Arula *et al. Helgol Mar Res (2017) 71:7*
DOI 10.1186/s10152-017-0487-x

Helgoland Marine Research

ORIGINAL ARTICLE

Open Access

Maturation at a young age and small size of European smelt (*Osmerus eperlanus*): A consequence of population overexploitation or climate change?

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Abstract

Age of fish at maturation depends on the species and environmental factors but, in general, investment in growth is prioritized until the first sexual maturity, after which a considerable and increasing proportion of resources are used for reproduction. The present study summarizes for the first the key elements of the maturation of European smelt (*Osmerus eperlanus*) young of the year (YoY) in the North-eastern Gulf of Riga (the Baltic Sea). Prior to the changes in climatic conditions and collapse of smelt fishery in the 1990s in the Gulf of Riga, smelt attained sexual maturity at the age of 3–4 years. We found a substantial share (22%) of YoY smelt with maturing gonads after the collapse of the smelt fisheries. Maturing individuals had a significantly higher weight, length and condition factor than immature YOY, indicating the importance of individual growth rates in the maturation process. The proportion of maturing YoY individuals increased with fish size. We discuss the factors behind prioritizing reproduction overgrowth in early life and its implications for the smelt population dynamics.

Keywords: *Osmerus eperlanus*, Early maturation, Young of the year (0+), Commercial fisheries

Background

Age of fish at maturation depends on the species and environmental factors but, in general, investment in growth is prioritized until the first sexual maturity, after which a considerable and increasing proportion of resources are used for reproduction, and thus growth rates decrease from maturity onwards [1]. Nevertheless, extreme environmental conditions may give rise to increased risk of mortality in adulthood, selecting for early maturation, high reproductive investment as well as short lifespan [2, 3]. Highly exploited fish stocks have been shown to produce individuals that start first maturation at a younger age and smaller size [4]. This phenomenon can be accompanied by size-selective harvesting that eliminates the faster-growing genotypes, favouring slow-growing individuals that mature at smaller sizes and younger ages [5–8]. Such shifts time of maturation might have drastic consequences for fish population dynamics, as the share of early maturing individuals will increase in population [9].

A number of studies have been undertaken to explore how mean age or size at first sexual maturation has changed over time and the implications of this with respect to fish populations (for a review, see [4]). For instance, size-selective harvesting of late maturing cod (*Gadus morhua*) has caused remarkable changes to the North Atlantic cod stock; from the 1930s to the 1970s age at maturity decreased from 9–6 years in the Arcto-Norwegian Sea [10]. Other studies have demonstrated that fishing can induce a decrease in the mean length or age at maturation of target species ([11] and references therein). A decreasing population growth rate resulting from high exploitation might lead to individuals maturing earlier, with this trait retained by future generations even when the population size increases again. This indicates that size-selective harvesting has removed the faster-growing

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genotypes from the population. Therefore, the change in maturation age had probably genetic background, rather than related to growth rate change advocating for domination of slow-growing individuals as an expression of overexploitation and not as a result of food-limited growth regulation, when population size changes [12]. In the Gulf of Riga (GoR), intensive size-selective fishing led to a decrease in size at maturation of female pikeperch (*Sander lucioperca*) [13]. However, there are also studies that show the reverse growth pattern at intensive exploitation [14].

The European smelt, an anadromous fish species, inhabiting oceanic, brackish, and freshwater environments, forms several distinct populations in the Baltic Sea [15]. Smelt spawn in rivers and brackish water estuaries in the Baltic Sea region and attain sexual maturity at the age of 3–4 years when total length (TL) equals 12–16 cm and total weight (TW) 11–25 g [15]. These matured individuals are already at the pre-spawning stage by December but do not commence spawning migration to rivers, e.g. Pärnu River (Estonia), until March or April. In the GoR spawning shoals of smelt consist of age groups 2–10+, prevailing ages 3–6 [15].

Growth conditions, in terms of prey availability and temperature facilitating metabolism during the early stages of life has an important role in the initiation of maturation, as temperature may have a permissive effect on the rate of oocyte growth and development [16], possibly due to a temperature response in the expression and activity of regulatory proteins that influence maturation [17]. GoR smelt larvae hatch at a size of 5.0–5.4 mm, depending on water temperature during the incubation period [18], and larvae start to prey upon copepod nauplii at a length of 7–9 mm [19]. When GoR smelt reaches a length of 6–9 cm, the dietary share of Mysidae rapidly increases and that of zooplankton decreases (Shpilev unpubl. data). The adult smelt, after reaching maturity at the age of 2–4 years, preys upon smaller fish species in the GoR [20].

GoR smelt is an important and highly exploited commercial fish species, caught both by trap nets in the spawning grounds and as a bycatch [15]. Due to the heavy and size selective exploitation and environmental pressure as river damming and extensive eutrophication, smelt recruitment and yields in the GoR dropped since 1970 until the 1990s but have increased again since early 2000 [21].

In the present study, we used information from survey trawl hauls performed in the Pärnu Bay (NE Gulf of Riga), a pre-wintering YoY smelt nursery ground in 1958, 1965, 1967, 1974, 1978–1980 and 2012. We addressed the following questions in our study: (1) whether the changes in YoY smelt maturation rate are temporally persistent; (2) whether the individual characteristics of immature/mature YoY smelt differ between 1978 and 1980 and 2012 and within 2012; (3) whether the long-term dynamics in the environment and fisheries can explain observed changes in YoY smelt maturation rate. The results of the present study are discussed in terms of how the hydroclimate and feeding conditions, combined with the collapse of smelt population in the 1990s, may have resulted in early maturation of the smelt, and how it could shape the future of smelt stock and commercial fishery in the GoR.

Methods

Study site

The Pärnu Bay (PB), located at the north-eastern part of the Gulf of Riga (Baltic Sea; Fig. 1), is a shallow (maximum depth 10 m) sea area covering 700 km^2 with a total volume of 2 km^3. Average annual freshwater inflow from the Pärnu River is about 2 km^3 [22]. In most years, the bay is fully ice-covered during winter, usually from December/January to March/April. Sea surface temperature (SST) fluctuates seasonally from regularly sub-zero degrees °C in winter to >20 °C in summer; salinity varies between three and six PSU (Practical Salinity Unit) and water is typically well mixed down to the bottom year around [23]. The currents are weak (velocities of <10 cm s^{-1}) and mainly wind-induced, but modified by coastline morphology and bottom topography. Owing to the shallowness of the PB, water temperatures are quickly influenced by changes in air temperature. The hydrographic conditions of PB are formed by a complexity of multiple influences, including ice conditions, freshwater input from Pärnu River, and water exchange with the main basin of the GoR.

Environmental data and sampling

YoY smelt was collected from monthly experimental trawl catches conducted by the Estonian Marine Institute (EMI) during ice-free periods using the R/V Johanna (L = 10.1 m, engine = 275 HP). Experimental hauls were conducted along five stationary transects in PB during daylight hours on the 8th and 12th of November and 1st of December 2012, with each haul lasting 30 min (Fig. 1). Mesh size of the trawl net was 10 mm and its height and width during hauling two and six meters, respectively. Water depth in the trawl transects varied between five and ten meters, and hauls were made as close to the bottom as possible at a speed of four knots. All collected fish were measured for TL and TW to the nearest 1 mm/0.1 g and aged using otoliths. Comparative historical data collected from October to December (1958, 1965, 1967, 1974, 1978–1980) were obtained from the EMI's analysis protocols and there were no trawls conducted targeting YoY smelt in 1981–2012 (EMI database). To compare

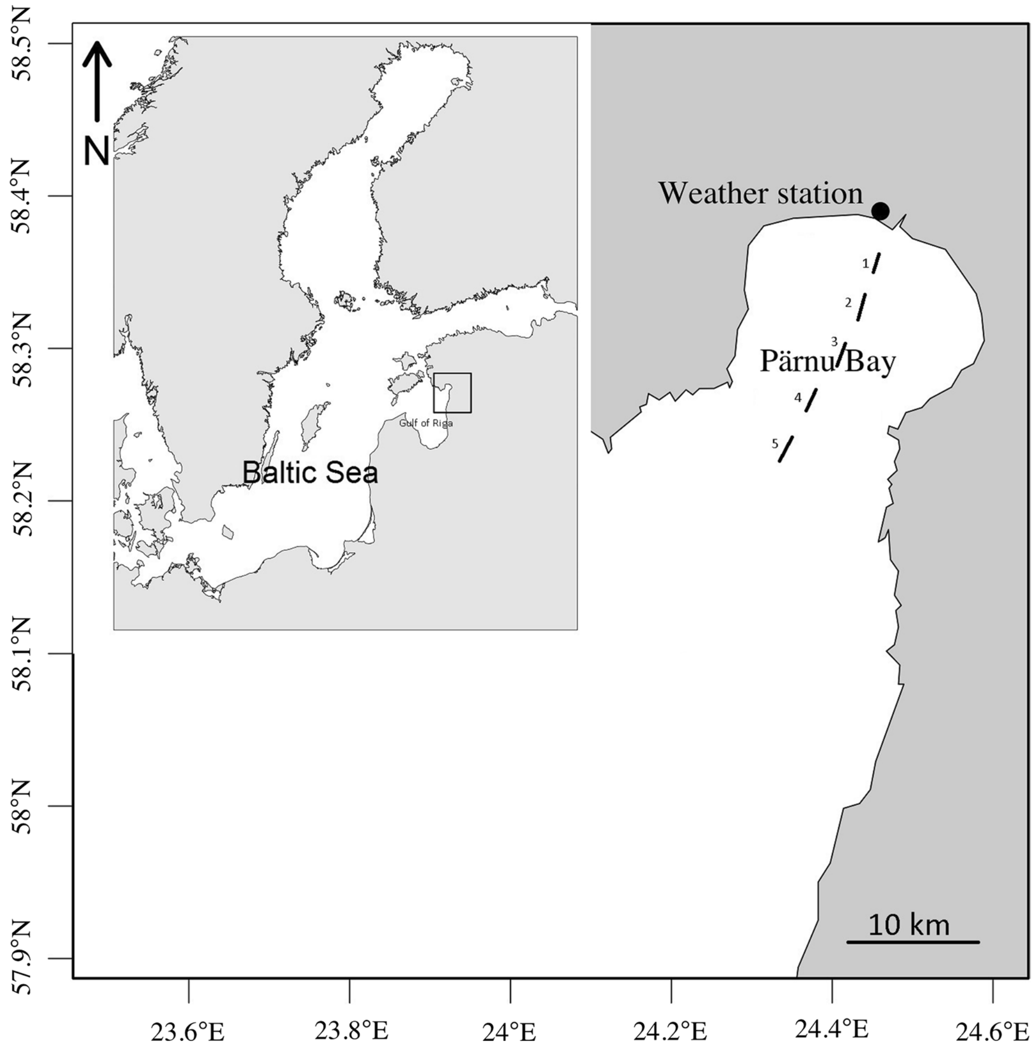

Fig. 1 Young of the year (YoY) European smelt trawling transects (*1–5*) in the Pärnu Bay in 2012

individual TL, TW and condition factor (K) of immature smelt, original data on immatures from October to December in 1978–1980 were compared with similar data from 2012. All the data used prior the 1980s were critically examined before adding into the analyses in terms of applicability for comparison with the data in 2012. In 2012 gender and maturation stage were determined using methods developed by the Workshop on Sexual Maturity Staging of Herring and Sprat Working Group [24], and for the former years individuals that showed signs of maturation were distinguished from immatures. The scale includes six stages: (I) immature; (II) maturing; (III) spawning; (IV) spent; (V) regeneration; and (VI) abnormal. The collected samples contained both immature and maturing individuals (ovaries/testes containing visible oocytes/sperm) that should be ready to spawn in the next spring. As the inspection of YoY maturation stage was performed visually, it was not possible to sex the immature individuals (stage I).

Zooplankton samples were collected weekly during the calendar weeks 20–30 over the years 1982–2013, from PB fixed sampling station (N 58°20′; S 24°26′). A Juday net (mouth opening of 0.1 m^2, mesh size of 90 µm) was used to sample the whole water column vertically by pulling the net once from the seabed to the surface (see also [25–27]). The samples were immediately preserved in a 4% formaldehyde/seawater solution. To characterize the prey assemblage of smelt larvae when they started to feed, we calculated the average weekly abundance of copepod nauplii (hereafter: nauplii) during mid-May to the end of July. Parallel to the zooplankton sampling, once a week SST was measured using a mercury thermometer, and the mean value for the period of mid-May to the end of July was calculated per annum.

The sum of monthly mean air temperature in Pärnu (for the location of the weather station, see Fig. 1) over the period January–March was used as background information. The sum was preferred to average values because the cumulative effect does not smooth data over a longer period. Therefore, it was used as a proxy value to estimate the potential overwintering mortality of YoY smelt per annum as severe winters have been shown to cause considerable overwinter losses and size-selective mortality among YoY of small pelagic species in northern seas [28]. Many studies demonstrate that decreased food availability in winter cause fish to starve and exhaust their energy reserves [29]. At the same time, at extremely cold temperatures, acute thermal stress can disrupt osmoregulatory function and become the primary cause of death [30]. Official annual landing statistics on smelt used in the study originates from the Estonian Ministry of Rural Affairs and its predecessors (prior to 1990). Winter air temperature data was obtained from the Estonian Environment Agency (http://www.ilmateenistus.ee/ilm/prognoosid/mudelprognoosid/eesti/?lang=en#layers/temp2mv2).

Analyses

Fulton's condition factor (K, Eq. 1), which assumes that the total weight of a fish is proportional to the cube of its length, was used to measure fish condition [31]:

$$K = 100 \times TW/TL^3 \quad (1)$$

where TW is total wet body weight in grams and TL total length in cm; the factor 100 is used to bring K close to a value of one.

To test any differences in median values (i.e. K, TW, and TL) between maturing females, males and immatures in 2012, and immatures between 1978–1980 and 2012, one-way analyses of variance (ANOVA) were used. First, data were analysed for normality of distribution (Wilkinson–Shapiro tests) and equal variance. As the assumptions for normal distribution were not met, Dunn's method in Kruskal–Wallis One Way Analysis of Variance on Ranks test was applied for pairwise comparisons.

To test for annual temporal trends in SST, winter air temperature, abundance of nauplii and smelt landings, a best fit linear or nonlinear regression model was applied using SigmaStat 12 software. For the statistical tests, alpha was set at <0.05.

Results

Total length, weight, and condition of maturing and immature YoY smelt

The proportion of YoY smelt with maturing gonads caught during the experimental trawls in 2012 was 22% (N = 634). Sampling conducted before 1980 (n = 1017) included one individual with maturing gonads (Table 1).

Table 1 Number of analysed young of the year (YoY) smelt by year and month, including the number of maturing individuals

Year/month	No. of analysed individuals	No. of maturing individuals
1958/Nov.	85	0
1965/Oct.	53	1
1967/Oct.	171	0
1974/Nov.	13	0
1978/Oct.–Dec.	412	0
1979/Oct.	100	0
1980/Oct.	183	0
2012/Nov.–Dec.	634	139
Sum	1651	140

The smallest observed maturing individual was a male, with a TL of 6.5 cm and TW of 1.2 g. In general, the percentage of maturing individuals in 2012 increased with fish length groups. Among the shortest TL group (5.1–6.0 cm), all individuals were immature; in the middle two TL groups (6.1–7.0 and 7.1–8.0 cm), there was a higher proportion of males (100 and 60%, respectively) among the maturing individuals; in the two biggest TL groups (8.1–9.0 and 9.1–10.0 cm), there was a slightly higher proportion of females (55 and 54%, respectively) among the maturing individuals (Fig. 2).

In 2012, median TL, TW, and K of maturing females and males were significantly higher than the corresponding values of immatures (Kruskal–Walls One-way

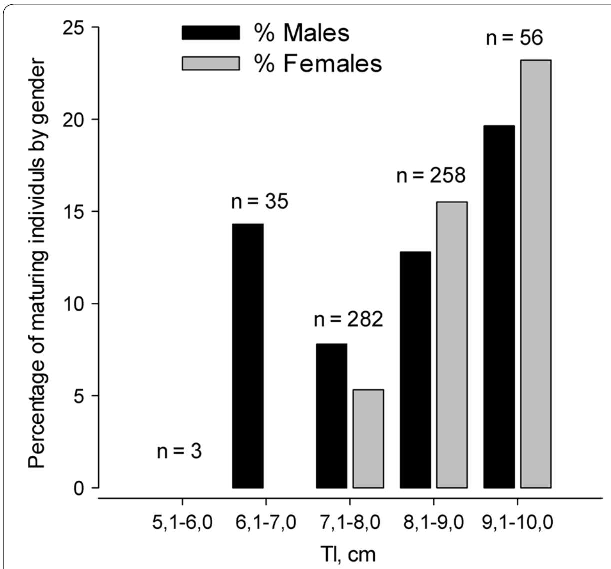

Fig. 2 The proportion of maturing YoY European smelt in 2012 by gender and total length (TL) groups. The *numbers above the bars* (*N*) are equal the total number of individuals per TL group

ANOVA, $P < 0.01$, Fig. 3). The differences in median values (TL, TW, K) between females and males were not significant (Kruskal–Walls One-way ANOVA, $P > 0.05$). Median K of immatures was significantly lower in 1978–1980 compared to immatures 2012 (Kruskal–Walls One-way ANOVA, $P < 0.01$); median TL and TW of immatures were significantly higher in 1978–1980 compared to immatures in 2012 (Kruskal–Walls One-way ANOVA, $P < 0.05$).

Changes in SST, abundances of nauplii, winter air temperature, and smelt landings

The abundance of nauplii significantly increased during 1982–2013 (nonlinear regression: $y = -83{,}336.4 + (82.6 \times x) - (0.02 \times x^2)$, $r^2 = 0.66$, $P < 0.01$, $N = 32$; Fig. 4a). The lowest nauplii abundance was observed in 1987 (3.2×10^3 ind. m^{-3}) and the highest in 2002 (45.1×10^3 ind. m^{-3}). Mean weekly SST varied between 14.6 °C (1994) and 18.4 °C (2013), and significantly increased over the period 1982–2013 (linear regression: $y = -133.8 + (0.08 \times x)$, $r^2 = 0.39$, $P < 0.01$, $N = 32$; Fig. 4b). The sum of mean monthly winter air temperature varied between −26.8 °C (1985) and 3.2 °C (1989). In general, winter air temperatures increased from 1982 until the mid-1990s and then gradually decreased (nonlinear regression: $y = -159{,}568.2 + (159.8 \times x) - (0.04 \times x^2)$, $r^2 = 0.17$, $P < 0.05$, $N = 32$; Fig. 4c).

Estonian smelt landings in the GoR have fluctuated significantly with the largest landings in 1972 (1331 t). This was followed by significant decreases during the 1980s and a collapse in the 1990s (nonlinear regression: $y = 2\,005.6. - (0.04 \times x) + (0.00002 \times x^2)$, $r^2 = 0.73$, $P < 0.01$, $N = 43$; Fig. 5). Since the 1990s there has been a gradual increase in landings.

Discussion

We detected a number of changes in winter air temperature, SST and prey abundance in the environment inhabited by GoR smelt in early life stages in PB that could be linked to the relatively high number of maturing YoY smelt observed in 2012. In general, smelt attains sexual maturity first at the age of 3–4 years in the Baltic Sea [15]. However, in the current study, we demonstrated for the first time a relatively high (22%) proportion of YoY smelt with maturing gonads during November and December of 2012. Further we will discuss the observed YoY maturation regarding why the GoR smelt shows such a distinct change in a life history with nearly a quarter of specimens maturing as YoY and ask: (1) does the feeding condition and SST favor early maturation, which implies that phenotypic responses to temperature are the most important to consider as temperature directly influences gonadal development as well as growth rate via food availability [32]; (2) does a milder winter in the 1990s favor survival of early maturing smelt, which implies that matured YoY may have a higher overwintering mortality rates than immatures due to a lack of energy reserves and limited abundance of food in winter [28]; (3) the overfishing and drastic smelt population decrease in the 1990s imply that commercial fisheries that select on the basis of size could be expected to favor the genotype for maturation at smaller sizes (and/or younger ages), given that rapidly maturing individuals will be more likely to reproduce prior to capture [33].

Feeding conditions

Fish mature at a younger age when growth conditions during their early life improve as a plastic response to reduced competition/increased availability of food [4, 16,

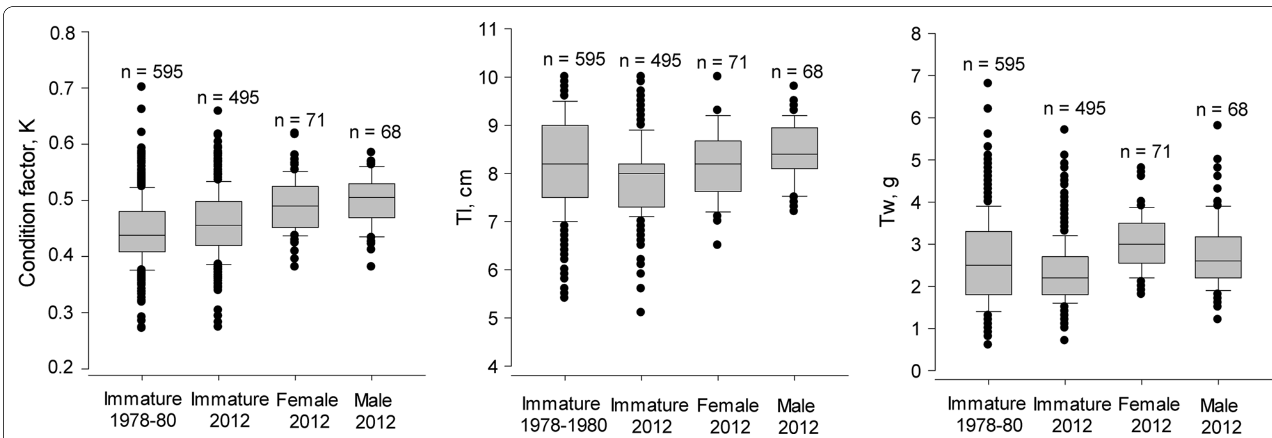

Fig. 3 *Box plots* of the Fulton condition factor (*left panel*), total length (*middle panel*) and total weight (*right panel*) of YoY European smelt maturing females, maturing males, and immatures in 1978–1980 and in 2012. *Vertical boxes* denote quartiles, the *line inside the box* median, *whiskers* 10th and 90th percentiles, and *dots* extreme values

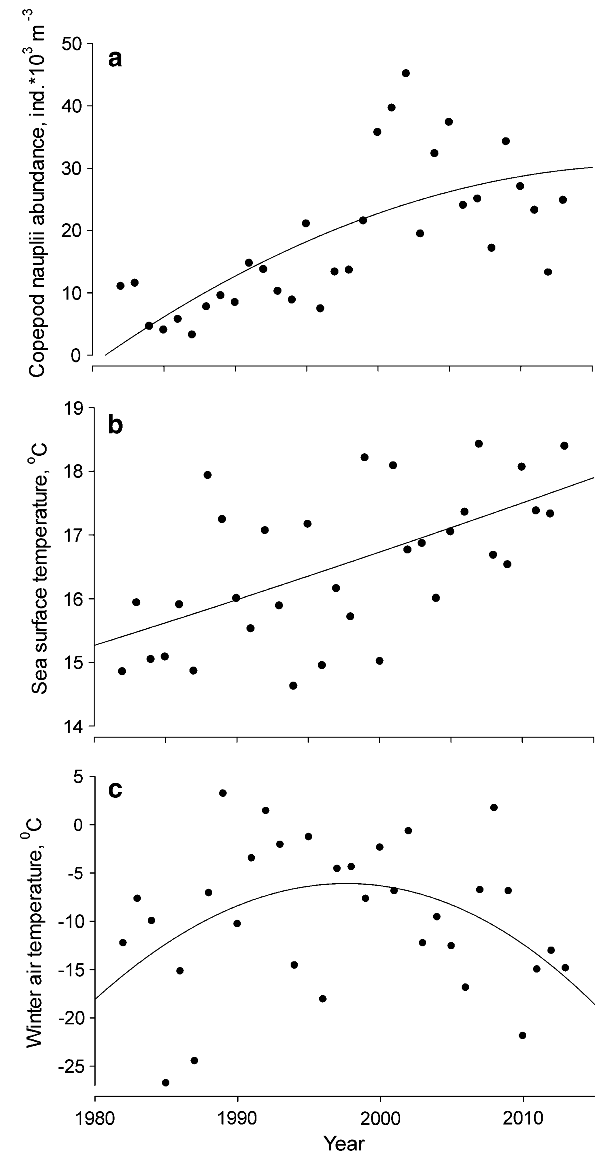

Fig. 4 **a** Temporal trend in mean long-term mean abundance of copepod nauplii from mid-May to late-July, **b** sea surface temperatures from mid-May to late-July, **c** and the sum of mean monthly winter (January–March) air temperature in European smelt larval and YoY retention grounds in 1982–2013

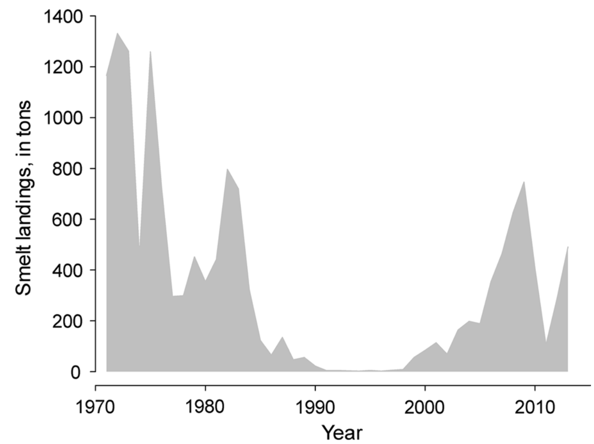

Fig. 5 Estonian commercial landings of European smelt in the Gulf of Riga (Baltic Sea) in 1971–2013 (*Source*: Ministry of Rural Affairs)

34]. GoR smelt landings decreased by more than a factor of three from the 1970s until the 1990s, resulting in fewer spawners and offspring, thus reducing competition during its early life stages. The abundance of copepod nauplii—the first prey of larval smelt—increased substantially since 1982, improving the feeding conditions for smelt larvae [26]. The feeding condition hypothesis is further supported by the fact that the abundance of herring larvae—main potential food competitor of smelt larvae—significantly decreased in the 1990s [19, 25–27]. Since we found K to be significantly higher in 2012, compared to the former period, we assume that improved feeding conditions during the early stages of life had a notable effect on the early maturation of smelt.

Sea surface temperature

Increased SST elevates individuals' metabolic demands that in ad libitum feeding conditions result in faster larval growth rate which, in turn, enables individuals to switch earlier to consuming energetically more profitable prey, e.g. mysids, and allocate energy to reproduction, as we observed in the current study. The importance of eurybionts (*Eurytemora hirundoides*, *Mysis mixta*, and *Neomysis integer*) in the diet of YoY smelt has increased since the 2000s in the GoR (Shpilev unpubl. data). This might be related to the cumulative effect of changes to temperatures during different life stages, coupled with a sufficient amount of prey. Water temperature and abundance of nauplii constantly increased since the 1980s in the retention grounds of smelt larvae and were both significantly higher in the 2000s compared to the 1980s, implying an elevated metabolic demand combined with better feeding conditions for smelt larvae. Simultaneously, significantly larger fish lengths and better condition of YoY smelt were observed in 2012 compared to an earlier period. The earlier maturation due to improved feeding conditions and elevated temperature has also been shown for Baltic sprat (*Sprattus sprattus balticus*), where the increase in water temperature resulted in the decrease of length-at-50% maturity by approximately 1.5 cm [35]. However, an important link to support this hypothesis is missing, and detailed studies on the growth rates of smelt larvae in the PB are needed in order to establish the actual mechanism of earlier maturation of smelt. Shifts towards maturation at younger ages or smaller sizes have been detected in many regions where warming trends in SST appeared [36]. Therefore, we hypothesise that observed warming trend in SST could be an important agent responsible for smelt early maturation in the present study.

Winter air temperature

Mean winter air temperature in the PB shows a decreasing trend since the 2000s, and it has been shown that YoY's overwintering mortality affects the size of fish populations at temperate latitudes [28]. The main reason for low survival is a poor condition (limited energy reserves), as decreased food availability in winter forces fish to starve and utilize all energy reserves (for a review, see [29]). Maturation is an energetically demanding process, which influences fish condition and, thereby, population recruitment dynamics [37]. It has been shown that, if K is too low during the feeding season, herring maturation is less likely to occur [38]. As in general, investment in growth is prioritized until the first sexual maturity, after which a considerable and increasing proportion of resources are used for reproduction, and thus growth rates decrease from maturity onwards [1]. Therefore, individuals that have achieved early maturation and survived due to milder winters will transfer genetic material to next generations. This, in turn, will result in more such early maturing and with low weight at age individuals in the population.

Commercial fishery

Commercial fishery can only be managed sustainably if the population characteristics, like age or size at first maturity, show stability over time [39]. Following the period of high exploitation rate, nearly a quarter of the analysed YoY smelt started to mature at a tenfold lower TW and 2–3 years younger than before the 1980s. 22% of individuals with a TL of <10 cm had maturing gonads in 2012, while only one maturing YoY smelt was observed in pre-1980, which indicates that these changes may be human-induced by overfishing or triggered environmentally [9].

Alterations in spawning stock demographics when evolutionary change is driven by selection for novel and potentially maladaptive phenotypes [40] may affect the ecosystem and the fishing industry. Since smelt are targeted for human consumption in the Baltic Sea, fish processors prefer landings consisting of large individuals. Unsuitable environmental conditions for forming abundant year-classes coupled with overfishing resulted in the collapse of smelt fishery in the GoR during the 1990s [15]. Therefore, early maturing smaller individuals, which were less targeted by size selective fishing, started to prevail in spawning stock after its recovery during the early 2000s [15]. Such a reduction in age and size at maturation has a drastic impact on the stock since reproduction is more reliant on early maturing individuals. Smaller and younger individuals produce offspring with similar genotypes that are characterized by early maturation and low absolute fecundity, as the latter depends on fish weight [41]. Older/larger fish, to the contrary, tend to spawn a higher number of eggs; thus, a shift to earlier maturation in a population reduces the survival potential of embryos and larvae and increases annual recruitment variability [42, 43]. Considering this, it is likely that smelt population overfishing had a significant effect on observed rates of smelt early maturation. Considering this, it is likely that smelt population overfishing, having caused early maturation, also had a significant effect on its recruitment abundance.

Long-term changes or short-term variation

An important question that remained in the present study is to what extent observed YoY smelt maturation can be explained by the long-term trends in the environment or by short-term variations resulting in anomalous environmental conditions in 2012. Generally, observed changes in YoY smelt maturation correspond to studied long-term temporal trends in environmental characteristics and fishery. However, because we have been able to compile too few number of years on YoY smelt maturation rate, none of the variables can be linked to our findings. Yet, we can suppose that YoY smelt early maturation is strongly influenced by the direction of long-term environmental changes and was not triggered by extreme conditions in the environment in 2012. Such mechanisms between early maturation and changes in climate and fisheries have been demonstrated by the number of studies [28, 32, 33]. It is further supported by the fact that we have found a number of early maturing YoY smelt after the 2012 (Arula unpubl. data).

In conclusion, we found that maturing YoY's were in a better condition and larger compared to immatures, which implies a faster growth and conditions favouring early maturation. While a remarkable proportion of YoY smelt were mature, this does not necessarily mean that they will spawn during the next spring. It can be expected that they (or at least some) may skip spawning, as the bulk of their energy has been invested in somatic growth, not reproduction, during the first year of their life. It has been hypothesised that skipping spawning may be an adaptive life-history strategy, given the potential to gain fecundity in improved condition [44]. Nevertheless, while it was assumed that iteroparous fish has an annual reproductive cycle spawn, it has become clear that resting or skipped spawning can often occur [45]. This phenomenon has not been studied in smelt, but signs of skipped spawning have been observed in a number of individuals of age groups 4–8 (Shpilev unpubl. data). Such a shift to earlier maturation in a population due to changed climatic conditions reduces the survival potential of embryos and larvae and increases the variability of annual recruitment [42, 43]. This, in turn, makes the population vulnerable to external conditions and results in unstable smelt fishery with implications to the performance of fishery.

Abbreviations

YoY: young of the year; GoR: Gulf of Riga; TW: total weight; g: grams; mm: millimeters; PB: Pärnu Bay; SST: sea surface temperature; °C: degrees in Celsius; s^{-1}: in one second; m^2: square meters; µm: microns; EMI: Estonian Marine Institute; L: length; HP: horse power; TL: total length; K: condition factor; ANOVA: one-way analyses of variance; N: number; T: tons.

Authors' contributions

TA carried out statistical analyses and drafted the manuscript. HS collected and analysed material. TR and MV and AA participated in data analyses, interpretation of the data and ms writing/correction. All authors read and approved the final manuscript.

Acknowledgements

The authors would like to thank two reviewers and the editor for their comments that helped to improve the quality of the article. We are grateful to Mr. Holger Jänes, Mr. James Philips and Mrs. Isabel Arula for language correction and their comments on earlier versions of the manuscript, and Dr. Mart Simm for providing copepod nauplii data.

Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

Data will be made publicly and freely accessible on the database of Estonian Marine Institute right after publication of this manuscript.

Ethics approval and consent to participate

No specific permits were required for the described field studies. This work was done in collaboration with the relevant governmental agencies aimed at enhancing knowledge-base on the dynamics of YoY life history of the regionally important commercial fish—smelt. The study area is not privately-owned and the field studies did not involve endangered or protected species.

Funding

The research was partly financed and conducted as part of the national data collection framework.

Publisher's Note

Received: 19 November 2016 Accepted: 6 April 2017
Published online: 17 April 2017

References

1. Heino M, Kaitala V. Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. J Evol Biol. 1999;12:423–9.
2. Sutherland WJ, Orafen A, Harvey HP. Life history correlations and demography. Nature. 1986;320:88.
3. Winemiller KO, Rose KA. Patterns of life history diversification in North American fishes: implications for population regulation. Can J Fish Aquat Sci. 1992;49:2196–218.
4. De Roos AM, Boukal SD, Persson L. Evolutionary regime shifts in age and size at maturation of exploited fish stocks. Proc R Soc B Biol Sci. 2006;273:1873–80.
5. Conover DO, Munch SB. Sustaining fisheries yields over evolutionary time scales. Science. 2002;297(5578):94–6.
6. Enberg K, Dunlop ES, Jørgensen C, Heino M, Dieckmann U. Implications of fisheries-induced evolution for stock rebuilding and recovery. Evol Appl. 2009;2:394–414.
7. Nussle S, Bornand CN, Wedekind C. Fishery-induced selection on an Alpine whitefish: quantifying genetic and environmental effects on individual growth rate. Evol Appl. 2009;2:200–8.
8. Sharpe D, Hendry A. Life history change in commercially exploited fish stocks: an analysis of trends across studies. Evol Appl. 2009;2:260–75.
9. Feiner SZ, Bunnell BD, Höök ÖT, Madenjian PC, Warner MD, Collingsworth DP. Non-stationary recruitment dynamics of rainbow smelt: the influence of environmental variables and variation in size structure and length-at-maturation. J Great Lakes Res. 2015;41(1):246–58.
10. Borisov VM. The selective effect of fishing on the population structure of species with a long life cycle. J Ichthyol. 1979;18:896–904.
11. Dieckmann U, Heino M. Probabilistic maturation reaction norms: their history, strengths, and limitations. Mar Ecol Prog Ser. 2007;335:253–69.
12. Beacham TD. Variability in size and age at sexual maturity of American plaice and yellowtail flounder in the Canadian Maritimes Region of the northwest Atlantic Ocean. Canadian Technical Report of Fisheries and Aquatic Sciences 1983;1196:75 p.
13. Lappalainen A, Saks L, Sustar M, Heikinheimo O, Jürgens K, Kokkonen E, Kurkilahti M, Verliin A, Vetemaa M. Length at maturity as a potential indicator of fishing pressure effects on coastal pikeperch (*Sander lucioperca*) stocks in the northern Baltic Sea. Fish Res. 2016;147:47–57.
14. Engelhard GH, Heino M. Maturity changes in Norweigan spring-spawning herring before, during, and after a major population collapse. Fish Res. 2004;66(2–3):299–310.
15. Shpilev H, Ojaveer E, Lankov A. Smelt (*Osmerus eperlanus* L.) in the Baltic Sea. Proc Estonian Acad Sci Biol Ecol. 2005;54(3):230–41.
16. Olin T, Von der Decken A. Vitellogenin synthesis in Atlantic salmon (*Salmo salar*) at different acclimation temperatures. Aquaculture. 1989;79:397–402.
17. Pankhurst NW, Porter MJR. Cold and dark or warm and light: variations on the theme of environmental control of reproduction. Fish Physiol Biochem. 2003;28:385–9.
18. Arula T, Shpilev H. Early ontogenesis of European smelt (*Osmerus eperlanus*) in variable environments. 39 Annual Larval Fish Conference 2015. Vienna, Austria; 2015.
19. Shestakov V. Feeding of smelt in Pärnu Bay and the Gulf of Riga. Tr BaltNIIRH. 1970;4:349–60 **(in Russian)**.
20. Taal I, Saks L, Nedolgova S, Verliin A, Kesler M, Jürgens K, Svirgsden R, Vetemaa M, Saat T. Diet composition of smelt *Osmerus eperlanus* (Linnaeus) in brackish near-shore ecosystem (Eru Bay, Baltic Sea). Ecol Fresh Fish. 2014;23(2):121–8.
21. Shpilev H. The European smelt (*Osmerus eperlanus*) in the North-Eastern Baltic Sea: biology, stock history and management. The European smelt *Osmerus eperlanus*: a workshop on the current knowledge base. Bangor University, North Wales, 26–27.03.2013.
22. Suursaar Ü, Kullas T, Otsmann M. Flow modelling in the Pärnu Bay and the Kihnu Strait. Proc Estonian Acad Sci Biol Ecol. 2002;3:189–203.
23. Kotta J, Lauringson V, Martin G, Simm M, Kotta I, Herkül K, Ojaveer H. Gulf of Riga and Pärnu Bay. In: Schiewer U, editor. Ecology of Baltic coastal waters: ecological studies, vol. 197. Berlin: Springer; 2008. p. 217–43.
24. ICES 2011. Report of the workshop on sexual maturity staging of herring and sprat (WKMSHS), 20–23 June 2011, Charlottenlund, Denmark. ICES CM 2011/ACOM: 46. 143 pp. http://www.ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/acom/2011/WKMSHS/WKMSHS%20Report%202011.pdf.
25. Arula T, Kotta J, Lankov A, Simm M, Põlme S. Diet composition and feeding activity of larval spring-spawning herring: importance of environmental variability. J Sea Res. 2012;68:33–40.

26. Arula T, Gröger PJ, Ojaveer H, Simm M. Shifts in the spring herring (*Clupea harengus membras*) larvae and related environment in the Eastern Baltic Sea over the past 50 years. PLoS ONE. 2014;9(3):e91304.
27. Arula T, Raid T, Simm M, Ojaveer H. Temperature-driven changes in early life-history stages influence the Gulf of Riga spring spawning herring (*Clupea harengus m.*) recruitment abundance. Hydrobiologia. 2016;767(1):125–35.
28. Anderson DA, Scharf FS. The effect of variable winter severity on size-dependent overwinter mortality caused by acute thermal stress in juvenile red drum (*Sciaenops ocellatus*) –. ICES J Mar Sci. 2013;71(4):1010–21.
29. Hurst PT. Causes and consequences of winter mortality in fishes. J Fish Biol. 2007;71:315–45.
30. McCollum AB, Bunnell DB, Stein RA. Cold, northern winters: the importance of temperature to overwinter mortality of age-0 white crappies. Trans Am Fish Soc. 2003;132:977–87.
31. Nash RDM, Valencia AH, Geffen AJ. The origin of Fulton's condition factor—setting the record straight. Fisheries. 2006;31(5):236–8.
32. Kuparinen A, Cano J, Loehr J, Herczeg G, Gonda A, Merilä J. Fish age at maturation is influenced by temperature independently of growth. Oecologia. 2011;167:435–43.
33. Marshall CT, Browman HI. Disentangling the causes of maturation trends in exploited fish populations. Mar Ecol Prog Ser. 2007;335:249–51.
34. McBride RS, Somarakis S, Fitzhugh GR, Albert A, Yaragina NA, Wuenschel MJ, Alonso-Fernández A, Basilone G. Energy acquisition and allocation to egg production in relation to fish reproductive strategies. Fish Fish. 2015;16:23–57.
35. Haslob H, Tomkiewicz J, Hinrichsen HH, Kraus G. Spatial and interannual variability in Baltic sprat batch fecundity. Fish Res. 2011;110(2):289–97.
36. Baudron AR, Needle CL, Marshall CT. Implications of a warming North Sea for the growth of haddock *Melanogrammus aeglefinus*. J Fish Biol. 2011;78:1874–89.
37. Roff DA. The evolution of life histories: theory and analysis. New York: Chapman and Hall; 1992.
38. Kennedy J, Skjaraasen JE, Nash RDM, Thorsen A, Slotte A, Hansen T, Kjesbu OS. Do capital breeders like Atlantic herring (*Clupea harengus* L.) exhibit sensitive periods of nutritional control on ovary development and fecundity regulation. Can J Fish Aquat Sci. 2009;67:16–27.
39. Darimont CT, Carlson SM, Kinnison MT, Paquet PC, Reimchen TE, Wilmers CC. Human predators outpace other agents of trait change in the wild. Proc Natl Acad Sci USA. 2009;106:952–4.
40. Coltman DW, O'Donoghue P, Jorgenson TJ, Hogg TJ, Strobeck C, Festa-Bianchet M. Undesirable evolutionary consequences of trophy hunting. Nature. 2003;426:655–8.
41. Hutchings JA. Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci. 2005;62:824–32.
42. Heyer CJT, Miller J, Binkowski PF, Caldarone ME, Rice AJ. Maternal effects as a recruitment mechanism in Lake Michigan yellow perch (*Perca flavescens*). Can J Fish Aquat Sci. 2001;58:1477–87.
43. Andree SR, Feiner SZ, Bledsoe WJ, Cragun MA, Höök OT. Ontogenetic variability of maternal effects in an iteroparous fish. Ecol Freshw Fish. 2014;24:384–96.
44. Folkvord A, Jørgensen C, Korsbrekke K, Nash RDM, Nilsen T, Skjæraasen JE. Trade-offs between growth and reproduction in wild Atlantic cod. Can J Fish Aquat Sci. 2014;71:1106–12.
45. Rideout RM, Tomkiewicz J. Skipped spawning in fishes: more common than you might think. Mar Coast Fish. 2011;3:176–89.