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Dying for a canape: the welfare implications associated with both traditional and "ethical" production of caviar from sturgeon

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The farming of sturgeon to produce caviar is increasing globally, even though little is known about the welfare implications of aquaculture for these unique, long-living, and large animals. The use of non-lethal methods for egg harvesting is increasing, as these methods are thought to offer a more ethical alternative to traditional methods where the female is killed. However, these "non-lethal" methods raise significant welfare concerns including routine handling, surgical procedures, and painful procedures, and could potentially perpetuate suffering. Consequently, there is an urgent need for significant exploration and research into this field. This review presents and discusses some of the welfare concerns associated with producing caviar from sturgeon, including the traditional and non-lethal methods of egg harvesting and the concerns associated with rearing them in aquaculture systems. It concludes in stating that the welfare issues involved with non-lethal caviar production are too sizeable to warrant its description as an "ethical or humane" alternative to traditional caviar production.

KEYWORDS
sturgeon (acipenseridae), caviar, ethical caviar, aquaculture, fish, no-kill caviar

1 Introduction

The demand for caviar is increasing, partly because of the rise in farmed caviar, which offers consumers a more affordable alternative to wild caviar, and the expansion in luxury consumers (Sicuro, 2019). Despite this, aquaculture practices involved in caviar production have received relatively little scrutiny from a welfare perspective. Although there have been some efforts to explore the welfare of farmed sturgeon (e.g., Williot et al., 2018), much of the focus has been on developing a sustainable alternative to harvesting endangered sturgeon from the wild and breeding individuals for repopulation programmes (Cámara-Ruiz et al., 2019; Sicuro, 2019; Raposo et al., 2023; White et al., 2023). As a result, the welfare of caviar-producing sturgeon in aquaculture varies considerably, especially with the development of the so-called ethical caviar production. This review tackles some of the most important welfare issues pertaining to caviar-producing sturgeon, including both the traditional method of producing caviar, in which fish are killed during egg removal, and the recent development of "ethical caviar," which involves routine egg removal without slaughter.

2 Scope of caviar production

Wild populations of sturgeon have declined as a result of both legal and illegal overfishing and significant habitat fragmentation and loss (Scarnecchia et al., 2014; Stokesbury et al., 2014; Wu et al., 2019; Tavakoli et al., 2021). As a result, all 27 species of sturgeon are listed in the appendices of the CITES treaty, significantly restricting the fishing of wild individuals due to their worsening conservation status (CITES, 2002). Despite this, the demand for caviar, and to a lesser extent meat from sturgeon species, has continued to grow (Raposo et al., 2023). Prior to 1997, when CITES protected all sturgeon species, nearly all caviar was sourced from wild-caught sturgeon, primarily from sturgeon in the Caspian Sea (Tavakoli et al., 2021). Since the CITES restrictions came into force, aquaculture production of sturgeon rapidly developed to fulfil the demand and develop new income avenues (Bronzi et al., 2019; Tavakoli et al., 2021). Today, nearly all caviar comes from aquaculture (Tavakoli et al., 2021).

Approximately 17 different sturgeon species are recognised for caviar production, and a further four hybrids and two Polyodontidae species are also used (Bronzi and Rosenthal, 2014). China is the number 1 exporter of caviar, followed by the USA, Italy, France, and Germany (Raposo et al., 2023). Global production is estimated at approximately 700 tons of caviar per year (Degani and Yom Din, 2022). Many countries now producing caviar had no prior involvement in the industry (Tavakoli et al., 2021). This has led to both a diversification of the quality of products and varying regulations and standards regarding welfare and best practices (Bronzi et al., 2019; Tavakoli et al., 2021).

The systems used for caviar production in aquaculture vary depending on the life stage of the fish, the farm, and its geographical location. For instance, running water ponds and cage farming are commonly used for sturgeon farming in China, with recirculating aquaculture systems (RAS) increasing in recent years (Yang et al., 2018). Elsewhere, ponds, cages, and RAS may all be used for sturgeon farming, with separate facilities or holdings corresponding with the different life stages (Chebanov and Galich, 2013).

3 Welfare implications of caviar production in aquaculture

Sturgeon are slow to mature, and young sturgeon can take 7–10 years to produce eggs (Raposo et al., 2023). During this time, the rearing environment, husbandry practices, and procedures can all impact their welfare (see *Section 3.2*). Once females reach sexual maturity and produce eggs, they are either killed or have their eggs harvested using a variety of non-lethal techniques, all of which can introduce significant welfare concerns.

3.1 Egg harvesting

3.1.1.Traditional methods

Traditionally, sturgeon are typically killed before egg harvesting, which means that only the method of killing is relevant from a welfare perspective. From an industry and consumer perspective, traditional methods are often preferred, as they are considered to produce a higher quality product, as no artificial hormone stimulation is required (Chebanov and Galich, 2013). However, from a sustainability perspective, traditional harvesting is wasteful, as it can take up to a decade to reach the harvesting stage, and the fish can produce more than one harvest (Stephen, 2022). From a welfare perspective, there are also significant concerns regarding the typical stunning and killing methods used for sturgeon (Williot et al., 2018; Clemente et al., 2023).

Percussive stunning and electronarcosis are recommended by the World Organisation for Animal Health (WOAH) and the European Food Security Association (EFSA) as humane methods for stunning sturgeon (EFSA, 2004; WOAH, 2023). Consequently, these methods are commonly used on farms, as are ice slurries, for stunning and killing sturgeon (Williot et al., 2018). However, there is considerable variation between farms regarding how the methods are performed. For example, differences in the type of instrument used for percussive stunning, whether or not the fish is removed from the water, and the operator's skills can all significantly impact the fish's experience and the efficiency of the process (Clemente et al., 2023).

Furthermore, although sturgeon are very different in behaviour and size from other farmed fish species, there has been little species-specific scientific research into slaughter methods (Williot et al., 2018). Consequently, there are no validated indicators for monitoring unconsciousness in sturgeon (Clemente et al., 2023). As a result, a lack of shared best practices, variation between farms in methodologies, and a lack of reliable indicators of unconsciousness may mean that individual sturgeon are subjected to prolonged and inhumane deaths. Further research is therefore needed to establish validated methods and indicators for the humane slaughter of these animals.

3.1.2 Non-lethal methods

In response to the concerns over sustainability and ethics, there has been a rise in efforts to use non-lethal methods of egg harvesting so that the same fish can be used to produce multiple batches of eggs (Stephen, 2022).

Non-lethal methods vary in the degree of invasiveness, from caesarean sections performed under general anaesthesia through to non-surgical methods where the fish is massaged. Non-lethal methods are typically used in combination with hormone therapy to induce labour artificially so that the female releases the eggs before being stripped (Tavakoli et al., 2021; Raposo et al., 2023). This produces "ovulated caviar," which is where the eggs ripen and form a shell (chorion), which swells and hardens when exposed to water, in order to protect the embryo inside (Chapman and Van Eenennaam, 2016). Such caviar has to be labelled as "ovulated caviar," as the eggs have to undergo artificial treatment to prevent the swelling and water-hardening process (Bronzi and Rosenthal, 2014; Chapman and Van Eenennaam, 2016). Traditionally harvested caviar, on the other hand, is harvested before it is released from the follicular layer, retaining its egg membrane, which is responsible for the characteristic texture, dissolvability, and aesthetic of traditional caviar (Chapman and Van Eenennaam, 2016). Caviar produced using non-lethal methods may also be marketed as "no-kill caviar," intended to promote a more sustainable and ethical product (Stephen, 2022). However, there are significant welfare concerns associated with non-lethal methods of caviar harvesting, which have been largely neglected by the scientific literature, and mortalities are an inherent risk (Bani and Banan, 2010; Tavakoli et al., 2021).

3.1.2.1 Caesarean section

Caesareans are the most invasive of the non-lethal methods of caviar harvesting and require the fish to be placed under general anaesthetic. The method is typically used for very large individuals, as other less labour-intensive and invasive methods are preferred for smaller fish (Chebanov and Galich, 2013). The procedure involves an open laparotomy, which is an incision of between 8 cm and 14 cm long into the abdomen so that the ovulated eggs can then be extracted. The fish is then sewn up using silk or kapron-coated thread and monitored for a few weeks (Chebanov and Galich, 2013).

In addition to handling (see *Section 3.1.3.2*), sturgeon undergoing caesareans experience other welfare issues from the procedure and the general anaesthetic. Anaesthetics are widely used on fish to avoid stress during certain procedures, and some studies suggest they can successfully reduce the stress caused by confinement and handling (Zahl et al., 2012). However, there are also indications that the anaesthetic itself may also induce a stress response in fish (Zahl et al., 2012). For example, in Siberian sturgeon, the anaesthetics MS-222 and clove oil induced a stress response, with significant responses to mS-22 at concentrations of 140 mg/L and 160 mg/L (Feng et al., 2011). Similarly, concentrations of 180 mg/L and above for clove oil were also found to induce significant differences in blood biochemical parameters indicating a stress response. However, clove oil was considered to have better results overall, providing optimum concentrations of between 60 mg/L and 90 mg/L were used (Feng et al., 2011).

Suturing sturgeons can be difficult and even professionals invariably pull through the musculature (Mims et al., 2004). In addition, muscular stress on the incision can result in the sutures rupturing (Aramli et al., 2014). As a result, mortality rates have been reported to be higher than 75% in paddlefish (Mims et al., 2004) but as low as 10% for beluga sturgeons and 15% for Russian sturgeons (Chebanov and Galich, 2013). Mortality rates often depend on the aftercare, the operator's skills, and the fish's condition.

3.1.2.2 Key-hole surgery

A common non-lethal method for harvesting the eggs is key-hole surgery. Key-hole surgery may be performed whilst the fish is conscious, which means that it is less labour-intensive and, therefore, more popular than a caesarean section (Chebanov and Galich, 2013). Key-hole surgery has been widely used since 1986 and reportedly has low mortality rates (Podushka, 1999; Parandavar et al., 2006; Chebanov and Galich, 2013, 1986).

To perform the procedure, a scalpel is used to open the female's abdominal cavity, creating a small incision, ranging from anywhere between 1 cm and 8cm, depending on the size of the fish (Parandavar et al., 2006; Bani and Banan, 2010; Chebanov and Galich, 2013). The eggs are then manually stripped through this incision by massaging the abdomen whilst the incision is kept open (Chebanov and Galich, 2013). The stripping process may then be repeated once or twice until all the eggs are removed. The female may be conscious during this process, as general guidance only suggests sedating the larger females for ease (Chebanov and Galich, 2013).

According to the "Sturgeon Hatchery Manual," suturing of small 1–2cm incisions is unnecessary, as there is no increase in mortality risk, even when the kidney or blood vessels of the rectum are damaged in the process (Chebanov and Galich, 2013). Although this manual is over 10 years old, the approach is still widely applied (Leavitt, 2022) and does not account for the fact that these sentient beings can feel pain and suffer during and after the procedure (Lambert et al., 2022). Larger incisions are usually sutured, which is considered the most challenging part of the process due to dermal denticles in the sturgeon's skin (Chebanov and Galich, 2013).

Key-hole surgery is considered to be an efficient egg-harvesting method, taking, on average, between 5 min and 17 min per fish, depending on the size of the female (Bani and Banan, 2010). This is equal to or shorter than the time needed for traditional harvesting and is faster than the caesarean method, which typically takes 30 min per fish, plus suturing time (Mims et al., 2004; Bani and Banan, 2010).

Overall, key-hole surgery is considered low risk, as it poses a low risk of serious infection due to the small size of the wound, and the risk of mortality from handling stress is also minimised due to the shorter handling period (Mims et al., 2004; Bani and Banan, 2010). However, there are still risks involved, particularly following the procedure. For instance, mortalities can result when the fish fail to feed following the procedure or are exposed to poor conditions (Parandavar et al., 2006; Bani and Banan, 2010).

There has been little to no investigation into the welfare impacts of this procedure, especially when anaesthesia is not used. The fact that poor feeding behaviour is commonly seen is a particular concern (Parandavar et al., 2006), as it may indicate long-term pain and distress in the fish. As far as we are aware, there is no mention of pain relief in the literature when discussing these procedures, and so although the procedure may not be fatal, it may still inflict suffering, pain, and distress on the fish involved, and this may be long-lasting as the incision heals.

3.1.2.3 Non-surgical methods

Non-surgical methods may also be used to harvest eggs from sturgeon. These involve massaging the fish's abdomen to remove the eggs without incisions. However, this method is considered less efficient and more labour-intensive than key-hole surgery and is considered to result in a poorer quality of eggs (Chebanov and Galich, 2013; Leavitt, 2022).

From a consumer perspective, a non-surgical method could be considered the most humane and sustainable option. The potential from a marketing perspective is therefore surmountable. However, little attention has been given to the welfare implications of this method in the scientific literature, so further investigation is needed.

Stripping eggs in other fish species is known to be a significant stressor, not only because they must be handled, usually out of the water (see *Section 3.1.3.2*), but the process itself can cause skin injury and considerable stress (Conte, 2004; Broom, 2007). Stripping the female of her eggs in this way requires considerable manipulation, and research is required to explore both the short and long-term effects on welfare.

3.1.3 Overarching welfare issues associated with egg harvesting

3.1.3.1 Fasting

Prior to both traditional and non-lethal egg harvesting methods, farmed sturgeon are typically fasted to empty their guts. Research indicates that long-term fasting significantly increases oxidative stress, weakens immunity, and increases mortality risk in sturgeon (Feng et al., 2011). However, short-term fasting of <2 days may be less problematic (Cai et al., 2017). In particular, juvenile sterlet sturgeon (*Acipenser ruthenus*, Linnaeus 1758) only show significant effects on their swimming efficiency when fasted for over 2 days (Cai et al., 2017). Furthermore, starvation appears to suppress cortisol stress responses in juvenile great sturgeon (*Huso huso*) when they are captured and handled (Poursaeid and Falahatkar, 2022). However, despite the handful of studies in this area, much more needs to be done to account for the different species of sturgeon farmed for caviar and explore the effects on mature individuals in terms of physiological, metabolic, and mental indications of welfare.

3.1.3.2 Capture and handling

Sexually mature sturgeon are large fish, so for ease, many farmers will seek to anaesthetise individuals before egg harvesting to immobilise or sedate them (Williot et al., 2018). As already discussed, anaesthesia may be aversive to the fish, representing a welfare concern (Williot et al., 2018). However, without it, the experience of being kept out of the water and handled by humans is a significant welfare concern for fish, resulting in considerable distress and potentially also pain and injury (Conte, 2004; Broom, 2007; Simide et al., 2018; Williot et al., 2018).

Although studies have found that sturgeons appear to be more resistant to handling stress, compared with most teleost species, they still show elevated levels of stress following handling, which can negatively affect their mental and physical welfare (Falahatkar et al., 2009; Falahatkar and Poursaeid, 2013). For instance, great sturgeon show elevated plasma cortisol levels following handling, with peak levels recorded at 6 h after handling and significant increases in plasma glucose levels recorded at 3 h after handling (Falahatkar and Poursaeid, 2013). However, further exploration is needed, as cortisol levels can vary depending on the time of day, the technique used, how long the fish is handled, and being dependent on exposure to other stressors (Simide et al., 2016). For example, cortisol levels appear to vary in sturgeon who have been kept at different densities, with those kept at high densities showing greater stress responses when handled compared with those kept at lower densities (Falahatkar et al., 2009).

Catch and release studies of wild white sturgeon (*Acipenser transmontanus* Richardson, 1836) also show that capture stress can significantly impact the fish (McLean et al., 2019). In particular, one study found that individuals showed reduced activity following their release, and tagged sturgeon were found to gravitate towards the shore (McLean et al., 2019). These behaviours were considered indicative of a potential refuge-seeking behavioural strategy for recovery.

3.2 Rearing sturgeon for caviar

Despite sturgeon being around since the dinosaurs, we still know surprisingly little about them, an issue that has become more pressing since their increasing popularity in aquaculture. Sturgeon fish are unique in that they grow far larger and live much longer than other species typically seen in aquaculture production (Chebanov and Galich, 2013; Clemente et al., 2023). Consequently, they are exposed to particular welfare issues and pressures when reared in aquaculture systems.

Sturgeon can take 6–10 years to reach sexual maturity and produce eggs. During this long rearing period, they are susceptible to many factors that can improve or worsen their welfare. The main, overarching concerns of aquaculture production and the impacts on sturgeon are summarised below.

3.2.1 Water quality parameters

As with all farmed fish species, water quality and associated parameters, such as levels of dissolved oxygen and temperature, are critical in ensuring the wellbeing of farmed sturgeon. Maintaining stable and optimum conditions is paramount for sturgeons, as variations can significantly impact their welfare.

3.2.1.1 Dissolved oxygen

Sturgeons have relatively high requirements for oxygen content in water (Nikolova and Bonev, 2020) and have a limited capacity to adapt to hypoxia, particularly when young (Sullivan et al., 2003). For instance, in one study where shortnose sturgeon (*Acipenser brevirostrum*) were exposed to 2.5mg/L dissolved oxygen for 6 h, 100% of the 25-day-old, 96% of the 32-day-old, and 85% of 64-day-old individual fish died, compared with only 12% of the 104- and 310-day-old fish (Jenkins et al., 1993). Similar results were found with juvenile Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*), as all individuals died when they were kept in water with only 3 mg/L of dissolved oxygen (Secor and Gunderson, 1998).

There are also notable species differences in oxygen requirements (Baker et al., 2005). For instance, the Siberian sturgeon (*Acipenser baerii*) reportedly has a higher tolerance for hypoxic conditions than other species (Secor and Niklitschek, 2002). In particular, studies have shown that they prefer dissolved oxygen levels of between 5.9 mg/L and 13.2 mg/L (Khakimullin, 1987), compared with white sturgeon, who have been caught in areas with dissolved oxygen levels of between 8 mg/L and 16 mg/L (Lepla and Chandler, 1995).

Dissolved oxygen levels vary in natural water bodies, with different areas fluctuating more than others (Sullivan et al., 2003). Sturgeons have certain adaptations to hypoxic conditions. For example, wild white sturgeon show deliberate behavioural changes in response to low levels of dissolved oxygen (6 mg/L), moving laterally onto elevated ledges where levels exceed 6 mg/L of dissolved oxygen (Lepla and Chandler, 1995). Individuals can also reduce their dissolved oxygen consumption by reducing their activity levels. However, this is only a short-term measure, as doing so over a long period would increase the risk of starvation and impact fecundity (Sullivan et al., 2003). However, in aquaculture systems, sturgeon are prevented from being able to move to areas with higher levels of dissolved oxygen. This means that the effects of hypoxic conditions can result in considerable welfare issues.

Low levels of dissolved oxygen can lead to respiratory distress for sturgeon and potentially suffocation, as they struggle to extract enough oxygen from the water (Nonnotte et al., 2018c). This is particularly stressful for fish, and Amur sturgeon (*Acipenser schrenckii*) exposed to hypoxic conditions show significant increases in serum cortisol levels (Ni et al., 2014). Similar findings have been found with other species of sturgeon, including Siberian sturgeon, which show rapid increases in serum cortisol levels 1 h into a hypoxic challenge before peaking at 3 h and then beginning to decline at 6 h (Wang et al., 2021).

Hypoxic conditions can also negatively impact immune responses in sturgeon by causing physiological changes in key parameters. For instance, in Amur sturgeon, hypoxia stress leads to a significantly decreased spleen-somatic index (SSI) and reduced spleen size (Ni et al., 2014). This may be indicative of an adaptive response in the fish in order to improve oxygen-carrying capacity in hypoxic conditions (Ni et al., 2014). However, as the spleen plays an important role in immune response regulation, reductions in the SSI may also indicate reduced immune function and response (Ni et al., 2014).

The negative effects of hypoxia on sturgeon also have production impacts. For instance, embryo hatching is negatively affected by low oxygen levels, as there is insufficient oxygen for the increased activity required for hatching (Delage et al., 2014). For instance, at oxygen saturation levels of 50% and 30%, embryos fail to hatch, and hatching only occurs at 90% oxygen saturation when the temperature is optimum (Delage et al., 2014). Growth rates can also be negatively impacted by as much as 20%–43% due to a lower feed consumption rate in hypoxic conditions (Cech and Crocker, 2002; Secor and Niklitschek, 2002; Nonnotte et al., 2018c).

3.2.1.2 Temperature

Temperature requirements vary according to the sturgeon's age, life stage, body condition, and the time of year, as sturgeon are naturally often exposed to lower temperatures over winter (Chebanov and Galich, 2013). Water temperature can influence the time taken for sturgeon to mature and produce eggs and, critically, can also impact their physical welfare (Máté et al., 2018). For instance, water that is too warm can result in lowered immunity and higher mortality rates in sturgeon (Mai et al., 2014; Wang et al., 2023). Furthermore, Siberian sturgeon lose the ability to stay upright (loss of equilibrium) in temperatures of 33°C and show metabolic changes indicative of stress (Wang et al., 2023). Sturgeon growth rate is also significantly affected by temperature, with optimum growth occurring at 20°C and decreased growth seen at lower and higher temperatures (15°C–19°C and 21°C–25°C) (Máté et al., 2018).

Temperature also interacts with levels of dissolved oxygen and can exacerbate and accelerate the negative effects of hypoxic conditions (Sullivan et al., 2003; Nikolova and Bonev, 2020). In particular, sturgeon's metabolic rate increases at increased temperatures, resulting in increased oxygen consumption (Nonnotte et al., 2018c). Therefore, if the dissolved oxygen levels are too low, the increased temperature will accelerate the onset of hypoxic stress (Nikolova and Bonev, 2020).

3.2.1.3 Toxins

The concentration of toxins such as ammonia, nitrite, and nitrates can also negatively impact the welfare of farmed sturgeon. Moreover, the effects can be exacerbated by crowdedness and confinement (Williot et al., 2018). In addition, systems that recirculate water (RAS) are increasing in popularity but pose the risk of giving rise to unhealthy levels of toxins that may have considerable welfare implications (Gisbert, 2018).

Ammonia toxicity in sturgeon can be lethal and, at sublethal levels, can cause hypertrophies and necrosis in the gill epithelium in Siberian sturgeon (Nonnotte et al., 2018a). Ammonia toxicity can also cause fish to lose equilibrium and perform erratic and irregular swimming patterns (Williot et al., 2018). Younger sturgeon are more sensitive to ammonia toxicity than adults, but all sturgeon are vulnerable, especially in crowded aquaculture systems where ammonia can quickly accumulate to toxic levels (Williot et al., 2018). Furthermore, sturgeon cannot control their ammonia uptake, which means that managing ammonia concentration is critical for their welfare and survival (Nonnotte et al., 2018b).

Similar to ammonia, both nitrite and nitrate toxicity can have significant welfare impacts on sturgeon (Williot et al., 2018). For instance, juvenile Siberian sturgeons show changes in behaviour, including increased breathing rate, erratic swimming, and a loss of equilibrium in response to nitrite toxicity (Gisbert, 2018). An accumulation of nitrites can also lead to multiple physiological effects in sturgeon, including liver damage, cardiovascular issues, ionic unbalance, and oxidation of haemoglobin, all of which can result in mortality (Gisbert, 2018).

Siberian sturgeon are particularly sensitive to nitrate toxicity compared with other species, which raises particular issues regarding their increasing use in aquaculture and the trend to recirculate water (Hamlin, 2006). Historically, nitrate levels have been managed by exchanging water, but the increase in RAS technology poses significant challenges in this regard (Hamlin, 2006). High levels of nitrates can cause anaemia in sturgeon, as immature red blood cells increase in number and mature blood cells decrease (Williot et al., 2018). Sturgeon also become more sensitive to nitrate as they age, and females show elevated levels of plasma glucocorticoids and plasma sex steroids in response to 30 days of exposure to 50 mg/L nitrates (Hamlin et al., 2008). This is concerning because 50 mg/L is considered an acceptable and average concentration in aquaculture (Hamlin et al., 2008). Too high levels of both nitrites and nitrates can also negatively impact the oxygen-carrying capacity of sturgeon, further exacerbating issues with poor levels of dissolved oxygen (Williot et al., 2018).

3.2.2 Population density

The density at which sturgeon are kept can positively or negatively affect other welfare concerns, including the water quality, disease prevalence, and their ability to behave normally. Furthermore, population densities also affect physiological wellbeing and development in sturgeon. For instance, high densities (12.68 kg m^2) were found to negatively affect the growth rate, stress, and immune responses in juvenile Chinese sturgeon (*Acipenser sinensis*), compared with low (4.80 kg m^2) and medium (8.99 kg m^2) densities (Long et al., 2019). Similar findings were found with juvenile hybrid sturgeon (♀*Acipenser baerii* × ♂*Acipenser schrenckii*) in RAS, where high densities (12 kg/m^2) were found to negatively impact growth performance and welfare indicators because of chronic stress (Bi et al., 2023). In addition, in Siberian sturgeon, high densities (40 kg/m^2) are thought to negatively impact reproductive development and increase the prevalence of infertility in females (Barulin, 2022).

The density at which sturgeon are reared in commercial farms is likely to vary depending on the life stage of the fish and the system used. In Chinese cage farms, densities are typically between 35 kg/m^2 and 40 kg/m^2, 50 kg/m^2 in RAS, and 25–30 kg/m^2 in running water ponds (Yang et al., 2018). All of these are above the threshold known to result in welfare concerns in a range of sturgeon species.

3.2.3 Diseases

Farmed sturgeon are susceptible to a range of health concerns and diseases, and the prevalence of these is often impacted by other variables, including population densities, diet, and water quality (Ciulli et al., 2016; Radosavljević et al., 2019). Furthermore, the stressful procedures of egg harvesting may also result in compromised immunity, increasing disease prevalence.

The sturgeon nucleocytoplasmic large DNA virus (NCLDV) is a common disease in farmed sturgeon (Mugetti et al., 2020) and is associated with a mortality rate of approximately 50% (Ciulli et al., 2016). NCLDV can cause symptoms of anorexia, lethargy, lighter skin colouration, ulcers and lesions on the dorsal fin, gill damage, pale organs, and marbled liver in sturgeon, causing considerable pain and distress to infected fish (Ciulli et al., 2016).

The pathogen *Streptococcus iniae* is also associated with high mortality rates in sturgeon. Mortality rates of infected fish range between 50% and 75% of cultured fish, causing significant economic losses across the aquaculture industry (Muhammad et al., 2020). *Streptococcus iniae* is also zoonotic and has been reported to cause several illnesses in humans, including meningitis (Lau et al., 2003). *Streptococcus iniae* is also resistant to important antibiotics, posing a significant threat to aquatic and human health (Muhammad et al., 2020).

Infection with *S. iniae* is not only often fatal, but sturgeon suffer from lethargy, erratic, and listless swimming behaviour, including sporadic whirling, skin lesions, haemorrhages on the base of fins, and petechial haemorrhages (Deng et al., 2017). Given the potential for *S. iniae* to cause widespread suffering to sturgeon in both captive and wild populations and the potential risk to human health and antibiotic resistance, addressing the causes of disease outbreaks is critical. As antibiotics are becoming less effective, strategies such as improving farming practices, including water quality and biosecurity measures, and lowering stocking densities to reduce stress and improve immune function in fish are widely recommended (Deng et al., 2017; Muhammad et al., 2020).

The white sturgeon iridovirus (WSIV) and the Acipenserid herpesvirus 2 (AciHV-2) are also significant pathogens for sturgeon that cause considerable suffering. Both are typically fatal, with mortality rates averaging approximately 95% in juvenile sturgeon (Radosavljević et al., 2019). Sturgeon infected with WSIV cease feeding, which then causes a deterioration in body condition. Infected fish also develop oedematous and pale gills, which can cause issues with oxygen uptake and a reddening along the ventral plates, which can lead to petechiae (Hofsoe-Oppermann et al., 2020).

Symptoms of AciHV-2 include extensive haemorrhagic ulceration of scutes and skin areas, changes in skin colouration, paleness in internal organs, signs of haemorrhagic inflammation in fingerlings, enlarged and altered swim bladder, fin necrosis, hyperaemia, and petechial haemorrhages on the skin (Doszpoly et al., 2017). The severity and presentation of the symptoms vary depending on age, but as with WSIV, mortality is highly likely (Doszpoly et al., 2017).

At the time of writing, none of the aforementioned diseases were regulated by the WOAH despite their significant impacts on sturgeon and the aquaculture industry. There is limited knowledge regarding epizootiology and disease control methods for sturgeon aquaculture, which poses considerable welfare concerns and risks the sustainability of the industry (Radosavljević et al., 2019).

Sturgeon are farmed alongside and in league with efforts to conserve wild populations of sturgeon. Although many of the pathogens affecting farmed sturgeon are also present in wild populations, industry practices, such as transporting captive fish across river basins, can introduce novel sources of diseases to wild individuals (White et al., 2023). The impact of novel pathogens can be particularly high when captive individuals are released into the wild as part of restocking conservation programmes, as individual sturgeon will move through a range of habitats throughout their lifecycle, spreading the novel pathogens as they go (White et al., 2023). As the native wild sturgeon have had no previous exposure to the pathogens, they have not yet developed any natural immunity, and the result can be widespread and devastating disease outbreaks.

In fact, restocking events are known to be responsible for population declines, loss of entire spawning year classes, and complete extirpation of species in some areas (Zholdasova, 1997). Many of the diseases affecting sturgeon have already been detected in multiple species and countries (White et al., 2023). As the sturgeon aquaculture industry continues to expand, the spread and scale of outbreaks are likely to worsen.

3.2.4 Behaviour

Captivity may also impact the behaviour of sturgeon, which can have wide-reaching consequences. For example, in the wild, Siberian sturgeon are typically benthic from 4 days of age and have relatively low mobility (Gisbert, 1999; Gisbert et al., 1999), whereas sturgeon reared in farms show a higher preference for swimming in the middle and upper areas of the tank and may even show inverted swimming patterns, which would normally make them more susceptible to predation (Gebauer et al., 2021). There are several, potentially interconnected, reasons for these changes in behaviour. First, sturgeon may be adapting to the feeding techniques used in aquaculture, as commercial feed pellets float on the surface, drawing hungry individuals up to feed. Second, the sturgeon may be showing an adaptive response to the absence of predators in aquaculture, allowing them to exploit the feed resources and forage more boldly without incurring predatory risk (Gebauer et al., 2021). Third, such changes in behaviour can indicate weakness, physical stress, and starvation in sturgeon, especially as they are contrary to natural behaviours (Kasumyan and Kazhlayev, 1993; Ross and Bennett, 1997). Lastly, a fourth potential reason could be that the changes in feeding and swimming behaviour may result from genetic selection. Farmed sturgeon are exposed to new selective reproductive pressures, which may render them less adaptive to natural conditions (Garcia, 2017). In particular, the individual sturgeon who successfully reproduce in captivity have undergone adaptations to the captive environment that enable them to reproduce. In contrast, wild individuals who could not adapt to captivity would die or have low reproductive success. Therefore, the selection pressures of captivity can mean that captive-bred individuals become increasingly different in physiology and behaviour from wild individuals (Garcia, 2017).

Environmental cues also play a role, however, as captive sturgeon will spend more time foraging at night when the water is turbid, compared with when it is clear (Wishingrad et al., 2015). Feeding predominantly at night can be a significant constraint on foraging success and may be driven as part of anti-predator behaviour (Wishingrad et al., 2015). Therefore, the pressures and influences upon sturgeon behaviour may be multi-faceted and complex. This poses particular challenges for conservation restocking efforts.

Survivability is often low in restocking programmes (Cámara-Ruiz et al., 2019; Gebauer et al., 2021; Wassink et al., 2022). In particular, post-release mortality is greatest in the immediate days following release and is considered to be due to the fish showing reduced life fitness traits such as foraging and anti-predator behaviour (Cámara-Ruiz et al., 2019). Commercial feeding techniques tend to prevent captive-reared sturgeon from practising their foraging skills, which can be detrimental to their survivability in the wild, especially as it appears to play a role in changing their swimming behaviour and rendering them vulnerable to predators (Gebauer et al., 2021).

It is also unclear to what extent the behavioural changes are characteristic of changes in affective state in the fish. For instance, most species of sturgeon have evolved to migrate long distances, and it is unclear whether being unable to fulfil these behaviours has any negative effect on their mental state. Sturgeon are sentient animals, yet science is lagging behind in its ability to assess all aspects of their welfare, including their mental states (Lambert et al., 2022). Until such developments are made, it is unclear to what extent captivity of an animal used to travel thousands of miles in a lifetime may have on their mental state.

4 Limitations and further research

This review has explored some of the key welfare concerns affecting farmed sturgeon, including the implications of both no-kill and traditional caviar harvesting. Since the farming of sturgeon in aquaculture is relatively new yet growing in scope, this is a critical area for further research and discussion. This review was limited by its reliance on existing literature, which is lacking in places, especially regarding the development of non-lethal egg harvesting techniques and the subjective experiences of sturgeon in captivity. Therefore, research is needed to explore the welfare of sturgeon in aquaculture systems to fully explore the impacts of captivity on these fish. In particular, a discussion and exploration into the impacts of restricting migratory animals, such as sturgeon, is urgently needed to explore the impacts on their emotional wellbeing. Future work would, therefore, benefit from including assessments of mental wellbeing and emotional states so that the subjective states of farmed sturgeon can be considered, too (Lambert et al., 2022).

5 Ethical considerations

The rise in farmed sturgeon has come about in response to both consumer demand for caviar and, from a conservation perspective, to protect and repopulate wild populations of sturgeon. The need for such a conservation drive is due to the overexploitation of these animals for a luxury product with a considerable price tag and the loss of critical habitats (White et al., 2023). Some suggest that despite claims that farming sturgeon will support conservation efforts to repopulate wild sturgeon, the opposite is occurring, as there is now little financial incentive to protect the remaining wild individuals (Raposo et al., 2023). Furthermore, this is particularly pertinent given the poor success of restocking programmes due to critical behavioural and health differences in cultured sturgeon (Cámara-Ruiz et al., 2019; Gebauer et al., 2021; Wassink et al., 2022).

Moreover, illegal harvesting of wild sturgeon continues to be an issue despite the abundance of farmed alternatives (van Uhm and Siegel, 2016). The scarcity of wild caviar has only increased the demand from those who can afford the exorbitant price tag and who are willing to break the law. The illegal trade in wild caviar is worth millions of euros each year, and organised crime has stepped up to fulfil the demand by illegally fishing, smuggling, and trafficking sturgeon across numerous countries (van Uhm and Siegel, 2016).

The farming of sturgeon is another example of industry seeking to prioritise the consumptive commercial use of wild animals at the expense of both the sturgeons' welfare and their conservation status. This is in direct contrast to the growing calls for a more systematic change of mindset, to shift away from consumptive forms of wildlife use towards non-consumptive use, reducing the demand for wild animals and wild-animal-derived production and replacing them with humane alternatives (Moorhouse et al., 2020; Green et al., 2023; Lambert et al., 2024). Given that the farming of sturgeon raises considerable welfare concerns, the full extent to which is not yet fully understood, farming sturgeon cannot be considered a suitable replacement for wild caviar, and other alternatives should be explored. Furthermore, we recognise that sturgeon and other fish may be farmed for other purposes, including sustenance, as opposed to the luxury market of caviar. However, whilst ensuring food security is essential, it should never come at the expense of fish welfare. Therefore, no matter what they are farmed for, fish deserve ethical and humane treatment throughout their lives and death.

6 Animal welfare implications

This review has summarised the key welfare concerns regarding the methods used for extracting eggs from sturgeon and the factors influencing their welfare during rearing. Although the concerns regarding rearing are not necessarily unique to sturgeon, their responses and experiences on farms are. Until relatively recently, sturgeon were not farmed for caviar and were only wild caught, so caviar farming is new to both the humans and the fish. Therefore, given the unique nature of this group of species, the most likely challenge to their welfare will be the fact that these wild species of fish are being farmed in artificial environments, under controlled conditions, far removed from their wild habitat.

Little attention has been paid to the welfare of sturgeon in caviar production, which is concerning as they are not only kept in captivity for years, but the procedures they undergo during egg harvesting can be severe. Therefore, the longevity and severity of the welfare concerns of caviar production render this subject as one requiring further attention from welfare scientists and policymakers. This is ever the more critical, considering that consumers are being marketed "no-kill" caviar as a more ethical choice when such a product may actually be perpetuating suffering. In this review, we have endeavoured to outline some of the key welfare impacts affecting farmed sturgeon and to show that both traditional and no-kill methods of egg harvesting cause considerable suffering to farmed sturgeon. Therefore, despite beliefs that caviar production can be performed humanely, the welfare concerns outlined show evidence to the contrary.

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HL: Formal analysis, Investigation, Methodology, Visualization, Writing – original draft. WE: Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Validation, Writing – review & editing.

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