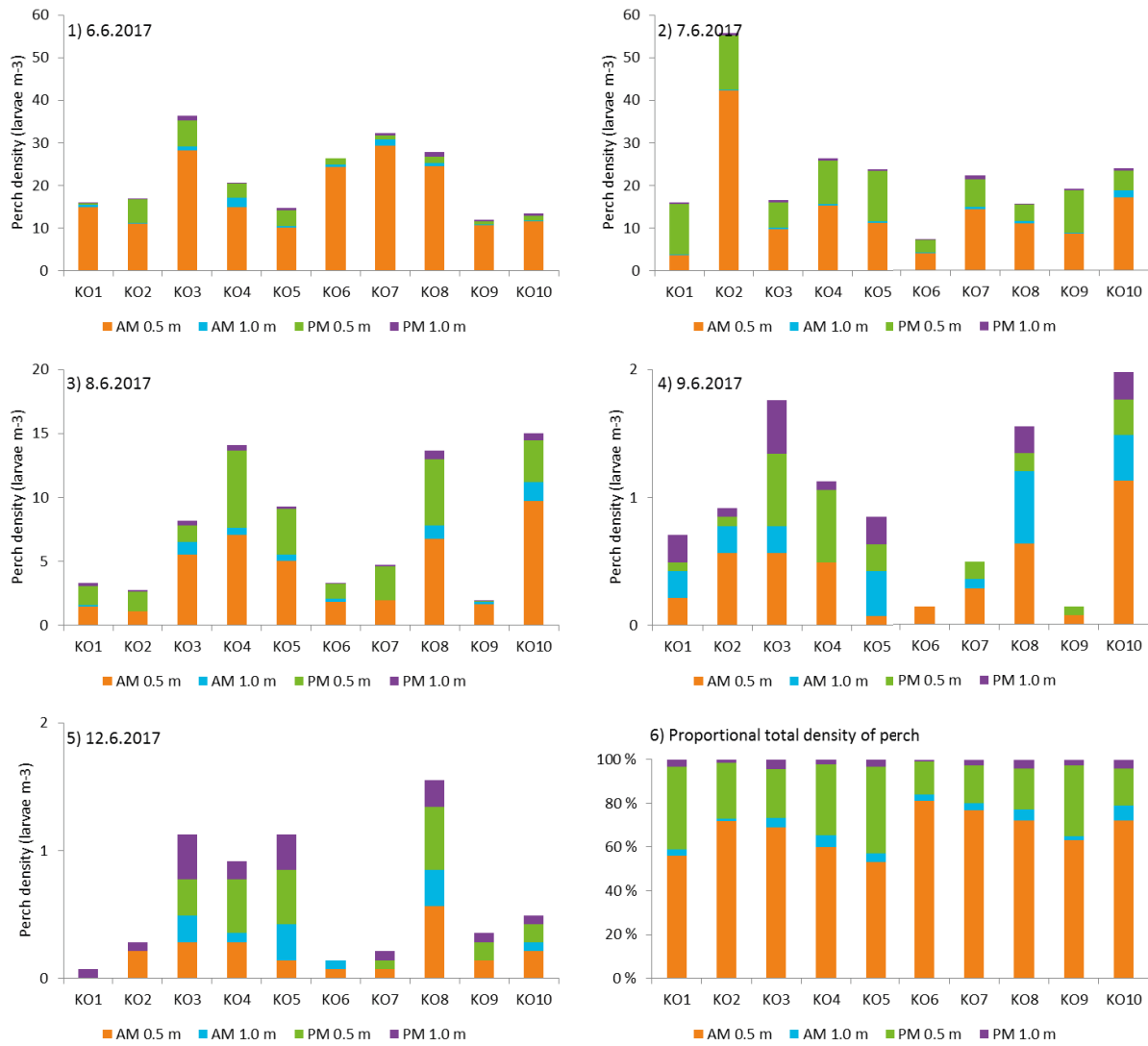
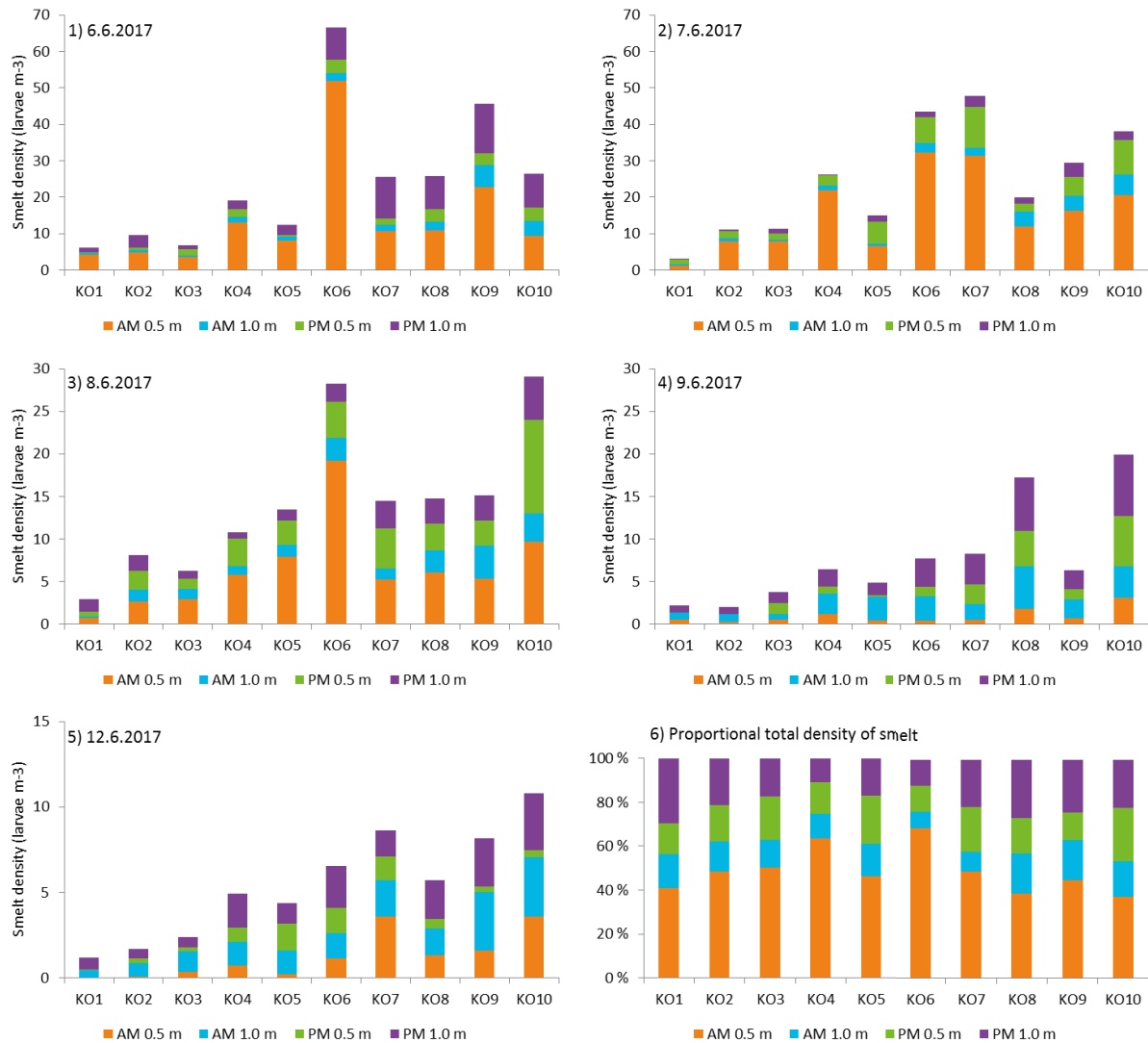


Figure 2. Mean total density of perch and smelt by sampling date.





**Figure 3.** Average density for perch per sampling transect (KO1 – KO10) by date (graphs 1 – 5), and proportional total density for all dates (graph 6). Stacked bars display the density by sampling time (AM / PM) and depth (0.5 m / 1.0 m). Note the difference in y-axis scale in graphs 1 – 5.



**Figure 4.** Mean density for smelt per sampling transect (KO1 – KO10) by date (graphs 1 – 5), and proportional total density for all dates (graph 6). Stacked bars display the density by sampling time (AM / PM) and depth (0.5 m / 1.0 m). Note the difference in y-axis scale in graphs 1 – 5.

### 3.2. Effect of environmental parameters and weather conditions

When examining data from FMI observational stations on wind speed and air pressure, no events of extreme weather occurred during the relatively short period of sampling. Air pressure rose to near mean sea level pressure (1013 hPa) during the first day, and varied little throughout the first four days of sampling. A low pressure system coincided with the final day of sampling, but did likely not affect overall larval abundance, as these had started decreasing already during normal pressure conditions.

Mean hourly wind speed fluctuated within and between sampling days, but never exceeded 10 ms<sup>-1</sup>. Estimated wind speed during sampling largely corresponded to the meteorological observations from Vaasa and Valassaaret stations (Figure 8). Wind estimates were similar during the first three days of sampling, on average 4–5 ms<sup>-1</sup>, and calmer during the final two days, averaging 1.3 and 2.5 ms<sup>-1</sup> respectively. Field observations of wind direction were likely consistently skewed, as estimated directions plotted in a wind rose diagram exhibited the same shape as the recorded corresponding FMI

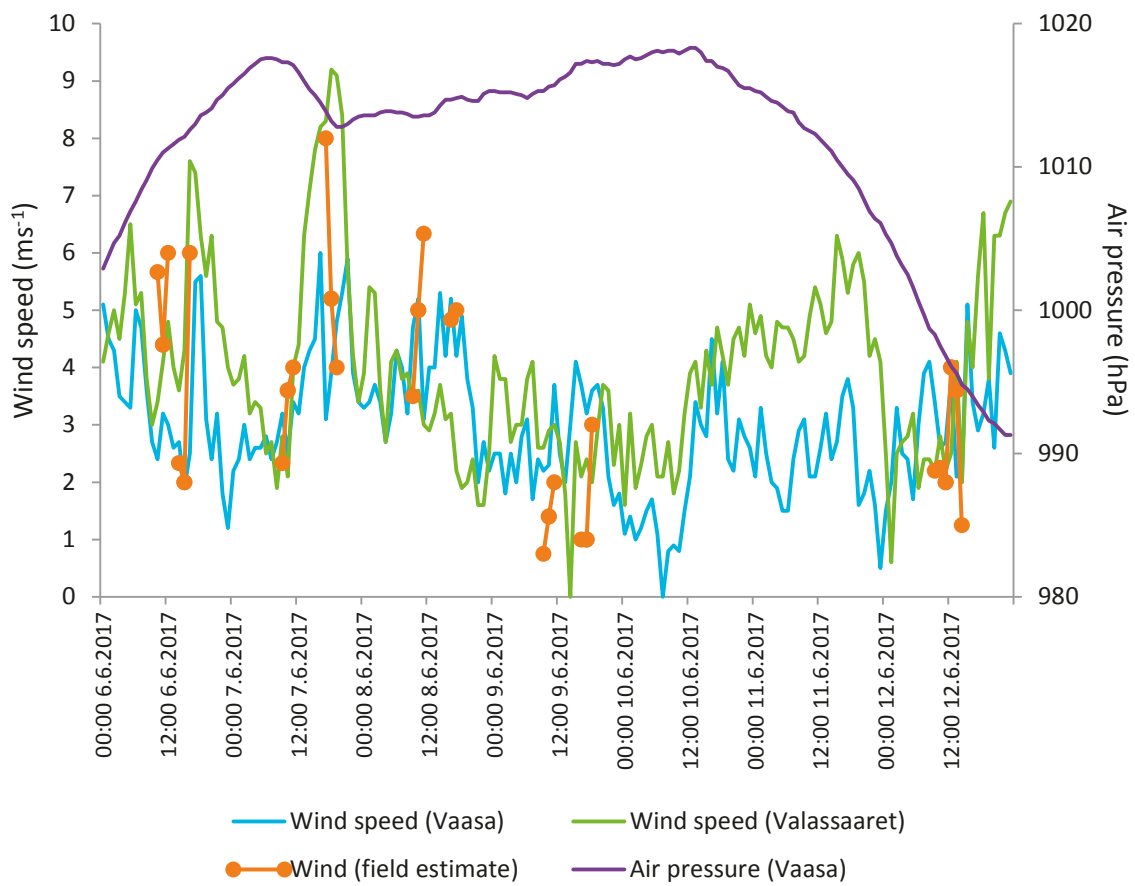
measures, but were larger by + 45° to + 90° degrees (Figure 9). Wind direction did likely not impact larvae abundance in the fairly sheltered sampling area, as the highest larvae densities were encountered during the first and second sampling days, between which wind direction changed from South-Western to North-Eastern.

Field measures of weather and water quality parameters are compiled in table 2. Wave height did not exceed 0.3 m during sampling, and varied in accordance with wind speed (Figure 10). Wind speed and direction was therefore excluded from further use within the mixed model analysis, as wave height was assumed to have the most direct effect on larval distribution.

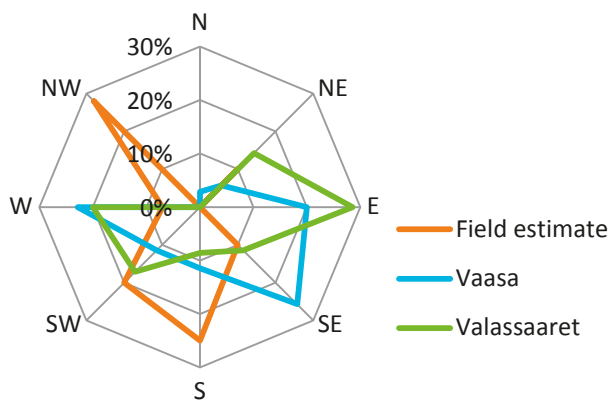
Air temperature measured in field increased during the first three days, but decreased with several degrees before the 4<sup>th</sup> day, remaining low until the last day of sampling. The water temperature measured at 0.5, 1.0, 2.0 and 3.0 m, exhibited a continuous increase during the sampling period for all depths (Figure 11). The temperatures for the four depths measured did not show any large variation, on average decreasing by only 0.1 °C between consecutive, increasing depths. Water temperatures were omitted from statistical analysis, as they were deemed to have low overall explanatory effect on larval abundance due to the small variations and continuous increase, compared to the marked decrease over time of larvae. Air temperature was omitted as it correlated with larval abundance, and therefore likely would have resulted in a false positive effect.

Water quality parameters did not differ notably between sampling dates (Figure 12) or transects. Salinity was on average slightly higher (by 0.1 psu) in the North-Western part of the sampling area, where water exchange with the more saline outer archipelago is strongest. Turbidity and pH decreased slightly during the last two days of sampling, likely as an effect of calm winds and lower wave height. Dissolved oxygen increased most the first two days of sampling, but it could have been due to a measuring probe issue, as the intra-variation during the 1<sup>st</sup> sampling day was by far larger than during any of the consecutive sampling times. None of the water quality parameters was used in the mixed model analyses, as any variation found between sampling time or transect was small-scaled.

After cross-examining cloud cover estimates with available recorded illuminance from a nearby flat, illuminance was chosen for further analysis due to the likely stronger explanatory effect of numeric data (Figure 10). The 2<sup>nd</sup> sampling day was the brightest, and the two last days the most overcast – likely an effect of different wind conditions. Illuminance was generally higher during morning sampling (AM) compared to afternoon (PM). When interpreting the result, however, it must be kept in mind that illuminance was measured at ca. 1.8 m depth, albeit in an area of low relative turbidity, and is not directly applicable on either of the two sampled depths. Illuminance would likely have been higher if measured at sampling depth, and the results of the analysis should only be viewed as a guideline of whether brightness has a positive or negative general effect on larval abundance.



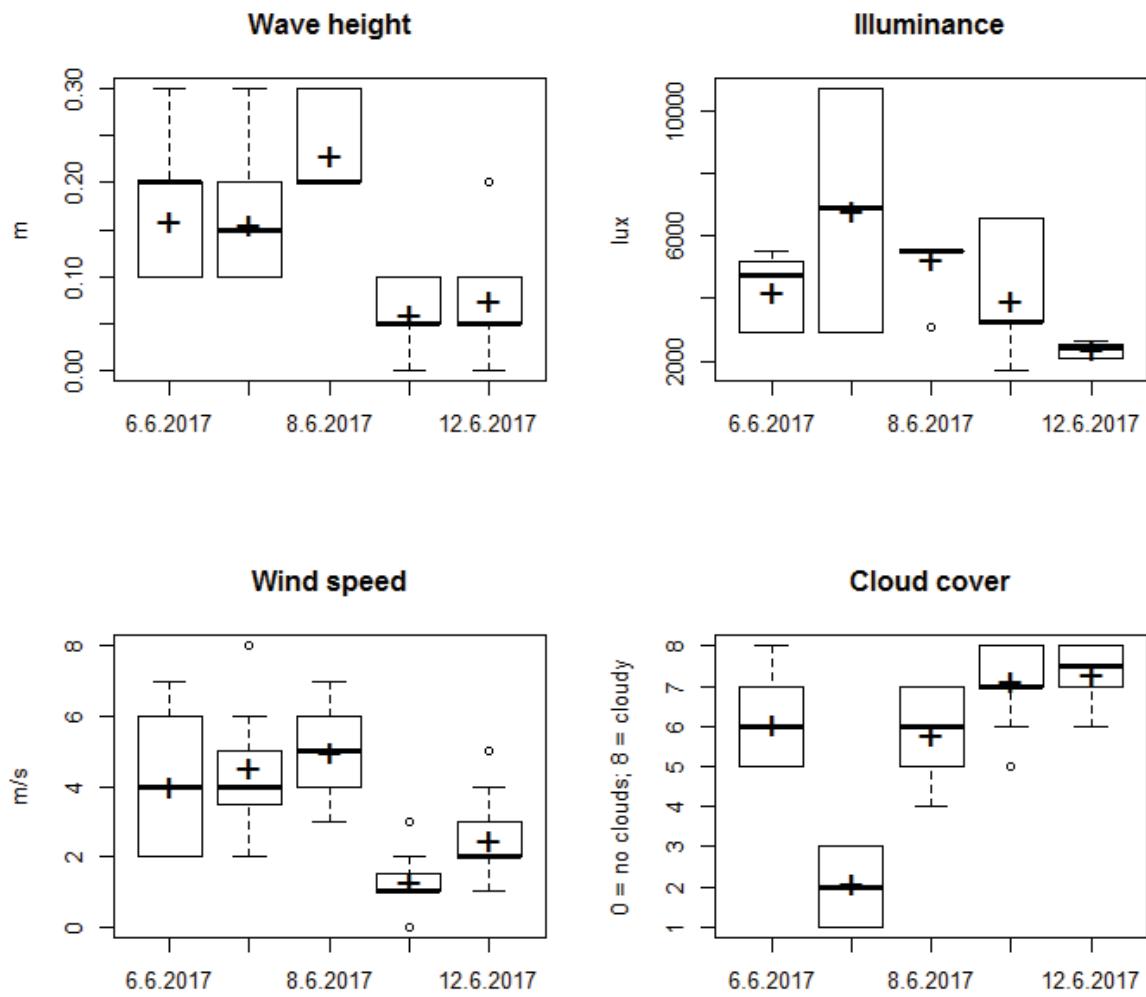
**Figure 5.** Hourly average of wind speed and air pressure measured at the nearest meteorological observation stations during the week of sampling, and the average estimated wind speed during sampling.



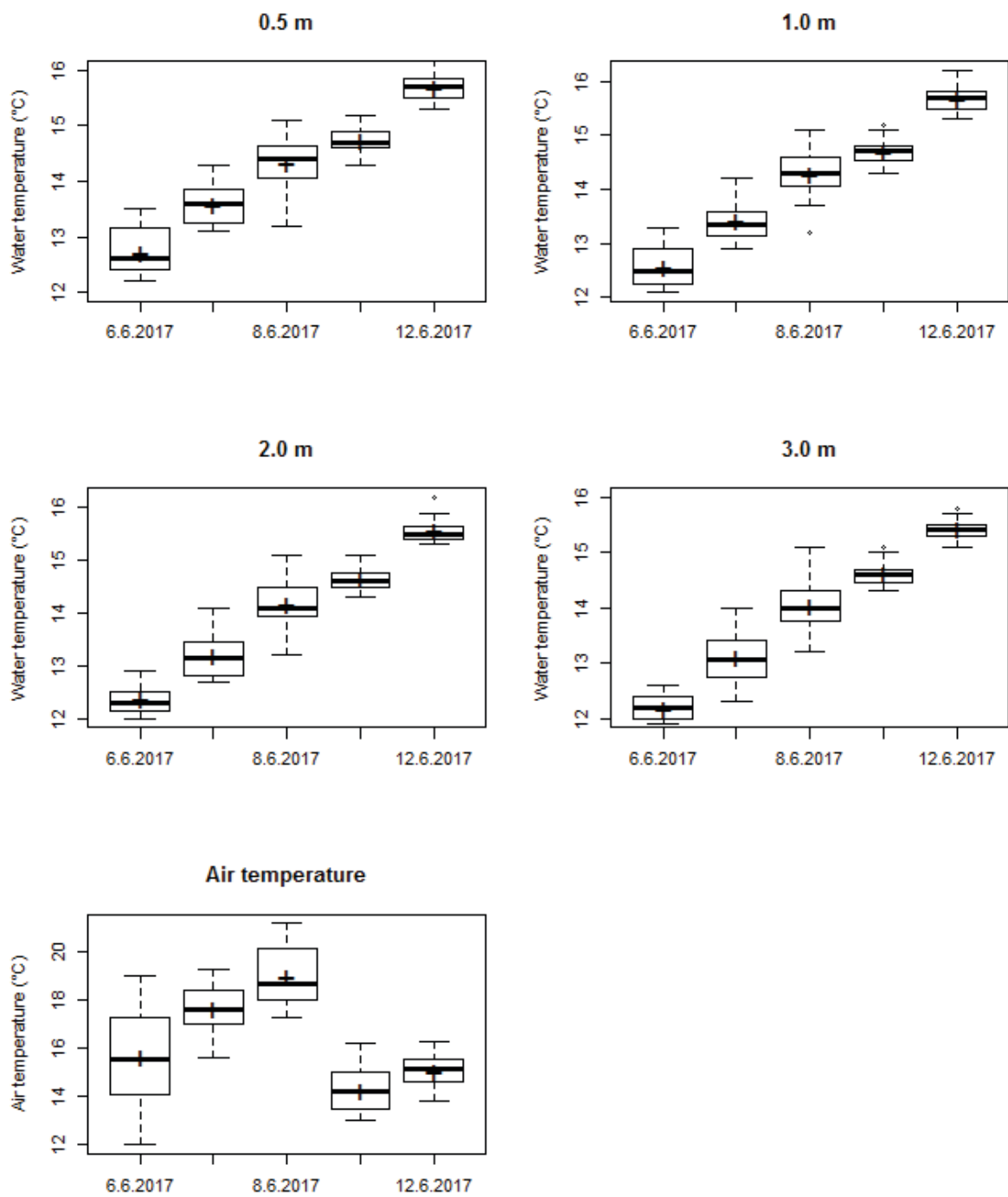
**Figure 6.** Wind rose diagram showing estimated wind direction during sampling in field, and corresponding recorded wind direction from meteorological data (Vaasa and Valassaaret).

Table 2. Mean measure and standard deviation for weather and water quality parameters.

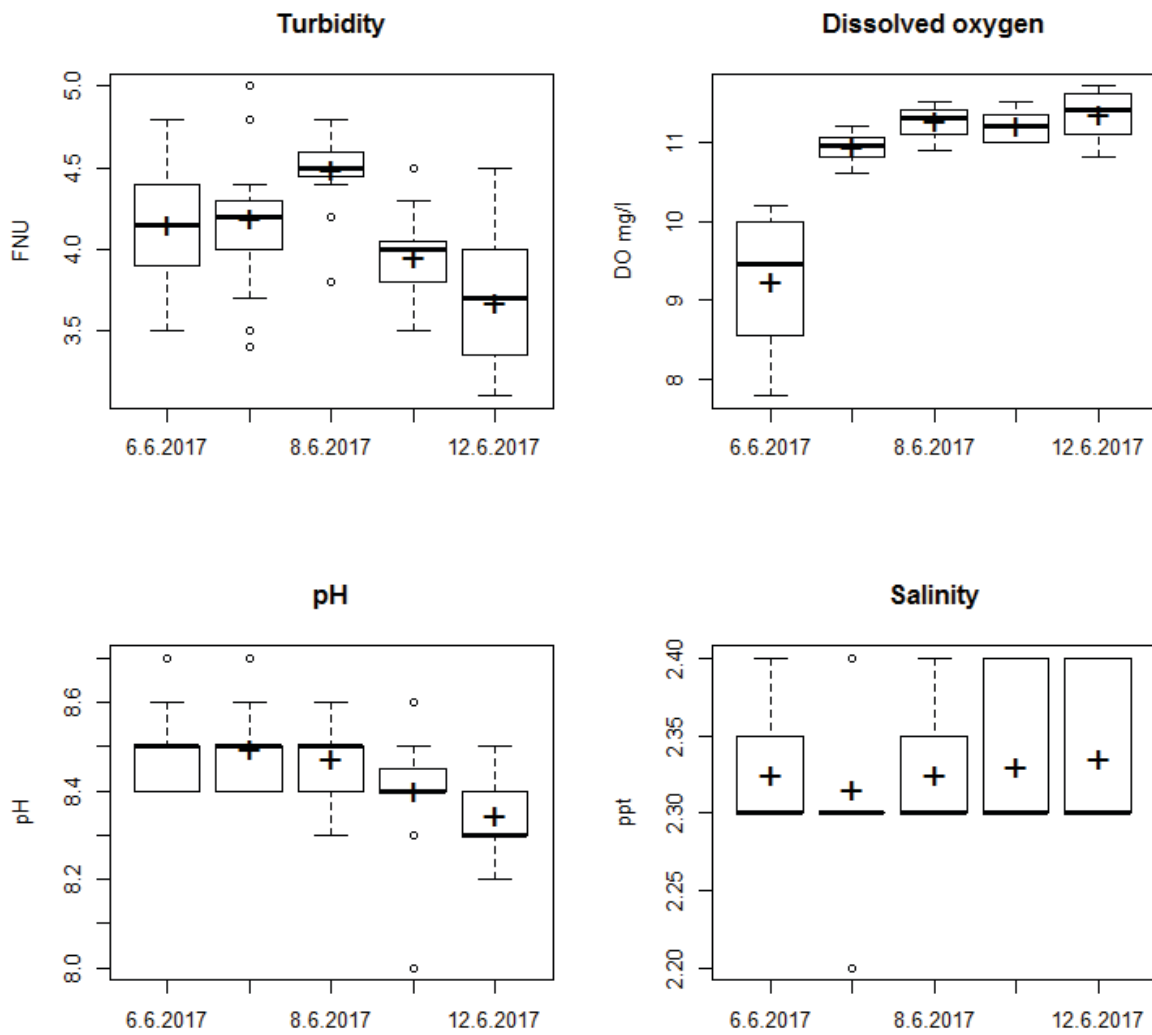
Parameter	6.6.2017		7.6.2017		8.6.2017		9.6.2017		12.6.2017		TOTAL	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Wind speed (ms <sup>-1</sup> )	4,0 ± 1,8		4,6 ± 2,0		5,0 ± 1,0		1,3 ± 0,7		2,5 ± 1,1		3,5 ± 2,0	
Wave height (m)	0,2 ± 0,1		0,2 ± 0,1		0,2 ± 0,0		0,1 ± 0,0		0,1 ± 0,1		0,1 ± 0,1	
Air temperature (°C)	15,7 ± 1,9		17,7 ± 1,1		19,0 ± 1,2		14,3 ± 0,8		15,1 ± 0,7		16,3 ± 2,1	
Water tmp. 0.5 m (°C)	12,7 ± 0,4		13,6 ± 0,3		14,3 ± 0,5		14,7 ± 0,2		15,7 ± 0,2		14,2 ± 1,1	
Water tmp. 1 m (°C)	12,6 ± 0,3		13,4 ± 0,4		14,3 ± 0,5		14,7 ± 0,2		15,7 ± 0,2		14,1 ± 1,1	
Water tmp. 2 m (°C)	12,4 ± 0,3		13,2 ± 0,4		14,2 ± 0,4		14,6 ± 0,2		15,6 ± 0,2		14,0 ± 1,2	
Water tmp. 3 m (°C)	12,2 ± 0,2		13,1 ± 0,5		14,0 ± 0,4		14,6 ± 0,2		15,4 ± 0,2		13,9 ± 1,2	
Salinitu (psu)	2,3 ± 0,04		2,3 ± 0,05		2,3 ± 0,04		2,3 ± 0,05		2,3 ± 0,05		2,3 ± 0,05	
Turbidity (FNU)	4,2 ± 0,4		4,2 ± 0,4		4,5 ± 0,2		4,0 ± 0,3		3,7 ± 0,4		4,1 ± 0,4	
pH	8,5 ± 0,1		8,5 ± 0,1		8,5 ± 0,1		8,4 ± 0,1		8,3 ± 0,1		8,4 ± 0,1	
Diss. oxygen (ml/l)	9,3 ± 0,8		10,9 ± 0,2		11,3 ± 0,2		11,2 ± 0,2		11,3 ± 0,3		10,8 ± 0,9	
Illuminance (lux)	4219 ± 1121		6829 ± 3669		5270 ± 742		3961 ± 1841		2372 ± 231		4530 ± 2407	
Cloud cover (0-8)	6,1 ± 1,0		2,1 ± 0,9		5,8 ± 1,0		7,2 ± 1,0		7,3 ± 0,8		5,7 ± 2,1	



**Figure 7.** Box-plots describing the mean (+), median, 25% and 75% quartiles, min and max parameter values of daily wave height, illuminance, wind speed and cloud cover. Wave height is dependent on wind speed, exhibiting similar plotted patterns. Illuminance is reflected in cloud cover by opposite trends, as high illuminance corresponds to low cloud cover.



**Figure 8.** Box-plots describing the mean (+), median, 25% and 75% quartiles, min and max parameter values of daily water temperature for the four depths measured, as well as mean daily air temperature. Water temperature increased at all measured depths over time, while air temperature dropped between the 3<sup>rd</sup> and 4<sup>th</sup> sampling day.



**Figure 9.** Box-plots describing the mean (+), median, 25% and 75% quartiles, min and max parameter values of daily measure of turbidity, dissolved oxygen, pH and salinity measured at 0.5 m depth. Turbidity varied with wave height, lowest on average during days with calm weather. Other water quality parameters (dissolved oxygen, pH, and salinity) remained similar across the sampling period, indicating homogeneity of the sampling area (the difference in dissolved oxygen on the first day may be due to a measuring probe failure).

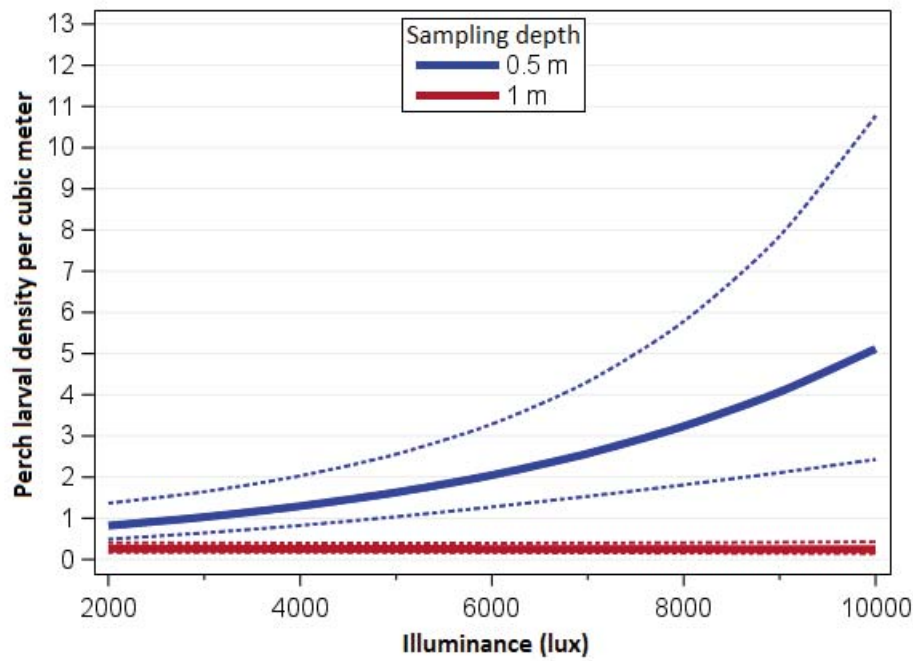
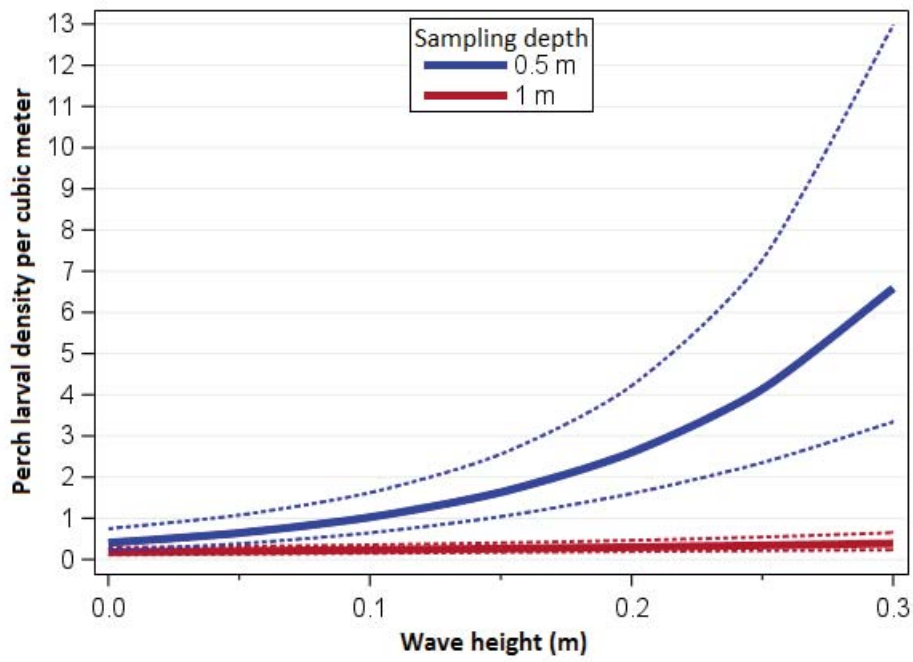


### 3.3. Result of linear mixed model analysis

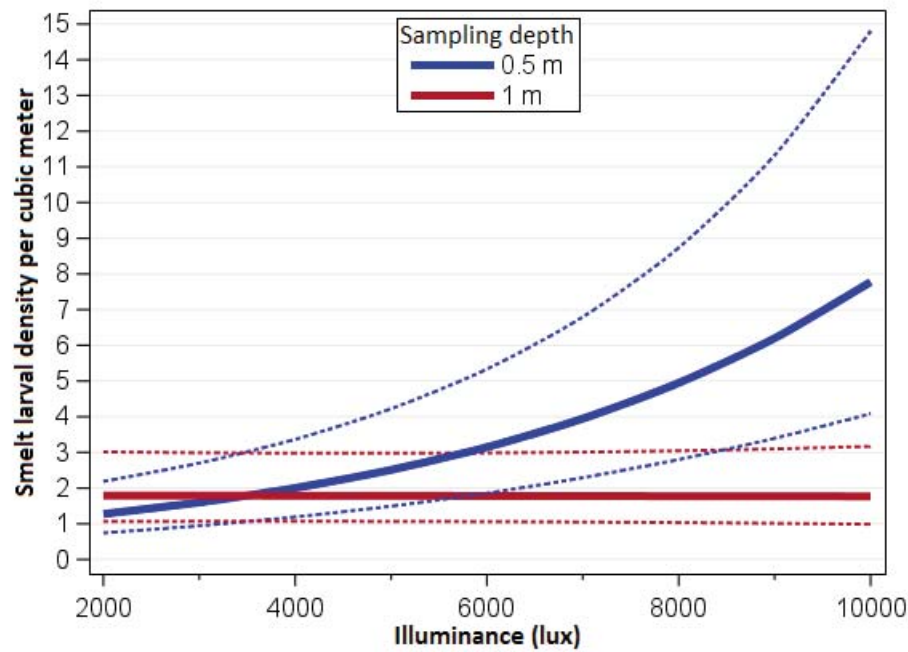
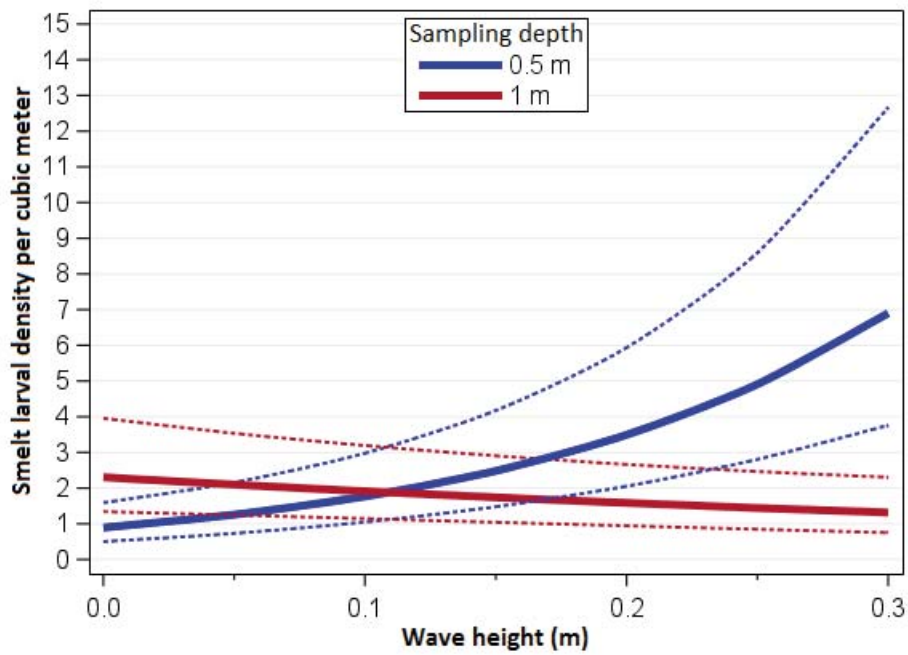
Results of the linear mixed model (LMM) analysis on log-transformed larval density showed overall higher larval densities at the sampling depth closer to the surface (0.5 m) than at the deeper (1 m) sampling depth. For perch ( $n=181$ ), mean larval density was higher at 0.5 m depth ( $1.5 \text{ larvae m}^{-3}$ ) than at 1 m depth ( $0.25 \text{ larvae m}^{-3}$ ) ( $p < 0.0001$ ). For smelt ( $n=197$ ), mean larval density was higher at 0.5 m depth ( $2.3 \text{ larvae m}^{-3}$ ) than at 1 m depth ( $1.8 \text{ larvae m}^{-3}$ ) ( $p = 0.014$ ).

Wave height and illuminance had an effect on larval density. For perch, wave height and illuminance had increasing effect on larval density at 0.5 m depth ( $p < 0.006$ , Figure 13). Larval density increased 16-fold, when wave height increased from 0 m to 0.3 m, and 6-fold, when illuminance increased from 2 000 to 10 000 lux (less cloud cover). For smelt, wave height and illuminance had increasing effect on larval density at 0.5 m depth ( $p < 0.0001$ , Figure 14). Larval density increased 8-fold, when wave height increased from 0 m to 0.3 m, and 6-fold, when illuminance increased from 2 000 to 10 000 lux.

No variation was found between sampling transects for neither perch nor smelt, indicating that the sampling area was homogenous according to larval density. Neither was the effect of sampling time (AM/PM) significant.



**Figure 10.** Linear mixed model-predicted average larval density for perch with 95 % confidence interval in relation to wave height (top) and illuminance (bottom), for sampling depths 0.5 and 1.0 m.



**Figure 11.** Linear mixed model-predicted average larval density for smelt with 95 % confidence interval in relation to wave height (top) and illuminance (bottom), for sampling depths 0.5 and 1.0 m.

## 4. Discussion

Wave height was found to correlate positively with larval abundance at 0.5 m samples, with a 16-fold and 8-fold increase in perch and smelt density respectively, following a change in wave height from 0 m to 0.3 m. This may be due to larvae being able to aggregate above 0.5 m depth during calm conditions, whereas higher waves will cause the uppermost layer of water to mix and larvae to distribute more evenly within it. The effect of wave height larger than our measured maximum of 0.3 m remains unknown, but larval densities would likely have started to decrease again after waves would have exceeded a certain height, as both perch and smelt larvae are likely to migrate deeper during windy conditions (Margoński 2000; Wanzenböck et al. 1997).

Both perch and smelt larvae density at 0.5 m samples was found to correlate positively with increased levels of light, while no significant effect of either categorical (AM/PM) or hourly time of sampling was found. Our modelled results predicted six times greater near-surface densities of both perch and smelt larvae to be caught during the brightest measured illuminance, compared to the most overcast conditions. This may be an effect of diurnal migration cycles, but as perch and smelt are both visual predators, it might also be a response to prey availability and optimal light levels for feeding, as has been found to be the case with herring larvae (Munk et al. 1989). Illuminance measures might therefore be better fitted than simply time of day for determining surficial density peaks. Larval densities at 1.0 m depth were not found to significantly correlate with light availability. Other studies have found smelt larvae to aggregate closer to the bottom during daytime, although patterns are inconsistent (Žiliukiene 2002; Urho 1997). Smelt daytime larval distribution has also been found to correlate positively with increasing depth, and negatively with increasing proximity to dense stands of submerged vegetation, indicating a general preference for pelagic habitats for feeding activity (Urho et al. 1990), and possibly explaining why increasing depth was of lesser consequence to larval density of smelt. Perch pelagic larval density has been found to correspond positively to increased vegetation cover and proximity to shallower depths (Urho et al. 1990). In perch, the onset of active habitat selection also takes place early, at a larval length of merely 8 mm, after which larvae will move from the pelagic to shallow vegetated areas (Urho 1996). This may explain the sudden drop in perch density towards the end of the sampling period, as well as why so few larger perch larvae were present in the samples, further stressing the importance of timing of sampling.

Sampling with Gulf Olympia paired ichthyoplankton samplers at 0.5 m depth yielded more larvae than at 1.0 m depth. This may be an effect of water temperature increasing towards the surface, as temperature is a strong determining factor for survival and distribution of fish larvae (Stoner 2004; Žiliukiene 2002; Urho 1996). The sampling depths for this study were chosen as warmer surface waters are known to be preferred by newly-hatched, developing larvae (Kallasvuo et al. 2016). However, the depth interval was likely too small to allow for any effects of temperature variations to emerge in this study, as the daily mean temperature difference between the two depths was less than 0.2 °C. Water temperature has been found to impact the vertical distribution of larval perch more strongly than diurnal cycles (Wang & Appenzeller 1998). This could not be examined within our study, as larval sampling depth, water temperature measures and sampling duration were too limited for analysing and modelling of vertical patterns. However, due to the sheltered and shallow nature of the study area, near-surface temperature is likely to vary in accordance with prevailing weather conditions, as the surface water layers will warm and cool by the impact of light intensity and magnitude of mixing through waves.

The marked drop in larval abundance over the course of the study emphasizes the importance of choosing sampling period and frequency according to the area and species being studied. This study might have gained in explanatory power, had sampling started at an earlier date, as the chosen sam-

pling period now seemingly overlapped at least partly with the cohort tail. Also, seeing as larval density had largely decreased towards the end of the study, coinciding with the calmest weather conditions as well as the lowest light levels encountered, the results would have benefitted from a more comprehensive data set. In order to draw asserted conclusions on the proportional importance of wave height and illuminance, a larger sample would be needed, where sampling is carried out within the cohort maximum, and weather variations are well represented there within.

As the sampling times were inconsistent and varied, it was not possible to examine diurnal dependencies. Temporal trends in larval abundance in relation to sampling time would have been more likely to emerge, had sampling effort per unit of time been kept constant. Both perch and smelt are known to migrate vertically depending on diel cycles (Wanzenböck et al. 1997; Hudd & Urho 1985), and our study suggests that morning (AM) sampling might return higher larval densities compared to afternoon (PM), but not of a magnitude that would render PM sampling discommendable. Furthermore, this may be true only in cases where larval density is high, as the difference in AM to PM density ratio was smaller and inconsistent towards the end of the sampling period.

The impact of atmospheric pressure on general fish catchability is not well known, but large-scale pressure systems should be taken into consideration when conducting Gulf Olympia sampling in surface waters, as weather conditions will impact wave height and light availability (through cloud cover and turbidity) (Stoner 2004), which were the only variables in our analysis found to significantly explain larval density variations.

Water quality was not found to significantly explain larval density patterns in this study, but as measures were limited to only the uppermost 0.5 m of the water column, knowledge of any potential vertical variation is not available. Environmental parameter dependency will also vary by species, e.g. Veneranta et al. (2011) found turbidity to more accurately explain the larval occurrence of pikeperch, a visual predator, than the initially hypothesized surface water temperature. In a study by Sandström and Karås (2002) higher densities of smelt larvae were similarly found in more turbid, eutrophicated areas compared to less eutrophic ones, whereas perch larvae exhibited the opposite distribution pattern. The highest densities of smelt within Skinnarfjärden-Köklotfjärden Bay were caught along transects closest to the mouths of the two largest rivers within the catchment area, both known to be strongly affected by eutrophication (Westberg & Lax 2016). The proportion of perch to smelt larvae therefore increased further away from the rivers, potentially as a result of spatial preference for less eutrophicated waters, or decreased resource competition from smelt. Despite finding no significant effect of spatial variation of smelt or perch within the area, prevalent environmental condition and water quality gradients should be taken into account when choosing sampling area extent and placement criteria for sampling points. Furthermore, night-time sampling could be considered in order to weaken the effect of light availability, as brightness will naturally vary less during night compared to daytime.

The seemingly large importance of Gulf Olympia sampling depth for evaluating the effects of weather and environmental parameters on larval density is a key finding of this study. The difference between sampling depths was merely 0.5 m, but evidently large enough to remove almost all effects of light availability and wave height. However, it must also be noted that the density of perch decreased nearly threefold with the 0.5 m increase in depth. Hence, straightforward recommendations on sampling depth are not possible within the context of this study, as there will be a weigh-off of either catching more larvae or reducing the effects of weather variability depending on depth. The relationship between larvae, time and environmental variation across different depths needs further investigation, but simultaneous sampling at two different depths with the Gulf Olympia provides more detailed knowledge on the larval assemblage, and a standardization of the method should be considered.

## 5. Conclusions and recommendations for future sampling

In conclusion, sampling depth, wave height and light availability should be taken into consideration when planning and analysing the results of Gulf Olympia sampling of pelagic larvae of coastal fish species such as perch and smelt. Despite generally encountering larger densities of larvae during morning than afternoon, this study did not find any consistent effect of time on larval abundance patterns, due to the forementioned variation in sampling times. Many prior studies have, however, recorded diurnal shifts in larval distribution, and we would recommend that future sampling is carried out in such a way that sampling effort is kept similar between the units of time that are to be compared, in order to reduce confounding effects of small-scale temporal variations. Additional sampling during night-time is recommended if temporal variations related to diurnality are to be explained.

Sampling depths should be chosen according to the species and larval developmental stage being studied, as well as to the depth and temperature profile of the sampling area (Wang & Appenzeller 1998). The near-surface samples in our study returned considerably larger densities of larvae than the slightly deeper ones, despite sampling water layers only 0.5 m apart, while in a similar study by Härmä & Lappalainen (2009) on larval herring abundance sampled at the same depths of 0.5 and 1.0 m, the opposite was found, highlighting the importance of considering small-scale variability. Choosing to sample two different depths, instead of replicates over one, might generally benefit ichthyoplankton studies, as it opens up for several possibilities in regards to analysis. Replicates can instead easily be obtained by driving parallel stretches alongside the initial transect, or by sampling in a triangular pattern. Despite the Gulf Olympia generally being well-suited for examining ichthyoplankton microdistribution (Hudd & Urho 1985), potential sampler avoidance may be better accounted for by including replicates (Wanzenböck et al. 1997). Replicates might also have aided this study, as larval densities had decreased strongly by the last day of sampling, likely affecting catchability.

The analysis on effects of weather and environmental parameters would also have been more robust, had a larger data set been collected, e.g. by using accurate measures of weather conditions instead of estimates, and by sampling temperature and water quality parameters over a larger depth span. Explanatory power would likely have increased further, if measures between sampling times had been available. Reliability and availability of field measurements for weather and water quality parameters in future studies could be improved by the use of automatic logging devices, deployed within the study area for the duration of the sampling period. Considering the importance of light availability in explaining larval vertical distribution, it would have been especially beneficial for this study if, prior to the sampling, light intensity loggers would have been deployed and set at the relevant depths within the immediate study area.

As no events of weather extremes occurred during the limited time frame of sampling, the full effect of weather still remains to be understood. It is unlikely that sampling would take place in winds exceeding 10 m/s, as waves would start to impact the sampling quality, but weather extremes do likely temporally affect the larval distribution both horizontally and vertically (Margoński 2000; Wanzenböck et al. 1997), and it remains to be studied how soon after such events the larvae will display normal distribution patterns again. The effect of wave height should be further investigated by conducting near-surface sampling over smaller depth spans, to find out whether larvae aggregate at the surface during calm conditions.

Despite the dependencies found between larval density and wave height, illuminance and depth, the study is still too limited to readily have the results applied to other areas, where other local factors might act as stronger drivers. The results do, however, stress the importance of taking note of prevailing conditions during Gulf Olympia sampling, and we emphasise the need for further studies on the matter, to be able to account for and eliminate possible bias due to sampling conditions when working with large data sets on larval habitats.

## References

- Aneer, G., Blomqvist, E.M., Hallbäck, H., Mattila J., Nellbring, S., Skóra, K., & Urho, L. 1992. Methods for Sampling of Shallow water fish. Baltic Marine Biologists Publication No. 13, 33 pp.
- Backer, H., & Frias, M. (ed.) 2013. Planning the Bothnian Sea - key findings of the Plan Bothnia project. HELCOM, 153 pp. Available at: <http://www.helcom.fi/Lists/Publications/Planning%20the%20Bothnian%20Sea.pdf>
- Borg, J., Mitikka, V., & Kallasvuo, M. 2012. Menetelmäohjeisto rannikon taloudellisesti hyödyntämättömien kalalajien lisääntymis- ja esiintymisalueiden kartoittamiseen. Riista- ja kalatalous. Tutkimuksia ja selvityksiä 4, 36 pp.
- Breilin, O., Kotilainen, A., Nenonen, K., Virransalo, P., Ojalainen, J., & Stén, C.G. 2004. Geology of the Kvarken Archipelago. Geological Survey of Finland, 47 pp.
- HELCOM 2010. Ecosystem Health of the Baltic Sea 2003–2007: HELCOM Initial Holistic Assessment. Baltic Sea Environment Proceedings No. 122, 68 pp.
- Hudd, R. 1983. Assessment of Smelt (*Osmerus eperlanus* (L.)) stock in the Vaasa Archipelago, Gulf of Bothnia. ICES C.M. 1983/J: 27, 25 pp.
- Hudd, R., & Urho, L. 1985. Abundance and distribution of smelt (*Osmerus eperlanus* (L.)) yolk sac larvae in the Northern Quark, Gulf of Bothnia. ICES C.M. 1985/J: 28, 14 pp.
- Hudd, R., Hilden, M., Urho, L., Axell, M.B., & Jåfs, L.A. 1984. Fiskeriundersökning av Kyro älvs mynnings- och influensområde 1980-82. National Board of Waters, Finland. Report 242B, 277 pp.
- Härmä, M., & Lappalainen, A. 2009. Sampling of herring larvae in shallow archipelago – are surface samples sufficient? ICES C.M. 2009/I: 05, 7 pp.
- Ljunggren, L., Sandström, A., Bergström, U., Mattila, J., Lappalainen, A., Johansson, G., Sundblad, G., Casini, M., Kaljuste, O., & Eriksson, B.K. 2010. Recruitment failure of coastal predatory fish in the Baltic Sea coincident with an offshore ecosystem regime shift. ICES Journal of Marine Science, 67, p. 1587–1595.
- Kallasvuo, M. 2010. Coastal environmental gradients – Key to reproduction habitat mapping of freshwater fish in the Baltic Sea. PhD-thesis, Faculty of Biological and Environmental Sciences, University of Helsinki, 38 pp. Available at: <http://urn.fi/URN:ISBN:978-952-10-6392-3>
- Kallasvuo, M., Vanhatalo, J., & Veneranta, L. 2017. Modeling the spatial distribution of larval fish abundance provides essential information for management. Canadian Journal of Fisheries and Aquatic Sciences 74: 5, p. 636–649.
- Kjellman, J., Hudd, R., & Urho, L. 2003. Monitoring 0+ perch (*Perca fluviatilis*) abundance in respect to time and habitat. Annales Zoologici Fennici 33: 3, p. 363–370.
- Kraufvelin, P., Pekcan-Hekim, Z., Bergström, U., Florin, A.B., Lehikoinen, A., Mattila, J., Arula, T., Briekmane, L., Brown, E.J., Celmer, Z., Dainys, J., Jokinen, H., Kääriä, P., Kallasvuo, M., Lappalainen, A., Lozys, L., Möller, P., Orio, A., Rohtla, M., Saks, L., Snickars, M., Støttrup, J., Sundblad, G., Taal, I., Ustups, D., Verliin, A., Vetemaa, M., Winkler, H., Wozniczka, A., & Olsson, J. 2018. Essential coastal habitats for fish in the Baltic Sea. Estuarine, Coastal and Shelf Science 204, p. 14–30.
- Margoński, P. 2000. Impact of Hydrological and Meteorological Conditions on the Spatial Distribution of Larval and Juvenile Smelt (*Osmerus eperlanus*) in the Vistula Lagoon (Southern Baltic Sea). Bulletin of the Sea Fisheries Institute, Gdynia 3: 151, p. 119–133.
- Munk, P., Kjørboe, T., & Christensen, V. 1989. Vertical migrations of herring, *Clupea harengus*, larvae in relation to light and prey distribution. Environmental Biology of Fishes, 26: 2, p. 87–96.
- Nilsson, J., Andersson, J., Karås, P., & Sandström, O. 2004. Recruitment failure and decreasing catches of perch (*Perca fluviatilis* L.) and pike (*Esox lucius* L.) in the coastal waters of southeast Sweden. Boreal Environmental Research 9, p. 295–306.
- Sandström, A., & Karås, P. 2002. Effects of eutrophication on young-of-the-year freshwater fish communities in coastal areas of the Baltic. Environmental Biology of Fishes 63, p. 89–101.



- Sandström, O., Abrahamsson, I., Andersson, J., & Vetemaa, M. 1997. Temperature effects on spawning and egg development in Eurasian perch. *Journal of Fish Biology* 51: 5, p. 1015–1024.
- Seitz, R.D., Wennhage, H., Bergström, U., Lipcius, R.N., & Ysebaert, T. 2014. Ecological value of coastal habitats for commercially and ecologically important species. *ICES Journal of Marine Science* 71, p. 648–665.
- Snickars, M., Sandström, A., Lappalainen, A., Mattila, J., Rosqvist, K., & Urho, L. 2009. Fish assemblages in coastal lagoons in land-uplift succession: The relative importance of local and regional environmental gradients. *Estuarine, Coastal and Shelf Science* 81, p. 247–256.
- Snickars, M., Sundblad, G., Sandström, A., Ljunggren, L., Bergström, U., Johansson, G., & Mattila, J. 2010. Habitat selectivity of substrate-spawning fish: Modelling requirements for the Eurasian perch *Perca fluviatilis*. *Marine Ecology Progress Series* 398, p. 235–243.
- Stoner, A.W. 2004. Effects of environmental variables on fish feeding ecology: implications for the performance of baited fishing gear and stock assessment. *Journal of Fish Biology* 65, p. 1445–1471.
- Sundblad, G., & Bergström, U. 2014. Shoreline development and degradation of coastal fish reproduction habitats. *AMBIO* 43, p. 1020–1028.
- Sundblad, G., Bergström, U., Sandström, A., & Eklöv, P. 2014. Nursery habitat availability limits adult stock sizes of predatory coastal fish. *ICES Journal of Marine Science* 71, p. 672–680.
- Urho, L. 1996. Habitat shifts of perch larvae as survival strategy. *Annales Zoologici Fennici* 33: 3, p. 329–340.
- Urho, L. 1997. Controlling bias in larval fish sampling. *Archiv für Hydrobiologie. Special Issues: Advances in Limnology* 49, p. 125–135.
- Urho, L. 1999. Relationship between dispersal of larvae and nursery areas in the Baltic Sea. *ICES Journal of Marine Science* 56 Supplement, p. 114–121.
- Urho, L., & Hildén, M. 1990. Distribution patterns of Baltic herring larvae, *Clupea harengus* L., in the coastal waters off Helsinki, Finland. *Journal of Plankton Research* 12: 1, p. 41–54.
- Urho, L., Hildén, M., & Hudd, R. 1990. Fish reproduction and the impact of acidification in the Kyrönjoki River estuary in the Baltic Sea. *Environmental Biology of Fishes* 27, p. 273–283.
- Veneranta, L., Urho, L., Lappalainen, A., & Kallasvuo, M. 2011. Turbidity characterizes the reproduction areas of pikeperch (*Sander lucioperca* (L.)) in the northern Baltic Sea. *Estuarine, Coastal and Shelf Science* 95, p. 199–206.
- Veneranta, L., Hudd, R., & Vanhatalo, J. 2013. Reproduction areas of sea-spawning coregonids reflect the environment in shallow coastal waters. *Marine Ecology Progress Series* 477, p. 231–250.
- Voipio, A. (ed.) 1981. *The Baltic Sea*. Elsevier Oceanography Series 30, Amsterdam, 418 pp.
- Voss, R., Schmidt, J.O., & Schnack, D. 2007. Vertical distribution of Baltic sprat larvae: changes in patterns of diel migration? *ICES Journal of Marine Science* 64, p. 956–962.
- Wang, N., & Appenzeller, A. 1998. Abundance, depth distribution, diet composition and growth of perch (*Perca fluviatilis*) and burbot (*Lota lota*) larvae and juveniles in the pelagic zone of Lake Constance. *Ecology of Freshwater Fish* 7, p. 176–183.
- Wanzenböck, J., Matena, J., & Kubecka, J. 1997. Comparison of two methods to quantify pelagic early life stages of fish. *Archiv für Hydrobiologie. Special Issues: Advances in Limnology* 49, p. 117–124.
- Westberg, V., & Lax, H.G. 2016. Rannikkovesien ja pienten vesistöjen vesienhoidon toimenpideohjelman 2016–2021. Etelä-Pohjanmaan ELY-keskus. Raportteja 51, 135 pp.
- Westberg, V., Aaltonen, E.K., Axell, M.B., & Storberg, K.E. (ed.) 2009. Åtgärdsprogram för vattenvården för kustvattnen och de små vattendragen till och med år 2015. Västra Finlands Miljöcentral. Report, 122 pp. Available at: <http://www.ymparisto.fi/download/noname/%7B58E52CAD-E7A6-40D4-9C55-EA808B439793%7D/52407>
- Žiliukienė, V. 2002. The occurrence, food and size structure of smelt (*Osmerus eperlanus* L.) larvae in the Lithuanian part of the Curonian Lagoon. *Bulletin of the Sea Fisheries Institute, Gdynia* 2: 156, p. 33–43.

Žiliukienė, V., & Žiliukas, V. 2009. Species composition, abundance and distribution of ichthyoplankton of the pelagic zone in the Lithuanian part of the Curonian lagoon in early June. *Acta Zoologica Lituanica* 19, p. 18–24.



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