



Population growth correlates with increased fecundity in three-spined stickleback populations in a human-disturbed environment

Ulrika Candolin¹ · Heinz-Rudolf Voigt¹

Received: 21 August 2019 / Accepted: 3 January 2020 / Published online: 10 January 2020
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Abstract

Human activity is altering the dynamics of populations through effects on fecundity, mortality and migration. An increased abundance of three-spined stickleback (*Gasterosteus aculeatus*) in the Baltic Sea has been attributed to a human-caused decline of top predators. However, recent research indicates that a top-down effect cannot fully explain the population growth, but the contribution of a bottom-up effect has not been investigated. Yet, anthropogenic eutrophication has increased algae biomass at the spawning sites of the stickleback and, thus, the abundance of benthic prey. We investigated if increased fecundity could have contributed to the population growth of the stickleback by analysing a two decade time series of stickleback abundance, fecundity, and body size at three spawning sites. The results show an increase in the proportion of gravid females in the populations, which correlates with the population growth. In particular, the proportion of gravid females late in the spawning season has increased, which indicates enhanced food intake at the sites during the spawning season. Thus, a bottom-up effect could have contributed to the growth of the populations by increasing the number of egg clutches females produce. These results stress the importance of considering both bottom-up and top-down processes when investigating the mechanisms behind human impact on population dynamics.

Keywords Bottom-up effect · Environmental change · Eutrophication · Population dynamics · Population regulation · Reproduction

Introduction

Human activity is altering the dynamics of populations through habitat degradation, pollution, climate change, harvesting, and species introductions. The abundance of the three-spined stickleback (*Gasterosteus aculeatus*) has increased in many parts of the Baltic Sea during the last decades at the same time as the sea has undergone a range of other human-induced changes, such as eutrophication and overfishing of top predators (Bergström et al. 2015; Candolin et al. 2016b). The population growth has been ascribed to the decline of top predators and subsequent mesopredator

release, i.e., to a top-down effect (Casini et al. 2008; Eriksson et al. 2011; Ljunggren et al. 2010). However, mismatches between the timing of the piscivore decline and the stickleback growth in some parts of the sea suggest that the top-down effect is not the sole explanation for the growth of the stickleback population, as noted by Bergström et al. (2015). Other changes could have contributed to the growth, such as human-induced eutrophication and climate change, as these have increased primary production and, thus, most likely food abundance for stickleback (Andersen et al. 2017; Salovius and Kraufvelin 2004). Yet, the possible contribution of a bottom-up effect has not been investigated.

The determination of the relative contribution of top-down and bottom-up effects to population growth is generally difficult, and particularly so in disturbed environments where the contribution of the two processes could change (Lynam et al. 2017; Perkins et al. 2018; Shurin et al. 2012). In the Baltic Sea, human-induced eutrophication has increased the growth of filamentous algae at the spawning sites of the three-spined stickleback: shallow coastal areas with vegetated rocky bottoms. This has increased the

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00027-020-0695-3>) contains supplementary material, which is available to authorized users.

✉ Ulrika Candolin
ulrika.candolin@helsinki.fi

¹ Organismal and Evolutionary Biology, University of Helsinki, PO Box 65, 00014 Helsinki, Finland

abundance of their preferred prey, especially of amphipods and dipterans (Candolin et al. 2016a; Jakubaviciute et al. 2017a; Kraufvelin and Salovius 2004; Kraufvelin et al. 2006; Olafsson et al. 2013; Salovius and Kraufvelin 2004). In addition, climate change has prolonged the spawning season (Hovel et al. 2017; Olsson et al. 2013), while rising water temperature has increased the feeding rate of the stickleback (Lefebure et al. 2011, 2014). However, whether these environmental changes correlate with the growth of the stickleback population is unknown.

The improved foraging conditions in the spawning habitats of the stickleback could have increased the fecundity of females and, thus, contributed to the population growth of the stickleback, as increased food intake during the spawning season shortens the interspawning interval and increases the number of egg clutches females produce, while not influencing the size of the clutches (Ali and Wootton 1999; Fletcher and Wootton 1995; Leloutre et al. 2018; Wootton and Fletcher 2009). An increased offspring production could in turn have interacted with the relaxed top-down control, caused by the decline of predator populations, in promoting population growth, as reduced predation rate should allow a larger number of offspring to reach the adult stage.

Three-spined stickleback in the Baltic Sea migrate in spring to shallow coastal waters to spawn, after spending the winter at deeper water (Candolin and Voigt 2003). Males establish territories and build nests to which they attract females to spawn (Wootton 1976). After spawning, the female leaves and the male alone cares for the eggs in the nest until hatching. Females can produce several clutches of egg during the spawning season, and males can complete several breeding cycles (Wootton 1976). Most individuals, of both sexes, complete only one spawning season at the age of +2 (Candolin 2000).

We performed the first test of a correlation between fecundity and population growth in the three-spined stickleback in the Baltic Sea. We hypothesised that fecundity should have increased during the last decades when human-induced eutrophication and climate change have increased the abundance of prey at the spawning sites, and that the increase should correlate with the growth of the population. In particular, we expected the proportion of gravid females to have increased later in the season, as the increased food availability should improve the probability of reproduction later in the season. To test these hypotheses, we analysed time-series data on the abundance of adult three-spined stickleback, the proportion of gravid females in the spawning populations, and the body size of the fish at three spawning sites in the Northern Baltic Proper from 1994 to 2015, with data for nine of the years. In addition, we analysed data on the size of the egg clutches of females at the three spawning sites during the same period, with data for 13 years from 1994 to 2017.

Materials and methods

The density of spawning three-spined stickleback has been monitored from 1994 to 2015 at three spawning sites in the Northern Baltic Proper; Långskär, Vindskär and Klobben bays (see descriptions of the bays in Candolin et al. 2018; Candolin and Voigt 2003). The bays are close to Tvärminne Zoological Station (60° N, 23° E), and the distances between them are 2–2.5 km (Fig. S1 in Supplementary Material). All three bays have a dense growth of algae, mainly of *Fucus vesiculosus* and the filamentous algae *Cladophora glomerata*.

Stickleback have been caught using transparent Plexiglas traps (20×20×40 cm) that have wings (20×60 cm) that direct fish toward the opening of the traps (1.5×20 cm) (Candolin and Voigt 2001). A minimum of six traps have been set out 1–2 times a week from early May to mid-July in each bay. They have been placed at two different depths, 30 and 80 cm, at each of three or more locations within each bay (see Candolin and Voigt 2003). They have been set in the evening at about 6 pm and collected the following day at noon. The number and body length (± 1 mm, standard length) of three-spined stickleback caught in each trap have been recorded, and their sex and maturity stage determined when possible, i.e. when they have been in reproductive condition. All stickleback have been returned unharmed to their habitat after measurements.

The fecundity of individual females has been recorded from 1994 to 2017 by catching females from the same area, but from different spawning sites to prevent the collection of females from influencing the dynamics of the monitored populations. The selected sites have similar environmental conditions as the monitored sites in terms of bottom structure, vegetation and water conditions. Females have been collected using Plexiglas traps, and transported to Tvärminne Zoological station within half an hour. They have been kept in flow-through tanks under natural light and temperature conditions until fecundity measurements. Fecundity has been determined by placing a female into a tank containing a male in reproductive condition, with a newly build nest, and allowing her to spawn in the male's nest. Females release all mature eggs when spawning. The male and the female have been removed immediately after fertilisation, and two hours later—when the eggs have hardened—the clutch of eggs has been collected and weighed (± 0.01 g). Female body size has been measured after spawning as standard length (± 1 mm) and wet weight (± 0.01 g). Different males have been used for each spawning.

Data analyses

To ensure the selection of appropriate models to analyse the data, we inspected the distribution of the residuals and transformed the data when needed. To analyse changes in the abundance of three-spined stickleback over the years, which

represents count data, we used a generalized linear mixed model (GLMM) with negative binomial error distribution and a log link. We used the number of stickleback per trap as response variable, year and Julian date as covariates, and spawning site as a random factor. To consider curvilinear relationships between abundance and year, we run models with quadratic, cubic or logarithmic year terms, and selected the model that explained most of the variation in stickleback abundance.

To analyse changes in the proportion of gravid females in the populations, we used a GLMM with binomial error distribution and an identity link, with the proportion of gravid females in each trap as response variable (in proportion to all stickleback in the trap), year and Julian date as covariates, and spawning site as a random factor. To assess curvilinear relationships, we run models with different year terms, as described for total number of stickleback. To assess if the proportion of females has changed over the season, we added an interaction term between year and Julian date. To analyse if the proportion of gravid females correlates with the size of the population, we used a GLMM with binomial error distribution and an identity link, with the proportion of gravid females in each trap as response variable, number of stickleback caught per site per year as covariate, and spawning site as a random factor.

To analyse temporal changes in body size, we used a Linear Mixed Model with log-transformed body length as response variable, year and Julian date as covariates, and spawning site and trap (nested within site) as random factors.

To analyse changes in egg clutch size, we used egg clutch weight, rather than egg number, because data on egg number were not available for the first years of the time series. We modelled clutch size as an allometric function of body size by log transforming (\ln) the two variables. We used a linear mixed model to analyse the data, with log transformed clutch size as response variable, log transformed female body length and year as covariates, and spawning site as a random factor.

Results

The abundance of three-spined stickleback at the three spawning sites has increased from 1994 to 2015, with the increase having levelled off during the last years, as the model that explained most of the variation included a quadratic year term (full model: $F_{1,3041} = 169.92$, $P < 0.001$, quadratic year term: $F_{1,3041} = 16.66$, $P < 0.001$, Fig. 1a, see also Fig. S2a in Supplementary Material). A rapid population growth occurred from year 1994–98 to 2003–05, after which a more stable state with high abundance has prevailed up to 2015.

The proportion of gravid females shows a similar increase that has levelled off during the last years, as the model that explained most of the variation included a quadratic year term (full model: $F_{1,2089} = 123.44$, $P < 0.001$, quadratic year term: $F_{1,2089} = 19.14$, $P < 0.001$, Fig. 1b, see also Fig. S2b in Supplementary Material). The proportion of gravid females later in the season has increased, as indicated by a significant interaction between year and Julian date ($F_{1,2089} = 39.74$, $P < 0.001$, Fig. 2). The increase in the proportion of gravid females over the years correlates with the increase in the abundance of stickleback ($F_{1,2091} = 137.77$, $P < 0.001$).

The body size of the stickleback has slightly decreased over the years (-0.026 mm/year (SE 0.006), $F_{1,6760} = 4.74$, $P = 0.030$), but that of gravid females shows no change ($F_{1,2035} = 0.24$, $P = 0.62$, Fig. 3), probably due to the lower sample size and the extremely small size change across all fish. Clutch size has remained unchanged over the years and depends allometrically on female body length, with an allometric coefficient of 3.58 (SE 0.20) (year: $F_{1,340} = 0.41$, $P = 0.52$, body length: $F_{1,338} = 311.08$, $P < 0.001$, Fig. 4). Body mass after spawning has not changed across years ($F_{1,341} = 0.01$, $P = 0.91$).

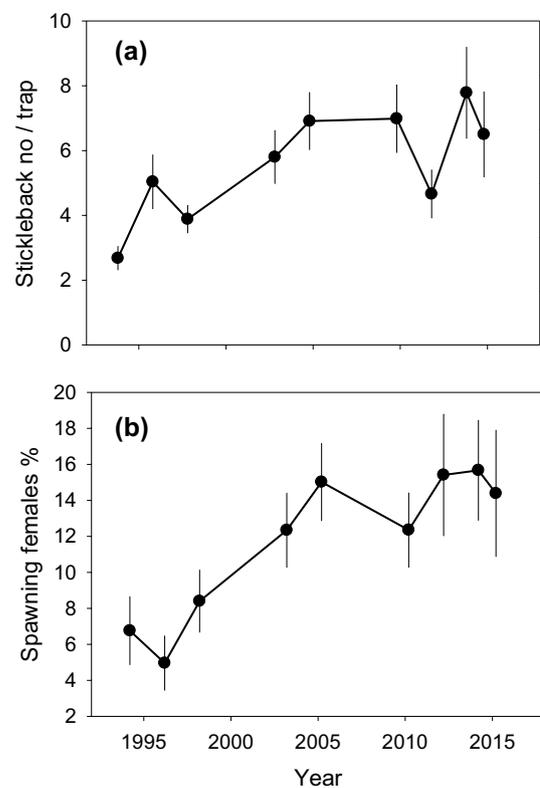


Fig. 1 **a** The number of adult three-spined stickleback captured from 1994 to 2015 at three spawning sites, and **b** the proportion of these that were gravid females. For simplicity, data presented are pooled means and 95% confidence intervals for sites and dates within each year

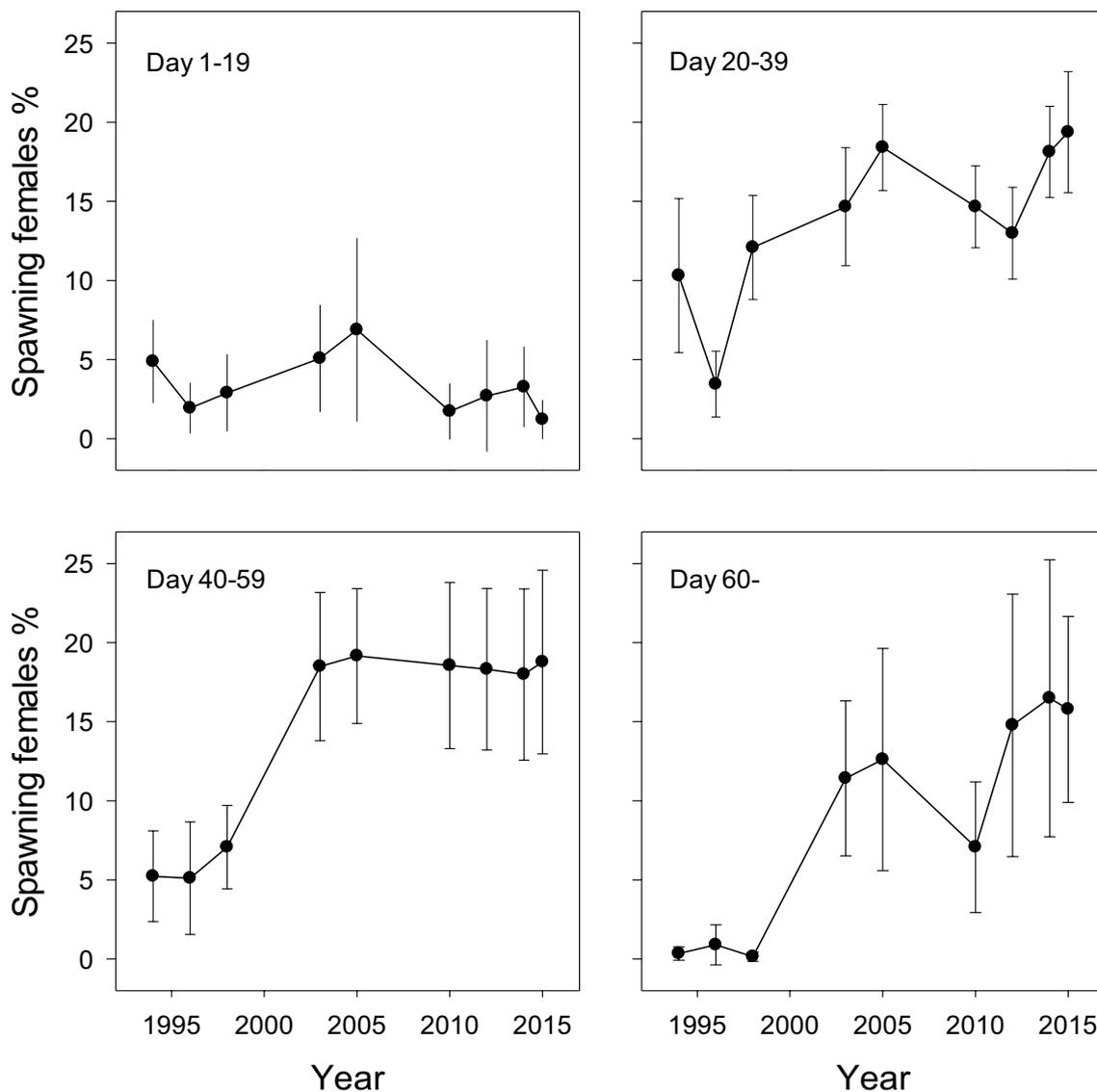


Fig. 2 The proportion of gravid three-spined stickleback females at three spawning sites during four time periods of the spawning season. Day 1 = 1st of May. Data are pooled means and 95% confidence intervals for sites and dates within periods

Discussion

The abundance of three-spined stickleback at the monitored spawning sites has increased during the investigated period, 1994–2015. The population growth is associated with an increased proportion of gravid females in the populations, particularly later in the season, while the size of the egg clutches has not changed. These results suggest that enhanced female fecundity—in terms of number of clutches females produce—could have contributed to the population growth. Earlier work has attributed the population growth of the stickleback in the Baltic Sea to the decline of top predators, through a mesopredator release (Casini et al. 2008; Ljunggren et al. 2010). However, the decline does

not explain the growth of stickleback populations in all parts of the Baltic Sea, and other factors could consequently have contributed to their growth (Bergström et al. 2015; HELCOM 2018). This study suggests that one such factor could be an increased number of egg clutches produced by females during their lifetime, i.e., increased lifetime fecundity.

The cause of the increased fecundity is probably favourable conditions at the spawning sites, as the proportion of gravid females has increased, especially later in the season when females have spent some time at the sites. The number of clutches females produce and, hence, total spawning season fecundity, depends on environmental conditions at spawning sites, as vitellogenic oocytes are recruited during the spawning season (Ali and Wootton 1999; Fletcher and

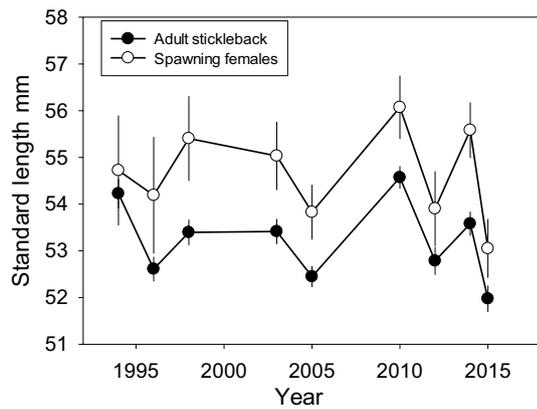


Fig. 3 Standard length of three-spined stickleback captured from 1994 to 2015 at three spawning sites. Data are pooled means and 95% confidence intervals for sites and dates within each year

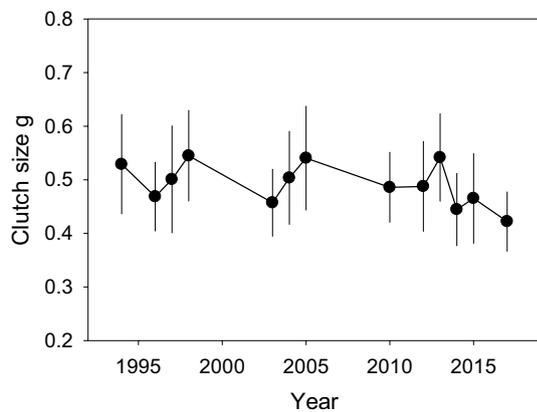


Fig. 4 Clutch size of three-spined stickleback females from 1994 to 2017 at three spawning sites. The data presented are pooled means and 95% confidence intervals for the sites

Wootton 1995; Wootton and Fletcher 2009). An increase in fecundity during the last decades is possible, as the availability of food has increased at the spawning sites when eutrophication and climate change have promoted the growth of filamentous algae (Andersen et al. 2017; Takolander et al. 2017), as algae biomass correlates with the abundance of benthic prey (Kraufvelin and Salovius 2004; Kraufvelin et al. 2006; Salovius and Kraufvelin 2004). In addition, climate change could have prolonged the spawning season, while the rise in water temperature (BACC II Author Team 2015) could have increased the feeding rate of the stickleback (Lefebure et al. 2014). Changes in species composition could in turn have reduced the intensity of competition for food (Candolin 2019; Candolin et al. 2018). Moreover, infections with the energetically expensive tapeworm *Schistocephalus solidus* decreases with eutrophication, which could have freed up energy for reproduction (Budria and

Candolin 2015). Females can produce up to ten clutches of eggs under favourable conditions (Ali and Wootton 1999; Fletcher and Wootton 1995; Wootton and Fletcher 2009).

Clutch size of females has not increased over the years. This is in line with earlier research that found no significant effect of food intake during the spawning season on clutch size (Wootton and Fletcher 2009). This is probably because clutch size is mainly determined by body size, which has not increased over the years. On the contrary, it has slightly decreased among adult stickleback, but the decrease is too small to be biologically meaningful.

The increase in the proportion of gravid females later in the season suggests that conditions at the spawning sites are responsible for the increased fecundity, rather than conditions outside the sites. Yet, factors other than prey availability could have contributed to the increased proportion of gravid females, such as altered sex ratio over the season, or altered behaviour of individuals. Males are more susceptible to predation than females during reproduction, because of their conspicuous reproductive behaviour and coloration (Johnson and Candolin 2017), and could suffer from higher mortality rate. However, the decline of predators in the area, especially of pike and perch (Bergström et al. 2016; Byström et al. 2015; Ljunggren et al. 2010), should have increased the proportion of males, not females. Regarding behavioural alterations, spawning females could have become more active at the spawning sites and more often caught in the traps, but we see no obvious reason for such changes.

A further possibility is that females have started to delay mate choice and retain their eggs for longer, which would increase the proportion of gravid females in the populations. This is possible as the increased growth of filamentous algae has reduced visibility and made mate choice more difficult (Candolin et al. 2007; Engström-Öst and Candolin 2007; Heuschele et al. 2012). However, prolonged mate choice should depress rather than promote population growth, as more females could release their eggs outside nests, or develop overripe eggs that cannot be released, which eventually kills them (Lam et al. 1978; Roufidou et al. 2016).

Irrespective of the exact mechanism(s) behind the increased fecundity, the results suggest that the fecundity increase could have contributed to the growth of the stickleback populations in the Baltic Sea. This is supported by a higher number of spawned eggs and emerging fry at spawning sites with a denser growth of filamentous algae (Candolin et al. 2014). However, the ultimate impact of offspring production on population dynamics depends on the survival of the juveniles after hatching. Density-dependent factors are expected to control population growth (Murdoch 1994). Thus, the reduced predation pressure—because of the decline of top predators—could have relaxed the top-down control and altered the equilibrium density of the populations, allowing a larger proportion of the juveniles to reach

adulthood. An interaction between bottom-up and top-down processes could then have contributed to the growth of the stickleback populations. This possibility deserves further attention, considering the multitude of disturbances that stickleback populations are exposed to in the Baltic Sea.

The very slight decrease in body size detected could in turn be a consequence of the increased population size, as the increased number of individuals competing for food in the pelagic area could constrain body growth. The plankton community in the area has shifted towards smaller species, which has been attributed to eutrophication and climate change (Suikkanen et al. 2013). However, increased predation pressure from mesopredators, such as stickleback, could as well have contributed to the shift in plankton size, as stickleback prefer larger zooplankton prey (Candolin et al. 2016a; Jakubaviciute et al. 2017a, b). Clearly, more investigations are needed on the relative importance of the various factors that regulate the abundance and population structure of the three-spined stickleback in the Baltic Sea, as well as the consequences that changes in the population could have for other components of the ecosystem.

To conclude, the results suggest that a bottom-up effect through increased female fecundity could have contributed to the growth of three-spined stickleback populations in the Baltic Sea. An interaction with top-down effects is likely, as the weakened top-down control (because of the decline of top predators) could have allowed more offspring to reach adulthood. These results emphasise the importance of considering both top-down and bottom-up effects, as well as their interaction, when investigating the effects of multiple human disturbances on the dynamics of populations.

Acknowledgements Open access funding provided by University of Helsinki including Helsinki University Central Hospital. We thank Elina Bertell, Julia Hämäläinen, Anna Johanson, Jarkko Kallio, and Tiina Salesto, for assistance in the field and in the lab, and Tvärminne Zoological station for providing facilities and equipment. Two reviewers provided excellent comments that improved the paper. Funding was provided by the Swedish Cultural Foundation in Finland. This study was approved by regional ethics committees, permits 86-06, STH421A and ESAVI/5421/04.10.07/2016, and conducted according to national guidelines.

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