

How is Freshwater Fish Reproduction Affected From Changing Climatic Patterns

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Review Article

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ABSTRACT

There are multiple literatures with evidence of changing climatic pattern and their effect on the freshwater ecosystem. The habitat within it is highly vulnerable to these changes because many species have limited abilities to get dispersed with the changing environment. Specifically, “what are the impacts and upshot of global climate pattern shift on the freshwater fish reproductive physiology and phenology?” is the interesting question to seek. Notable observations have been made in temperatures, hypoxia, and hydrology regimes, presumably affecting spawning (timing, pattern, and habitats), endocrine (HPG) axis, sexual maturation, gamete formation, sex differentiation, embryonic development, and hatching. Phenological changes are primarily driven by abrupt fluctuations in temperature - increasing temperature along with hypoxia disrupts the endocrine and brings reproductive impairment. Freshwater fish respond to changing climatic patterns by shifting their distribution range, changing migration times, and spawning. Similarly, Temperature-Dependent Sex Differentiation (TSD) species are more affected and the effect is projected to increase in the near future. In the meantime, there are several concerns regarding the harm to freshwater fish, either due to changes in climate trends or due to anthropogenic activities, but there is growing evidence of the impact of change in climatic patterns on the reproduction, development, structure, and abundance of freshwater fish populations.

INTRODUCTION

Multiple indicators of weather and climate cycle have been shifted and creating a threat [1] and it is understood that this may have negative impacts on many species [2]. Observed and potential expected impacts of global climate change on freshwater environments around the Arctic (Arctic Climate Impact Assessment, 2004), temperate and tropical climate zones [3] and areas where data currently limit our understanding of how and when global climate change affects freshwater fisheries [4]. Freshwater fish strain faces particular challenges [5] dry inland waters,

hypoxia, fluctuating water levels, and in particular, rising water temperatures will affect numerous species within the future - fish stocks will decline, and more species end up with extinction. Globally averaged combined land and ocean surface temperature evidenced warming of 0.85 [0.65 to 1.06] °C, over the period 1880–2012 [6]. In freshwater water bodies, changes are being observed in temperature, oxygen levels, currents, and circulation (IPCC, 2007), which are vital growth-regulating indicators of their ecosystem. Though their consequences are often difficult to differentiate from damage caused by overfishing and pollution; however, these climatic changes are having impacts on the breeding behavior of freshwater fish, also structure and diversity [7] of fish communities in rivers.

Patterns of climate change are capable of exacerbating existing problems, since fish are poikilothermic animals strongly suffering from ambient water temperature [8] the consequences of global climate change on their physiology and behavior are going to be particularly pronounced, especially to fish growth, metabolism, food consumption, reproductive success, and habitat range [9]. Fishes display an outsized number of reproductive strategies. “They possess an indeterminate capacity for growth, and thus the climate affects the energy balance and therefore the current trade-offs between growth and reproduction that maximize reproductive success. These interchange strongly influence the temporal pattern of reproduction: timing of sexual maturation, the periodicity of the reproductive cycle, and spawning seasonality [10]. With this alteration, the general non-market ecosystem service value will get decrease, and hence, the natural wealth may decrease. “Climate change is predicted to progressively shift the freshwater environments that favor alien fishes over native species. There are likely to be more restricted populations of native species, and a few could also be eliminated. Due to lower flows and elevated air temperatures, stream-dependent species may decline as portions of streams dry or become warmer [11]. Changes in certain physiological characteristics in response to a rise in water temperature have in successfully resulted in changes in fish performance [12] reproduction, growth, and seasonal rhythms. Besides, some species have moved upriver [13] extending their migration range regulated by temperature difference [14]. These movements have led to changes in the composition of communities with as a consequence modifications in species richness and the number of dominant species [15]. This could impact the ecology of freshwater environments, which already acutely feel the consequences of a changing climate. Furthermore, surface water, which determines the quality and availability of aquatic freshwater habitat, depends heavily on rainfall and temperature regimes [5] which can be drastically suffering by global climate change [16]. Relatively few studies have explored the implications of global climate change for freshwater fish reproduction. Predicted impacts of global climate change on fish included habitat loss and fragmentation, exceeding physiological tolerances and therefore the spread of alien species [17]. Normal changes in environmental temperature can affect endocrine function and either advance or retard gametogenesis and maturation, but above-normal temperatures have deleterious effects on reproductive processes [18]. During the maturing phase, exposure to high temperatures impairs gonadal steroidogenesis [19], delaying or inhibiting the pre-ovulatory shift from androgen to maturation-inducing steroid production [20]. This paper aims to determine the effect of changing climatic patterns on the reproductive performance of the freshwater fish. And assessing the consequences on reproductive physiology and phenology. The adjacent sections describe the methodology of reviewing papers followed by findings and conclusions.

MATERIALS AND METHODS

A comprehensive analysis of the impact of climate change on the reproduction of freshwater fish is presented, primarily to deduce the expected changes and related results. This analysis was performed using knowledge from various scientific articles and literature published in various ways in peer-reviewed journals, Google Scholar, Semantic Scholar, Elsevier, Research Gate, Science Direct, Springer, magazines, reports, and news media.

RESULTS AND DISCUSSION

Here we are describing the type of climate change indicators and their impacts on reproduction of freshwater fish, systematically under relevant headings.

Rising temperature/global warming

In the past century, global warming has increased the Earth's mean surface temperature by 0.6 ° C, and the temperature is expected to increase by a further 3 °C by 2100 [21]. "Change in climatic patterns alters water temperatures and current flow velocities in the river system on a global scale. This creates critical issues for local as well as migratory fishes with complex life histories that use rivers to reproduce" [22]. "Water temperature features a very marked effect on the physiological and biochemical processes in fish, and a raised temperature regime has complex effects on fish reproductive, nerve and endocrine systems. Increased temperature affects fat synthesis, metabolism, and the endocrine system which fails in the generative process" [23]. Freshwater environments and their fishes are especially sensitive to the effects of climate change as the persistence and quality of aquatic habitats are strongly reliant on climatic and hydrologic regimes [17]. Thermal tolerance levels vary depending on the latitude and at low or high temperatures are distinguished by oxygen restrictions [24]. Thus, it represents that the freshwater is likely to be more vulnerable to these changing climatic patterns. The fish species in the freshwater ecosystem have limited abilities to disperse as the environment changes.

"Temperature is one of the most important physiological factors deciding the overall functioning of aquatic ecosystems. Global temperature changes on freshwater have an impact on both the reproduction and early development of fish populations" [25,26] Okuzawa suggest that high water temperature is the proximate driver of the termination of the spawning season. The effect appears to be mediated by the suppression of gene expression in the B-P-G axis [23]. "Water temperature plays a vital role in the reproductive success of fish species. The elevated temperature has a direct effect on the pituitary gonad axis. This leads to impairment of the reproductive ability of the fish" [27-29] elevated summer temperature delay spawning and reduced redd construction for resident brook trout (*Salvelinus fontinalis*). Increased temperature affects reproductive behavior and morphology in a salmonid (*Salmo trutta*) [30].

Hypoxia

Hypoxia refers to oxygen deficiency in biotic environments. Hypoxia is a widespread phenomenon in marine and freshwater systems [31]. The spread of hypoxia poses a threat to aquatic ecosystem functions and services, and biodiversity [32]. Hypoxia started spreading before 1900 AD and the establishment of stable hypoxic conditions accompanied by increasing global nutrients emission from industries and climate change [33]. In the marine ecosystem, "Dead zones" have now been reported from more than 400 systems, affecting a total area of more than 245,000 square kilometers [34]. After the great 1993 flood of the Mississippi River, the hypoxic (or low-oxygen) "dead zone" in the Gulf of Mexico more than doubled in scale, hitting an all-time high of over 7,700 square miles in July 1999 [35], and in July 2008 hypoxic bottom waters extended across 20,720 square kilometers [36]. Hypoxia in the East China Sea: one of the largest coastal low oxygen areas covered an area estimated at greater than 12,000 km² [37]. Episodes of low (< 5 mg L⁻¹) to hypoxic (< 2 mgL⁻¹) concentrations of dissolved oxygen (DO) near Bordeaux were occasionally reported in the tidal Garonne River, about 100 km from the mouth [38]. With continued changing climatic patterns, the frequency of hypoxic events, and short, mild winters are expected to increase, possibly leading to unforeseen consequences for aquatic ecosystems [39].

"The effect of hypoxia includes inhibition of fish spawning even though the gonad and oocytes develop under hypoxia exposure. Luteinizing Hormone levels of female carp were significantly decreased upon chronic exposure to hypoxia, and the final oocyte maturation in hypoxic females was significantly retarded. The results indicated that hypoxia may inhibit fish spawning through LH-dependent final oocyte maturation [40].

According to Rudolf [41] behavioral studies revealed that hypoxia affects courtship behaviors, mate choice, and reproductive

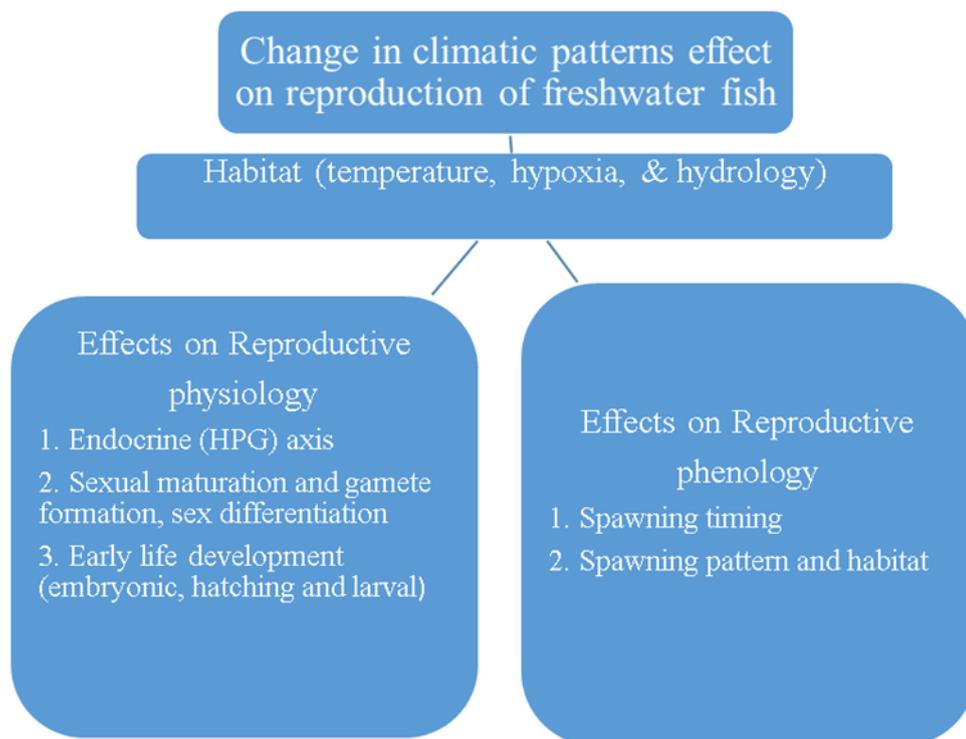
efforts in fish. He showed that hypoxia causes major reproductive impairments by inhibiting testicular and ovarian development, affecting production and quality of sperm and egg, reducing fertilization and hatching success, and affecting larval survivorship as well as the quality and fitness of juveniles. Evidence by Eva further showed hypoxia affects sex differentiation and sex development of zebrafish (*Danio rerio*), leading to a male-biased population in the F1 generation (74.4% +/- 1.7% males in the hypoxic groups versus 61.9% +/- 1.6% males in the normoxic group) [42]. The increase in males was associated with down-regulation of various genes controlling the synthesis of sex hormones as well as an increase in the testosterone/estradiol ratio. The male-dominated populations caused by hypoxia will have reduced reproductive success, [44] thereby threatening the sustainability of natural fish populations. Long-term cyclic hypoxia can affect valuable fishery resources and the structure of the fish population by impairing reproductive efficiency and inducing estrogenic effects in male [42-44]. "Hypoxia is additionally endocrine disruptor and poses a significant threat to the reproduction and hence sustainability of fish populations. The serum levels of testosterone, estradiol, and triiodothyronine significantly decreased in carp (*Cyprinus carpio*) upon chronic exposure to hypoxia, suggesting adverse effects of hypoxia on reproductive efficiency as a result of endocrine disruption [45]. Hormonal changes were associated with delayed gonadal development, decreased spawning success, sperm motility, fertilization success, hatching rate and larval survival [46].

Hydrology

Global climate change influences hydrology, which changes the timing and amount of precipitation and soil moisture, changes lake levels, and affects the quality of water [46]. Such changes give rise to the potential for environmental dislocations [47]. The pattern of flooding has a major influence on the evolution of life-history strategies of fishes in large river floodplains [48]. Specifically, habitat variability [49] and predictability seem to forge the reproductive strategies of fishes. Reproductive dynamics and flood regimes were closely correlated [50], the timing of reproduction in relation to the long-term hydrograph is related to life-history traits [51,52]. Correlations identified that the duration and timing of floods had negative effects on body condition, whereas amplitude and mean annual water level improved feeding activity [53]. The reproductive peaks of fishes using all four strategies (long-migrant, short migrants, parental care, and internal fertilization) always preceded flood peaks. Intense floods favored the gonadal growth of long-distance migrants and parental care, but for internal fertilization and short migrants were less important. Concerning juvenile survival, the occurrence of floods appeared to be crucial for the strategies of long-distance migrant, parental care, and internal fertilization [54], because such floods increased fish survival in the period of initial development. In contrast, short migrants are less dependents on floods for reproduction [55]. The seasonal fluctuations in hydrology regimes effects on species oocytes number, timing of reproduction, and parental care to their offspring [56]. Results by Winemiller suggest that both hydrology and habitat heterogeneity interact with fish life history strategy to determine optimal conditions for recruitment [52]. The water level has an impact on the hatching, time of spawning and survival of largemouth bass and spotted bass in Normandy reservoir [57]. The combination of climate change and increased water withdrawal would lead towards the extinction of local species up to 75% by the year 2070 [58] (Figure 1).

Figure 1: Modified, Potential consequences of changing climatic patterns on reproduction of freshwater fish [3,25,59-65].

Effects on reproductive phenology (spawning timing, pattern and habits)



Effects on reproductive phenology (spawning timing, pattern and habits)

The shift in phenology is the indicator of the effects of climate change on ecological communities [66]. As a result of climate change, many species are forced to change their breeding pattern, timing, and habitat [13,67-70]. Temperature and water flow maintains the density and size of habitats needed for successful spawning and recruitment [74]. Temperature is the primary driver of the phenological changes [72] and Freshwater fish respond to changing environments by shifting their distribution range, changing migration times, and spawning [73]. The impact of warm water and altered flow conditions have difficulty for migratory fishes during reproduction [22]. As the predictions by Ruiz-Navarro [74] suggest that there is potential for considerable alterations to the climate spaces of freshwater fishes. Specific habitats requirement for spawning display bottle-neck in the life cycle of fishes [75]. Some invasive species will be established and occupy the ecosystem permanently due to their voracious feeding and proliferative breeding habits under changing climatic conditions [76]. This type of invasions by exotic fish shifting the spawning habitat as well as communities of endemic fish in a freshwater environment which has a limited range of expansion. Coldwater fisheries spatial distribution is projected to contract, replacing warm/cool water, and high-thermal tolerance species [77]. Climate change has accelerated the change of migration pattern of spawning, declining in fecundity, and shifting of Hilsa catch from inland water to sea [61]. The increase in temperature and water level in the Estonian part of the Narva river basin caused by climate change has affected the spawning of Bream (*Abramis brama*) and Roach (*Rutilus rutilus*) [78]. Within forty years (1951-1990), bream spawning shifted, on average, to ten days earlier but the spawning temperature range remained unchanged, while there was no shift in roach spawning time, which began spawning at about three degrees higher water temperature than before [79]. The brook trout eggs and alevins reared at normal 5°C and elevated 9°C temperatures show variation in metabolic rates. It indicates that the predicted increase in water temperature under climate change scenario have significant variation in eggs, alevins and fry metabolic rates [80].

Effects on reproductive physiology

All organisms respond to global climate change that allows them to organize the timing and duration of life-history stages that make up their life cycles. Climate change has deleterious effects on life-history [81] stages such as migration, and reproductive function [82]. Global climate change, environmental disturbance, and endocrine disruption are increasingly likely to pose additional stresses that could have a major impact on freshwater fish reproductive behavior. Changes in water temperature, hypoxia and hydrology have profound effects on fish reproductive endocrine (HPG) axis [45], sex differentiation, gamete maturation, early life histories [63], spawning pattern [13] and timing as well as reproductive success [83].

Endocrine (HPG) axis

Fish reproduction is regulated by the interaction of the nervous and endocrine systems [84], and this interaction is carried out by the hypothalamus-pituitary-gonad or brain-pituitary-gonad (BPG) axis [85]. The organs that compose the axis produce and release, as internal factors, the hypothalamic, pituitary, and gonadal hormones, regulated by kisspeptins [86,87]. In addition, and interacting with the hormones produced by the axis, several internal factors such as neurotransmitters and neuromodulators and external factors such as temperature, photoperiod, and rainfall are involved [88].

Temperature, hypoxia, and change in hydrology regimes are the main direct and indirect factors resulting from the global climatic changes that are likely to influence fish reproductive behavior and reproductive endocrine axis [25]. This change has the capacity to affect the endocrine HPG axis at multiple sites through its reaction-rate-determining effects on hormone synthesis and action, and its effects on hormone structure. These gonadotropins stimulate steroidogenesis by the gonads through a complex pathway of specific enzymes [88]. Common carp (*Cyprinus carpio*) subjected to hypoxia (1.0 ± 0.2 mgO₂ L⁻¹) resulted in reduced LH level leading to failure of oocyte maturation [40]. Fish exposed to hypoxia resulted from a change in climate has the ability to disrupt endocrine and reproductive impairment in fish population [89].

Heat has action on the synthesis, secretion, and metabolism of hormones. Consequently, endocrine profiles may be significantly altered above-average temperatures [90]. Pejerrey fish (*Odontesthes bonariensis*) kept under a control-temperature regime (19°C) and two experimental temperatures (23° and 27°C) for 8 days. The effect of elevated temperature results in the reduction of plasma estradiol in females and testosterone in males [27]. Both temperature and hypoxia have interactive effects on the growth and survival of juveniles [91]. Shifting global climate change brings severe complexities of aquatic endocrine disruption in fishes [92,93] Chronic exposure of fish *Oryzias melastigma* [94]. Nearly 2000 fish *Oryzias melastigma* were exposed to hypoxic (1.5 mg L⁻¹) and normoxic (6.0 mg L⁻¹) conditions for 30 days and the result shows that majority of the immune-related parameters and steroidogenesis genes in HPG axis are modulated [95]. Thus this change results in a change in hypoxia-responsive mRNAs and protein in both steroidogenesis and immunomodulatory pathways.

Sexual maturation and gamete formation, sex differentiation

Negative impacts of direct and indirect thermal changes caused by global climate change on river water effects on the sperm quality of brown trout (*Salmo trutta*) [96]. Sperm motility is a key factor in allowing us to determine semen quality and fertilizing capacity [97]. Fertilizing ability and velocity of spermatozoa, as well as the duration of the motility period [98], depending on the temperature [99]. “High water temperatures due to changes in the aquatic environment before sexual maturation and spawning may result in hermaphroditic dysfunction of *Kryptolebias marmoratus*” [100]. Due to the consequences of climate change the European smelt (*Osmerus eperlanus*) anadromous fish mature at a young age [101].

Temperature-dependent sex differentiation occurs more frequently in fish species [102], and in the scenario of global warming, temperature-dependent Sex Determination would increase. “Increasing temperatures inevitably lead to extremely male-based sex ratios, which can dramatically alter the sex ratio from 1 to 31 (male / female) in freshwater to minor shifts of just 1 to 2 °C” [103]. At temperature 36°C Nile tilapia (*Oreochromis niloticus*) increased the proportion of male up to 33-81 % and Sex reversal by the genotypic female population of in response to temperature, shows the effect of temperature on sex differentiation [104]. In blue tilapia (*Oreochromis aureus*), higher temperature produces a high male ratio while intermediate temperature give a balanced ratio and lower temperature delay the differentiation of gonads [105]. 17α-ethinylestradiol effects at different water temperatures on zebrafish sex differentiation and gonad development, Luzio show low-temperature delays gonad differentiation and maturation while high temperature masculinizes Zebrafish [106]. “The results by Hattori suggest a function of cortisol in the masculinisation of pejerrey (*Odontesthes bonariensis*) and the possible connection of stress and testicular differentiation in this gonochoric TSD species” [107] (Table 1).

Table 1: Evidence of fish reproduction affected by changing climatic patterns.

Change in Climatic patterns	Effects on Reproductive Mechanism	Species	References
Hydrology			

Change in water level & seasonal destabilization of lake	Decreased Reproduction & Loss of breeding ground	Sarotherodon galilaeus, Oreochromis aureus	David ^[115]
Hydrological alteration	Change in habitat and spawning	Cyprinus carpio Coreius heterodon	Yang ^[116]
Increase in flood frequency Mississippi-Missouri river	Successful reproduction (sporadic recruitment) and invasion	silver carp Hypophthalmichthys molitrix and bighead carp H. nobilis	Gibson-Reinemer ^[117]
Water quality (sulfate soils)	Overall reproduction	Burbot (Lota lota)	Toivonen ^[46]
Hypoxia			
Prolonged diel cyclic hypoxia	Endocrine disruptor	Cyprinus carpio	Rudolf ^[44]
Hypoxic Condition	sex differentiation and sex development	zebrafish (Danio rerio)	Eva ^[42]
Hypoxic hypoxia	Transgenerational Impairment of Ovarian Development and Hatching Success	(Oryzias melastigma)	Lai ^[94]
Reduced oxygen	Effects on embryos and Larvae	Lake Trout (Salvelinus namaycush) & Largemouth Bass (Micropterus salmoides)	Carlson ^[118]
Diel cyclic hypoxia	Impairs reproduction	Goldfish (Carassius auratus)	Bera ^[43]
Global warming/temperature			
Warmed Winter Water Temperatures	Out of season spawning	Fathead Minnows (Pimephales promelas)	Firkus ^[28]
Elevated temperature	Impairment of reproductive	pejerrey Odontesthes bonariensis	Warren ,Federico ^[28,29]
Increased temperature	Reproductive behavior Sperm quality	Salmonid (Salmo trutta)	Fenkes ^[96]
Temperature fluctuation	Egg quality and malformation rate	Rainbow trout Oncorhynchus mykiss	Aegerter ^[119]
Temperature	Sperm motility and fertilizing	salmonids, cyprinids and sturgeons	Alavi ^[97]
Warming	Change in reproductive Phenology	Cyprinid fish Gymnocypris selincuoensis	Tao ^[120]
High temperature	Sex reversal	Nile tilapia Oreochromis niloticus	Baroiller ^[104]
Early ice break	Timing and frequency of breeding	Lacustrine fish Three-spine stickleback (Gasterosteus aculeatus)	Hovel et al ^[64]
Variable and constant thermal conditions	Embryonic and early larval development	Cyprinids (Leuciscus leuciscus, L. idus, L. cephalus, Cyprinus carpio)	Kupren, El-Gamal ^[112,113]
Incubation temperatures	Egg development dynamics	(Coregonus albula) and European whitefish (Coregonus lavaretus)	Karjalainen ^[114]

Early life histories

Temperature plays a vital role during the reproduction process which directly effects on embryonic duration [108], eggs survival, hatching, development rate, larval duration, and survival [63]. Result by Shang implies that hypoxia may have a teratogenic effect on fish and delay fish embryonic development, which may subsequently impair species fitness leading to natural population decline [109]. Diversification on water temperatures due to changing climatic patterns plays a critical role during the time of hatching, growth, and development of juveniles [110,111]. Variable and constant thermal conditions have effects on embryonic and early larval development of Cyprinids fish [112,113]. Temperature change alters the egg development dynamics in cold-water adapted coregonids primarily effects on the survival of embryo, hatching, and growth of larvae [114].

CONCLUSION

In this paper, we reviewed the previous literature that explored possible impacts of change in climatic patterns on the reproduction of freshwater fish. This review revealed that the changing climatic patterns have profound effects on the reproduction of freshwater fish and will continue to impact on reproductive physiology and reproductive phenology. These changes affect spawning timing and pattern, endocrine (HPG) axis, sexual maturation, gamete formation, sex differentiation, and early life histories of fish. Fish exposed to hypoxia and elevated temperatures as a result of changing climatic patterns has the ability to disrupt endocrine and reproductive impairment in the fish population. It is concluded that the changing climatic patterns effects are typically species-specific, with cold-water fish being generally negatively affected and warm-water fish positively affected.

This review provides insight into some evidences and potentials, how changing climatic patterns effects on reproductive performance of fish. We suggest that to improve our understanding of the effects of changing climatic patterns, future research needs to cover every aspect of fish reproduction, integrating interdisciplinary studies of migratory, reproductive, and behavioral physiology. Consideration of all aspects of fish reproduction can be effective ways of managing and ensuring their continued abundance in the face of current and future climate change.

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