



Behavioral Complexity of *Oreochromis* Species: A Review for Sustainable Fisheries and Aquaculture

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ABSTRACT

Climate change-mediated physicochemical conditions and environmental disturbances necessitate robust freshwater species, especially for African aquaculture. The *Oreochromis* genus is a commonly reared fish due to its remarkable behavioral and ecological adaptability through its unique social structures, reproductive strategies, environmental resilience, and foraging habits. These traits significantly determine the species' capability for ecological distribution, dominance, and as aquaculture potential candidates. Despite the general characteristic traits, *Oreochromis* species are native to specific ecological zones, compelling an understanding of the behavior of each species. Therefore, this review synthesized research on the behavioral dynamics across most *Oreochromis* species, focusing on social interactions, feeding strategies, survival, and cognitive traits. The adaptive mechanisms that enhance growth, establishment, and resilience in diverse environments were also highlighted. Findings indicated that the *Oreochromis* species exhibit remarkable tolerance to extreme environmental conditions like high salinity, temperature fluctuations, and alkalinity stress. From the literature, the mentioned attributes contributed to the success of *Oreochromis* species in natural ecosystems and aquaculture conditions. Future research should explore genetic and environmental behavioral traits for unmapped *Oreochromis* species, accentuating the impact of climate change on behavioral adaptability for sustainable fisheries and aquaculture innovations.

INTRODUCTION

Cichlids play a significant role in global aquaculture due to their extensive taxonomic, phenotypic, ecological, and behavioral diversity. This family of teleost fishes includes more than 1,300 species and exhibits remarkable biodiversity, particularly in the East African Great Lakes, which are considered major evolutionary hotspots (Salzburger, 2018). Among these cichlids are the non-haplochromine tilapia of the *Oreochromis* genus, native to Africa and the Middle East. These species have been

widely introduced to other regions for aquaculture and fisheries development (**Vajargah, 2021**).

Given their rapid production rates and economic significance, behavioral studies of *Oreochromis* species have attracted increasing attention in both aquaculture and evolutionary biology research (**Day *et al.*, 2019**). *Oreochromis* species serve not only as a major food source but also as effective biocontrol agents for aquatic vegetation. Along with other cichlid groups, they are now recognized as a ‘model system’ for evolutionary and ecological studies (**Li *et al.*, 2017**).

Behavioral complexity

Behavioral strategies that contribute to the ecological adaptability and complexity of *Oreochromis* species are of particular interest. These fish exhibit unique social structures, reproductive behaviors, and resilience to challenging environments—traits that distinguish them from many other freshwater fish species (**Abd El-Hack *et al.*, 2022**). Unlike many freshwater species confined to narrow ecological niches, *Oreochromis* are highly adaptable and can survive under extreme environmental conditions. For example, the *Oreochromis amphimelas* lineage is especially well-adapted to environments with high salinity, temperature, and alkalinity (**Day *et al.*, 2019**).

Their advanced reproductive and social behaviors, such as parental care and hierarchical social systems, contribute to higher offspring survival rates and enhanced aquaculture productivity (**Gonçalves-De-Freitas *et al.*, 2019**). However, traits like aggression, territoriality, and heightened stress responses can pose challenges to effective management in intensive aquaculture settings (**Rodriguez-Barreto *et al.*, 2019**).

Literature gap

Despite the wide distribution and importance of *Oreochromis*, there is a lack of comprehensive behavioral studies on lesser-known species such as *Oreochromis karongae*, *Oreochromis shiranus*, *Oreochromis tanganicae*, and *Oreochromis andersonii*. These species hold significant ecological and aquacultural value, particularly in their native habitats. Yet, behavioral data on them remain limited or outdated.

There is a critical need for region- and species-specific behavioral research to inform localized aquaculture and fisheries management strategies. This review addresses these gaps and highlights the importance of behavioral diversity studies to support the development of resilient and diversified aquaculture systems that incorporate native and indigenous species within their respective ecosystems.

BEHAVIOR STRATEGIES IN *OREOCHROMIS* SPECIES**1. Social behavior**

Fish utilize a range of visual, olfactory, and chemical cues in social interactions. These cues are influenced by environmental factors and group dynamics, such as composition and size. In *Oreochromis* species, social behavior plays a pivotal role in dominance, resource allocation, and reproduction.

1.1 Hierarchy establishment

The stability of social hierarchies is essential, as prolonged instability can lead to elevated stress levels and increased injury rates among individuals (**Gonçalves-De-Freitas *et al.*, 2019**). Under aquaculture conditions, factors such as water renewal rate, stocking density, lighting conditions, and fish size influence the frequency and intensity of aggressive interactions (**Chifamba & Mauru, 2017**).

1.1.1 Rate of water renewal (Chemical Cues)

Chemical communication is vital for social interaction. Changes in water quality can interfere with chemical signaling. For example, in *Oreochromis mossambicus*, urine contains specific chemical compounds that signal social rank, particularly dominance in males (**Barata *et al.*, 2007**). Aggression is not only used to establish hierarchy but also to secure critical resources such as food, territory, and mates (**Da Silva *et al.*, 2021**).

1.1.2 Environmental lighting

Oreochromis niloticus possesses seven cone opsin genes, allowing perception across the full visible spectrum. This spectral sensitivity enables them to detect both shortwave and longwave colors. Environmental lighting influences several behavioral and physiological responses in this species, including aggression, stress, growth, feeding efficiency, and reproduction (**Maia & Volpato, 2013**).

1.1.3 Stocking density, fish size, and group composition

Fish size, sex, and group structure are key predictors of aggression and dominance behaviors in culture systems (**Rodriguez-Barreto *et al.*, 2019**). Larger individuals typically exhibit more aggressive behavior and dominate social interactions. In a study involving *O. niloticus* and *O. mortimeri*, aggression levels were influenced by relative size differences (**Chifamba & Mauru, 2017**).

Fattah *et al.* (2020) found that high stocking densities of juvenile *O. niloticus* increased aggressive behaviors, likely due to competition for food and shelter. However, **Rodriguez-Barreto *et al.* (2019)** reported contrasting results: at high densities, aggression decreased, possibly due to stress-induced changes in gene expression—particularly in hypothalamic stress-related genes like somatostatin (*sst1*)—leading fish to shift from hierarchical to shoaling behaviors.

1.2 Territoriality

Male *Oreochromis* exhibit territorial behavior, especially during breeding, vigorously defending nest sites or "craters." Related males have been shown to tolerate each other more than unrelated males, promoting social stability under crowded conditions (**Gonçalves-De-Freitas *et al.*, 2019**).

Oreochromis tanganicae, in particular, is highly territorial. Males show no tolerance to intrusions, especially during breeding, and are aggressive toward both conspecifics and other territorial species. These behaviors often result in prolonged and intense conflicts as males defend sandy or muddy breeding grounds (**Kalima *et al.*, 2020**).

1.3 Cooperative interactions

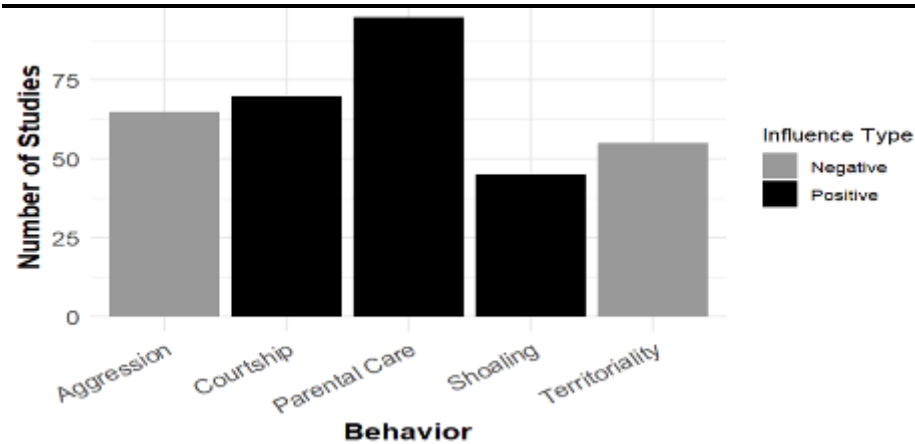
Despite their aggressive tendencies, *Oreochromis* also engage in cooperative behaviors. During territory establishment and reproduction, males coordinate with females to improve mating success and offspring survival (**Gonçalves-De-Freitas *et al.*, 2019**).

Oreochromis karongae demonstrates group foraging behavior, enhancing feeding efficiency and reducing predation risk. These species also exhibit a wide range of parental care strategies—both biparental and uniparental (**Balshine & Sloman, 2011**).

Social learning is another cooperative behavior observed in tilapia. In one study, both trained and untrained fish learned to forage more efficiently when in groups, demonstrating the ability to acquire and share information in a social setting (**Mesquita *et al.*, 2016**).

Fig. (1) presents a graphical summary of how environmental and social factors influence the social behavior of *Oreochromis* species. The data were compiled in Excel and visualized using R statistical software based on the literature discussed above.

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Positive- The behavior **encourages** social interactions and cooperation

Negative- The behavior **reduces** social behavior, increases aggression, and disrupts normal interactions

Fig. 1. Summary of *Oreochromis* social behavior and its influence on social interactions from the articles reviewed

2. Foraging and feeding behavior

Feeding behavior among *Oreochromis* species is highly diverse and closely tied to their habitat and the availability of dietary resources. These species exhibit various specialized adaptations that allow them to exploit a broad range of food sources, including algae, detritus, plankton, and small invertebrates (**Beveridge & Baird, 2000**) (Table 1).

In aquaculture, feeding strategies for tilapia typically rely on a combination of natural and supplemental food sources. According to **El-Sayed (2020)**, tilapia fish obtain approximately 30–50% of their nutrition from natural food organisms, which play a vital role in supporting their growth. The remaining 50–70% is met through supplemental feeding, with the exact proportions depending on fish size, growth stage, and production system.

Table 1. Feeding habits and habitats of major African *Oreochromis* species

Species	Diet	Feeding category	Foraging behavior	Feeding Habitat	References
<i>Oreochromis tanganycae</i> and <i>Oreochromis karongae</i>	Algae, periphyton, detritus, small invertebrates or zooplankton, diatoms (<i>Pinnularia</i> and <i>Navicula</i>), sand grains, and small fish	Opportunistic, primarily herbivorous	Skimming the surface film in sheltered waters to access floating algae and microorganisms	Benthic zones and open waters	(Kapute <i>et al.</i> (2008); Saikia (2015); Kalima <i>et al.</i> (2020))
<i>Oreochromis andersonii</i> and <i>Oreochromis macrochir</i>	Vegetative detritus (main diet; 90.88%), aquatic invertebrates, diatoms, and pelleted feed	Opportunistic detritivores	Sifts through sediment to extract food particles	Lagoons, slow-flowing or standing water bodies	(Winemiller and Kelso, 2003)
<i>Oreochromis shiranus</i> , <i>Oreochromis aureus</i> and <i>Oreochromis lidole</i>	Detritus, phytoplankton, and pelleted feed	Microphagous detritivore	Picks food from the water column, grazes on surfaces, and picks up detritus from substrates.	Shallow waters, floodplains, and lagoons	Saikia (2015)
<i>Oreochromis squamipinnis</i>	Phytoplankton, diatoms, and sand sediments	Opportunistic herbivorous grazer	Substrate feeder, picking up its food items and grazing on algae	Semi-pelagic, shallow, vegetated bays	(Reinthal and Konings, 1991)
<i>Oreochromis niloticus</i> and <i>Oreochromis mossambicus</i>	Phytoplankton, Zooplankton, Detritus, Periphyton, and pelleted feed	Omnivorous	Grazes periphyton and phytoplankton on submerged surfaces, picks up detritus, and filters suspended food particles.	Feeds both in shallow waters and in open water column	El-Sayed (2020)

3. Reproductive behavior

Oreochromis species are renowned for their high reproductive capacity, which is largely unaffected by environmental extremes—whether favorable or harsh (Trewavas, 2013). All members of the genus are maternal mouthbrooders, and they generally exhibit sexual dimorphism, with females acting as the choosy sex while males display pronounced sexual traits (Fig. 2).

Dominant males typically exhibit larger body size, brighter skin coloration, and higher levels of aggression—traits used to attract females. Some species develop secondary sexual features such as enlarged jaws (*O. mossambicus*), elongated soft dorsal and anal fins, and pronounced genital papillae (Turner *et al.*, 2000). Polygamous mating systems are a hallmark of the genus, with males often mating with multiple females (Turner *et al.*, 2000).

Spawning in *Oreochromis* is primarily influenced by environmental cues such as temperature and rainfall. For instance, *Oreochromis niloticus* in Lake Victoria breeds year-round, with spawning peaks typically observed during the rainy season (Santos *et al.*, 2023). In contrast, *O. karongae*, *O. squamipinnis*, and *O. lidole* exhibit species-specific seasonal spawning peaks in Lake Malawi (Turner *et al.*, 2000).

A key reproductive strategy of *Oreochromis* species is mouthbrooding. After fertilization, the female collects the eggs in her mouth for incubation, offering protection from predators and environmental stressors (Fig. 2). Fry remain in the mother's mouth until they are capable of independent swimming and feeding, which significantly increases their survival and adaptability.

Oreochromis niloticus is the most studied species within the genus, contributing to over 90% of the available reproductive research (Omwenko *et al.*, 2024; Refaey *et al.*, 2025). Sexual maturity is typically reached at a total length (L_{50}) of 14–15 cm in females and 15–17 cm in males (Shoko *et al.*, 2015). Fecundity is more strongly correlated with total length and body weight than with gonadal development alone. However, in species such as *O. macrochir* and *O. andersonii*, a strong positive correlation exists between body length and the number of eggs produced (Kefi, 2011).

In terms of reproductive output, *O. mossambicus* demonstrates relatively high fecundity, averaging 921 ± 604.6 eggs per female and a relative fecundity of 8.36 ± 3.09 eggs per gram of body weight. This exceeds the fecundity levels of *O. niloticus* under similar environmental conditions (Urbano *et al.*, 2024).

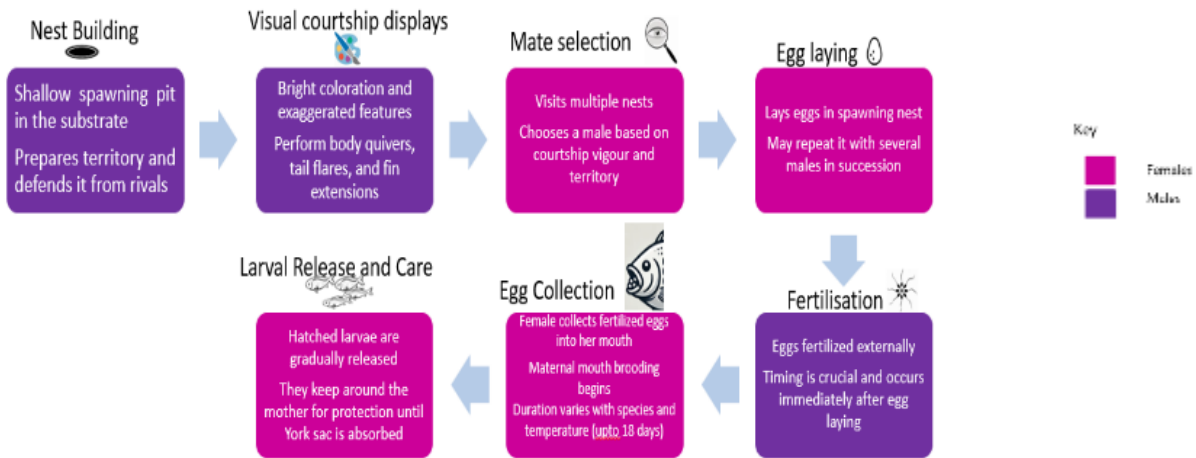


Fig. 2. The reproductive behavior cycle diagram of *Oreochromis* species

4. Survival behavior

Oreochromis species display a wide array of survival behaviors that include predator avoidance, environmental tolerance, flexible feeding strategies, and reproductive adaptations (Xu *et al.*, 2006) (Fig. 3).

a) Environmental tolerance and stress adaptation

Due to their ability to withstand harsh environmental conditions, *Oreochromis* species are widely used as research models for studying water quality tolerance and stress adaptation. They can survive in low-quality aquatic environments impacted by rainfall, flooding, drought, and fluctuating water levels. Their tolerance to temperature shifts, salinity changes, and resistance to many diseases and parasites makes them valuable in climate change adaptation and aquaculture resilience (Kunda *et al.*, 2024).

Schofield (2007) assessed the survival of invasive *Oreochromis niloticus* in coastal Mississippi following Hurricane Katrina and found that the species survived for over a year in isolated ponds and drainage ditches post-flooding, demonstrating remarkable environmental resilience.

b) Genetic adaptations for survival

In *O. niloticus*, genetic analysis has revealed specific genes associated with hypoxia tolerance. Li *et al.* (2017) identified *GPR132* and *ABCG4* as key genes involved in

hypoxia response, linked to processes such as liver development, signal transduction, and steroid hormone mediation—mechanisms that contribute to survival in low-oxygen environments.

O. mossambicus is another species with exceptional survival capabilities in extreme euryhaline conditions. This species can expand its osmoregulatory range from 335–360 mOsmolal up to 550 mOsmolal. It also tolerates a wide thermal range of 15–37 °C, with some individuals demonstrating even broader tolerance, making it one of the most adaptable freshwater fishes (Moorman *et al.*, 2015).

c) Predator avoidance strategies

Predator evasion is another critical survival mechanism in *Oreochromis* species. *O. niloticus* engages in shoaling and schooling behaviors that reduce individual predation risk through the "confusion effect" and collective vigilance (Pitcher, 1986; Khalil & Emeash, 2018).

In addition, their ability to alter body coloration provides camouflage that aids in avoiding predators—a behavioral adaptation effective in various ecological scenarios (Fujii, 2000). Chen *et al.* (2013) demonstrated that erythrophores in *O. niloticus* respond to different wavelengths of light, enhancing camouflage and providing a chromatically tuned visual defense mechanism.

d) Thermoregulation strategies

Skin color modulation also plays a role in thermoregulation. Changes in pigmentation help *Oreochromis* species adapt to thermal fluctuations in their environment. In *O. niloticus*, cone opsin gene expression was detected in the caudal fin, where photosensitive chromatophores reside. These opsins facilitate color changes and enable the fish to detect and respond to changes in ambient light and temperature (Chen *et al.*, 2013; Kumar *et al.*, 2022). This form of photoregulatory adaptation allows for efficient thermoregulation and enhances survival across varying environmental conditions.

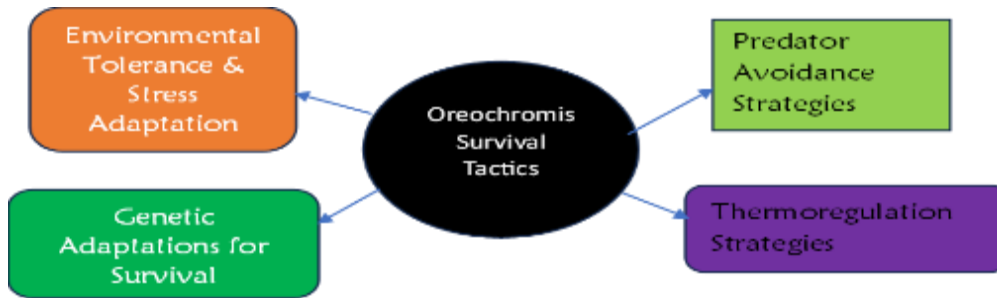


Fig. 3. Summary of the different *Oreochromis* survival strategies

5. Cognitive behavior

In fish, cognitive behavior is expressed through learning from past experiences and storing information related to predator recognition, food sources, and spatial navigation. These behaviors are often based on associating specific environmental cues with prior outcomes. In *Oreochromis* species, cognitive abilities are critical for survival, social organization, and ecological adaptability.

Oreochromis niloticus has been studied for its capacity to exhibit time–place learning, where the fish can associate specific times with food availability at particular locations (Delicio & Barreto, 2008). Such behavior demonstrates a level of spatial and temporal memory that aids in efficient foraging and avoidance of predators or unfavorable conditions.

Overall, cognitive behavior in *Oreochromis* species is vital for adaptability in dynamic environments. However, these cognitive functions are highly sensitive to environmental stressors, pollution, and social interactions. Stressful or degraded environments can impair learning, memory, and decision-making capabilities, ultimately affecting survival and productivity.

To support cognitive performance and improve outcomes in fisheries and aquaculture, it is essential to minimize environmental pollutants and maintain optimal water quality and social conditions in rearing systems (Reda *et al.*, 2025).

FUTURE RESEARCH PROSPECTS

This review provides valuable insights into the behavioral ecology of *Oreochromis* species, with approximately 40% of the existing literature focusing on *Oreochromis niloticus*, while nearly 60% of behavioral data on other *Oreochromis* species remains underexplored due to limited scientific research. To advance our understanding of the

genus, there is a critical need to focus on the behavioral complexities of lesser-studied species—particularly those endemics to the ecologically unique environments of Lakes Malawi and Tanganyika.

Expanding research beyond *O. niloticus* and *O. mossambicus* is essential, especially in regions where these two species are considered invasive. Exploring the behavior of native *Oreochromis* species will not only enrich ecological and evolutionary knowledge but also offer practical benefits by identifying alternative species for aquaculture. This is particularly important in light of increasing global demand for animal protein and the stagnation of wild fish stocks.

Furthermore, enhanced knowledge of underrepresented *Oreochromis* species will contribute to species diversification in aquaculture, improve conservation planning, and support the development of sustainable and region-specific aquaculture practices. These advancements will also provide critical data to inform future capture fisheries management and drive innovations that align with global food security goals.

REFERENCES

- Abd El-Hack, M.E.; El-Saadony, M.T.; Nader, M.M.; Salem, H.M.; El-Tahan, A.M.; Soliman, S.M. and Khafaga, A.F. (2022).** Effect of environmental factors on growth performance of Nile tilapia (*Oreochromis niloticus*). *International Journal of Biometeorology*, 66(11):2183–2194. <https://doi.org/10.1007/s00484-022-02347-6>
- Barata, E.N.; Hubbard, P.C.; Almeida, O.G.; Miranda, A. and Canário, A.V.M. (2007).** Male urine signals social rank in the Mozambique tilapia (*Oreochromis mossambicus*). *BMC Biology*, 5:54. <https://doi.org/10.1186/1741-7007-5-54>
- Balshine, S. and Sloman, K.A. (2011).** Social and reproductive behaviors: Parental care in fishes. In: “*Encyclopedia of Fish Physiology: From Genome to Environment*.” Farrell, A.P. (Ed.). Vol. 1–3, Elsevier, pp. 670–677. <https://doi.org/10.1016/B978-0-12-374553-8.00098-8>
- Beveridge, M.C.M. and Baird, D.J. (2000).** Diet, feeding and digestive physiology. In: “*Tilapias: Biology and Exploitation*.” M.C.M. Beveridge and B.J. McAndrew. (Eds). Springer Netherlands, pp. 59–87. https://doi.org/10.1007/978-94-011-4008-9_3
- Chen, S.C.; Robertson, R.M. and Hawryshyn, C.W. (2013).** Possible involvement of cone opsins in distinct photoresponses of intrinsically photosensitive dermal

- chromatophores in tilapia *Oreochromis niloticus*. *PLoS ONE*, 8(8), e70342. <https://doi.org/10.1371/journal.pone.0070342>
- Chifamba, P.C. and Mauru, T. (2017).** Comparative aggression and dominance of *Oreochromis niloticus* (Linnaeus, 1758) and *Oreochromis mortimeri* (Trewavas, 1966) from “paired contest in aquaria.” *Hydrobiologia*, 788(1):193–203. <https://doi.org/10.1007/s10750-016-2997-y>
- da Silva, M.C.; Canário, A.V.M.; Hubbard, P.C. and Gonçalves, D.M.F. (2021).** Physiology, endocrinology and chemical communication in aggressive behaviour of fishes. *Journal of Fish Biology*, 98(5):1217–1233.
- Day, J.J.; Ford, A.G.P.; Bullen, T.R.; Pang, L.; Genner, M.J.; Bills, R.; Flouri, T.; Ngatunga, B.P.; Rüber, L.; Schliewen, U.K.; Seehausen, O.; Shechonge, A.; Stiassny, M.L.J. and Turner, G.F. (2019).** Molecular phylogeny of *Oreochromis* (Cichlidae: *Oreochromini*) reveals mito-nuclear discordance and multiple colonisation of adverse aquatic environments. *Molecular Phylogenetics and Evolution*, 136:215–226.
- Delicio, H. C.; and Barreto, R. E. (2008).** Time-place learning in food-restricted Nile tilapia. *Behavioural Processes*, 77(1): 126–130. <https://doi.org/10.1016/j.beproc.2007.06.005>
- El-Sayed, A.-F.M. (2020).** Tilapia Culture, second ed. Academic Press.
- Fattah, A.F.A.; Ahmed, F.A.; Saleem, A.-S.Y.; Mohammed, H.H.; Youssef, M.I. and Said, E.N. (2020).** Effect of the different stocking density on behavior, performance and welfare of the Nile tilapia (*Oreochromis niloticus*). *Egyptian Journal of Aquatic Biology and Fisheries*, 24(5).
- Fujii, R. (2000).** The regulation of motile activity in fish chromatophores. *Pigment Cell Research*, 13(5):300–319.
- Gonçalves-De-Freitas, E.; Bolognesi, M.C.; Gauy, A.C.D.S.; Brandão, M.L.; Giaquinto, P.C. and Fernandes-Castilho, M. (2019).** Social behavior and welfare in Nile tilapia. *Fishes*, 4(2):1–10. <https://doi.org/10.3390/fishes4020023>
- Hirpo, A. (2013).** Reproductive biology of *Oreochromis niloticus* in Lake Beseka, Ethiopia. *Journal of Cell and Animal Biology*, 7(9):116–120. <https://doi.org/10.5897/jcab2013.0388>
- Kalima, S. and Kefi, A.S. (2020).** Growth performance of monosex and mixed sex of *Oreochromis tanganycae* (Günther, 1894) raised in semi concrete ponds. *Journal of*

Aquaculture Research & Development, 11:586. <https://doi.org/10.35248/2155-9546.19.11.586>

- Kefi, A. S.** (2011). Some aspects of reproductive biology of *Oreochromis andersonii* (Castelnau, 1869), *Oreochromis machrochir* (Boulenger, 1912) and *Oreochromis niloticus* (Linnaeus, 1758). *Malawi Journal of Aquaculture and Fisheries*, 1(2): 32–37.
- Khalil, F. and Emeash, H.** (2018). Behavior and stereotypies of Nile tilapia (*Oreochromis niloticus*) in response to experimental infection with *Aeromonas hydrophila*. *Aquatic Sciences and Engineering*, 33(4):124–130. <https://doi.org/10.26650/ASE2018407191>
- Kumar, S.; Dar, S.A. and Rani, S.** (2022). Effect of environmental variability on the pigmentation of fishes. In: “Outlook of Climate Change and Fish Nutrition.” *Springer Nature Singapore*, pp. 153–170. https://doi.org/10.1007/978-981-19-5500-6_12
- Kunda, M.; Chowdhury, A., Harun-Al-Rashid, A. and Pandit, D.** (2024). Optimizing feed restriction strategies for profitable *Oreochromis niloticus* culture in floating cages in riverine ecosystems. *Discover Animals*, 1(1):26. <https://doi.org/10.1007/s44338-024-00028-9>
- Li, H.L.; Gu, X.H.; Li, B.J.; Chen, C.H.; Lin, H.R. and Xia, J.H.** (2017). Genome-wide QTL analysis identified significant associations between hypoxia tolerance and mutations in the GPR132 and ABCG4 genes in Nile tilapia. *Marine Biotechnology*, 19(5):441–453. <https://doi.org/10.1007/s10126-017-9762-8>
- Maia, C.M. and Volpato, G.L.** (2013). Environmental light color affects the stress response of Nile tilapia. *Zoology*, 116(1):64–66. <https://doi.org/10.1016/j.zool.2012.08.001>
- Mesquita, F.O.; Torres, I.F.A. and Luz, R.K** (2016). Behaviour of proactive and reactive tilapia *Oreochromis niloticus* in a T-maze. *Applied Animal Behaviour Science*, 181:200–204. <https://doi.org/10.1016/j.applanim.2016.05.022>
- Moorman, B.P.; Lerner, D.T.; Grau, E.G. and Seale, A.P.** (2015). The effects of acute salinity challenges on osmoregulation in Mozambique tilapia reared in a tidally changing salinity. *Journal of Experimental Biology*, 218(5):731–739. <https://doi.org/10.1242/jeb.112664>
- Omwen, J.O.; Getabu, A.; Omondi, R. and Orina, P.S.** (2024). Water quality effects on growth and survival of *Oreochromis jipe* and *Oreochromis niloticus* species in

aquaculture. In: “Water Quality - New Perspectives”. IntechOpen. <https://doi.org/10.5772/intechopen.106361>

- Ogutu-Ohwayo, R.** (1990). The decline of the native fishes of Lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch (*Lates niloticus*) and the Nile tilapia (*Oreochromis niloticus*). *Environmental Biology of Fishes*, 27(2):81–96. <https://doi.org/10.1007/BF00001938>
- Pitcher, T.J.** (1986). Functions of shoaling behaviour in teleosts. In: “The Behaviour of Teleost Fishes.” T.J. Pitcher (Editor), Springer, Boston, MA, pp. 294–337. https://doi.org/10.1007/978-1-4684-8261-4_12
- Reda, R.M.; Zaki, E.M.; Aioub, A.A.; Metwally, M.M.M.; Yassin, A.M. and Mahsoub, F.** (2025). Behavioral, biochemical, immune, and histological responses of Nile tilapia (*Oreochromis niloticus* Linnaeus, 1758) to lead, mercury, and pendimethalin exposure: individual and combined effects. *Environmental Sciences Europe*, 37(1):11. <https://doi.org/10.1186/s12302-024-01047-9>
- Refaey, M.M.; Zghebr, F.E.; Mansour, A.T. and Mehrim, A.I.** (2025). Effect of different aquaculture systems on chronic hypoxia tolerance in Nile tilapia, *Oreochromis niloticus*: growth rate, physiological responses, oxidative stress biomarkers, and flesh quality. *Aquaculture International*, 33(2):130. <https://doi.org/10.1007/s10499-024-01799-4>
- Reinthal, P.N. and Konings, A.** (1991). Ad Konings’s Book of Cichlids and All the Other Fishes of Lake Malawi. *Copeia*, 1991(4):1165. <https://doi.org/10.2307/1446130>
- Rodriguez-Barreto, D.; Rey, O.; Uren-Webster, T.M.; Castaldo, G.; Consuegra, S. and Garcia de Leaniz, C.** (2019). Transcriptomic response to aquaculture intensification in Nile tilapia. *Evolutionary Applications*, 12(9): 1757–1771. <https://doi.org/10.1111/eva.12830>
- Salzburger, W.** (2018). Understanding explosive diversification through cichlid fish genomics. *Nature Reviews Genetics*, 19(11):705–717. <https://doi.org/10.1038/s41576-018-0043-9>
- Schofield, W.; Slack, T.; Peterson, M.S. and Gregoire, D.R.** (2007). Assessment and control of an invasive aquaculture species: An update on Nile tilapia (*Oreochromis niloticus*) in coastal Mississippi after Hurricane Katrina. Mississippi-Alabama Sea Grant Consortium Technical Report, <https://trace.tennessee.edu/>
- Shoko, A.P.; Limbu, S.M.; Mrosso, H.D.J. and Mgaya, Y.D.** (2015). Reproductive biology of female Nile tilapia *Oreochromis niloticus* (Linnaeus) reared in

monoculture and polyculture with African sharptooth catfish *Clarias gariepinus* (Burchell). *SpringerPlus*, 4:1027. <https://doi.org/10.1186/s40064-015-1027-2>

Trewavas, E. (2013). *Tilapia aurea* (Steindachner) and the status of *Tilapia nilotica exul*, *T. monodi* and *T. lemassoni* (Pisces, Cichlidae). *Israel Journal of Zoology*, 13:258–276. (Originally published in 1965; republished 2013.)

Turner, G.F. and Robinson, R.L. (2000). Reproductive biology, mating systems and parental care. In: “Tilapias: Biology and Exploitation.” M.C.M. Beveridge and B.J. McAndrew (Editors), *Springer Netherlands, Dordrecht*, pp. 33–58. https://doi.org/10.1007/978-94-011-4008-9_2

Urbano, T.; Velásquez, P.; Lodeiros, C. and Maeda-Martínez, A.N. (2024). Reproductive parameters of *Oreochromis mossambicus* in Laguna de Los Patos, Cumaná, Venezuela. *Brazilian Journal of Biology*, 84: e282485. <https://doi.org/10.1590/1519-6984.282485>

Vajargah, M. F. (2021). A review of the physiology and biology of Nile tilapia (*Oreochromis niloticus*). *Journal of Aquaculture & Marine Biology*, 10(5): 244–246. <https://doi.org/10.15406/jamb.2021.10.00328>

Winemiller, K.O. and Kelso-Winemiller, L.C. (2003). Food habits of tilapiine cichlids of the Upper Zambezi River and floodplain during the descending phase of the hydrologic cycle. *Journal of Fish Biology*, 63(1):120–128. <https://doi.org/10.1046/j.1095-8649.2003.00134.x>

Xu, J.; Liu, Y.; Cui, S. and Miao, X. (2006). Behavioral responses of tilapia (*Oreochromis niloticus*) to acute fluctuations in dissolved oxygen levels as monitored by computer vision. *Aquacultural Engineering*, 35(3):207–217. <https://doi.org/10.1016/j.aquaeng.2006.02.004>