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Salinity tolerance of fishes: experimental approaches and implications for aquaculture production.

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Abstract

The life history, distribution and diversity of fishes are largely influenced by environmental salinity. Changes in salinity affect a range of physiological processes, including metabolism, nutrition, reproduction, and growth. Therefore, fish can be conditioned to environmental parameters most suitable for production, where distinct traits are optimized through species-specific manipulation of salinities. The primary purpose of this review is to summarize the existing literature on the salinity tolerance of aquacultured fish. The various experimental approaches for determining salinity tolerance are compared, along with summarized information for key species employed in aquaculture, including their native distributions, life history stage, and optimal salinity for survival and growth. The implications for production were assessed by considering the effects of salinity on growth, reproduction, management, disease mitigation and marketability.

1. Introduction

Variations in salinity are among the physical parameters that drive the capacity of fish to survive and thrive in a range of environments; from freshwater (FW) habitats such as rivers, lakes, and marshes; to marine or seawater (SW) habitats such as coastal waters, bays, and the open ocean; to extreme environments, such as hypersaline ponds or estuaries that undergo tidal variations from FW to SW.[1] The capacity of fish to tolerate a given environmental salinity largely depends on their ability to regulate salt and water balance, or osmoregulate, and is closely tied to their life histories. To maintain hydromineral balance, fish spend significant energy on the uptake and secretion of ions in hyposmotic and hyperosmotic environments, respectively, thereby maintaining a relatively stable osmotic concentration of body fluids.[2,3] Fish inhabiting FW environments actively uptake ions and excrete copious amounts of dilute urine to counteract a passive loss of salt and gain of water, while those in SW actively secrete ions and retain water to compensate for osmotic water loss and diffusional ion gain (Figure 1). The physiological and molecular mechanisms underlying acclimation of fish to not only FW and SW steady-state environments, but also to environments characterized by frequent salinity changes, are distinct and diverse, and have been reviewed extensively elsewhere.[3-15] Reflecting these adaptive strategies, fish are capable of tolerating changes in salinities to varying extents. Based on their salinity tolerance and natural distribution, fish have been classified on a spectrum of stenohaline to euryhaline, describing narrower and broader salinity tolerance ranges, respectively.[6] Moreover, within euryhaline fishes, diadromous species spend periods of their life history in distinct salinity environments, with anadromy being characterized by spawning and larval development in FW and migration to SW in later stages, and catadromy by spawning and larval development in SW followed by subsequent migration to environments of lower salinity.[16] A comprehensive account of euryhalinity in fishes has summarized such diversity in salinity tolerance across species.[17] The evolution of salinity tolerance in fishes is believed to have occurred in a mosaic-like pattern across different taxonomic groups, with euryhalinity, for example, having evolved multiple times independently.[8,17] Here, we have categorized fish that can tolerate salinities ranging from FW to SW or higher salinity as euryhaline. Generally, most studies on the salinity tolerance and physiological responses of fishes have employed one-way salinity transfers, either in direct or gradual fashions. Additional approaches that more closely reflect how fish tolerate environments of highly variable salinities[11] or aim to investigate the genetic basis of salinity tolerance,[18,19] imprinting,[20] or inheritance of salinity tolerance traits,[21,22] have also emerged.

Understanding salinity tolerance in fishes provides fundamental information required for optimization of management, husbandry, and aquaculture production practices. In production systems where salinity varies, such as near-shore farms, understanding salinity tolerance grows ever more important as weather patterns shift. Thus, euryhaline species, for example, may become more suitable for production in such changing environments inasmuch as they possess a wider range of salinity tolerances that can facilitate environmental adaptation in face of climate change. Fish commonly employed in aquaculture can range in salinity tolerance according to species, life history stages, age,[23] and environmental temperature.[24] Moreover, the rearing salinity can maximize performance metrics such as growth, feed efficiency, reproduction, disease response, nutritional status, and palatability, or taste of the final product. Ultimately, enhancing these parameters can optimize time to market, product quality, and management of water resources.

This review summarizes the salinity tolerance of 22 commercially relevant and commonly aquacultured groups of finfish worldwide, including 52 species, as a resource that combines and synthesizes the experimental approaches (Figure 2) and practical applications over the past 40 years of study. An initial literature search was conducted combining the keywords "fish," "salinity tolerance," and "aquaculture" using the Aquatic Sciences and Fisheries Abstracts database, yielding 4,429 references up to 2023. Searches employing each common fish group name with the last two terms above were conducted, and references were further filtered according to relevance. To narrow the scope of our analysis, we targeted the Food and Agriculture Organization's list of the top 10 major finfish species globally produced each in inland aquaculture and in marine and coastal aquaculture,[25] while also considering the available literature on salinity tolerance of other, less commonly aquacultured species. Fish species were grouped by prevailing environmental salinity and by life histories characterized by distinct salinities (diadromy) to facilitate the discussion of salinity tolerance trials by direction of transfer, with FW and marine species being typically investigated for their capacity to tolerate increases and decreases in salinity, respectively. The combined and synthesized data from these references are visually summarized in Figure 3 and organized according to species and life stage.

2. Salinity tolerance

Salinity tolerance largely constrains the range of habitats where fish can grow and reproduce. In turn, this natural range of suitable salinities is important when evaluating potential aquaculture candidates. For example, understanding the hypersaline tolerance of species may be particularly relevant in regions affected by the scarcity of FW resources. Fish maintain their blood osmolality within a relatively narrow range, roughly 1/3 that of SW (~280-360 mOsm kg^{-1}) [26]. This process relies on osmoreception, or the capacity to perceive osmotic changes resulting from the passive movement of solutes and water across cell membranes to activate osmoregulatory responses that allow fish to adjust to specific osmotic demands.[27-29] The control of hydromineral balance is largely mediated by hormones, where specific endocrine systems are triggered by hypo- and hyperosmotic stimuli in species-specific manners.[11,15,30,31] As a consequence of combined endocrine action and direct osmosensing, a wide range of epithelial responses to modulate water and ion transport, mainly in gill, kidney, and intestines, are activated in fish acclimated to FW, SW, and undergoing salinity challenges.[5-8,10,12-14] These responses provide a comprehensive assessment of the adaptive strategies that different species of fish deploy when facing changes in environmental salinity, and enable salinity tolerance, typically expressed as percent survival. For the purposes of this review, the main environmental salinities discussed will be defined by FW at 0 parts per thousand (‰), SW at 35‰ unless stated otherwise, and brackish water (BW), as specified by the salinity ranging between FW and SW. Importantly, the adaptive mechanisms underlying salinity tolerance vary temporally. Fast-acting, transient cellular stress responses operate within minutes (min) to hours (h) to enable survival, while slower endocrine-mediated systemic responses require up to days (d) to facilitate acclimation into more permanent environments. Hence, in discussing the salinity tolerances of fish, it is important to outline the experimental time course and methodology employed. This information will, in turn, define salinity tolerance, which can last a few hours or indefinitely, depending on the experimental approach employed. Because of the inherent variability in defining the salinity tolerance of different species, several authors have calculated extrapolations based on survival rates following a salinity challenge, with the salinity leading to 50% mortality termed the lethal concentration 50 (LC50).[32-34] Here, studies reporting LC50 will be emphasized, as the method is useful for comparisons among species. Nonetheless, the experimental approach needs to be carefully considered when interpreting salinity tolerance data.

2.1. Approaches to determine salinity tolerance

Depending on the application, the focus of salinity tolerance studies may vary in both time and lethality of the salinity exposure. In addition to comparisons between steady-state salinities and the effects of one-way transfers to different salinities, several studies have investigated the effects of pre-exposure[35-37] and dynamically changing salinities[11] on salinity tolerance. Hybridization and, more recently, loci selection represent other approaches to studying and affecting salinity tolerance.[38-40] Here, we will discuss some of the advantages and limitations of these various approaches.

2.1.1. Steady-state comparisons

Comparing fish acclimated to two or more salinities is a straight-forward way to assess a myriad of salinity-sensitive traits. To control for species-specific traits associated with salinity tolerance, comparisons are usually made between individuals of the same species acclimated to distinct salinities. The acclimation periods prior to comparisons may range from weeks to years, or across generations, depending on the species and goal of the study, but are usually characterized by stable survivorship in groups of individuals being compared; euryhaline species typically allow for comparisons across a wider range in the salinity spectrum (i.e. FW vs SW). For example, steady-state comparisons can be useful for informing the optimal salinity for growth and resistance to disease.[41-44] The relative ease of maintaining fish in a steady-state salinity also enables long-term transgenerational studies of salinity tolerance and evolutionary insights into salinity adaptation.[45,46] Further, the consistent nature of steady-state salinity comparisons is ideal for studying the salinity-dependent effects of pollutants and other stressors on fish, especially euryhaline species. Comparing the toxicity of pollutants in fish kept at different salinities can indicate the salinity in which fish are most sensitive or resilient to the pollutant.[47] While the static nature of steady-state comparisons is advantageous for studying salinity tolerance, such comparisons may not accurately reflect all culture conditions, such as those susceptible to salinity changes due to rainfall, evaporation, and SW intrusion; especially at lower elevations.[48] Nonetheless, the insights into salinity tolerance gleaned from steady-state comparisons provide valuable information for aquaculture.

2.1.2. One-way transfers

One-way salinity transfers provide a direct way to assess the capacity of fish to tolerate a change in salinity and associated physiological responses. Rapid one-time transfers are useful in aquaculture tasks such as fish transport or disease treatment.[49] In the case of disease treatment, marine fish are often exposed to FW, with studies focusing on the duration of fish survival and recovery from the FW dip.[50] One-way transfers, between salinities suitable for long term survival, also inform the maximum rate of change that fish can tolerate between salinities. For example, the Mozambique tilapia (*Oreochromis mossambicus*) cannot survive a direct transfer from FW to SW despite having the ability to survive in hypersaline (up to 120‰) waters.[23,51] However, employing a series of one-way transfers to increase the salinity gradually, affords the study of hypersaline tolerance in fish that are often maintained in lower salinities.[6] Hence, two main approaches for conducting one-way transfers are often employed, one in which salinity is gradually changed from high to low or vice-versa (Figure 2A), and another where multiple direct transfers are conducted to investigate tolerances to low or high salinities (Figure 2B). In both cases, survival over time is often used as an outcome of salinity tolerance to various challenges (Figure 2C). One-way transfers can be more resource-intensive relative to steady-state comparisons if terminal sampling is required to collect data. Since multiple fish are sampled at multiple time points following transfer to capture the changes occurring during acclimation,[36] these experiments often require more fish and resources. Further, one-way transfer experiments also fail to capture the dynamic nature of natural salinity fluctuations, such as in estuarine environments or exposed ponds.

2.1.3 Pre-exposure

Early exposure to different salinities has been widely used to determine later effects on fish growth, development, and salinity tolerance of fish. The stages of development typically employed in early exposure experiments comprise eggs, sperm, embryos, and larval stages.[52-56] These early growth stages of fish could be exposed to different salinities to increase salinity tolerance and enhance other beneficial effects (Figure 2D). For example, exposure to different salinities alters fertilization, survival, and normal development of fish eggs.[57] In FW species, such as the Nile tilapia (*O. niloticus*), an elevation in salinity has been associated with a delay in hatching time, even though the larvae had increased salinity tolerance.[58] In contrast, both egg fertilization and sperm motility of the SW black bream (*Acanthopagrus butcheri*) were reduced at 5‰ while low egg hatchability, low larval survival, and high larval deformities were observed in salinities below 15‰.[59] In addition to reproduction, early exposure to different salinities can affect fish growth and development. Juvenile Atlantic salmon (*Salmo salar)* acclimated to FW increased growth hormone (GH) levels following exposure to SW.[60] Similarly, early exposure to high salinities increased growth performance in puffer fish (*Takifugu rubripes*) and Mozambique tilapia,[61,62] while striped catfish (*Pangasianodon hypophthalmus*) larvae reared in 5–10‰ showed higher tolerance to thermal stress than the fish reared in FW.[63] Early exposure to changes in salinity may, therefore, confer greater adaptive capacity.

2.1.4. Dynamically changing salinities

Coastal ecosystems such as estuaries can be characterized by frequently changing salinities in response to tides. Consequently, the fish species that live in those waters tend to be euryhaline, surviving and thriving in a wide range of salinities. In order to investigate the salinity tolerance of estuarine fish, researchers have simulated tidal environments, where the salinity periodically changes (Figure 2E). Mozambique tilapia reared in a tidal regimen (TR), characterized by dynamic changes between FW and SW every 6 h, were able to compensate for the large changes in salinity while maintaining their osmoregulatory parameters within a narrow range.[64] Interestingly, Mozambique tilapia reared in a TR grew faster than those in steady-state salinities, in part through the activation of the GH/IGF system, while maintaining a similar or lower feed conversion ratio (FCR) compared with fish reared in steady-state FW or SW.[41,65] Moreover, Mozambique tilapia reared in a tidal environment since larval stages were able to acclimate to direct and sustained transfer to SW as adults.[36] Other studies have shown that to survive a FW to SW transfer, this species requires a gradual change in salinity, typically a direct exposure to BW (25‰) for 48 h prior to a transition to SW.[23,36,66] Recently, it has also been found that Mozambique tilapia acclimated to steady-state FW or SW could successfully acclimate to a TR, showing similar adaptive responses as fish reared in TR from larval stages.[67] However, age also affects the salinity tolerance during these transitions, resulting in a decline of salinity tolerance in older fish.[23] Collectively, these studies employing a TR show that experimental simulation of salinity regimes that most closely approximate those of the native ecological distribution of the species under study may provide the most accurate assessment of their physiological capacity. Nevertheless, despite the adaptive and growth advantages observed in Mozambique tilapia reared in a TR compared with fish reared in steady-state salinities, the continuous maintenance of a TR system is costlier and more complex compared with steady-state salinity systems, and a TR is unsuitable for recirculating systems. Pre-exposing larval fish to dynamically changing salinities, however, may serve as a strategy to facilitate adaptive capacity to future environmental challenges.

2.1.5. Crossing and hybridization

Hybrid crosses have been used to examine the role of parental sex and species on inherited salinity tolerance, which in some cases resulted in differences between parental strains and their hybrids (Figure 2F). In comparing the salinity tolerance of Nile, Mozambique, and hybrid tilapia, it was reported that while there was no difference in survival between hybrid and Mozambique tilapia (99% and 98%, respectively), only ~68% of Nile tilapia survived a 30‰ challenge.[68] Offspring produced by crossing between different populations can exhibit enhanced salinity tolerance compared with parental strains as a result of heterosis. In guppies (*Poecilia reticulata*), F1 crosses between parental strains and their offspring resulted in offspring surviving longer following a transfer from FW to SW compared with both parental strains.[69] Crossing between fish populations adapted to different environments can also affect salinity tolerance. F1 offspring produced by crossing amphidromous ayu (*Plecoglossus altivelis*), which migrate between FW and SW during growth stages, and landlocked ayu, had an intermediate salinity tolerance compared with the purebred populations.[70]

A comparison between sunshine bass (male striped bass, *Morone saxatilis* × female white bass, *M. chrysops*) and palmetto bass (male white bass × female striped bass) revealed similar salinity tolerances, with a 24 h LC50 of ~28‰.[71] In flounder, however, it was shown that salinity tolerance was affected by parental sex. The FW tolerance of starry flounder (*Platichthys stellatus*), stone flounder (*Kareius bicoloratus*), and their reciprocal hybrids (female starry flounder × male stone flounder as hybrid Sb, and male starry flounder × female stone flounder as hybrid Bs) revealed that starry flounder exhibited relatively high survival (44% and 100%), followed by hybrid Bs (40% and 60%) and hybrid Sb (23.6% and 88%) at juvenile and immature stages, respectively. Stone flounder, in contrast, did not survive the challenge at both life stages.[72] Therefore, the effects of hybridization on the salinity tolerance of offspring are variable and species-dependent.

3. Freshwater species

Most aquacultured fish are produced inland, in waters comprising FW and some BW salinities.[25] In addressing salinity tolerances of species occurring in these waters, studies have typically investigated fish challenged with a rise in salinity, comparing fish reared in FW with those transferred to increasing salinities up to SW. Here, the salinity tolerances of some of the main fish groups cultured primarily in FW are discussed.

3.1. Tilapia

Tilapia (Cichlidae) represent the second most cultured fish group globally.[25] Nile tilapia, the most commonly grown species of tilapia, have been extensively studied to understand and extend its upper salinity tolerance. When Nile tilapia (~26 g) were exposed to salinities ranging from 6–34‰ for 6 months, survival was >90% up to 12‰, optimal growth occurred at 16‰, and LC50 was 24‰.[73] Spawning frequency was greater between 5–15‰ compared with other salinities between 0–32‰.[74] Nonetheless, Nile tilapia are less tolerant to high salinity when compared with its congener, Mozambique tilapia, a euryhaline species that can grow well in ponds up to 40‰, spawn in 49‰,[75] and survive salinities as high as 120‰.[76] When the acute salinity tolerance of Nile and Mozambique tilapia were compared, the former did not survive a 24 h transfer from FW to 20‰, while 100% of the Mozambique tilapia survived the same challenge.[77] While some authors have estimated the optimum salinity for growing Mozambique tilapia at 17.5‰ when directly transferred from FW,[78] others have clearly shown that fish reared in a TR or SW grow faster than those reared in FW or BW.[41,62,79-82]

Because of its high salinity tolerance, Mozambique tilapia is widely used in hybridization programs. Hybridization between Nile and Mozambique tilapia (*O. niloticus* × *O. mossambicus*) resulted in elevated salinity tolerance and growth of offspring. These hybrid tilapia showed better growth and survival in BW, with the optimum salinity range at 15–32‰.[22,68] Similarly, the Mozambique tilapia is used to develop another commonly grown hybrid, Florida red tilapia (*O. mossambicus* × *O. urolepis hornorum*), which is reported to survive in 37‰ outdoor flow-through pools for several months with a 97% survival rate.[83] Although the optimal salinity for seed production of red tilapia is 5‰, their reproduction rates at 18‰ and >30‰ are considerably high when compared with FW tilapia strains.[84] Last, the blue tilapia (*O. aureus*) is another species widely used in hybridization for its capacity to adapt to cold water, and reported to survive salinities up to 45‰.[85] Blue tilapia were able to withstand a direct transfer from FW to 27‰ for 2 d with 80% survival. When the transfer was gradual, from 0 to 18‰ (BW) and then acclimated to 36‰, no mortalities were reported for 6 d.[86] A recent study concluded 12‰ as the optimal salinity for blue tilapia growth with no mortalities, while salinities over 20‰ resulted in >50% mortality of the population.[87]

3.2. Cyprinids

Carp (Cyprinidae) form both the oldest domesticated and most aquacultured fish group globally.[25] Silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*Aristichthys nobilis*) are two of the most aquacultured species of carp for which salinity tolerance studies have been conducted. Juvenile silver carp were reported to survive a 3–4‰ for a short time.[88] Bighead carp fry at 35 d post-hatch (dph) had higher salinity tolerance (7.6‰) than younger fish at 11 and 18 dph (2.3 and 6‰, respectively); 18 dph fry grew faster when reared at 0–2‰ compared with 4–6‰ over 4 weeks.[89] Early trials with grass carp (*Ctenopharyngodon idella*) revealed a 24 h LC50 of 16‰.[90] More recently, acute (4 d) and chronic (8 weeks) salinity challenges ranging from 0 to 20‰ indicated that over an 8-week period, grass carp reared at 6‰ grew slower than fish at 2‰.[91] In the acute trial, mortality initiated by 24 h at 12‰; all grass carp kept in salinities ranging from 0 to 8‰ survived over the course of 4 d.[91] The fertilization rate of common carp (*Cyprinus carpio*) was reduced to 13.4% at 6‰, compared with 98% in FW controls.[92] While the authors suggested that common carp could tolerate 3–4‰ without visible changes during early development, it is clear that this and other species of carp have limited tolerance to elevations in salinity.

The three major species of carp (rohu, catla, and mrigal) indigenous to the rivers of the Indian subcontinent, also known as Indian major carps, are widely aquacultured in the region. In rohu (*Labeo rohita*), the 48 and 96 h LC50s were calculated at 9.6 and 7.7‰, respectively;[93] sub-lethal exposures to salinities up to 4.5‰ over 90 d demonstrated that growth decreased with a rise in salinity.[93] Another study reported that the LC50 for salinity exposure was modulated by temperature; rohu were less tolerant of high salinity at the high temperature (28°C; 7 d LC50s of 6‰), when compared with 14°C (7 d LC50 of 10‰).[94] In hybrids (male *L. rohita* x female *Catla catla*), the salinity tolerance decreased in higher temperatures when compared with rohu.[94] Mrigal (*Cirrhinus mrigala*) fingerlings survived up to 6‰ for 10 d with no mortalities or morphological changes.[95] At 8‰ and 10‰, however, survival rates were 93.33% and 86.67%, respectively, suggesting that 6‰ could be regarded as the maximum salinity tolerance for that species.[95]

Like carp, other cyprinids are also usually stenohaline exhibiting limited salinity tolerance.[96] Increasing salinity to as little as 4‰ negatively affected egg production, fertilization rate, number of spawning days, and clutch size in the fathead minnow (*Pimephales promelas*), leading the authors to recommend that salinity should not exceed 1‰ for rearing this species.[97] Another commonly cultured group of cyprinids, especially in the ornamental industry, are goldfish (*Carassius auratus*). Goldfish can survive over 72 h in salinities under 10‰, but only for 8 h following acute transfer to 20–25‰.[98] Another study reported 6‰ as the upper salinity before negative stress effects were noted; at 8–10‰, growth and food intake decreased, FCR increased, muscle was dehydrated, and plasma cortisol was elevated.[99] These findings were corroborated by an additional report where growth rate and FCR were similar between goldfish grown at 6‰ and FW controls, regardless of water temperature (23°C and 27°C).[100]

3.3. Sunfish

Sunfish (Centrarchidae) are native to FW and BW habitats of North America, and have been cultured largely to provide fingerlings for stocking recreational ponds and lakes.[101] Salinity tolerance of sunfish, including basses and bluegills, varies with developmental stage, acclimation history, and species. For example, largemouth bass (*Micropterus salmoides*) larvae collected from a tidal river (<3‰) were transferred to salinities ranging from 0–16‰ for 48 h. While fish transferred to 4 and 12‰ showed 100% survival, those transferred to 0 and 8‰ had 80% survival, and only 20% of fish exposed to 16‰ survived.[102] Juvenile largemouth bass collected from BW canals (3–4‰) and from a FW lake grew fastest at 0‰ while fish stopped feeding and died within a week of exposure to 12‰.[103] The bluegill (*Lepomis macrochirus*) naturally inhabits saltmarsh systems where salinity fluctuates between 0 and 10‰.[104,105] In a salinity preference trial, juvenile bluegills spent the same amount of time in tanks at 0 and 10‰.[105] Another study found that growth was unaffected at 10‰ compared with FW controls.[104]

3.4. Catfish

Catfish are highly diverse and widely used in aquaculture. The striped catfish or swai (Pangasiidae, *Pangasianodon hypophthalmus*), is native to tropical FW habitats of the Mekong River basin. A 10 d salinity tolerance trial of striped catfish larvae showed a relatively high survival rate (~86%) in salinities up to 10‰. Survival dropped to ~29%, however, following exposure to 20‰.[63] Fingerlings exposed to different salinities for 96 h survived up to 13‰, with an LC50 of ~15‰ estimated by probit analysis, and 100% mortality at 17‰.[106] The authors also reported the highest growth rate at 4‰ when compared with fish reared at 0, 8, and 12‰ over 56 d. These results are consistent with another study that reported the highest growth rates of juvenile striped catfish between 2–10‰, with no differences in survival rates within that salinity range.[107] This study reported the lowest survival rate (~39%) at 18‰.

Hatch success and post-hatch survival of channel catfish (Ictaluridae, *Ictalurus punctatus*) is largely influenced by salinity. Embryos had the highest hatching rate (82%) at 4‰ but exhibited high post-hatching mortality (55%) by 4 d.[108] By contrast, 2‰ was an optimal salinity for treating eggs and increasing profitability, where the hatching rate was slightly lower (75%), but survival post-hatch was 100%.[108] Survival of channel catfish fry, was highest (99%) at 1‰ compared with those kept at 0 and 2‰; at 4‰, survival decreased to >20%.[109] Catfish fingerlings reared at 1‰ also grew faster than fingerlings reared at 0‰ or other salinities.[110] The salinity tolerance of channel catfish is also influenced by acclimation history. Yearlings acclimated to 10‰ had a better survival rate than those acclimated to 5‰ when exposed to 12‰, but neither group had high survival above 12‰ (>50% survival).[111] Moreover, the transfer of market-size fish from 0‰ to a low salinity environment (>5‰) did not affect production and FCR.[110]

Similar to channel catfish, hatching rates of African catfish (Clariidae, *Clarias gariepinus*) ranged from ~57 to 69% in salinities from 0–5‰, with the highest hatching rate observed at 1‰, and sharp declines at 6, 7, and 8‰ with 21, 9, and 0% hatching rate, respectively.[112] Another study reported hatching rates ranging from 45 to 60% between 0–6‰, with the highest at 4‰, though 52% had deformities.[113] Survival rates of African catfish larvae in salinities ranging from 0–10‰ for 16 d, were lower at 7.5‰ (60%) compared with those exposed to 0–5‰ (77 to 80%), with an LC50 at 8.5‰; growth rates also decreased at higher salinities.[114] Generally, juvenile African catfish are more tolerant to higher salinities than larvae, based on reported survival rates ranging from ~82 to 97% in salinities from 0-12‰.[115]

3.5. Pacu

Pacu (Serrasalmidae) is a commonly aquacultured group of FW fishes native to South American river systems.[116] One study concluded that tambaqui (*Colossoma macropomum*) could tolerate 10‰, though it is unclear if survival could be sustained as the study was based on acute short-term salinity challenges. The investigators found that a 1 h exposure to 15‰ resulted in elevated plasma glucose levels, while at 25‰ both plasma glucose and osmolality rose above the FW controls.[117] In juvenile tambaqui, specific growth rate, mean daily feed intake, and final weight decreased while FCR increased at 15‰ compared with 0-10‰ over 84 d.[118]

4. Marine species

Despite the disproportionate amount of water in oceans (~10,000-fold greater) compared with inland lakes and rivers, only ~60% of fish species inhabit marine environments,[119] and only ~8% of aquacultured fish are marine.[25] Unlike the approaches employed in FW species, studies on salinity tolerance of marine fish have primarily focused on assessing their capacity to tolerate lower salinities than those in which they are reared in. Many aquaculture facilities for marine fish are often situated inland or in sea-cage farms, exposing them to weather events (e.g., storms, typhoons, FW run-off, etc.) which can significantly decrease salinity within enclosures.[120] Thus, understanding the lower salinity tolerance of marine fishes is crucial for determining optimal siting, rearing conditions, and species selection to optimize production.

4.1. Grouper

The three most commercially aquacultured species of grouper (Serranidae), especially in Southeast Asia, are the brown-marbled or tiger grouper (*Epinephelus fuscoguttatus*), orange-spotted grouper (*E. coioides*), and the giant grouper (*E. lanceolatus*).[121,122] Juvenile tiger grouper have a wide salinity tolerance (0–32‰) when acclimated to lower salinities at a gradual rate of 2‰ h^{-1} in a 96 h trial,[123] versus 20–31‰ after directly transferred for 14 d.[124,125] Juvenile goliath groupers (*E. itajara*) tolerated salinities between 0 and 31‰ for 12 d (100% survival) in both gradual (from 29‰ to FW over 3-4 d) and direct transfer to low salinities.[126] Another study on the same species demonstrated 100% survival for 28 d with gradual salinity decrease (from SW to FW over a 3 d period), but observed that only 60% survived the direct transfer to <1‰ in 96 h.[127] All juvenile white grouper (*E. aeneus*) survived salinities between 4 and 43‰ over a 10 d study.[128] Another study on rearing *E. aeneus* found that juveniles reared for 92 d while consuming a 3% dietary salt supplement could tolerate salinities as low as 3‰ with 78% survival while improving growth and FCR compared with controls on a standard diet.[129]

4.2. Snapper

Snappers (Lutjanidae) are generally regarded as marine; however, some species exhibit euryhalinity.[130] Mangrove red snapper (*Lutjanus argentimaculatus*) aquaculture relies on the collection of wild fingerlings.[131] The optimal salinity for 21 dph larvae ranged between 16–32‰; by 28–50 dph, their salinity tolerance range increased to 16–50‰.[131,132] One study on juvenile mangrove red snapper analyzed the interaction between habitat structures and salinity (10, 17, and 25‰) and reported 17‰ as optimal for survival while in 15–20‰, hard, complex structures (e.g., rock piles or mangrove roots) improved survival rate by 20% and growth by ~10%, without changing diet or stocking rates.[131] Adult amarillo snapper (*L. argentiventris*) gradually acclimated at a rate of 1–2‰ d^{-1} between 23–44‰ had 100% survival with optimal salinity for growth at 23‰.[133] The red snapper (*L. campechanus*), popular in the Gulf of Mexico region, spends its entire life in offshore waters (34‰).[134] Larvae have been reared successfully in salinities ranging between 31–38‰.[135] There were no significant differences in survival over 96 h or FCR (6-week trial) in juveniles acclimated to 8 or 32‰ by the addition of FW or crystalline sea salt at a rate of 2‰ d^{-1}.[136] There were no survivors, however, within 24 and 72 h of exposure to 2 and 4‰, respectively; the LC50 was estimated at ~5.6‰. In the same study, fish grew faster at 32‰ compared with those in 8‰.

Juvenile gray snapper (*L. griseus*) tolerated between 5–45‰ with >90% survival rate when acclimated to target salinities (5, 15, 25, 35, and 45‰) at 5‰ d^{-1} over a 15 d period.[137] These results are consistent with the natural conditions that juveniles experience in the wild, where they inhabit both nearshore and estuarine areas before migrating to reefs as adults.[138,139] Both sub-adult and adults were found to tolerate direct transfers to salinities ranging between 0–60‰, with no mortalities observed during the 8 d experimental period, suggesting that gray snappers exhibit a higher range of salinity tolerance compared with other snappers.[140]

4.3. Halibut and Flounder

Halibut is the common name of right-eyed flounders of the genus *Hippoglossus* (Pleuronectidae). Atlantic halibut (*Hippoglossus hippoglossus*), which are commercially aquacultured, undergo a 50 d yolk-sac larval stage, during which they are the most sensitive to the influence of environmental parameters, including salinity.[141-143] Sac larvae reared between 29‰ and 32‰ exhibit reduced deformities and mortality compared to other salinities.[141,143] As juveniles and adults, halibut are surprisingly tolerant of intermediate salinities (15 and 25‰). Juvenile Atlantic halibut showed improvements in specific growth rate and feed conversion efficiency in reduced salinities (13–25‰) compared with 27 and 32‰.[144,145] In a long-term study, adult Atlantic halibut also showed a 20% improvement in growth and feed efficiency with no indications of stress at 15‰ compared with 27‰.[146]

Flounders (Paralichthyidae) are of great commercial importance and amenable to aquaculture in part due to the wide salinity tolerance of both juveniles and adults.[147,148] Larval summer flounder (*Paralichthys dentatus*) can tolerate salinities from 0‰ to 38‰, but they exhibit best growth and development rates at 8‰ compared with other salinities tested.[149,150] Juveniles of this species have a remarkable salinity tolerance range of 5–50‰ with a 100% survival rate.[149] Southern flounders (*P. lethostigma*), are found frequently in brackish bays, estuaries, and occasionally in FW, with a reported optimal salinity for survival between 15–35‰ for egg incubation, 20–34‰ for larvae, and 5–30‰ for juveniles.[147,151,152] The LC50 for Southern flounder larvae was <10‰ in both direct transfer[151] and gradual acclimation trials.[152]

4.4. Cobia

Cobia (Rachycentridae, *Rachycentron canadum*) are distributed in tropical and subtropical waters of salinities between 23–45‰.[153] In aquaculture settings, however, juvenile cobia have been grown in salinities as low as 10‰[154] and 5‰ (68.3% survival over an 8-week trial).[155] In addition, juvenile cobia were able to withstand 30 min treatments in FW for removal of marine parasites, including *Amyloodinium sp.*[156] During the larval stages, their salinity tolerance is highly age-dependent (down to 20.1‰ at 3 dph and 7.5‰ at 7–9 dph).[33] Moreover, the standard lengths of larval cobia (1, 4, 7, 13 dph) were unaffected by decreases in salinity (5‰ d^{-1} and down to 5‰ for 10 d),[33] but juveniles grew slower at lower salinities.[156] These findings indicate that the effects of salinity on growth, especially at early developmental stages, are age-dependent.

4.5. Sea bream

Sea breams (Sparidae) inhabit multiple near-shore habitats, including estuaries and river mouths. They are thereby capable of tolerating a wide range of salinities in aquaculture operations, including FW, depending on the rate of salinity change. Juvenile yellowfin sea bream (*Acanthopagrus latus*) acclimated to 33‰ had an upper LC50 of 37.8‰ at 32°C; however, when transferred gradually at a rate of 2‰ h^{-1}, the upper LC50 was 66‰. The upper LC50 was also temperature-dependent, with greater salinity tolerance (71‰ following gradual transfer) observed as the temperature lowered (10°C).[157] In the same study, when fish were directly transferred from 33‰ to lower salinities, lower temperatures also increased hyposmotic tolerance on direct transfers (LC50 was 2.5‰, 7.2‰ and 11.6‰ at 10°C, 25°C and 32°C, respectively); all fish transferred gradually at a rate of 2‰ h^{-1} survived in FW despite thermal regime.

The gilthead sea bream *Sparus aurata* inhabits brackish to hyper-saline estuaries, lagoons, and coastal waters of the Mediterranean and eastern Pacific.[158] Juveniles survived a direct transfer from 39 to 3.9‰ and as low as 2‰ when salinity was gradually reduced.[159] When gilthead sea bream were transferred from 39 to 7‰, plasma osmolality initially decreased and recovered by 30 d post-transfer; plasma cortisol, however, rose and remained elevated compared with pre-transfer levels, suggesting a role in hyposmotic conditions.[158]

4.6. *Jacks*

Jacks (Carangidae) are globally distributed and typically found in deep coastal waters. The rise in commercial aquaculture of jacks of the genus *Seriola* and pompano is relatively recent. Of the Seriolids, the most widely farmed species include *Seriola quinqueradiata*, *S. rivoliana, S. dumerlii* and *S. lalandi*, with studies on salinity tolerance primarily focusing on the last two. Young (6.38 ± 1.33 g) *S. dumerlii* can survive a direct transfer from 35 to either 20 or

40‰ for at least 30 d; in the same study, all fish transferred to 10‰ died after 10 d.[160] Similarly sized *S. dumerlii* in a separate study survived a direct transfer to 10‰ for at least 3 d.[161] Juvenile *S. lalandi* (11.6 ± 0.6 g) grew faster at 14, 18, and 22‰ than 26 and 30‰ after 29 d due to an increase in food intake.[162] Responding to hypersaline challenges, *S. lalandi* juveniles decreased food intake, FCR, and survival at 41 and 45‰ compared with 37‰.[163] The eggs of *S. rivoliana* hatched at the highest rate in 35, 40, and 50‰ compared with a range of salinities between 15 and 30‰.[164] In that same study, larval survival was highest at 35 and 40‰ compared with 50‰.[164]

Pompano (*Trachinotus ovatus*), is widely consumed throughout China, Japan, and Australia.[165] Juvenile pompano (48 dph), tolerated 10–34‰ with >90% survival when acclimated at 1‰ d^{-1} for 24 d.[166,167] The highest specific growth rate occurred at 34‰ with no differences observed between 18 and 26‰.[166] Another gradual acclimation trial on juvenile *T. ovatus* increased or decreased salinity from 31‰ (4‰ d^{-1}) to 5, 15, 25, and 35‰ with 100% survival observed after 56 d.[168] The main difference between both gradual acclimation experiments was stocking density, with the first trial[166] stocked at aproximately 4-fold higher density than the second,[168] suggesting that increasing stocking density may decrease salinity tolerance. Juveniles of this species reared for 8 weeks in sea cages, with salinities reported to range between 20–33‰ due to heavy rainfalls, had >97% survival.[169-171]

4.7. Rabbitfish

Rabbitfish (Siganidae) are reef herbivores widely distributed throughout the Indo-West Pacific that have been increasingly cultured due to some species possessing favorable traits for aquaculture production, including acceptance of formulated diets, schooling behavior, and mass spawning.[172] The golden rabbitfish (*Siganus guttatus*) is typically cultured in salinities ranging from 10–35‰.[173] While there are no differences in specific growth in salinities ranging from 5 to 35‰, survival of golden rabbitfish began to decline 9 d following exposure to FW, with no survivors by 27 d.[174] Moreover, breeding, fecundity, gonadal development, and egg quality of adult broodstock were similar in salinities ranging between 25 and 35‰.[175] Once hatched, the optimal survival of golden rabbitfish yolk-sac larvae was between 14 and 37‰[176]. The rivulated rabbitfish (*S. rivulatus*), introduced into the eastern Mediterranean Sea following the opening of the Suez Canal, can survive up to 3 weeks in salinity as low as 10‰ or as high as 50‰,[177] but the effect of salinity on growth is less clear, at least in juveniles. In one study, growth was highest in 34‰ with decreased growth at salinities ranging from 5–25‰,[178] while in another, growth only decreased in 10‰ when compared with fish reared in 15–40‰.[177] Further, the standard metabolic rate of rivulated rabbitfish was lower in 30–40‰ compared with 25‰, suggesting that the higher salinity range minimizes metabolic expenditure while maximizing growth in this species.[179]

4.8. Drums

Drums or croakers (Sciaenidae) inhabit marine and coastal areas and are characterized by the ability to produce a "croaking" sound through the beating of abdominal muscles against the swim bladder. The red drum (*Sciaenops ocellatus*) is native to the Gulf of Mexico and the Atlantic Ocean, forming an important commercial fishery, with aquaculture efforts targeting both food production and wild stock enhancement.[180] The salinity tolerance of red drum varies with life stage. For example, lower hatching success was observed in fish exposed to salinities greater than 37‰ and the LC50 of larvae was 37.7‰ by 72 h.[53] Juveniles were more tolerant than larvae to salinity changes, reflecting their natural environment, ranging from 0.8–45‰.[181] While 95% of juvenile red drum survived a transfer to FW for 96 h, only 5% and 70% of larvae and post larvae, respectively, survived. Although juvenile red drum can survive FW, they grow faster and have lower FCR when reared in SW.[181]

The culture of large yellow croaker (*Larimichthys crocea*) has developed rapidly, especially through marine and coastal cage aquaculture, though high levels of disease, limited coastal area, and increasing pollution threaten healthy production.[182] The main pathogen to this species, *Cryptocaryon irritans*, cannot survive in low-salinity environments, hence low salinity aquaculture is seen as a potential mitigation strategy.[183] Juvenile yellow croaker directly transferred to 5, 10, 20, and 25‰ had survival rates >90% during a 6-week trial.[184] Though in the same study, fish exposed to 15‰, had a survival rate of 69%. Gradual acclimation for juveniles of this species (4 ‰ d^{-1}) produced a wider range in salinity tolerance, between 4–28‰ with 97–100% survival.[183] After 24 h in 2 and 0‰, survival rate decreased to 88.26 and 53.91%, respectively. Optimal growth in juveniles that were gradually acclimated for 40 d was found to be 4‰.[185] Adult yellow croaker (1–2 years old), directly transferred to 5, 15, 25, and 35‰ in land-based recirculating aquaculture systems for 48 h had 100% survival.[182] The maximal metabolism of adult yellow croaker was reported at 25‰ and 26°C.[182] Likely due to their environmental range spanning coastal and marine habitats, both the red drum and yellow croaker represent marine species that are highly tolerant to decreases in salinity.

5. Euryhaline species

Euryhaline fish represent a broad range of taxa that can thrive in a wide range of salinities from FW to SW and higher. This adaptability makes them particularly valuable in aquaculture, providing practitioners leeway for salinity range and fluctuations in culture.[186] As observed in FW and marine species, there are various levels of euryhalinity among species of a given family, where the temperature, age, and life history influence optimal salinity conditions for survival and growth. Typically, euryhaline fish include species whose natural life histories require acclimation to FW and SW environments either continuously, such as in estuarine species, or at least once during their life cycle, such as observed in diadromous fishes. Estuarine environments form at the transition zone of FW rivers and the ocean. This intersection renders the salinity of estuaries highly variable and dependent on the tides. Therefore, estuarine species include some of those described above, under FW and marine species. For example, the Mozambique tilapia as described in Section 3.1, also inhabit estuaries and are euryhaline as an adaptation to cope with the frequently changing salinities. Likewise, predominantly marine fish, such as the red drum and yellow croaker (described in Section 4.8) may spend part of their life cycle in estuarine environments. For the purpose of this review, the groups of euryhaline species discussed below are diadromous, and further subdivided according to the salinity in which they naturally spawn and hatch.

5.1. Anadromous species

Anadromy is a life history strategy in which eggs hatch in FW, juvenile fish migrate to SW where they mature, and adults return to FW to spawn. Euryhalinity can vary in anadromous fishes during their life stages. For example, hybrid striped bass, retain tolerance to a wide range of salinities throughout their life stages,[187] while Atlantic salmon exhibit narrow salinity tolerance ranges during some stages.[188]

5.1.1. Temperate basses

Temperate basses (Moronidae) comprise predominantly marine and anadromous species of commercial interest to aquaculture in Europe and North America. The European sea bass

(*Dicentrarchus labrax*) ranges from Norwegian and Scottish coasts to the Mediterranean and Black Sea,[189] where they undertake seasonal migrations from SW to estuarine and sometimes FW environments. European seabass is a commercially valuable species with 94% of its total production in the Mediterranean.[190] While European seabass are generally considered euryhaline, they have high intraspecific variation in salinity tolerance depending on age, location-based population genetics, and water temperature.[191,192] Juveniles and adults have been reported in waters between 0 and 40‰. Juvenile European sea bass were shown to successfully acclimate following direct transfer from SW to FW, though a more gradual acclimation was suggested to minimize long-term stress effects.[193] In some studies, optimal growth of European seabass occurred in FW compared with 20, 30, and 40‰,[192,194] while another found that ~30% of fish had phenotypes incompatible with FW tolerance including erratic swimming, isolation from the shoal, low reflexes, and increased pigmentation.[195] In larvae, it was shown that a gradual increase from low (15‰) to high salinity (37‰) at 93 d post-fertilization increased the percentage of males (87 to 93%), suggesting an effect of environmental salinity on sexual differentiation.[191]

Striped bass (*Morone saxatilis*) is an anadromous species native to the northeastern shores of North America. The hybridization of striped bass with white bass (*M. chrysops*) led to heterosis of traits, including improved disease resistance, survival, and growth.[196] One study found that striped bass hybrids, commonly called sunshine bass and palmetto bass, were able to withstand direct transfers from FW to SW and vice-versa.[187] Another study reported that both hybrids had similar 24 h LC50 of 28‰, suggesting other factors, such as population age, genetics, preconditioning, diet, and temperature are considerable factors in the outcomes of these salinity tolerance experiments.[71,197] The hybrid striped bass in FW are more sensitive to aqueous copper compared to those reared in BW (15‰).[198] Salinity (0–30‰) had no effect on the growth rate of juvenile hybrid striped bass.[199] This is also the case during the larval stage (0–10‰); however, survival was optimized at 10‰.[200]

5.1.2. Salmonids

Many salmonids (Salmonidae) undergo anadromous life cycles, where juveniles smoltify, a process that involves extensive physiological modifications to prepare for SW adaptation. The salinity tolerance of Atlantic salmon is dependent on their developmental stage and size.[188,201] For example, 65%, 94%, and >99% of parr survived a direct transfer from FW to full-strength

SW, 20‰, or 10‰, respectively. By contrast, all smolts survived the same regime.[188] Similarly, 5 dph chum salmon (*Oncorhynchus keta*) can survive the direct transfer from FW to 45‰ for 24 h, but they lose that capacity by 10 dph.[202] Adult Atlantic salmon acclimated to SW show signs of osmotic stress, including increased plasma osmolality and cortisol and high mortality when exposed to temperatures above 18°C; the stress is ameliorated when fish are transferred to 28‰.[203] Sockeye salmon (*O. nerka*) smolts did not survive the transfer from FW to SW at temperatures above 15.8°C, but nearly all survived the transfer below 14°C.[204] These studies indicate that high temperatures may reduce the salinity tolerance of salmon.

Rainbow trout (*O. mykiss*) are native to western North America and exhibit dynamic life history strategies, though most are produced in the European Union.[205] Eggs are released and hatched in rivers, but adults can mature in FW (resident) or SW (anadromous; steelhead trout). The plasticity of rainbow trout life histories is influenced by interactions between environmental conditions, genotype, sex, and individual growth rates and lipid storage.[206,207] The spatial and temporal separation of rainbow trout has resulted in several subspecies, including the coastal rainbow trout *O. m. irideus*, which displays both resident and anadromous life histories.[208]

As observed with other species, the salinity tolerance of rainbow trout is affected by temperature and life stage. FW-acclimated fish did not survive by 7 d when directly transferred to 26‰ at 1°C, while all fish transferred to 26‰ at 8°C and the controls survived.[209] High water temperatures also reduce salinity tolerances of *O. m. irideus.* Alevin and fry were acclimated to 13, 16.4, and 19°C water and directly transferred to 18‰ for 24 h while 4 week-old fry were acclimated to the same 3 temperatures as the alevin but transferred to SW. Alevin and fry survival following the salinity challenge decreased significantly with an increase in temperature. Further, while none of the alevin exposed to 19°C survived, 50% of fry exposed to 19°C survived the salinity challenge.[52] Combined, these studies suggest that salinity tolerance is maximized within an optimal thermal range.

5.1.3. White Sturgeon

The white sturgeon (Acipenseridae, *Acipenser transmontanus*) has been historically found in coastal marine environments along Northern Mexico to Alaska and into major river systems, where adults inhabit estuaries and only return to FW to spawn.[210] Habitat segmentation from dams and overfishing have resulted in major population declines.[211,212] Produced primarily for its meat and caviar, white sturgeon can be reared exclusively in FW under aquaculture conditions.[213] Adults can tolerate gradual transfers (5‰ h^{-1}) from SW to FW and vice-versa.[214] In that study, it was concluded that size, rather than age, influenced the salinity tolerance of juvenile white sturgeon. Those weighing less than 1 g could not tolerate salinities above 10‰, while those weighing 4.9–50 g could tolerate direct transfers to 15‰. This was confirmed by another study where the survival of white sturgeon weighing 10 g was lower than those weighing 30 g from the same cohort, following transfer from FW to higher salinities.[215] These studies indicate that a larger size increases the salinity tolerance of white sturgeon.

5.2. Catadromous species

Catadromous fish typically spawn in SW, migrate to near-shore environments and mature in FW. Salinity tolerances of catadromous fish often vary with developmental stages, thereby complicating their aquaculture production.[216]

5.2.1. Eels

Eels (Anguillidae) of the genus *Anguilla* are catadromous, with larvae hatching in marine environments and developing into glass eels which migrate to estuarine environments where they metamorphose into pigmented elvers and finally move into FW. Adult eels return to marine environments as silver eels to reproduce. Overexploitation of American eels (*Anguilla rostrata*), European eels (*A. anguilla*), and Japanese eels (*A. japonica*), along with habitat degradation from dams, have led to dramatic declines in populations.[216-218]

The aquaculture of Anguillids is complicated by their life histories, with early developmental stages requiring SW or BW and adult stages requiring FW. For example, while glass European eels grow faster in 33‰ compared with FW, some glass eels preferentially choose to be in FW.[219] Spawning European eels in captivity can be achieved in SW and enhanced with injections of carp pituitary extracts.[220] Glass eels and semi-pigmented elvers collected from estuaries (12‰) had 100% survival when transferred to 34‰ and FW.[216] Japanese eel larvae (5 dph) survived for 13 d without food in 10‰ and 17‰, but only 6 d in FW and 3‰ and 9 d in 24‰ and SW.[221] Conversely, only 30% of fully-pigmented eels collected from the mouth of a river (0‰) survived in 34‰ by 10 d.[216]

5.2.2 *Barramundi*

The barramundi (Latidae, *Lates calcarifer*), also known as Asian seabass, is a catadromous species native to tropical and subtropical coastal areas of the Indo-Pacific. Their suitability for aquaculture stems from their rapid growth, tolerance to a broad range of environmental conditions, and sustained high market demand.[222] Juvenile barramundi can be cultured in salinities ranging from 0–55‰, though at 45‰ and above, potassium supplementation may be needed.[223,224] A salinity range of 5–20‰ has been recommended for optimal feed conversion efficiency and metabolic activity[225] and 20–36‰ for commercial farming of barramundi, with juveniles growing optimally at 20‰.[222] Barramundi are protandrous hermaphrodites that naturally spawn in BW near the mouths of rivers (28–36‰).[226] Early studies showed a connection between increasing salinity and gonadal development,[227] with one study showing landlocked FW populations in Papua New Guinea having abnormal gonadal development.[228] In culture settings, either increasing salinity and temperature or hormonal injections can be used to induce spawning; salinities between 28 and 32‰ are optimal for hatching and larval stages.

5.2.3. Mullet

The striped mullet (Mugilidae, *Mugil cephalus*) is globally distributed in coastal tropical and sub-tropical waters with salinities ranging from 0 to 122‰.[229,230] Despite their remarkable euryhalinity, wild fish reproduce exclusively in SW (34‰).[231] The optimal salinity for egg survival and hatching ranges between 30 and 40‰.[232-234] The tolerance of larval and juvenile fish to direct FW transfer is dependent on life history stage; fish under 4 cm (at least 7.5 months old) cannot survive direct transfers from brackish to FW, but 6-week old fingerlings can survive a 7 d transition from BW to FW.[235,236] In another study, juvenile mullet (~2.5 cm) were transferred from 20‰ to salinities ranging from 35–80‰ with a calculated LC50 of 50.4‰; when gradually acclimated, fish survived a transfer from 34 to 120‰ for at least several days.[237] Consistent with their life history, growth rate, and FCR varies with developmental stage, with the optimal salinity, 5–20‰ for adults and juveniles, generally decreasing later in life.[235,238-240]

5.2.4. Milkfish

The milkfish (Chanidae, *Chanos chanos*) is the only species in the genus *Chanos* and is typically found in waters throughout the tropical and subtropical Indo-Pacific.[241] Generally, their life history starts off as pelagic larvae in SW, followed by settlement as juveniles in shallow nearshore habitats such as estuaries, mangrove swamps, and lagoons. Juveniles will enter FW habitats if available, though these habitats appear unnecessary for proper survival and development, with sub-adults moving into deeper coastal waters to feed and reproduce when nearshore resources are insufficient to support the growing fish.[241] Some populations, however, spend their entire lives in FW lakes and rivers,[242,243] and others are naturally landlocked in hypersaline lagoons in the Christmas Islands where they can remarkably survive and breed in waters up to 158‰.[241,244] Originating in converted mangrove swamps in Southeast Asia, the culture of milkfish typically involves the collection of wild seed stock and the grow out of juveniles and adults in natural ponds of salinities that can range from 10–60‰ as a result of evaporation and precipitation.[245] The optimal salinity for growth generally increases as fish grow older and larger. For example, milkfish fry grew the fastest at 0‰ followed by 16‰ then 34‰,[246] while fingerlings (8-week old) grew the fastest at 25‰ compared with 0, 10, 15 or 20‰,[247] and adults (25 cm, <2 years-old) grew the fastest in 55‰.[248]

5.2.5. Pacific threadfin

The Pacific threadfin (Polynemidae, *Polydactylus sexfilis*) is distributed throughout coastal waters of the tropical Indo-Pacific[249] and is known as moi in Hawai‘i, where efforts to optimize its culture began in the 1970’s.[250] In the wild, breeding occurs in inshore BW habitats; eggs drift offshore where pelagic larvae develop until they metamorphose and eventually settle in nearshore habitats including estuaries.[251] Pacific threadfin larvae survived best at 26–34‰; higher (42‰) or lower (10 or 18‰) salinities increased larval mortality.[252] As juveniles, they could survive a decrease in salinity from 34 to 1‰ in 1 h for at least 30 min, but only 60% survived at 0‰, when simulating a FW dip to remove parasites.[253] In the same study, the fish that survived the 1‰ dip also survived at 5–15‰ with no ill effects for up to 40 d.[253] While the study highlighted the potential for BW culture of Pacific threadfin even after a FW dip at 1‰, to our knowledge, there are no studies on the relationship between salinity, growth, and reproduction in this species.

5.2.6. Japanese sea bass

Japanese sea bass (Lateolabracidae: *Lateolabrax japonicus*) is a catadromous species native to the Western Pacific, ranging from Japan to the South China Sea.[254,255] Because of its euryhalinity, Japanese sea bass are widely cultured in both sea cages and inland FW ponds. One study found that juveniles increased specific growth rates at 13, 20, and 27‰ compared with 34‰.[256] Moreover, rearing Japanese sea bass in SW increases omega-3 content, compared with fish reared in FW, leading to improved nutritional, flavor, and texture qualities and fetching higher market prices.[257,258] As a catadromous species, Japanese sea bass typically reproduce in SW, but one study found that a reduced salinity (29.6 - 31‰) improved fecundity relative to SW

(34.5 - 35.1‰).[259] While the rate of embryonic development is unaffected by salinity (22 - 34.5‰), hatching success is optimal between 33.8 and 34.5‰.[256,260]

5. Implications for production

Aquaculture operations may target commercial production, broodstock maintenance, and wild restocking. In commercial production, reducing operational costs and time to market are often targeted through the selection of conditions that accelerate growth, increase feed conversion efficiency and improve fillet quality. In contrast, broodstock and wildstock management often target the raising of robust fish that can produce quality offspring. In all instances, understanding and applying species- and age-specific salinity tolerances may inform best management practices while mitigating stress and disease susceptibility. In a practical sense, whether raised for production, broodstock, or release, salinity challenges during various early life stages may be employed to improve their salinity tolerance in later life stages, thereby increasing their chances of survival and resilience to environmental stressors. Multiple endpoints have been employed to assess performance in response to salinity, including aerobic scope/ metabolic rates and stress responses.[24,179,207,248,261-263] Here, some of the physiological aspects that most directly impact the production of aquacultured species, including growth, reproduction, disease resistance and nutrition are further discussed.

6.1. Growth and feed utilization

Salinity imparts major effects on growth across all developmental stages in multiple species. Generally, salinity-dependent growth in controlled environments parallels the natural history of the species. For example, most FW fish grow fastest when reared in a FW environment or moderately elevated salinities. African catfish showed optimal FCR and growth rates when reared in FW and signs of increased energy allocation for maintaining normal function and metabolism, such as elevation of plasma cortisol and oxidative stress, were seen with increasing salinity.[115] Grass carp and common carp grew fastest with the lowest FCR at 0 and 2‰, compared with slightly higher salinities.[264,265] Tambaqui, another stenohaline FW species, grew fastest at 0‰ with no difference in FCR observed between 0 and 10‰,[118] while the Nile tilapia, naturally occurring in FW and tolerant of BW, grew the fastest between 0 and 8‰, with optimal FCR at 8‰ at 32℃.[266] Compared with FW fish, euryhaline species generally exhibit optimal growth rates at intermediate salinities. Goldlined seabream (*Rhabdosargus sarba*) showed the highest growth rate and protein efficiency ratios at 15‰ relative to other salinities.[267] Similarly, SW fish with tolerance for low salinity, such as Atlantic cod (*Gadus morhua*) and turbot (*Scophthalmus maxiinus*), exhibited optimal growth rates and FCR at 14‰ and 19‰, respectively.[43,268,269]

Salinity has been shown to control growth rate through changes in metabolic rate, food intake and conversion, and hormonal regulation.[270-272] Growth in fish is primarily regulated by the growth hormone/insulin-like growth factor (GH/IGF) system which also involves interactions with their respective receptors and binding proteins.[273-275] The GH-IGF system in fish is highly responsive to changes in salinity. For example, elevated plasma GH was reported in channel catfish and rainbow trout following transfer from FW to BW.[276,277] When transferred from FW to SW, Mozambique tilapia doubled growth rates while upregulating GH and IGF-1[278] and grew even faster through further activation of the GH-IGF system when reared in tidally changing salinities compared with those reared in FW or SW.[41]

6.2. Reproduction

As observed with growth, fish reproduction is also directly impacted by salinity. Broadly, for fish acclimated to FW, reproductive output may be reduced when exposed to increasing salinities, and vice-versa for fish acclimated to SW. Typically factors other than salinity are employed for modulating reproduction in aquacultured fish (i.e., hormone therapy, changing temperature, and photoperiod).[279-281] Nonetheless, salinity has a significant role in modulating reproduction in aquaculture. In males, spermatozoa are quiescent until motility is triggered during release into hyposmotic environments for FW fish or hyperosmotic environments for marine species;[282] thus, when fish are exposed to different salinities, spermatozoa quality may also be affected. For example, a low holding salinity of 5‰ significantly reduced the sperm motility of black bream compared with those held at 20‰ or 35‰.[59] Osmotic stress also affects gonadosomatic index (GSI): FW and 7‰ BW resulted in the highest GSI in male Nile Tilapia compared with those acclimated to 14 and 21‰ BW.[283] Further, a population of the European flounder (*P. flesus*) that spawns in BW (6–9‰) has larger testes than a population that spawns in 10–18‰ and another that spawns at 30–35‰, potentially highlighting a trade-off between osmotic challenges and sperm production.[284]

While the underlying mechanisms of how salinity affects egg development, fertilization, and hatch rate have not been fully elucidated, several studies show that salinity can affect these parameters. In Nile tilapia, the fecundity of females is reduced at salinities 30‰ and above[285] while the hatch rate is suppressed at salinities above that of FW.[58] The more salinity tolerant red tilapia did not change fecundity when acclimated to 1, 25, or 33‰. However, at 39‰ fry production was lower and at 42‰ there were no fry produced.[286] By contrast, black bream acclimated to 5‰ reduced ovulations, egg volumes, and fertilization rates compared with those held at 20‰ or 35‰.[59] In practice, salinity exposure during early developmental stages can be employed to enhance the salinity tolerance of offspring. For example, exposure to elevated salinities during time of fertilization and egg incubation increases the salinity tolerance of Nile tilapia larvae.[287] Given the specificity of salinity tolerances and plasticity when fish are exposed to different salinities at early life stages, a species-specific understanding of salinity requirements and tolerances is key for maximizing reproductive output in aquaculture.

6.3. *Disease management*

With the increase in aquaculture production, mitigation of disease, while minimizing the use of antibiotics and other chemicals has become a major challenge in the industry. Sodium chloride (NaCl) is one of the most critical tools used for controlling parasitical, bacterial, and fungal infections in fish. Reflecting the plethora of studies showing that fish are typically most amenable to gradual salinity changes than to direct transfers (See Figure 2), most salt treatments are used in short-term increments. Salt treatments are usually employed with the notion that there are generally no detrimental health effects when both NaCl concentration and time of exposure are carefully applied. For example, many FW fungi, including *Saprolegnia diclina*, *S. parasitica*, and *Aphanomyces sp*. cause Saprolegniasis, leading to losses in aquaculture production.[288] Those fungi have distinct tolerances to NaCl, (12 and 8‰, for *S. diclina* and *Aphanomyces* sp., respectively), thereby informing the minimum concentration of NaCl that could be effective for treatment.[288] *S. parasitica* exhibit an even higher tolerance for NaCl. Exposure to 15‰ was unable to control infection in Chinook salmon; however, exposure to 30‰ controlled the fungal infection but led to egg mortality.[289] Survival of channel catfish infected with bacterial pathogen, *Edwardsiella ictaluri,* increased as a result of raising salt concentration from 1 to 3‰.[290] Another study, however, reported that treatment in higher salt concentration (4‰) after artificial exposure to *E. ictaluri*via abdominal injection did not improve survivability, nor prevented infection to naive individuals,[291] corroborating the need for further investigation on the use of NaCl as a bacterial disease treatment.

The most effective uses of NaCl for disease treatment have been reported in the control of parasites. Capable of surviving in aquatic environments without a host, ectoparasites attach to the gills and skin of fish, thereby affecting the immune system and, in severe cases, causing lethal damage.[49] The use of 6‰ NaCl reduced the number of the gill-specific *Piscinoodinium* sp. in red-tailed Brycon (*Brycon cephalus*) by 96 h of immersion following transport, compared with untreated controls.[292] In juvenile arapaima (*Arapaima gigas*), researchers found that 9, 10, and 11‰ NaCl solutions were effective at inducing 60–100% mortality of external *D. cycloancistrium* following 1 h of treatment.[293] Combating the skin ectoparasite ich (*Ichthyophthirius multifiliis*) with salt has produced mixed results depending on the species. While 2–3‰ NaCl controlled ich infections in the silver perch (*Bidyanus bidyanus*), following exposure for 8 d,[294] the treatment did not prevent mortality of channel catfish (*Ictalurus punctatus*) fingerlings.[295] Overall, salt treatments have been effectively used to induce antiparasitic effects at low concentrations in FW fish. SW fish are also often treated with limited low salinity or FW exposures. For example, the use of hyposaline (as low as 4‰) treatment was effective in combating sea lice attached to Atlantic salmon,[296] and FW exposure for at least 5 min in *S. dumerlii,* while stressful, did not induce mortality, indicating that abrupt lowering of salinity may be a useful strategy for parasite treatment.[297] Nonetheless, further studies are needed to elucidate species-specific responses and optimal protocols for hyposaline treatments for mitigating disease and parasitic infections.

6.4. Nutrition and flesh quality

Water salinity has been shown to affect fillet flavor and nutritional composition in several aquacultured species of fish. For example, largemouth bass reared at 9‰ had lower water content and flesh tenderness but higher density of muscle fibers compared with fish reared in FW, thereby affecting flesh texture. Moreover, compared with FW fish, bass reared in 9‰ had a higher content of sweet and umami amino acids but fewer bitter amino acids and greater amounts of inosine monophosphate (IMP), a flavor enhancer, and the essential fatty acids EPA and DHA.[298] A short salinity treatment also influences the muscle quality and flavor of carps. Grass carp and black carp (*Mylopharyngodon piceus*) exposed to 7.5‰ for 24 h had higher levels of polyunsaturated fatty acid (PUFA) and increased muscle hardness compared with those reared in FW.[299]

Nile tilapia exposed to 12‰ had increased levels of the flavor-enhancing amino acids glutamic acid and proline along with EPA, DHA, and PUFA content compared with fish kept in FW.[300] A rise in salinity also affected fatty acid composition in rainbow trout, where 1.7‰ increased n-3 PUFA, EPA, and DHA content while decreasing monounsaturated fatty acid (MUFA) and n-6 PUFA compared with FW controls[301] and Japanese seabass (*Lateolabrax japonicus*), where rearing at 26.2‰ increased n-3 PUFA, EPA, and DHA in muscle compared with fish reared in a FW pond.[257]

6. **Conclusions**

In this review, we aggregated and summarized the literature on the salinity tolerance of several fish species commonly produced in aquaculture along with the various approaches for assessing salinity tolerance. The wide variety of approaches employed in different studies, however, necessitates caution when comparing results side by side (Figure 3). Consequently, the definition of salinity tolerance can also vary depending on the experimental approach taken, making it challenging to establish a standardized framework. Evaluating the trade-offs between each method of determining salinity tolerance is crucial for interpreting the results and implementing them effectively. As one of the primary environmental factors regulating the physiology of fish, salinity impacts multiple aspects of aquaculture production, from growth and reproduction to disease management and finished flesh quality. Generally, in the early stages of production, natural environmental distributions of fish inform the optimal salinities in which they can be reared. In contemporary aquaculture, understanding salinity tolerances can inform possible coping strategies in the face of ongoing and impending consequences of climate change, including added salinity stresses. Advancements in our capacity to detect and control environmental salinities has enabled a variety of experimental and applied salinity paradigms, including early exposure to salinity changes and crossing between strains and related species of distinct salinity tolerances leading to phenotypic improvements of offspring stocks. For example, hybridizing FW species with those more tolerant to salinity can allow for heterosis of growth traits and improved nutritional content and flavor when grown in saline conditions. Though most aquaculture currently occurs in FW, production in saline environments holds potential for future growth considering dwindling land space, decreased FW resources, and high market demand for seafood. The use of various experimental approaches to investigate the salinity tolerance of fishes has improved our understanding of environmentally mediated mechanisms that affect efficiency and quality endpoints in aquaculture production, ultimately enhancing management practices towards greater sustainability and resiliency in the industry while bolstering the economic value of cultured species.

Figure legends

Figure 1: Summary of osmoregulatory challenges faced by fish in fresh water (FW; A) and seawater (SW; B). Orange and blue arrows represent fluxes of ions and water, respectively. Solid and dotted arrows depict active and passive modes of transport, respectively.

Figure 2: Different experimental approaches to determine the salinity tolerance of fish acclimated to low salinity (light blue) and high salinity (dark blue). Intermediate tones of blue represent intermediate salinities. A) gradual transfer from high salinity to low salinity and low salinity to high salinity; B) direct transfer from high or low salinity to a range of salinities; C) effect of direct salinity transfer on fish survival, where the magnitude of salinity challenge is inversely proportional to survival ; D) early life stage exposure to different salinities to test their adult salinity tolerance such as, for example, the initial exposure to alternating salinities facilitates acclimation to either low or high steady-state salinities ; E) tidal regime paradigm designed to test the effects of alternating salinities and; F) effects of crossing and hybridization on salinity tolerance of F1 generation.

Figure 3: Summary of salinity tolerance of species discussed in this review. Colored bars indicate the recorded salinity tolerance level (‰) of the species at different life stages. Two open diamonds (◊) within a bar indicates the optimal salinity range and a single open diamond indicates the reported optimum salinity for growth. The LC50 salinity following direct transfer is indicated by an open circle (○), while the LC50 following a gradual transfer is indicated by "<" and ">" corresponding to decreasing and increasing salinities, respectively. Numbers next to bars indicate the references used to gather the information for each species reported.

Author contributions

The preparation of this review was a component of a graduate level course on advanced topics in aquaculture taught by APS to KC, RJAC, TG, GHTM, RSM, TLP and JRR.

APS: Conceptualization; supervision; data curation; formal analysis; methodology; visualization; writing–original draft; writing-review; editing; KC, RJAC, TG, GHTM, RM, TLP and JRR contributed equally to manuscript and are listed alphabetically by last name: data curation; formal analysis; methodology; writing–original draft; writing-review; editing.

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Conflict of interest statement

The authors declare no conflict of interest.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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