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Ecological niche and life-history traits of redbelly tilapia (*Coptodon zillii,* Gervais 1848) in its native and introduced ranges

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Abstract – Redbelly tilapia (*Coptodon zillii*) is a member of a group of fishes in the Cichlidae family endemic to the northern half of Africa and the Middle East. In the literature, the name *C. zillii* is mostly associated with a negative impact on the ecosystem and biodiversity in the areas to which it was introduced. In its native range, it is not a much-appreciated fish species from both fisheries and aquaculture perspectives because of its small size and difficulty to catch when compared to Nile tilapia, *Oreochromis niloticus*. Although *C. zillii* has several desirable aquaculture traits such as feeding at lower trophic levels, high fecundity, saltwater and cold tolerance, the attempts to capitalize on this potential are lacking. Moreover, comprehensive studies that characterize its ecological niche in its native range and adaptive mechanisms of invasiveness in introduced areas are also limited. Notwithstanding, it is a species of invasion concern that requires continuous monitoring and implementation of mitigation actions in non-native regions. Compilation of information regarding the environmental requirements, feeding, and reproductive biology of *C. zillii* may serve as a starting ingredient for further research and management of its invasiveness, which is highly required in the face of freshwater ecosystem modifications as a result of climate change. This paper also addresses the current state and potential of *C. zillii* for utilization in capture fisheries and fish farming.

Keywords: Redbelly tilapia / freshwater invasion / non-native range / biocontrol and fisheries

1 Introduction

Redbelly tilapia (*Coptodon zillii*), formerly known as *Tilapia zillii,* is a fish species in the Cichlid family, which is native to the northern half of Africa and some areas in the Middle East (Philippart and Ruwet, 1982). Its former name was changed after a molecular systematics study by Dunz and Schliewen (2013), which resulted in the taxonomic revision of the group of Cichlid fishes collectively called "Tilapia". The native range of *C. zillii* includes the southern coast of Morocco, the Senegal River, Niger-Benue system, Volta System, Chad basin, and the Congo River basin in the northern and central part of Africa, and most of the Nile River basin as well as lakes such as Turkana and Albert in the northeastern part of Africa (Fig. 1). In the Middle East, it is naturally distributed along the coast of Israel, Jordan River system and Lake Kinneret (Trewavas, 1982; Philippart and Ruwet, 1982; Froese and Pauly, 2022). A comprehensive list of its native range is not available because of the difficulty to morphologically distinguish it from other closely related species (e.g., *Coptodon rendalli* or redbreast tilapia) which share the same native range, for instance, in the Congo River basin (Trewavas, 1982; Welcomme, 1988; Thys van den Audenaerde, 1998).

Currently, it is widely distributed both within Africa and elsewhere and has become an established species in many countries around the world because of deliberate and unintentional introductions for the purpose of aquatic weed control or fisheries enhancement (Philippart and Ruwet, 1982; Platt and Hauser, 1978; Roozbhfar et al., 2014; Fig. 1). Despite its widespread introduction within Africa, reports on its contribution to fisheries remain largely obscure, probably due to inefficient collection of production data (e.g., reporting all tilapias as a single entity or no reporting altogether) (FAO, 2018). The status and potential of *C. zillii* in fisheries and aquaculture in its native range are covered in Section 4.

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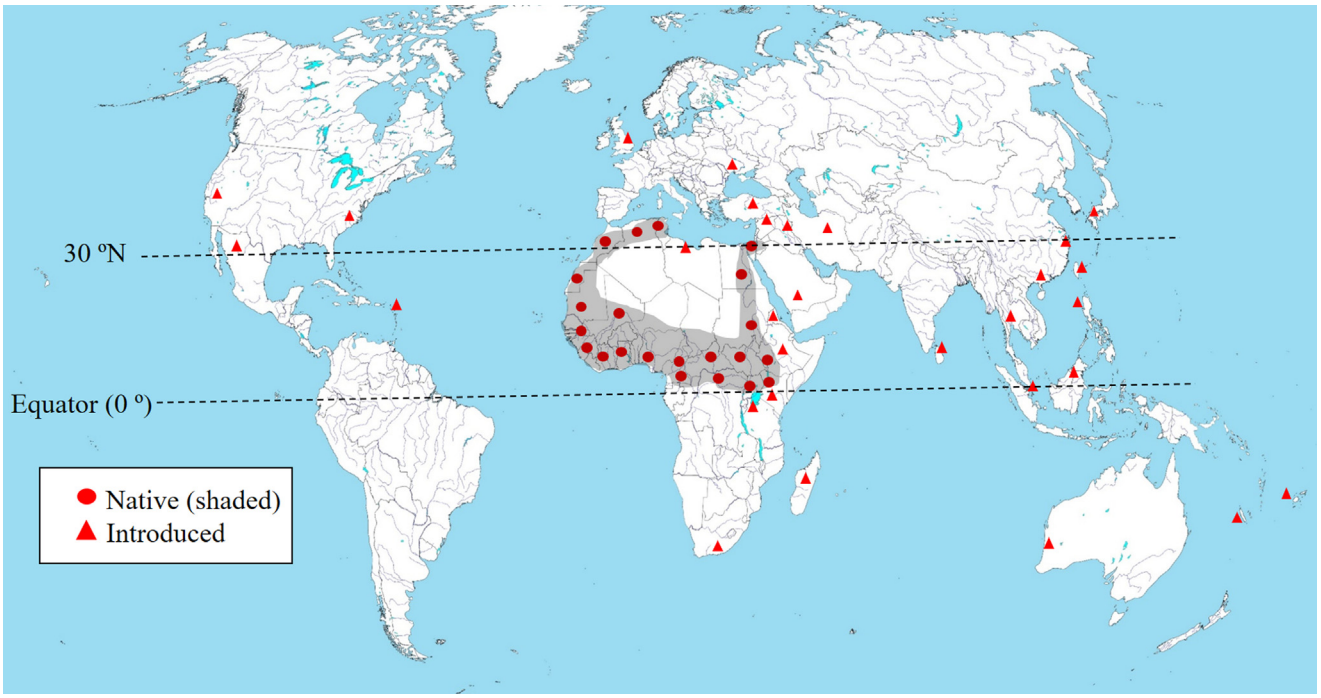

Fig. 1. *C. zillii* native and non-native distributions (Welcomme, 1988; De et al., 2004 De Silva et al., 2004; Tarkan, 2022). For year of introduction and purpose of introduction, see Tarkan (2022).

In general, between 1950–1980s, the introductions of tilapias was commonplace, mainly because of their wide range of environmental tolerances and feeding at lower trophic levels (Geletu and Zhao, 2022). It was in the later years, the trade-offs associated with tilapia introductions have become a topic of concern among aquatic ecologists and fishery managers (Deines et al., 2016). *C. zillii* is a hardy fish and is considered a potential competitor of native fish species for food and spawning areas (Tarkan, 2022; Costa-Pierce, 2003). Hence, several countries have reported its detrimental impacts on native fish species and ecosystems after introductions (Costa-Pierce, 2003; Gu et al., 2018b; Nico et al., 2019). Life-history traits and adaptive plasticity are among the main factors contributing to invasiveness and are important for predicting the invasive potential and associated risks of a species before introduction (Olden et al., 2006; Rosecchi et al., 2001; Liu et al., 2017; Lawson and Hill, 2022), especially if supported by information from studies such as epigenetics (Gozlan et al., 2020).

In recent years, the global introductions and distributions of tilapia have faced the dilemma of native biodiversity conservation and economic gain (Deines et al., 2016). Nile tilapia, *O. niloticus*, which contributes to about 80% of tilapia aquaculture production (FAO, 2018), remains as the species of choice for addressing the issue of food security and income generation for local communities in many countries around the world (Geletu and Zhao, 2022; El-Sayed and Fitzsimmons, 2023). However, economically less relevant species such as Mozambique tilapia, *O. mossambicus* (listed among the 100 worst invasive species in the world), and *C. zillii* are often associated with negative impacts on ecosystems in non-native regions (Deines et al., 2016; GISD, 2023). Given the recent phenomenon of climate change, which causes warmer water temperatures, alters existing freshwater ecosystem dynamics, and has a tendency to favor invasive species proliferation and expansion, active monitoring of such species to detect the signs of range expansion and its effect on local ecosystem health is required for the implementation of appropriate mitigation measures (Rahel and Olden, 2008; Rahel et al., 2008; Moyle et al., 2013; Britton, 2022).

In this review, the ecological niche characteristics and life-history traits of *C. zillii* in its native range and introduced areas are briefly discussed. In addition, reports on the use of *C. zillii* for aquatic weed control, its adverse impact on native species, and its current status and potential in contribution to fisheries and aquaculture are assessed. Furthermore, this review criticizes the gap related to the management of *C. zillii* invasiveness and suggests the implementation of an all-encompassing management approach for sustainable utilization as well as the elimination of its detrimental impacts.

2 *C. zillii* in native range

2.1 Habitat and environmental requirement

C. zillii is a highly adaptable fish that is known to tolerate and thrive under a wide range of water quality and environmental conditions (Froese and Pauly, 2022). Naturally it can be found in lakes, rivers, wetlands, estuaries, and in a few cases in marine habitats. Usually, it inhabits shallow vegetative areas in tropical Africa; however, it can also live over sand, mud, or rocks. Since *C. zillii* is of riverine origin as are other tilapias, their physiologies are not adapted to descend deeper into lakes, and are caught within a depth of 1–7 meters in a littoral zone (Philippart and Ruwet, 1982). Fry usually inhabits marginal vegetation, whereas juveniles are found in seasonal floodplains (Tarkan, 2022; Froese and Pauly, 2022). *C. zillii*

Table 1. Environmental requirements and tolerance ranges of *C. zillii* in its native range (some extreme conditions are reported only from experimental studies).

Physical/ chemical parameter	Tolerance range	Optimum range	Adverse effect in extreme conditions	References\
Temperature	6.5–42.5 °C	25–30 °C	In low temperatures (below 11 °C), feeding stops, vulnerability to disease increases, mortality occurs Minimum temperature for reproduction is 20 °C	Philippart and Ruwet (1982); Gophen, (2016)
pH	6–9	–		Froese and Pauly (2022)
Salinity	0.16–45 ppt	–	Established in the Red Sea, and Lake Qarun of Egypt (salinity 36–45 ppt), but the fish is considered a freshwater fish since almost all of its native distributions are in freshwater, and no reproduction occurs in seawater	Philippart and Ruwet (1982); El-Sayed (2006)
Dissolved oxygen	0.1–40 mg. L^{-1}	–	Most tilapias are known to tolerate very low DO level (as low as 0.1–0.5 mg. L^{-1}) as well as high level of CO_2 for varying period of time	Chervinski and Hering (1973); Philippart and Ruwet (1982); El-Sayed (2006)
Turbidity	–	–	Generally, tilapias are tolerant to high turbidity and resistant to water pollution by toxic substances	El-Sayed (2006)

predominantly occurs in tropical climates where the average water temperature is between 25 and 30 °C. This fish species is known to be one of the most salt-water tolerant species among tilapias, which can thrive in salinities as high as 45 parts per thousand (ppt), and it can withstand a pH range between 6 and 9 (Philippart and Ruwet, 1982; Tarkan, 2022). Physical and chemical tolerance ranges of *C. zillii* along with some reported adverse effects under sub-optimal conditions are summarized in Table 1.

2.2 Food, feeding habits, and natural predators

C. zillii is primarily considered as an herbivorous fish that feeds on aquatic macrophytes, terrestrial plant leaves that fall into the water, filamentous algae, and diatoms which comprise more than 80% of its diet (Philippart and Ruwet, 1982; Gownaris et al., 2015; Nico et al., 2019). However, several studies have indicated that the fish also consumes blue-green algae, zooplankton, crustaceans, insects, and fish eggs, particularly when aquatic plants are scarce (Philippart and Ruwet, 1982; Gophen, 2016; Nico et al., 2019). Generally, in larger individuals, animal-based diets constitute a higher proportion of the consumed food (Nico et al., 2019). The feeding characteristics of *C. zillii* can be highly influenced by the type of food available, the accessibility of food organisms, and the presence or absence of competing species (Philippart and Ruwet, 1982; Tab. 2).

Moreover, the feeding characteristics of *C. zillii* can vary in different seasons, especially in temperate/subtropical regions, where there are significant changes in species composition that occur in waterbodies. In subtropical regions, for example, Israel, *C. zillii* mainly feed on algae, insects, insect larvae, and pupae in winter and spring, and feed on zooplankton (Cladocera) in summer and autumn seasons (Spataru, 1978; Philippart and Ruwet, 1982). The types of food consumed by breeding and non-breeding adults may also vary. Breeding individuals remain in close vicinity to their eggs or larvae to provide protection, and therefore feed on benthic organisms. As such, feeding is not interrupted during breeding seasons. Non-breeding adults mostly capture prey from the surface in open waters (Philippart and Ruwet, 1982).

As a substrate spawner (guarder), *C. zillii* eggs and fry are more vulnerable to natural predators than mouth-brooding tilapia. Hence, fertilized eggs and fry are vulnerable to natural predators such as catfish (*Clarias gariepinus)*, Mozambique tilapia (*Oreochromis mossambicus)*, largemouth bass (*Micropterus salmoides*), and bluegill (*Lepomis macrochirus*), despite the efforts of protection by parent fishes (Crutchfield et al., 1992; Legner and Bellows, 1999; Yongo et al., 2020). Moreover, juvenile and adult *C. zillii* are prey for predatory fish species, including *Lates niloticus, Micropterus salmoides, Carasobarbus canis, Gymnarchus niloticus,* and *Mormyrops anguilloides,* in their native range (Tarkan, 2022; Froese and Pauly, 2022).

2.3 Conditions required for reproduction and development

C. zillii is a substrate spawner exhibiting a monogamous pair (during breeding season) and bi-parental guarding behavior (GISD, 2008; Nico et al., 2019). Its eggs and larvae are in close association with the substrate, since there is no mouth-brooding, in contrast to some related tilapia species (Tarkan, 2022; Froese and Pauly, 2022). In tropical systems,

Table 2. Studies on diets of *C. zillii* in different lakes and reservoirs in Africa and the Middle East.

Waterbody	Type of consumed food	Remarks	References
Lake Turkana, Kenya/Ethiopia	Insects and high trophic level zooplankton Macrophytes and Epilithic algae	Phytoplankton is rarely consumed Predominantly macrophytes	Sharapi (2022) Gownaris et al. (2015)
Lake Ziway, Ethiopia	Macrophytes, detritus and phytoplankton	Insects and zooplankton are also detected, but constitute less than 10% of the consumed food	Dadebo et al. (2014) Negassa and Prabu (2008)
Lake Nasser, Egypt	Detritus, plant, diatoms, zooplankton and insects	Green algae and blue green algae are also observed but in smaller proportions	Kariman et al. (2020)
Lake Ayamé, Côte d'Ivoire	Macrophytes, insects and mollusks parts	Food of plant origin constitute larger proportion	Shep et al. (2013)
Lake Kinneret, Israel	Algae, macrophytes and invertebrates	About half of consumed food is an arthropod	Spataru (1978)
Nile River Canal, Egypt	Macrophytes, algae, insect larvae and crustacean	More than 90 % of the consumed food is from macrophyes and algae	Khallaf and Alne-na-ei (1987)
River Otamiri, Nigeria	Aquatic plants, algae and insect larvae	Aquatic plants observed only in adults	Agbabiaka (2012)

Table 3. Reported breeding seasons and condition of breeding grounds of *C. zillii* in Africa and the Middle East.

Waterbody	Geographical region	Breeding season	Remarks	References
Lake Naivasha, Kenya	Tropical	Year round	Little seasonal variation in the intensity	Philippart and Ruwet (1982)
Lake Ziway, Ethiopia	Tropical	Year round	Peak activity during rainy season (between April and September)	Negassa and Getahun (2003)
Lake Ayata, Algeria	Subtropical	March–August	Peak in the month of June	Rabie et al., (2021)
Lake Qarun, Egypt	Subtropical	May–November	Hottest months of the year	Philippart and Ruwet (1982)
Lake Kinneret, Israel	Subtropical	April–August	Breeding in shallow sheltered and non-sheltered places	Bruton and Gophen (1992)

it is known to breed year-round, particularly when the water temperature is above 20 °C, but breeds only during hot or summer season in the subtropical waters (Bruton and Gophen, 1992; Rabie et al., 2021; Tab. 3). In subtropical waters (e.g., Lake Qarun), cold temperatures inhibit breeding during certain parts of the year, and the breeding season starts during the hottest times of the year (Philippart and Ruwet, 1982). In the northern part of its native range, the peak season of spawning coincides with times of maximum day length and water temperature (Coward and Bromage, 2000).

Mature individuals start mate selection and courtship when the water temperature exceeds 20 °C. The male establishes a territory, clears the area, and displays it to various females to attract one of them during the breeding season (Bruton and Gophen, 1992). Both of the parents participate in completion of the nest-building process, constructing small (20–25 cm in width and 5–8 cm in depth) saucer-shaped nests with bottoms containing sand, pebbles, or ample vegetation. Nests are constructed in shallow waters with depths not exceeding 2.5 meters (mostly 1.5 meters) (Bruton and Gophen, 1992; Tarkan, 2022).

Green, sticky, and interconnected eggs with a diameter of 1–2 mm are laid directly on the substrate within the constructed nest, and then the male fertilizes them externally. A single female is known to produce between 1000 and 6000 eggs in one spawning period (Coward and Bromage, 2000; Tarkan, 2022; Nico et al., 2019). However, observations under laboratory conditions indicate that the number of eggs produced in a single round of spawning is directly related to the size of the female (i.e., larger females produce more eggs than smaller ones) (Coward and Bromage, 2000). After fertilization, both parents guard and fan the eggs for oxygenation, and later feed on unfertilized eggs. In a breeding ground, several pairs of fish may breed near each other, forming a colony (Bruton and Gophen, 1992). The embryos hatch after 2–3 days of incubation and are then transferred by mouth or fin fanning to a nearby depression until the yolk sac is absorbed (usually 3–4 days after hatching). The larvae and

juveniles are guarded for approximately a month, and then another round of reproduction may occur, if conditions are favorable (Bruton and Gophen, 1992; Froese and Pauly, 2022).

The patterns of nesting and guarding behaviors can vary significantly between different habitats. In habitats with heavy waves, no vegetation and rocky bottoms/substrates, nest construction and guarding can be minimal. In such cases, larvae are fully independent within 2–3 days after hatching (Bruton and Gophen, 1992; Nico et al., 2019). On sandy or muddy substrates, brood care is usually interrupted during strong wave actions, and larvae swim into deep water to seek shelter and avoid predators (Bruton and Gophen, 1992). Generally, the guarding of eggs and juveniles is high in sheltered habitats and low in habitats without shelters or strong waves. Sheltered habitats provide the advantage of avoiding predators for adults and increase the survival rate of juveniles (Bruton and Gophen, 1992; GISD, 2008).

3 *C. zillii* in introduced areas

3.1 Interactions with other fish species in introduced areas within Africa

In its native range and introduced places, *C. zillii* has become an important component of an ecosystem. This is in part because of its high reproductive success and abundance in shallow vegetated waters, which results in competition for space and limits the availability of breeding grounds for other less-competitive fish species (Bruton and Gophen, 1992). Owing to its less selective and voracious feeding habits, *C. zillii* is often considered harmful to other commercially important species. By feeding on insect pupae, it diminishes the biomass of insects (Chrominids), which are a source of food for commercially valuable benthivorous fish species, such as common carp (Spataru, 1978). In addition, hybridization of *C. zillii* with related tilapia species (e.g., *Coptodon guineensis*, *C. rendalli*) may negatively affect local genetic diversity (Adépo-Gourène et al., 2006; Nico et al., 2019).

The introduction of a given tilapia species to a vacant ecological niche or a waterbody without other tilapia species or a species that is not vulnerable due to competition (e.g., *O. niloticus*) could be considered beneficial for fisheries enhancement when the translocated species is within its natural/native distribution range. However, this requires utmost caution and could be more suited to confined manmade waterbodies, such as dams and reservoirs. For fisheries and aquaculture purposes, the introduction of other tilapia species could be considered, but the selection process of a species to be introduced needs to account for factors such as the native range, presence or absence of competitive species, and overall condition of the receiving ecosystem (Lind et al., 2012).

The failure of introduction into waterbodies with other indigenous tilapia species can be exemplified by the introduction of *C. zillii* into Lake Victoria which is believed to have outcompeted and supplanted a native tilapia species, *Oreochromis viriabilis,* particularly by winning over breeding and nursery grounds (Lowe-McConnell, 1982; Philippart and Ruwet, 1982). However, it is important to mention other contributing factors for the disappearance of *O. viriabilis* because there are several species (e.g., Nile Perch, *Lates niloticus* and Nile tilapia, *O. niloticus*) that were introduced into Lake Victoria before the disappearance of *O. viriabilis* from the lake (Ogutu-Ohwayo, 1990; Twongo, 1995; Goudswaard et al., 2002;). Hybridization with introduced *O. niloticus*, overfishing, habitat degradation, and competitive dominance of introduced species are among the factors that may have contributed to the disappearance of *O. viriabilis* from Lake Victoria (Ogutu-Ohwayo, 1990; Twongo, 1995; Geletu and Zhao, 2022).

In contrast, elsewhere, populations of *C. zillii* have been negatively affected by other introduced invasive species, such as the common carp (*Cyprinus carpio*). In Lake Naivasha, Kenya, *C. zillii* has been among the major contributors to the catch from the lake, after it was introduced in 1956 to enhance fisheries production of the lake. After the accidental introduction of *C. carpio* in 1998/9, the catch contribution of *C. zillii* diminished (Hickley et al., 2004; Oyugi et al., 2011). It is speculated that this could be due to the alteration of the existing ecosystem by *C. carpio,* which may have resulted in competition for food as well as destruction of shelter and breeding grounds used by *C. zillii* (Mutethya and Yongo, 2021).

3.2 Feeding and reproduction (non-native regions)

Non-native regions into which *C. zillii* has been introduced include southeastern Asia, western Asia, western Australia, South Pacific Islands, USA, Europe and the Caribbean regions (Fig. 1). Most of the introductions took place between the 1950s and 1980s by government institutions, universities, and private companies for purposes such as aquatic plants and insects/mosquitoes control, evaluation of its aquaculture potential, and recreational fishery (Costa-Pierce, 2003; De et al., 2004 De Silva et al., 2004; GISD, 2008; Tarkan, 2022; Innal and Giannetto, 2017). There are a few reports on feeding habits and reproductive or life-history traits of *C. zillii* from its introduced areas, despite its widespread presence and ecological importance.

A report from the Shadegan wetland, Iran by Bavali et al. (2022) indicated macrophytes as the main consumed food along with a small proportion of food from animal origin and also indicated peak reproductive activity in the months of February, May, and September. Mohamed and Al-wan (2020) reported the presence of a higher proportion of detritus (44.6%) among the food ingested by *C. zillii* followed by algae (19.9%), macrophytes (19.7%) and diatoms (13.3%), and spawning season extending from April to June in Garmat Ali River, Iraq. The peak reproductive period in southern China is known to be between May and October (He et al., 2013). The variation in the feeding habits of *C. zillii* in these waterbodies could be attributed to the differences in the available food organisms and the ability of the fish to adapt to different feeding habits, depending on food availability and environmental conditions (Dill 1983; Wright et al., 2010).

3.3 Consequences of introductions

The trans-regional introductions of *C. zillii* into natural waterbodies have resulted in unintended consequences in many aspects (Philippart and Ruwet, 1982; Costa-Pierce, 2003). The introduction of *C. zillii* in California, USA, as a

biological control agent to control invasive aquatic weeds that clog irrigation canals, did not result in the anticipated outcome. The fish introduced in the first round were unable to establish themselves and have disappeared, those introduced during the second round have also become vulnerable to cold temperatures, and only those in the southern part have survived. In this region, *C. zillii* feeds on aquatic weeds only during the warm season and is also implicated in the decline of native killifish, *Fundulus lima,* and desert pupfish, *Cyprinodon macularius,* probably because of competitive interactions for habitat and breeding grounds (Varela-Romero et al., 2002; Costa-Pierce, 2003; Andreu-Soler and Ruiz-Campos, 2013). After unintentional introduction to a power plant reservoir in North Carolina, USA, it has eliminated aquatic macrophytes (Brazilian waterweed*, Egeria densa*) within 2 yr and has become one of the dominant fish species within 3 yr (Crutchfield, 1992). It is also implicated in the destruction of breeding grounds and declines in native fish species in the area (Crutchfield, 1995; Canonico et al., 2005; Cassemiro et al., 2018).

Moreover, negative impacts on ecosystems (e.g., degradation of water quality and decline of native fish communities) after introductions have been reported or mentioned from countries such as Iran (Bavali et al., 2022), Iraq (Mohamed and Al-wan, 2020), Japan (Ishikawa and Tachihara, 2008) and China (Gu et al., 2016; Xiong et al., 2022). However, details on the level of damage caused to the aquatic environment involved and the specific species affected remain largely unknown. Moreover, persuasive recommendations for its management have not yet been provided.

3.4 Management and control of invasiveness

The most effective way to manage non-native species invasiveness begins with the prevention of introductions, which is based on the precautionary principle, with the main aim of conserving local biodiversity (Vitule et al., 2009). Another alternative that is usually chosen by managers is the introduction of the non-native species first, and then taking actions to mitigate the impact (Gozlan et al., 2010). In an attempt to find a middle ground for both approaches, Gozlan et al. (2010) devised a guideline for the introduction of alien freshwater fish species, which involves pre-introduction screening of invasiveness (for decision on introduction or no introduction), and subsequent follow-up and taking remedial actions, such as eradication or control of expansion, if invasion occurs. More recently, WorldFish has started utilizing an integrated approach of risk assessment, which involves ecological, genetic, and pathogen risks to the receiving ecosystem before the dissemination of its genetically improved farmed tilapia (GIFT) strain, although this is strictly for aquaculture purposes (Amarasinghe, 2021; Arthur, 2021; Bartely, 2021). In general, the introductions of tilapias (including *C. zillii*) into non-native areas have been taking place in the absence of adequate studies on receiving aquatic ecosystems (Canonico et al., 2005). In most cases, negative consequences, such as prolific reproduction and rapid expansion and colonization of vast waterbodies, resulting in disturbance of native biodiversity and community structure, have been reported after introductions (Gu et al., 2018). This makes it difficult to conclude whether the ecological impact has occurred only because of the introduced tilapia species or other factors such as anthropogenic activities or climate change, since environmental disturbances are known to make native species vulnerable and facilitate invasion (Bernery et al., 2022).

In addition, most studies conducted on the ecological impact of tilapias in their introduced range, failed to include other contributing factors such as climate change, pollution, and fishing pressure on the reported ecological changes; hence, the perception of portraying tilapia as an invasive species to its introduced range remains disputed (Gozlan et al., 2008; Gozlan et al., 2010; Deines et al., 2016; Xiong et al., 2022). Obtaining more reliable information appears rather unattainable in the presence of widespread opinion about the negative ecological impacts of tilapia introductions without giving due credit to the contribution of tilapias in improving animal protein intake and serving as a source of income for low-income communities around the world (Canonico et al., 2005; Deines et al., 2016). Nevertheless, this is not to undermine the level of impact of introduced tilapias in general and *C. zillii* in particular, especially considering the strong correlation between introductions and the decline of native species (Crutchfield, 1995; Canonico et al., 2005). However, it is to advocate for more holistic research so that the true magnitude of the impact can be revealed and utilized for a better-informed decision in future management actions.

Yet, many conservation ecologists suggest that the ecological impact following any kind of non-native fish species introductions cannot be fully avoided, even if the effects are not apparent, they are waiting to be revealed (Gozlan et al., 2010). In some cases, introductions have been made to control invasive aquatic weeds, for example, in Southern California, USA (Costa-Pierce, 2003). However, these decisions relied on limited information about the introduced fish species and the receiving ecosystem. As it has been revealed over the course of time, important questions such as whether *C. zillii* can consume a particular plant species in the area, whether its introduction will impact native species, and whether it can adapt to the new habitat were not properly addressed before the introductions (Abdel-Tawwab, 2008; Costa-Pierce, 2003).

Currently, there are more resources and information available at the disposal of decision-makers; therefore, the possibility of making more informed decisions is high, only if all concerned bodies participate in the process. For instance, if the presence of *C. zillii* is deemed unnecessary and if its removal/reduction would benefit the ecosystem to which it has been introduced, options such as stocking with native fish species that have a competitive advantage over *C. zillii* can be considered. In Lake Naivasha, the introduction of common carp, *C. carpio* was implicated in the reduction of *C. zillii* abundance, although this finding was not from direct investigation (Yongo et al., 2022). However, the use of *C. carpio* as a biological control agent may not be a good alternative because it is also one of the most powerful invaders capable of degrading freshwater habitats, especially in the introduced range, albeit it can be a good alternative for increasing capture production (Britton et al., 2007; Piczak et al., 2023; Mutethya and Yongo, 2021). Although its feasibility and effectiveness is questionable, attracting *C. zillii* by releasing warm water to a location where they can be caught

during winter can be tried in subtropical/temperate regions (Ishikawa and Tachihara, 2008) in order to eliminate or reduce its populations. In southern California, during the winter season, *C. zillii* survives by seeking for thermal refuge around warm water produced by hydrothermal systems (Costa-Pierce, 2003). From Swan River, Western Australia, *C. zillii* was eliminated by using seine netting and rotenone in 1975 after it was observed in the same year before it became an established species (Fulton and Hall, 2014). Currently, it is known to be present in Western Australia, confined to the Chapman River, and no ecological impact has been reported (Corfield et al., 2008). Furthermore, direct removal by fishing and the use of predatory fish species as biocontrol agents may serve as an alternative strategy to control its invasion (Yongo et al., 2023).

Lastly, concomitant with climate change, an increase in winter water temperatures in temperate regions in countries such as China may favor its survival during the winter period and facilitate its expansion towards the north (higher latitude). Specifically, from the southern region of China (where it was already established), it may gradually expand its range towards the north (Gu et al., 2018a; Yongo et al., 2023). Hence, prevention of its further spread to the northern region necessitates continuous monitoring and utilization of conventional methods (e.g., direct physical removal, barrier construction, biological control, chemical control), since modern molecular techniques (e.g., genetic manipulation of sex ratio, gene editing, gene silencing) are at a relatively nascent stage for use in most invasive fish species (see Simberloff, 2021; Rytwinski et al., 2019).

4 Fisheries and aquaculture potential of *C. zillii*

The potential of *C. zillii* for capture fisheries and fish farming has not been fully explored and exploited. In larger lakes and reservoirs, it is usually confined to shallow muddy vegetated areas which is inconvenient for fishing; therefore, its contribution to fisheries is very small in its native range (Negassa and Prabu, 2008; Genner et al., 2018; Gu et al., 2018b). In Lake Kinneret, Israel, the contribution of *C. zillii* to capture fisheries is very small, and it is not appreciated by fishermen due to its small size when compared to other tilapia species (Chervinski and Hering, 1973; Spataru, 1978). In the aforementioned lake, the fish species can be captured both in near shore and in deep waters, and the reported figures of the catch may not reflect the stock proportion, since it can easily slip through the meshes of the net due to its size, and released back into the water by fishermen or sold in bulk combined with other small fish species (Spataru, 1978).

In Africa, it is known to grow to large size and is cultured in ponds for production as well as aquatic weed control (Spataru, 1978; Hepher and Pruginin, 1982). However, its growth rate is generally slower than that of other tilapia species, such as *O. niloticus* and *O. aureus,* both in natural habitats and aquaculture settings, including in its native range and introduced areas (Hepher and Pruginin, 1982; Gu et al., 2018b; Xiong et al., 2022). Both male and female *C. zillii* individuals reach sexual maturity at around 13–14 cm; however, the minimum length of sexual maturity in aquaculture ponds and some lakes can be as low as 5.1 cm (Dadzie and Wangila, 1980; Lowe-McConnell, 1982; Akel and Moharram, 2007). Obtaining mono-sex stock is also rather difficult since it requires growth to about 20–50 grams for manual sexing (Hepher and Pruginin, 1982).

Similarly, in Lake Ziway, Ethiopia, its contribution to capture production is very small when compared to that of *O. niloticus.* However, the amount of catch may not be proportional to the stock available since the fishermen mainly target *O. niloticus*, because of its size and market preference (Negassa and Getahun, 2003), and there has been no stock assessment study conducted in the aforementioned lake hitherto. Moreover, fishermen in Lake Ziway are not interested in selectively capturing *C. zillii* since it requires fishing near vegetated areas. Negassa and Prabu (2008) reported the predominance of *C. zillii* over *O. niloticus* in the catches of nearshore areas in Lake Ziway, and its rareness in open waters far away from the shore where most of the catch constitutes the latter species. In this lake, fishing activity mainly takes place in pelagic zones targeting *O. niloticus*. A small proportion of the captured *C. zillii* is sold together with *O. niloticus* at landing sites (unpublished data).

Likewise, in Lake Victoria and Lake Naivasha, *C. zillii* is seldom captured, and its contribution to these lake fisheries is limited (Yongo et al., 2021; Yongo et al., 2022). The level of its contribution to Lake Turkana fisheries is also not known since the catch of all tilapia (*O. niloticus, C. zillii,* and *Sarotherodon galilaeus*) has been reported as Nile tilapia (Gownaris et al., 2015). Furthermore, its catch from the Aswan region of the Nile River, Egypt, contributes approximately 12 %, and the remaining 88 % of the catch is from Nile tilapia (El-Bokhty and El-Far, 2014). In introduced areas, such as China, culture production of tilapia is highly dominated by *O. niloticus*, and *C. zillii* is not a desirable species by fish farmers because of its lower growth performance and lack of market demand (Gu et al., 2018a; Xiong et al., 2022).

Nevertheless, *C. zillii* could be a suitable species for aquaculture as a herbivorous fish that grows in eutrophic muddy conditions of fish ponds. So far, the level of its adaptability (e.g., acceptance of artificial feed) and growth performance under controlled conditions, such as in indoor aquaculture, are not known. Coward and Bromage (1999) reported a single female producing 11,640 eggs in a single spawning and inter-spawning period as short as one week under aquarium conditions. The fecundity of *C. zillii* is much higher than that of mouth-brooding tilapia species, including *O. niloticus*. In aquaculture, the problem of overcrowding in culture ponds can be prevented by the production of sterile or mono-sex seeds. Given its desirable aquaculture traits, such as feeding habits, fecundity, cold and salt tolerance, it has the potential to become an alternative species for tilapia aquaculture, which is currently almost entirely dependent on *O. niloticus*.

Production of hybrid seeds (e.g., *C. zillii* × *O. niloticus*) with desirable aquaculture traits specific to certain environmental conditions may also have unexplored potential, yet to be evaluated (Goni et al., 2020). Currently, a sought-after fish species, Nile tilapia, has also been less desirable for aquaculture due to the challenges related to excessive breeding in culture ponds and stunting. However, research outcomes from intensive selective breeding programs and the utilization of modern aquaculture techniques have enabled it to become

one of the most important fish species in aquaculture (Eknath and Hulata, 2009; Ponzoni et al., 2011). Overall, diverse research works in the areas of genetics, reproductive biology, breeding, nutrition, and culture conditions are required to reveal and improve the aquaculture potential of *C. zillii*.

5 Concluding remarks

The adaptability of *C. zillii* to a wide range of environmental conditions, flexibility in the type of food consumed, and high reproductive potential have enabled it to successfully establish itself, compete with native fish species, and impact ecosystems in its introduced areas (Cassemiro et al., 2018). Information on its ecological role in its native range is somewhat limited; however, in introduced areas, it can disturb freshwater ecosystem functions; for instance, by diminishing ecologically important submerged aquatic macrophytes that maintain water quality, provide shelter, and are used as spawning sites by native fish species (Cassemiro et al., 2018; Gu et al., 2019; Yongo et al., 2023). Hence, its negative effects on the freshwater ecosystems outweigh its benefits as a biocontrol agent. Moreover, *C. zillii* should not be considered for enhancing capture fisheries in non-native areas due to its slow growth and negative consequences to the ecosystem (Gu et al., 2018a). In its current state, it is not feasible to consider it for aquaculture; however, intensive research works in areas such as modern selective breeding approaches combined with genomic selection technologies may help to produce a strain with superior growth performance, which could be used in its native range (Lind et al., 2012; Houston et al., 2020; Yáñez et al., 2022).

Future research on the impacts of *C. zillii* introductions in aquatic ecosystems would provide more accurate information if they incorporate other contributing factors to change that has occurred in aquatic environments. If future introductions to new areas are sought, conducting baseline suitability assessments would help to avoid most of the failures previously encountered after introductions. For instance, understanding of the native species traits such as life-history, food habits, distribution patterns, and vulnerability to change in the ecosystem can be helpful in making decisions before the introduction of non-native species and also for impact assessment after introductions (Canonico et al., 2005). Since there is limited data available on its feeding habits and reproductive behavior from its introduced areas, more research works may help to better understand the underlying mechanisms that enabled it to adapt and successfully establish in most of its introduced areas. Genomic studies may also help to reveal the underlying genes responsible for its tolerance to a wide range of environmental conditions and could be applied to control and/or reverse invasions in non-native regions (Adrian-Kalchhauser et al., 2020; Matheson and McGaughran, 2022).

Data availability statement

No data available.

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Conflict of interest

The authors declare no conflict of interest.

Ethics approval statement

Not applicable.

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