



Anthropogenic noise disrupts early-life development in a fish with paternal care

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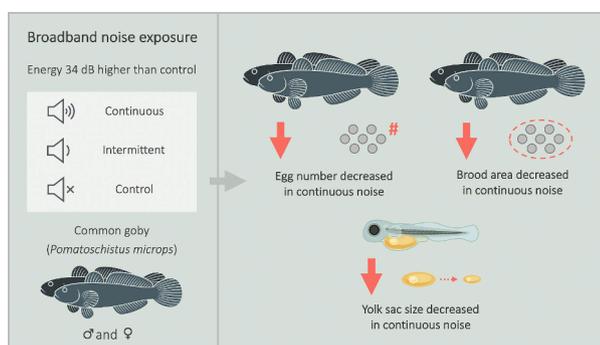
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HIGHLIGHTS

- Noise exposure during early life-stages affects fitness-related traits in fish.
- Noise exposure decreases the yolk sac reserve during early life of pelagic larvae.
- Brood size, brood area, and egg density decreased with increased noise.
- Noise pollution had a negative effect on egg and larval development.
- Highlights the wide-ranging impacts of anthropogenic noise on aquatic wildlife

GRAPHICAL ABSTRACT



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ABSTRACT

Anthropogenic noise is a global pollutant but its potential impacts on early life-stages in fishes are largely unknown. Here, using controlled laboratory experiments, we tested for impacts of continuous or intermittent exposure to low-frequency broadband noise on early life-stages of the common goby (*Pomatoschistus microps*), a marine fish with exclusive paternal care. Neither continuous nor intermittent noise exposure had an effect on filial cannibalism, showing that males were capable and willing to care for their broods. However, broods reared in continuous noise covered a smaller area and contained fewer eggs than control broods. Moreover, although developmental rate was the same in all treatments, larvae reared by males in continuous noise had, on average, a smaller yolk sac at hatching than those reared in the intermittent noise and control treatments, while larvae body length did not differ. Thus, it appears that the increased consumption of the yolk sac reserve was not utilised for increased growth. This suggests that exposure to noise in early life-stages affects fitness-related traits of surviving offspring, given the crucial importance of the yolk sac reserve during the early life of pelagic larvae. More

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broadly, our findings highlight the wide-ranging impacts of anthropogenic noise on aquatic wildlife living in an increasingly noisy world.

1. Introduction

Anthropogenic pollution has accumulated in aquatic environments around the globe (Häder et al., 2020). Research has shown that a diverse range of pollutants, such as chemical contaminants (Bertram et al., 2022), light pollution (Hölker et al., 2023), and heat stress (Luksiene and Sandström, 1994), can disrupt sensitive reproductive processes in a wide array of aquatic species, including fish (reviewed in Aulsebrook et al., 2020). One such pervasive pollutant in the aquatic environment is noise originating from human activities, including commercial shipping and recreational boating, naval sonar, oil exploration, and construction works, which is known to affect both wildlife (Duarte et al., 2021) and human health (Brown and van Kamp, 2017). For example, research has shown that anthropogenic noise increases larval mortality in zebrafish (*Danio rerio*; Lara and Vasconcelos, 2021), and can also disrupt the growth and development of early life-stages in various fish species (Fakan and McCormick, 2019; Faria et al., 2022; Lara and Vasconcelos, 2021; Nedelec et al., 2015). Furthermore, anthropogenic noise can compromise reproduction by directly influencing mating success in fish (Amorim et al., 2022; Blom et al., 2019; de Jong et al., 2018) and by causing stress-induced declines in egg quality (Li and Leatherland, 2012; Sierra-Flores et al., 2015). However, despite the fact that parental care is a critical reproductive strategy across many aquatic taxa, including teleost fish and amphibians, the potential impacts of anthropogenic noise on this key reproductive process—integral to the reproductive fitness of these species—remains poorly understood (Goldberg et al., 2020).

In fish with parental care, the parent can improve egg development by fanning and brooding, thereby providing oxygen and removing waste products, as well as cleaning and removing dead and infected eggs (Blumer, 1979), and protecting eggs from infections with antimicrobial mucus (Giacomello et al., 2008; Knouft et al., 2003). Hence, if parental care is compromised by aquatic noise, this would be expected to affect both developmental rate and viability of the embryos. The size of larvae and yolk sac at hatching are useful indicators of offspring condition, with reduced growth and increased yolk sac use indicating poorer condition (Nedelec et al., 2015). Furthermore, parentally caring fish often show filial cannibalism (i.e. a parent consumes some or all of the offspring under their care) (e.g. Bose, 2022; Manica, 2002; Pereira et al., 2017). Full-brood cannibalism is expected when the cost of care exceeds the reproductive value of the brood and means a termination of parental care, whereas a parent that only consumes a portion of the brood continues to care for the remaining offspring. Filial cannibalism and its causes have been extensively investigated and reviewed. Examples of well-studied species are the common goby *Pomatoschistus microps* (Krøyer, 1838), the three-spined stickleback *Gasterosteus aculeatus*, and the bluegill sunfish *Lepomis macrochirus* (Bose, 2022; Manica, 2002; Pereira et al., 2017). However, only a few studies have investigated the effects of aquatic noise on filial cannibalism and then in the context of brood failure. In the spiny chromis, *Acanthochromis polyacanthus*, motorboat-noise playback increased complete brood mortality. It was not recorded if the parents abandoned or cannibalised their offspring (Nedelec et al., 2017). Furthermore, aquatic noise increased the incidence of termination of care, sometimes involving filial cannibalism, in the maternally mouth-brooding cichlid *Astatotilapia burtoni* (Butler and Maruska, 2021). Thus, it is plausible that aquatic noise not only impacts parental care but also influences levels of filial cannibalism.

Here, we examine how exposure to broadband noise pollution affects traits directly associated with reproductive success in the common goby. Specifically, we investigated the hatching success and early-life development of broods spawned and subsequently reared by males in each of

three noise regimes: control, intermittent noise, and continuous noise. We quantified brood size (total number of eggs per brood), brood area (area covered by eggs), egg density, egg size, developmental rate, hatching success, and filial cannibalism. For hatched larvae, we measured yolk sac size and body length. We predicted that exposure to continuous and intermittent noise would negatively affect egg and larvae development but that continuous noise would be more detrimental than intermittent noise, as it represents a higher cumulative sound exposure level.

2. Materials and methods

The experiment was conducted at the Kristineberg Center for Marine Research and Innovation on the west coast of Sweden (58°15' N, 11°27' E) between May and August 2018.

2.1. Ethics statement

The experiment was conducted according to national and international guidelines for the care and use of laboratory animals. An ethical permit for the experimental procedures was obtained from the Swedish Animal Welfare Agency (dnr: 5.8.18-03920/2018). After the experiment, all adult fish were released back into their natural habitat.

2.2. Study species

The common goby is a small (3–6 cm) marine fish distributed in lagoons, coastal areas, and estuaries (Bouchereau and Guelorget, 1997; Kullander et al., 2012). The species is common in coastal areas of the north-east Atlantic Ocean, the Mediterranean Sea, and the Baltic Sea, and plays an important role in the food web structure and dynamics of those ecosystems (Leitão et al., 2006; Pockberger et al., 2014). It is a short-lived fish (1–2 years) that, during its single breeding season, can spawn multiple times with different mates (Kullander et al., 2012; Miller, 1986). Common gobies have a resource-based mating system, in which the males build nests out of empty bivalve shells or similar substrates (Borg et al., 2002; Vestergaard, 1976). When spawning, females attach their clutch of eggs in a single layer to the ceiling of the nest. The male alone provides care for the brood, which may consist of several female clutches (Magnhagen and Vestergaard, 1993), and filial cannibalism commonly occurs (Kvarnemo et al., 1998; Vallon and Heubel, 2017).

Males attract females using visual courtship signals but, as an additional component of courtship, males also produce a series of low-frequency pulses when accompanied by a female in the nest (Blom et al., 2016). Although it is not entirely known why male gobies produce sound, it is likely that it carries information about male quality to the female (Amorim et al., 2013; Blom et al., 2016; Pedroso et al., 2013). Many anthropogenic sound sources have the potential to overlap and mask the sounds that males produce during courtship (Slabbekoorn et al., 2010). It is also relevant to note that *Pomatoschistus* spp. have previously been used to assess the effects of environmental stressors such as aquatic noise, endocrine-disrupting chemicals, and various other chemical contaminants (e.g., Asnicar et al., 2018; Blom et al., 2019; Saaristo et al., 2009).

2.3. Study animals and husbandry

Fish were collected by hand trawling at a depth of 0.2–0.5 m in bays around Kristineberg and sorted by sex into four 50 L aquaria, with sifted sand in the bottom, placed in an outdoor greenhouse. All aquaria had a

continuous flow of natural deep seawater (salinity 32–34 PSU). Water temperature was checked daily (11–18 °C). All fish were fed daily with commercial fish food granules (Nutra HP, Skretting) and frozen *Artemia* sp. Fish were allowed to acclimate to their storage environment for at least three days (maximum of seven days) until the start of the experiment. No storage tank was exposed to any noise treatment.

2.4. Experimental setup

The experiment consisted of three treatments: a control treatment (no noise added), an intermittent noise treatment, and a continuous noise treatment. A polypropylene tube (Ø 56 mm) was vertically placed in the corner of each aquarium and filled with one decilitre of soft airgun balls. To generate noise, compressed air was bubbled from the bottom of the polypropylene tube, causing the soft airgun balls to tumble and bounce on the walls. This method avoids electromagnetic fields from speakers, which would have required an additional control (Nedelec et al., 2014). This method also created a similar broadband character as many anthropogenic noise sources, such as boats (Nichols, 2014; Simpson et al., 2016), with most of its energy being below 1000 Hz, frequencies within the common goby's hearing range (<1 kHz) (Bolgan et al., 2012).

In the intermittent noise treatment, the air pump was turned on and off randomly by a timer, creating on-and-off periods ranging from 1 to 15 min, with a total on-time of 50 %. In the continuous noise and the control treatments, the air pump was always on or off, respectively. All treatments were subjected to low levels of ambient noise caused by natural sources and human activities outside the greenhouse. When fish were exposed to their treatment, they were undisturbed by humans inside the greenhouse between measurements (see below).

We used 26 experimental aquaria (20L). To avoid acoustic interference between tanks and to isolate from ground-borne vibrations, the aquaria were placed on wooden planks. The aquaria were separated by opaque screens to avoid visual interaction between fish in adjoining replicates. Each aquarium contained sifted sand and a halved clay flower pot (65 mm inner diameter) that acted as an artificial nest site. The ceiling of the flower pot was lined with a plastic sheet, marked with 0.25 cm² squares, on which females were able to lay eggs. Further, we measured the total body length of all fish to the nearest mm before trials (males: $n = 159$, length: 40 ± 3.8 mm; females: $n = 318$, length: 41 ± 4.0 mm).

Males were randomly assigned to either the control treatment (no noise added), the intermittent noise treatment, or the continuous noise treatment, and were left for 36 h before being presented with two ripe females in a transparent plastic cup. The females remained inside the plastic cup for one hour to acclimatise to both the treatment and the new environment, and were then released into the aquarium. The females were allowed to freely interact with the male for 12 h, after which the female was removed and the nest was examined for eggs. The females were exposed to the same treatment as the males when present in the experimental aquaria.

If one or both of the females had laid eggs, the brood on the plastic sheet was briefly removed from the nest, photographed with a mobile phone (SM-G950F, Samsung) and then returned to the tank. If no eggs were found, the replicate was terminated. The broods were photographed again at 65 % and 75 % of the estimated time to hatching, using a stereo microscope (Leica M205 C, Leica Microsystems, Germany, using $\times 2.0$ zoom). To estimate when the brood would reach this stage in development, a formula that calculates developmental rate in sand gobies (*Pomatoschistus minutus*) was used. The formula is calculated as follows: $y = -0.073 + 0.012x$, where x = water temperature, and $1/y$ = 100 % hatching time (Kvarnemo, 1994). The water temperature was measured three times per day in the experimental tanks (morning, midday, and evening) to estimate the daily average temperature to use in the formula.

When a brood was ready to hatch according to the formula, the

plastic sheet was removed from the nest and moved to a water-filled petri dish for the larvae to hatch. After hatching, the larvae were euthanised with an overdose of MS-222 and photographed using a stereo microscope (the same model as above, using $\times 3.2$ zoom).

2.5. Acoustic measurements

The noise generated in the tubes had an elevated energy of 34 dB higher than the control (root-mean-square sound pressure level, SPL). Sound was registered at four locations inside the aquaria using a calibrated hydrophone (HTI-96-MIN with pre-amplifier, High Tech Inc., Gulfport MS; sensitivity -165 dB re 1 V/ μ Pa, frequency range 0.02–30 kHz) connected to a digital audio recorder (Song Meter SM2+, Wildlife Acoustics Inc., Maynard, US, sampling frequency 24 kHz). Note that frequencies of interest in the noise treatment should be unaffected by tank properties as they fall well below its resonant frequency of 4.9 kHz (Akamatsu et al., 2002). Full details of the noise profiles (e.g. frequencies and sound pressure levels) of the treatments are reported in Blom et al. (2019).

2.6. Data collection

From the photographs taken of the brood at spawning (0 %) and 65 % of development, we measured brood size, brood area, egg density, egg size, developmental rate, hatching success, and filial cannibalism. Brood area (cm² covered by eggs) and egg size (mm²) were measured using ImageJ (National Institutes of Health, Bethesda, Maryland, USA). We measured all of the eggs in five randomly selected squares (5×0.25 cm²) on the plastic sheets and calculated an average egg size for the brood (only at 65 % of development). For egg density (number of eggs per cm²), we calculated the average number of eggs per cm² by counting the number of eggs in five randomly selected squares on the plastic sheet. To estimate brood size (total number of eggs per brood), the egg density was multiplied by the brood area. Developmental rate was based on the number of days it took for a brood to reach hatching, defined as $1/x$, where x = the number of days to hatching. Based on our own observations, filial cannibalism in this species usually happens during the first half of the brood cycle. Filial cannibalism was therefore measured as the complete loss of eggs between 0 % of development and 65 % of development, indicating full brood cannibalism. Hatching success was based on the number of eggs (expressed as a proportion of the initial number of eggs) surviving to 65 % of development, excluding broods that had been cannibalised by the male and eggs that were underdeveloped. We assumed that all eggs reaching 65 % of development survived until hatching. From the photographs taken of hatched larvae, we measured the standard body length and yolk sac size (yolk sac area) of ten randomly selected larvae using the ImageJ measuring tool. These measurements were then used to calculate the average body length and yolk sac size for the larvae in each brood.

2.7. Sample sizes and statistical analysis

In this study, we had a total of 160 replicates (each replicate consisting of one male and two female gobies) divided between the three treatments, with 67 replicates in control, 28 in intermittent noise, and 65 in continuous noise. Before starting each trial, the total body length of the fish was measured to the nearest mm (males $n = 160$, L_T [mean \pm SD] 40.5 ± 3.8 mm; females $n = 320$, L_T [mean \pm SD] 40.9 ± 4.2 mm). The number of replicates where females successfully spawned and males received eggs was 66 (control $n = 33$, intermittent $n = 17$, and continuous $n = 16$).

All statistical analyses were performed in RStudio (version 2022.12.0). The effects of treatment on brood size (number of eggs), brood area, egg density, and egg developmental rate were investigated using generalised linear models (GLMs) developed with the *stats* package (version 3.6.2) in R. For each response variable, GLMs with

Gaussian, Gamma, and Poisson distributions were constructed, with noise treatment serving as the primary predictor. Additionally, the model for egg developmental rate incorporated average water temperature as a covariate. The suitability of these model distributions was determined using Akaike's information criterion (AIC). The *performance* package (version 0.10.3) was employed to validate model assumptions and performance, ensuring that the most parsimonious model conforming to the assumptions was chosen for subsequent analyses. Across all four response variables, Gaussian-distributed GLMs were identified as the best fit. The effects of noise treatment on hatching success and filial cannibalism were investigated using GLMs with a binomial distribution (model-based estimator, link function logit). Original brood size was included as a covariate for both models and average water temperature was included as a covariate for the hatching success model. Specifically, original brood size was included in both models as it has been shown to affect paternal investment and brood success in gobies (e.g., Karino and Arai, 2006). Average water temperature was included as a covariate for the hatching success model because it has been shown to influence this trait in gobies (e.g., Fonds and Van Buurt, 1974; Lopes et al., 2020), while no such effect is expected for filial cannibalism (e.g., Vallon et al., 2016). All GLMs were analysed with Wald's chi-squared tests. Significant predictor effects identified were further explored using Sidak pairwise comparisons, facilitated by the *emmeans* package (version 1.8.6). The model estimated trend between average water temperature and the response variables was also examined using the *emmeans* package.

We analysed the effects of noise treatment on egg size, length of the newly hatched larvae, and yolk sac size using linear mixed-effects models (LMMs) with the *lme4* package (version 1.1). This was because there were multiple measurements for each of these response variables for each brood and thus, we needed to include random effects to account for this nested structure. Specifically, the egg size model had noise treatment as a fixed factor. The larvae length model had noise treatment, yolk sac size, and temperature as fixed factors. The model for yolk sac size had noise treatment, larvae length, their interaction, and temperature as fixed factors. All models had brood ID as a random factor because of the nested structure of the experiment, whereby multiple eggs and larvae were measured from the same brood. All significant fixed factor effects were followed by pairwise comparisons with Tukey's adjustment using the *emmeans* package. The performance of all models was assessed where model fit, linearity, homogeneity of variance, normality of residuals, and normality of random factors were checked.

3. Results

3.1. Brood size, brood area, and egg density decreased with noise treatment

Among the males that received eggs, there was a significant effect of treatment on the number of eggs laid per brood (i.e., brood size; GLM, estimated means and 95 % confidence intervals [CI]: control 2234.5, CI = 1914.8–2554.3, $n = 33$; intermittent 2043.2, CI = 1251.4–2834.9, $n = 28$; continuous 1512.0, CI = 632.6–2391.4, $n = 16$; Wald $\chi^2 = 6.44$, $df = 2$, $p = 0.040$). Broods in the continuous noise treatment contained significantly fewer eggs compared to broods in the control, a difference of 723 eggs fewer on average (SE = 298.00, $p = 0.040$). There was no significant difference between the mean number of eggs in the continuous and intermittent treatments ($p = 0.208$) or the control and intermittent treatments ($p = 0.814$) (Fig. 1A).

Brood area was also significantly affected by noise treatment (GLM, control 13.9, CI = 12.1–15.7, $n = 33$; intermittent 12.5, CI = 8.1–167.0, $n = 28$; continuous 10.0, CI = 5.1–14.9, $n = 16$, Wald $\chi^2 = 6.17$, $df = 2$, $p = 0.046$). Broods in the continuous noise treatment covered a significantly smaller area compared to broods in the control treatment, with an average difference of 4.0 cm² (SE = 1.60, $p = 0.045$), but not compared to broods in the intermittent noise treatment ($p = 0.322$). There was also no significant difference of brood area between the control and the intermittent noise treatment ($p = 0.664$) (Fig. 1B).

Egg density was significantly affected by treatment (GLM, control 155.8, CI = 147.9–163.7, $n = 33$; intermittent 163.1, 143.5–182.7, $n = 28$; continuous 142.9, CI = 121.2–164.7, $n = 16$, Wald $\chi^2 = 7.68$, $df = 2$, $p = 0.022$). The egg density of broods in the continuous noise treatment was significantly lower compared to the intermittent noise treatment, by 20.1 eggs per cm² on average (SE = 7.27, $p = 0.021$), but not compared to the control ($p = 0.202$). There was no significant difference in egg density between the intermittent noise treatment and the control ($p = 0.537$; Fig. 1C).

3.2. Egg size was not affected by treatment

There was no significant difference in mean egg size across the control, intermittent, and continuous noise treatments (LMM, $F_{2,17} = 0.37$, $p = 0.696$).

3.3. Developmental rate was affected by temperature but not by treatment

Temperature influenced developmental rate significantly (GLM, Wald $\chi^2 = 10.19$, $df = 1$, $p = 0.001$), although there was no significant

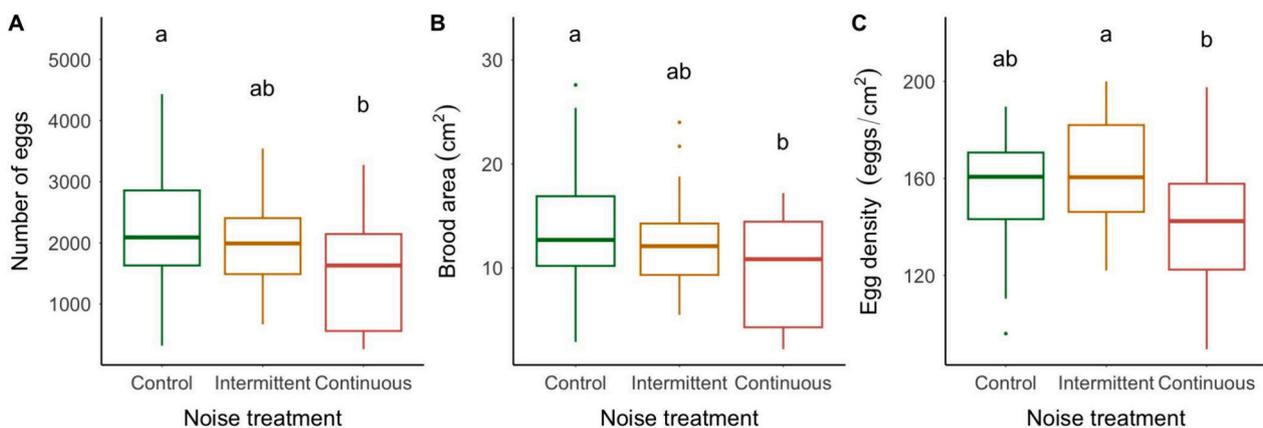


Fig. 1. Effects of anthropogenic noise on reproductive outcomes in common gobies from the control, intermittent noise, and continuous noise treatments. A) The number of eggs per brood, B) brood size based on the area covered with eggs (cm²), and C) egg density (eggs per cm²). Only replicates where spawning occurred are included. Boxplots show the 25th, 50th (median), and 75th percentiles. Whiskers show the range of the data, with outliers being represented by filled circles. Treatments without lowercase letters in common are significantly different. $\alpha = 0.05$.

effect of treatment (GLM, Wald $\chi^2 = 0.72$, $df = 1$, $p = 0.698$). The model estimate for the trend of the effect of temperature on developmental rate was -1.48 ($df = 21$, $CI = -2.44$ to -0.52), which means for every one-degree increase in average water temperature, the total time a brood takes to hatch will decrease by approximately 1.48 days.

3.4. Hatching success and filial cannibalism were unaffected by the noise treatments

Hatching success was unaffected by treatment (GLM; Wald $\chi^2 = 0.47$, $df = 2$, $p = 0.789$), original brood size (GLM; Wald $\chi^2 = 0.01$, $df = 1$, $p = 0.916$), and temperature (GLM; Wald $\chi^2 = 0.80$, $df = 1$, $p = 0.372$). Similarly, noise treatment had no significant effect on full brood cannibalism (GLM, Wald $\chi^2 = 1.04$, $df = 2$, $p = 0.594$). However, the original brood size did have a significant effect on the likelihood of full brood cannibalism (GLM; Wald $\chi^2 = 9.61$, $df = 1$, $p = 0.002$), where for each additional egg in the brood, the odds of full brood cannibalism decrease by a factor of 0.9988, holding other variables constant (log-odds effect size = -0.001 , $SE < 0.001$; Fig. 2). Put in the context of thousands of eggs, a brood containing 2000 eggs is 2.7 times more likely to be fully cannibalised than a brood containing 3000 eggs.

3.5. Continuous noise affected yolk sac size but not body length of the larvae

The size of the yolk sac was significantly affected by noise treatment (LMM; $F_{2,13} = 13.01$, $p < 0.001$). Pairwise comparisons showed that, on average, larvae reared in the continuous noise treatment hatched with yolk sacs 0.03 mm^2 smaller than those of control larvae ($SE = 0.01$, $df = 13$, $p = 0.001$), and 0.02 mm^2 smaller than those of intermittent noise-reared larvae ($SE = 0.01$, $df = 13$, $p = 0.006$; Fig. 3). On average, larvae reared in the continuous noise treatment and intermittent noise treatment did not differ significantly ($SE = 0.01$, $df = 12$, $p = 0.345$; Fig. 3). The body length of the larvae at hatching was not significantly affected by treatment (LMM; $F_{2,13} = 2.53$, $p = 0.117$), yolk sac size (LMM; $F_{1,178} = 0.15$, $p = 0.701$), or temperature (LMM; $F_{1,12} = 0.37$, $p = 0.554$).

4. Discussion

In this study, we investigated how different broadband noise regimes affected egg and larval development, as well as the paternal care of the common goby, a prevalent fish species in coastal waters in Europe. The results demonstrate that when spawning females and developing

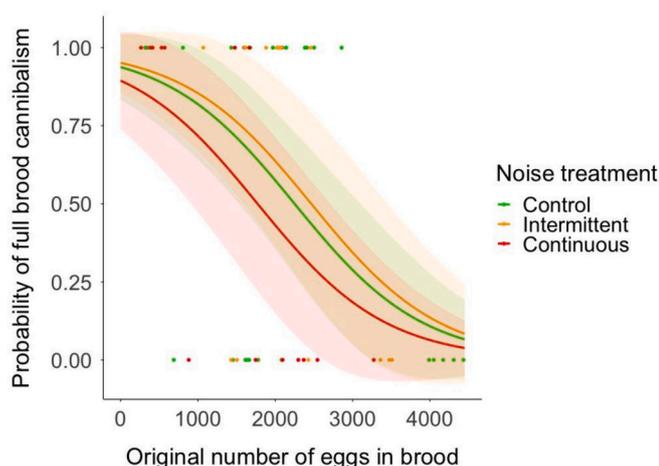


Fig. 2. The influence of the original number of eggs in a brood on the predicted probability of full brood cannibalism. There was no significant difference between noise exposure treatments: control (green), intermittent noise (yellow), and continuous noise (red).

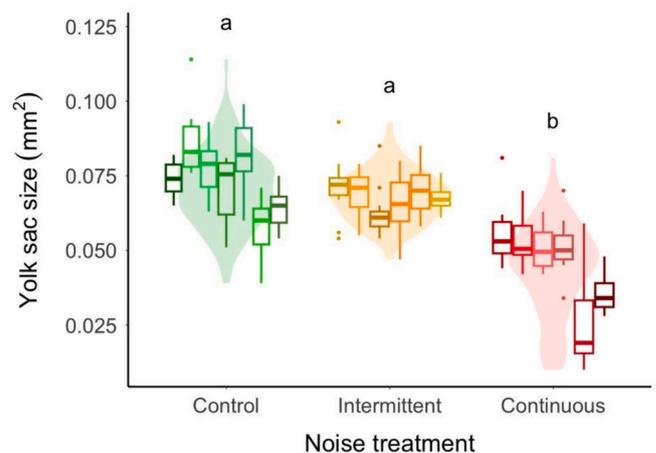


Fig. 3. The yolk sac size at hatching of larvae exposed to the control (green; $n = 7$), intermittent (yellow; $n = 6$), and continuous noise treatments (red; $n = 6$). The boxplots show the 25th, 50th (median), and 75th percentiles of the yolk sac sizes of fry within a single brood. The violin plots show the treatment-level distribution of yolk sac sizes. Treatments without lowercase letters in common are significantly different. $\alpha = 0.05$.

embryos were exposed to continuous noise, brood area, brood size, and yolk sac size decreased, whereas hatching success of the broods, larval size, and filial cannibalism by the nest-holding male were unaffected. Blom et al. (2019) showed that common goby females are reluctant to spawn and even refuse to do so in continuous noise, whereas male behaviours such as nest building and courtship were unaffected. Taken together, these results reveal that anthropogenic noise can have severe detrimental effects on common goby larvae recruitment.

4.1. Embryo development

Developmental rate did not differ between treatments, and hence broods did not hatch earlier or later in the control treatment. Small larvae can suffer from high mortality rates since it might be harder for them to capture food and avoid predators (Miller et al., 1988; Nedelec et al., 2015). All larvae measured in this study fall within the normal size range (2–3 mm) for common goby larvae (Fonds, 1970; Fonds and Van Buurt, 1974), and the body length of the larvae did not differ between treatment groups. Effects of noise on larval growth and survival in fish have been studied to a limited extent, and the effects seem to vary depending on species and noise source. For example, intermittent noise reduced growth in cod larvae (Nedelec et al., 2015), while chronic boat noise exposure did not affect the growth or survival of *Neolamprologus pulcher* cichlid fry (Bruinjtjes and Radford, 2014) but did reduce growth in Lusitanian toadfish at larval stages (Faria et al., 2022). A recent study also showed that larval fish of four investigated estuarine species potentially habituate to anthropogenic noise in less than ten minutes (Waddell and Širović, 2023). Furthermore, a caring parent may affect the developing young. For example, a single three-hour exposure to excess noise altered female mouth brooding behaviour of the African cichlid *A. burtoni*, and impaired larval condition and survival (Butler and Maruska, 2021). On the other hand, intermittent noise did not affect growth in spiny chromis larvae, although brooding male behaviour was affected and complete brood mortality increased (Nedelec et al., 2017).

Although there was no difference in larvae body size, we found that in the continuous noise treatment newly hatched larvae had smaller yolk sacs than in the other treatments. Continued noise exposure has previously been found to increase yolk sac consumption in larvae of damselfishes (*Amphiprion melanopus* and *A. polyacanthus*; Fakan and McCormick, 2019), zebrafish (*Danio rerio*; Lara and Vasconcelos, 2021) and Atlantic cod (*Gadus morrhua*; Nedelec et al., 2015), but not in Lusitanian toadfish (*Halobatrachus didactylus*; Faria et al., 2022). Noise

has also been shown to cause elevated heart rates in fish embryos (Fakan and McCormick, 2019; Jain-Schlaepfer et al., 2018), which is often a correlate of metabolic rate (Green, 2011), and may therefore be the mechanism behind the reduced yolk sac size seen in the present study. During the yolk sac stage, the mouth and gut become functional, allowing the switch from endogenous nutrition to exogenous feeding. This is the most crucial stage in development, often with substantial mortalities (Blaxter, 1988; Rønnestad et al., 2013). We do not know when common gobies absorb the yolk sac and start to feed exogenously. The sand goby *Pomatoschistus minutus* (own data) and the grass goby *Zosterisessor ophiocephalus* (Privileggi et al., 1997) start to feed a few days after hatching, despite hatching with their mouths open (Fonds, 1970; Privileggi et al., 1997). With a faster absorption of yolk sacs, larvae exposed to noise could use up their energy reserve before being able to gain energy from an external source. If surviving that transition, they would be more dependent on their success to catch their first prey than larvae from the other treatments. Larvae that are successful in catching prey may be able to compensate for a small energy reserve at hatching. However, studies indicate that larvae exhibit elevated stress responses and abnormal development, if noise exposure continues over time (de Soto et al., 2013; Nedelec et al., 2014, 2015). Therefore, it is likely that larvae reared in continuous noise will have a reduced chance to survive.

4.2. Parental effects

In the present study, the males tending eggs, as well as the spawning females, were subjected to noise. Thus, the effects on embryos could be caused by male parental care, female spawning decisions, and/or maternal effects.

Research has demonstrated a negative correlation between brood size and the likelihood of full brood cannibalism (Kvarnemo et al., 1998). In light of this, our analysis controlled for brood size to discern whether noise exposure had a direct or indirect (via changes in brood size) effect on paternal care. Our results indicate that brood size did indeed negatively correlate with the likelihood of full brood cannibalism. However, noise exposure neither directly nor indirectly influenced the likelihood of full brood cannibalism, suggesting that paternal care remained consistent regardless of noise exposure, and independent of any changes in brood size.

Females in the continuous noise treatment laid fewer eggs in total than those in the control and the intermittent noise treatments. This reduction in egg production is likely due to females being reluctant to spawn in the presence of continuous noise (Blom et al., 2019), resulting in either fewer females contributing eggs to each nest, individual females laying fewer eggs, or a combination of both. The hesitancy of female gobies to spawn in the presence of continuous noise may be a result of stress caused by the noise. In this regard, other stressors, such as the threat of predators, have been shown to impede the spawning of black gobies (Magnhagen, 1990). Continuous noise may also obscure the male gobies' courtship signals, thereby compromising the females' capacity to evaluate their suitability (Blom et al., 2022). In contrast, the lack of an impact of intermittent noise on spawning suggests that the periods of silence provided crucial opportunities for females to hear male courtship sounds and appraise male quality, which allowed for normal spawning behaviour.

There are thus alternative explanations for the treatment differences in yolk sac sizes seen in newly hatched larvae, other than increased yolk consumption. For instance, the females in the continuous noise treatment that were willing to spawn, despite these adverse conditions, may have included individuals with over-ripe or poor-quality eggs. In addition to maternal effects, noise exposure may have indirectly affected yolk sac size by altering the behaviour of the caring male. For example, by disrupting vital behaviours such as fanning and cleaning. This could, in turn, affect the developing embryos, through altering the oxygen levels or the build-up of waste products in the nest. However, by this

reasoning, we would also expect to see an effect on hatching success, which was not observed in this study, making this explanation less likely.

5. Conclusions

Our results show that exposure to noise during breeding can have detrimental effects on the early-life development of common gobies. During the daytime in European summer, common gobies are often exposed to continuous noise, as their reproduction coincides in time and space with the prime season for recreational boating and water sports. This might be especially true for the Nordic countries, since daylight persists for ~80 % of the day, resulting in more hours of recreational boating per day. However, we do not know whether the cessation of these activities during the short summer nights offers the essential respite we see in the intermittent noise treatment. The effect on mating success shown in previous studies (Amorim et al., 2022; Blom et al., 2019; de Jong et al., 2018), combined with the effect seen on developing larvae, show that anthropogenic noise may substantially decrease reproductive success in common gobies. To fully understand the impacts of noise exposure and inform mitigation measures, more work is needed to examine the mechanisms behind the responses observed in this study. Nevertheless, our findings clearly demonstrate that exposure to anthropogenic noise can have dire consequences for the early-life development of fish, with wide-ranging implications for aquatic wild-life subjected to anthropogenic noise.

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CRediT authorship contribution statement

Eva-Lotta Blom: Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Isabelle K. Dekhla:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Michael G. Bertram:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis. **Jack L. Manera:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation. **Charlotta Kvarnemo:** Writing – review & editing, Writing – original draft, Resources. **Ola Svensson:** Writing – review & editing, Writing – original draft, Visualization, Resources, Formal analysis, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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