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Welfare implications of closed-cycle farming of Atlantic bluefin tuna (*Thunnus thynnus*)

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There is an increased demand for tuna meat to supply the growing global sushi and sashimi market. Current methods to farm tunas, especially Atlantic bluefin tunas (ABFTs; *Thunnus thynnus*), are unsustainable. This is driving a movement towards closed-cycle ABFT aquaculture, i.e., farming tuna from spawning and hatching to slaughter on land, to try and meet the demand for these fish. Tunas are not domesticated species and thus face different challenges in terms of closed-cycle aquaculture when compared to other farmed fish species. Tunas also possess unique physiological traits such as regional endothermy and ram ventilation which affect their needs and how they are farmed. No current global standards exist to measure or monitor ABFT welfare in captivity, because there are many unknown factors surrounding ABFT welfare in aquaculture settings. There is a need to conduct studies that measure the baseline physiological parameters of ABFT in closed-cycle systems. Issues such as manipulation of breeding cycles, tank design, and slaughter procedures need attention and further research is required before such welfare indicators can be established. Stress is an overarching concern for animal welfare. In particular, pre-slaughter crowding and stress negatively affect the quality of the meat produced due to lactic acid buildup in the red muscle. Further research needs to be conducted throughout all life stages in terms of both animal welfare implications and the commercial viability of farmed ABFTs.

KEYWORDS

fish welfare, farming apex predators, fish behavior in captivity, humane slaughter, sashimi market, welfare standards, fish health, tuna ranching

1 Introduction

Tuna species are of great economic import because of the high international market demand for their meat (EFSA, 2009b; FAO, 2020). Increases in the popularity of sushi and sashimi as a luxury item in Japanese and international cuisine post-World War II has led to an exponential increase in demand for bluefin tuna, the preferred source for these dishes (Van Beijnen, 2017). Atlantic bluefin tuna (ABFT; *Thunnus thynnus*) is now officially the most sought-after fish in the world (Partridge, 2013; Van Beijnen, 2017).

Tunas have historically been overfished since the 1950s (Taylor et al., 2011). Traditionally, tuna aquaculture is based on the wild capture of younger fish for use in ranching systems, where they are kept in sea nets or cages until sufficiently grown and fattened for slaughter (Mylonas et al., 2010; Metian et al., 2014). In 2017, only 66.6% of tuna stocks were fished at biologically sustainable levels (FAO, 2020). Amidst growing global concerns about food source sustainability, interest has grown regarding closed-cycle tuna aquaculture (i.e., farming the complete fish life cycle from spawning and hatching until slaughter) (Naylor and Burke, 2005; Metian et al., 2014; Van Beijnen, 2017). Domestication of ABFT, with captive production of eggs and juveniles, would aid conservation efforts by reducing the number of wild-caught tunas.

2 Characteristics of Atlantic bluefin tuna

2.1 Physiological and anatomical attributes

These tunas are suited for closed-cycle aquaculture because they grow rapidly, produce significant quantities of meat, and have high fecundity levels (Fromentin and Powers, 2005; Pecoraro et al., 2017). However, aquaculture of ABFT is made challenging by their specific physiological needs, i.e., they are ram ventilators, have small swim bladders, are regionally endothermic, and struggle to reproduce in captivity (Graham and Dickson, 2001, 2004; Blank et al., 2007; Mylonas et al., 2010).

As obligate ram ventilators, tunas must swim continuously to extract oxygen from the water. This also helps maintain their hydrodynamic equilibrium and prevent sinking (Blank et al., 2007). Tunas have a small swim bladder, making their bodies denser than seawater (Pecoraro et al., 2017). A 1m-long tuna would need to swim approximately 43km per day at minimum speed to adequately ventilate and maintain hydrodynamic equilibrium (Graham and Dickson, 2004). Thus, long-distance swimming is not only an important behavior but also necessary for physical health.

Tunas are regionally endothermic, i.e., they conserve metabolic heat, allowing them to warm their red muscle, viscera, and brain above the ambient temperature (Graham and Dickson, 2001, 2004). Tunas swim to generate heat in their red muscle, which increases oxygen diffusion but also predisposes tunas to severe overheating, especially during times of stress and struggling (Graham and Dickson, 2001; Pecoraro et al., 2017).

2.2 Breeding

Controlled reproduction is a prerequisite for the successful aquaculture of any fish species (Zohar et al., 2016). Atlantic bluefin tuna have a short, irregular, and unreliable spawning season (Fromentin and Powers, 2005), necessitating manipulation of exogenous hormones and/or photoperiods to encourage breeding in captivity (Zohar et al., 2016; Higuchi et al., 2024). While sex hormone levels are similar in captive and wild tuna,

spermatogenesis and oogenesis are reduced in captive tuna. The lack of natural oocyte maturation in adult female ABFT is mainly due to the lack of appropriate environmental stimuli and/or the effects of chronic stress from captivity, which causes atresia of the female gonads (Partridge, 2013; Zohar et al., 2016). Hormonal implants (tags attached to the tuna using spear guns) are the primary means to stimulate spawning in both sexes (De Metrio et al., 2010; Zohar et al., 2016). This requires direct handling of the fish. It remains unclear whether tag application is painful for the broodfish, and what long-term impacts a permanent tag with constant hormone release would have.

3 Closed-cycle ABFT aquaculture

There is growing evidence to support the notion of fish sentience. Fish species have nociceptors like mammals, which are responsive to noxious stimuli (EFSA, 2009a; Sneddon, 2011). There are also arguments that all teleost fish are sentient and are capable of complex behavior, despite their basic brain anatomy being different from mammals (Woodruff, 2017, 2018). Fish have also been shown to demonstrate prolonged behavioral changes which could be indicative of discomfort or suffering (Sneddon, 2011). Overall, the balance of evidence supports that fish species, including tunas, can experience pain and therefore suffer (EFSA, 2009a; Sneddon, 2011; Woodruff, 2017). However, pain responses differ amongst teleost species, thus a generalized set of welfare indicators for all teleost species is unsupported (Sneddon, 2011).

Tunas have not been genetically selected to thrive in captivity, and so they experience chronic stress differently from other domesticated species (Partridge, 2013; Chandararathna et al., 2021), resulting in a multitude of challenges when attempting to breed and raise captive ABFT. Chronic stress has many consequences for the condition of animals in captivity (Dara et al., 2023). It is extremely difficult to evaluate tuna stress indicators during handling procedures because these procedures are intrinsically stressful (Chandararathna et al., 2021). Apart from direct factors affecting welfare, such as stocking density and water parameters, there are also indirect stressors unique to terrestrial fishery settings. Fish are highly sensitive to stressors such as light manipulation, noise, and vibrations (e.g., from passing traffic), which do not exist in the natural environment and are readily transmitted through water (EFSA, 2009a). Welfare assessments of farmed fish have not been investigated to the same degree as those of terrestrial animals, meaning that much knowledge regarding the welfare of intensively farmed fish is extrapolated from their wild counterparts (EFSA, 2009b; Dara et al., 2023). More research needs to be conducted regarding the wild ABFT ethogram to determine which behaviors are most crucial and should be fostered in captive ABFT.

3.1 Husbandry considerations

3.1.1 Tank design

The benefits of terrestrial tanks include the control and manipulation of environmental conditions to encourage

spawning, but factors such as water oxygenation and temperature and tank construction are important considerations.

Constant swimming is a physiological prerequisite of these giant fish, necessitating high-volume tanks with low stocking densities (Partridge, 2013). Stocking densities greater than 0.5kg/m³ result in increased incidences of death from a collision with the tank walls (Partridge, 2013). In one 1880m³ tank study, 91% of adult fish deaths were caused by a collision with the tank walls. Postmortems revealed trauma to the skin, skull, and spine, with no evidence of pathogens (Kadota et al., 2016; Higuchi et al., 2024). This indicates that the fish were swimming fast enough to cause fatal trauma when colliding with the tank walls. Tanks with reduced stocking density are preferential for fish welfare, but there is a greater risk of injury due to collision with the tank walls at a high swim speed. Conversely, if the tank design is too small for tunas to build up speed to try to prevent injuries, or if the stocking density is too great to allow for high-speed swimming, it would severely compromise captive ABFT welfare by restricting natural behavior and function. Partridge (2013) describes painting tank walls with black stripes to increase contrast and visibility for easier detection by tunas. Evidence suggests that tunas (especially juveniles) have poor scotopic vision (Ishibashi et al., 2009), so the efficacy of painted walls in dim lighting (when most deaths occur) is questionable. Studies into other potential solutions are required.

3.1.2 Water parameters

Water temperature and oxygenation levels are important because tunas must swim to adequately thermoregulate and oxygenate. Tunas are very sensitive to reductions in the ambient water oxygen concentration (Pecoraro et al., 2017) but can tolerate broader temperature ranges because of their endothermic abilities (Graham and Dickson, 2001). The suggested water temperature is 18 – 30°C (Pecoraro et al., 2017). Tunas typically spawn in water warmer than 24°C (De Metrio et al., 2010; Mylonas et al., 2010). Water parameters to hatch eggs, larvae, and juveniles have been described (De Metrio et al., 2010; Chen et al., 2016). However, little information is available regarding water parameters for adult ABFT in terrestrial tanks with controlled environments, as adult tunas are typically reared in natural seawater enclosures with variable conditions (Mylonas et al., 2010; Zohar et al., 2016).

3.1.3 Feeding

Most of the information about the nutritional requirements of captive tuna broodstock has been derived from consideration of tunas' natural diet, with many similarities between captive and wild diets (Partridge, 2013; Buentello et al., 2016). Sources of dietary fish for captive tunas are from fish feed, live pelagic fish, or 'trash fish' captured when trawling for other species (Naylor and Burke, 2005).

Larvae typically eat zooplankton, while juveniles eat crustaceans, fish, and cephalopods. Adult ABFT feed on other fish such as herring, sardines, and mackerel (Fromentin and Powers, 2005). Because ABFTs have not been bred for domestication, they still seek natural food sources (moving prey fish) in captivity as opposed to frozen, pelleted, or flake food (Chandararathna et al., 2021). A diet commonly fed to ABFTs during the fattening period mainly

consists of sardines and squid. However, this is not sustainable because sardine availability is limited to certain months and stored frozen products are less nutritious and more expensive than fresh fish. Daily feeding of mass quantities of fresh or frozen fish/squid results in an unreasonably high feed conversion ratio, because this diet does not meet tunas' metabolic needs and supplementation is usually required (Partridge, 2013; Buentello et al., 2016).

The sourcing of pelagic fish for tuna rations is also a concern. Prey species used as feed for large-scale fisheries need to be ethically and sustainably sourced to preserve their wild populations and by-catch of other vulnerable marine species, such as turtles, must be minimized (Naylor and Burke, 2005; Chandararathna et al., 2021). Current feeding strategies facilitate the spread of pathogens which have previously caused sardine fisheries in some parts of the world to collapse (Buentello et al., 2016).

3.1.4 Rearing

The natural mortality rates of wild tunas, especially ABFTs, are not well known and are extrapolated from the mortality rate of southern bluefin tuna (*Thunnus maccoyii*), where a constant mortality rate of 0.14 is assumed (Fromentin and Powers, 2005).

Currently, there is a high mortality rate of ABFT tuna larvae, with only 1% of larvae surviving until 7 days post-hatching, and 0.44% of larvae surviving the first 30 days of life (De Metrio et al., 2010; Van Beijnen, 2017). Such a low survival level is generally considered unacceptable in terms of both profitability and captive animal welfare (Van Beijnen, 2017). The highest cause of larval mortalities during the first 10 days post-hatching is caused by 'sinking syndrome' (Win et al., 2020). Larvae sink to tank floors and perish on collision during periods of darkness when larvae are less active and do not swim to maintain their hydrodynamic lift (Masuma et al., 2011; Win et al., 2020). From hatching, ABFTs are heavier than the surrounding seawater because of their heavy yolk sac and small swim bladder, causing them to sink due to their density (Fromentin and Powers, 2005; Pecoraro et al., 2017). Other causes for concern include stress-related deaths after inter-tank transfer (Van Beijnen, 2017), cannibalism, viruses, and diet for larvae and juveniles (Masuma et al., 2011). With the lack of validated indicators other than mortality rate to measure immature ABFT welfare, it is hoped that attempts to increase survival rates to improve commercial profitability will also positively affect fish welfare.

3.2 Health considerations

Increased stocking densities in fisheries, together with factors such as dissolved oxygen levels, water turbidity, nutrition, and age of juvenile fish have been shown to influence the spread of disease through reduced immunity and increased contact between individuals (Rodgers and Furones, 2009; Henriksson et al., 2018; Martos-Sitcha et al., 2020).

Little information is available regarding pathogens affecting captive tuna. A routine response to prevent challenges such as diseases and parasitic infections in many different fishery settings is

the prophylactic use of antimicrobials to combat outbreaks and mass mortalities (Henriksson et al., 2018). Antimicrobial use is especially prevalent during the transport of broodstock and early life stage development to prevent the introduction of microbes to new facilities (Ibrahim et al., 2020). For example, antibiotics are routinely added to the water used to hatch ABFT eggs (Higuchi et al., 2024). Routine antimicrobial use in aquaculture, such as the rapidly developing ABFT fisheries, provides a bridge between aquatic and human pathogens and could aid in the emergence of new trans-species antimicrobial-resistant pathogens (Rodgers and Furones, 2009; Henriksson et al., 2018; Ibrahim et al., 2020).

4 Slaughter

Tunas rapidly overheat during times of stress because of their endothermic nature (Graham and Dickson, 2001; Pecoraro et al., 2017). Crowding is the single greatest cause of pre-slaughter stress (EFSA, 2009b). Crowding restricts movement, preventing tunas from swimming and ventilating properly. Tunas also overheat as they struggle to escape before death (EFSA, 2009b; Mylonas et al., 2010). Overheating during pre-slaughter increases lactic acid buildup in tuna red muscles, rendering the meat unsuitable for use in sashimi or sushi, the prime markets for ABFT (de la Gandara et al., 2016). It is in the fisheries' best interests, from both an economic and welfare view, to ensure a swift and stress-free death to prevent lactic acid accumulation and preserve the value of the fish (EFSA, 2009b; de la Gandara, Ortega and Buentello, 2016).

All current forms of tuna harvesting involve increasing the stocking density of fish in shallow, smaller nets to facilitate handling, or chasing them into a smaller slaughtering cage (de la Gandara, Ortega and Buentello, 2016). During the pre-slaughter period, fish in the slaughtering space are exposed to a range of stimuli including crowding, handling, noise, transport, unfamiliar environments, and food deprivation. This causes fear, distress, and fatigue from attempts to escape (EFSA, 2009b).

In the European Union (EU), there are three described methods to slaughter tunas: lupara (underwater shooting), shooting from the water surface, and coring and spiking. The main influencing factor determining the slaughter method is the size of the fish (EFSA, 2009b).

Lupara involves the shooting of large (>80kg) individuals underwater. This method is considered the gold standard for current and future slaughter because the fish undergo only mild to moderate crowding and can swim around relatively normally before a diver kills individuals by a direct shot to the head. The fish are then brought to the surface and their lateral arteries are severed. Their brains are cored with a metal rod to prevent involuntary muscle movement. However, this method is inefficient for greater numbers of fish (EFSA, 2009b; Mylonas et al., 2010).

Surface shooting of large (>80kg) fish is the second slaughter method. The fish are briefly brought to the surface by hydraulically lifting the bottom of the sea cage (Mylonas et al., 2010). The tunas are then shot through the head with the same cartridge as used for lupara. This method is preferred because it is easier to slaughter many more fish per day but is less ideal in terms of welfare because

the fish are exposed to severely stressful conditions prior to death. There is a greater risk of error because the fish are moving targets, marksmen may be improperly trained, bullets may be misaimed, and/or death may not be immediate (EFSA, 2009b). These factors also apply to lupara.

The protocol for smaller (<80kg) fish requires them to be speared through the gills (gaffed) and brought to the water surface, where they are then crowded in a small net before being suffocated out of water and cored. Welfare concerns regarding this method are based on the slaughter being performed under extremely stressful circumstances, with crowding, gaffing, and no guaranteed immediate loss of consciousness (Mylonas et al., 2010; de la Gandara, Ortega and Buentello, 2016). This method is least preferable.

Pre-slaughter stunning would increase the accuracy and efficacy of shooting and coring, rendering these procedures less stressful for the fish and persons involved. Pre-slaughter electrostunning has been trialed successfully in other species (Bouwsema et al., 2022). Soto et al. (2006) researched types of electrical stunning for tunas in a natural seawater environment. They obtained the best meat quality results after slaughter using a mixed DCP/AC signal, which utilized moderate voltage and current but little power (Soto et al., 2006). This method was discontinued in the EU because of challenges due to the highly variable conductivity of the seawater rendering the stunning results too inconsistent and unreliable (de la Gandara, Ortega and Buentello, 2016). However, electrostunning merits further research, considering the controllable environment offered by terrestrial tanks, unlike open seawater. However, only meat color and spinal injury were scored by Soto et al. No research was conducted regarding brain electrical activity so the true efficacy and immediacy of different stunning methods could not be fully evaluated.

5 Conclusion

The global tuna industry is currently reliant on wild-caught tunas, resulting in long term sustainability issues. This has driven the development of closed-cycle terrestrial tuna aquaculture.

No current global standards exist to measure or monitor ABFT welfare in captivity. There is a need to conduct studies that measure the species-specific physiological parameters (e.g., core and red muscle temperature) of ABFT in closed systems. These measurements should ideally be combined with routine procedures so that baseline standards can be established. A range of feasible, valid, and reliable measurements and indicators can then be developed to guide humane and profitable ABFT aquaculture.

Sentience in teleost fish continues to be debated. Not all parties involved in ABFT aquaculture consider tunas sentient, and as such, producers may not take the initiative to promote fish welfare or intervene when suspected welfare violations occur. Slaughter methods must be adapted to suit the unique new challenges posed by land tanks. It is unclear whether nets such as those used in seawater enclosures could be adapted for use in fixed-feature terrestrial tanks or whether the bottom of land-based tanks could be made mobile. Whilst lupara remains

the ideal method of slaughter, a margin for error still exists and it is impractical and inefficient for greater numbers of fish. Other slaughter methods also require adaptations, especially regarding tank setup.

Aquaculture companies that intend to conduct closed-cycle farming of ABFTs should commit to improving husbandry and survival rates, and adapt slaughter methods as necessary.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Author contributions

BM: Writing – original draft, Writing – review & editing. WE: Conceptualization, Writing – review & editing.

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