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Review

Climate Change and Reproductive Biocomplexity in Fishes: Innovative Management Approaches towards Sustainability of Fisheries and Aquaculture

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Abstract: The ongoing rapid climate change, combined with the disturbance of fish breeding grounds, may impact reproduction by endangering successful breeding and survival, and thus affect the viable sustainability in aquaculture systems as well as in the sea. In this study we focus on the biocomplexity of fish reproduction in response to climate change. Further, we propose adaptive strategies, including technological advancements, using a noninvasive and non-lethal approach, and we outline an assisted reproduction and nutrigenomics approach to mitigating fish reproductive risks posed by climate change. This was done in an effort to monitor fish aquaculture and ensure that, as a livelihood, it may provide a useful source of nutrition for our society.

Keywords: aquaculture; fish sustainability; endocrine regulation; antioxidants monitoring; aquaculture biostatistics; germ cell transplantation; nutrigenomics

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1. Introduction

Climate change is undeniable and deserves effective solutions toward sustainability [1,2]. In the recent geological past it is evident that although the high specific heat coefficient of water buffered the oceans, they were not exempt from the effects of climate change and eco-evolutionary consequences [3]. Climate change alters fundamental ecological processes, profoundly impacting oceans as well as aquaculture systems, primarily through rising sea levels and temperatures, resulting in altered monsoon patterns and inducing intense weather events and water stress [4]. Climate change affects the physiologies, patterns of growth, and behaviors of aquatic organisms, which in turn reduces their geographic distribution and abilities for reproduction [5,6]. This ultimately results in mortality, changing the oceans' composition, production efficiency, and functionality of aquatic ecosystems [7,8]. Fish, being poikilothermic, are influenced by asymmetric climatic events affecting a range of factors, from metabolism to behavior, and the process of evolution [8]. Temperature change may lead to biodiversity loss, affecting the global fish stocks [9,10], having socio-economic consequences, and causing an increase in nutritional hunger [11].

Projections show that these spatial and temporal changes may intensify in the future [12,13], where the importance of the dynamic interplay between biological systems and their environment, known as "biocomplexity", is perceived [14]. Diverse physical habitats, the influence of shifting environmental factors, intra-species competition, nutrient cycling, and community dynamics are just a few of the facets of biocomplexity that aquatic ecologists have discussed, and that have an impact on the productivity of fish species [14].

The ongoing rapid environmental changes, combined with the disturbance of breeding grounds, may endanger successful breeding and survival, and thus the ability to maintain viable sustainability. Sexual reproduction, being an important and energy-intensive process for species survival and evolution in fish, is strongly reliant on specific environmental cues that trigger and regulate sexual maturation, breeding, and offspring survival [15]. The response of organisms to environmental stochasticity, whether driven by genetic (evolutionary) or non-genetic (plastic) processes [16], results in within-generation phenotypic plasticity, transgenerational plasticity, and genetic adaptation [17]. Some plastic responses may involve tradeoffs with fecundity [18], or they can result in interactions with different species or habitats that eventually lower survival rates [19].

In this review article, we focus on the biocomplexity of fish reproduction in response to climate change. Further, we propose innovative solutions to monitor and contrast the fish reproductive risk posed by climate change to secure aquaculture as a sustainable livelihood and as an abundant nutritional source for society.

2. Climatic and Aquatic System Changes

Climate change and resource sustainability have become global issues in recent decades. Marine animals are at a high risk from climate change due to the change in temperature in both the air and water simultaneously. The change may be limited to a certain area, or worldwide [1]. Climate changes, in oceans as well as in aquaculture systems, directly affect the physical behavior, the biological growth pattern, and the fertility of aquatic organisms, including fish [20]. Implicitly, this changes the structure and productivity of the aquatic environment [21], affecting individual organisms as well as whole species populations [22]. Aquatic organisms, including fish, are poikilothermic in nature. As a result, they are extremely sensitive to changes in the environmental temperature. Increased water temperature caused by climate change reduces fish's growth due to an increase in their metabolic rate. Only environmental spawners, whose spawning grounds move in response to variations in environmental properties such as temperature, are able to move to locations where their internal control systems can restore internal homeostasis when the ambient temperature exceeds their temperature tolerance [6,23]. This migration allows environmental spawners to migrate away from shallow coastlines and slightly enclosed areas in shallow water [24]. Sea level rise, increased tide frequency, lower pH, a higher concentration of carbonate ions in seawater, and an increase in disease risk in marine biota are all potential effects of climate change on marine ecosystems (Table 1). Climate change has an impact on the entire aquatic food chain, and consequently on fish production. The availability of nutrients in water is influenced by temperature and the amount of sunlight, which contributes to the resources available for fish productivity and sustainability [25]. Reduced rainfall due to climate change will result in a decrease in ground flow, which will starve wetlands and mangroves and harm local fisheries. Climate change has a significant impact on most small fishing grounds in the lowlands. In some areas, increased rainfall raises the level of nutrients in bodies of water, causing eutrophication and hypoxia in fish [25]. Light levels and temperature variations influence the availability of nutrients which, in turn, contributes to the main source of aquatic resources available for fish productivity and sustainability. De Silva and Soto [5] highlighted that the impacts of climate change on freshwater aquaculture in tropical and subtropical regions are difficult to predict. Increasing temperatures and increasing plankton growth, as a result of eutrophication, may increase the growth rates and productivity of cultured species [5].

Table 1. Potential impacts of climate change on fisheries and aquaculture (adapted from Barange and Perry [4]).

Drivers of Change	Impacts
Variation of the surface temperature of the waters	Expansion of harmful algae Lowering of dissolved O_2 levels Spread of disease and parasites Extension of growth stations Changes of position and ranges of suitable species Mortality decreases during the winter season Enhanced growth and food conversion rates Alteration of local ecosystems induced by competition, parasitism and predation of competitors and exotic species
Variation of oceanographic variables	Decreased flushing rates and food availability to shellfish Alteration in the richness of edible species and fishmeal
Sea level rise	Reduction of areas destined for aquaculture Reduction of areas that provide physical protection Increased risks of flooding Salt infiltration into groundwater
Increased frequency of storms	Larger waves More frequent storms Floods caused by rainfall Variation of salinity parameters Structure damage
Drought and water stress	Variation of salinity parameters Decrease in water quality Increased disease Uncertain water supplies

Changes in water availability, extreme weather events, vertical stratification, and nutrient supply may have negative effects on freshwater aquaculture production, depending on local conditions. Aquaculture activities in brackish waters may be affected by changes in salinity (increasing or decreasing), again depending on local conditions of runoff, marine circulation, etc. Further, aquaculture in temperate regions may be adversely impacted by an increased prevalence of pathogens, as temperatures warm at a greater rate than in low latitude regions [4].

3. Climatic Change Effects on Fish Reproduction

In the last few decades, alterations have been made in the classification and recording of relevant events in the reproduction of organisms, in particular those that are cold-blooded, i.e., those unable to regulate their own temperature independently from that of the environment (known as reproductive phenology) [5,7]. As in other vertebrates and invertebrates, these climate asynchronous changes potentially affect population dynamics, community structure, ecosystem processes, and the stability of ecosystems by changing recruitment success [5], impacting on mismatches between phytoplankton blooms and fish spawning phenology [6].

The long term assessment of the influence of climate has shown that precipitation, critical temperatures, along with the fish mortality rate were the main drivers of species abundance shifts [4,26]. The evidence of climate change on sex ratio, gonadal differentiation, gametogenesis, gametes quality, embryonic activity, reproductive cycle, sexual behavior, and recruitment success [7,27–32] has been extensively reported (Figure 1).

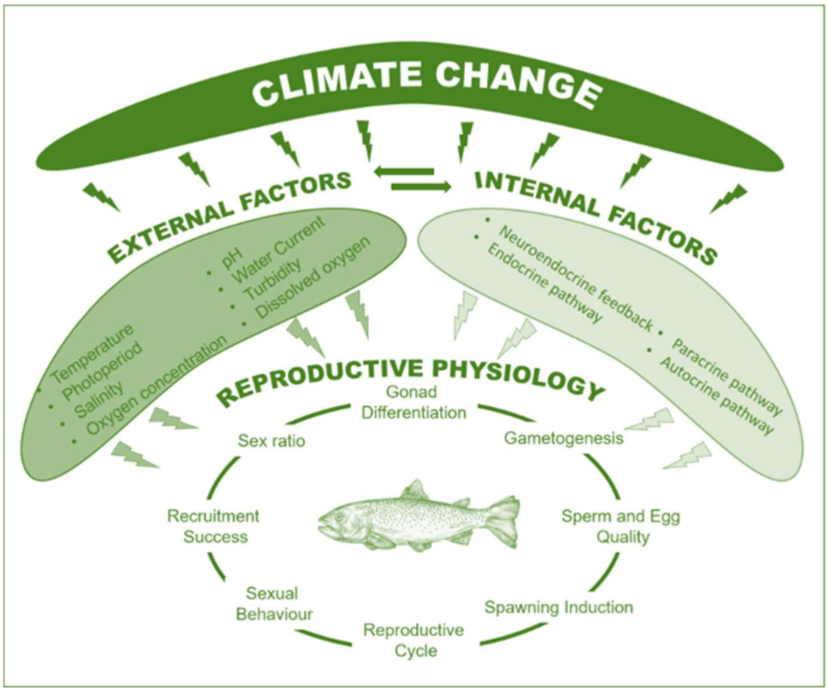

Figure 1. External and internal climate dependent factors affecting fish reproductive physiology.

Thus, under the changing climate scenario, knowledge of the interaction between different environmental variables that regulate the functioning of the brain-pituitary-gonad axis is critical for predicting ecological phenomena related to natural fish populations and controlling captive fish breeding. The central nervous system is known to play a critical role in the combination of various external (environmental) and internal (hormonal) signals that regulate reproduction via reaction-rate-determining effects on hormone synthesis and action, as well as effects on hormone structure [33] (see Figure 2). The sensory system influences the hypothalamus, which appears to be the most important brain area for controlling vertebrate reproductive processes and behaviors [34–36].

The endocrine control of reproduction depends on the hormones, gonadotropin releasing hormone (GnRH I, II, III), thyroid hormone, dopamine, neuropeptide Y (NPY), gamma-aminobutyric acid (GABA), and kisspeptin (Kiss), which stimulate specific enzymes to produce sex steroids and control gametogenesis [37]. All of these are influenced by the levels of free radicals and by the balance of free radicals, which is controlled by the physiological antioxidative defense mechanisms [7,38]. With geographic spans that cover a wide range of temperatures, many fish species may be able to adapt to changing temperatures [39]. However, high water temperature impairs the development of gonads, inducing gonadal regression and spawning impairment in association with the inhibition of the expression of specific genes, conformational changes in proteins, and the increasing propensity of steroid hormones to form water-soluble conjugates [40]. Studies have found that decreased stream flows and increased water temperatures, due to climate change, mainly affect the reproductive success of geographic spawners whose spawning grounds are fixed by geographic features [41,42]. An interesting earth system model reports the impact of a high-emissions, climate-warming scenario (RCP8.5) on the future spawning time of the two classes of temperate, epipelagic fishes: "geographic spawners" and "environmental spawners" [6]. Predictions of the synergistic effects of the phenology of blooms and temperature on the life cycles of fishes may lead to improved evaluations of the impact of climate change on existing fish populations, as well as leading to more informed management for species conservation. Water flow alters turbidity, channel geomorphology, and spawning habitat suitability. These factors may thus initiate migration or spawning events [43]. Fraser and colleagues [44] proposed that habitat reductions, under climate-change-induced flow reductions, would certainly reduce population abundance, which may be partially offset by upstream expansion to more thermally suitable habitats. According to Pottner and Farrell [45], a greater pCO_2, or increased acidification, may restrict the ability of mature fish to operate aerobically, which could have an impact on their reproductive productivity. Researchers have correlated hypoxia and high water temperature with unsuccessful migration and spawning in migratory species [46]. The reproductive impairments observed in fish due to increased pCO_2, as a result of the low perception of chemical cues and sexual pheromones, affect mating and other reproductive processes [47]. Additionally, data from transcriptomic and proteomic studies suggest that ocean acidification affects the circadian system, which may lead to downstream modifications in the control of neuroendocrine regulation of fish reproduction. Biswal and colleagues [48] reported that ocean acidification and hypoxia simultaneously pose a threat to larval survival by impairing both larval behavior and sensory capacity. Researchers have also reported that a shift in salinity may affect breeding and reproductive success, and parental behavior in fishes [49–51]. Changes in salinity can have an impact on fish spermatogenesis and testicular homeostasis, affecting gonadal cell proliferation, apoptosis [52], and male nesting behavior in marine fish [50]. The synergistic effect of freshwater salinization and rising temperatures results in complex interactions with significant implications on the physiological responses of freshwater fishes, and contributes to a growing body of research documenting complex multiple-stressor interactions [53,54]. The ability for genetic adaptation to rapid climate change in fish is, however, affected by a number of factors, including adaptive genetic variation, effective population numbers, generation times, and connectivity across populations that might promote the spread of tolerant genotypes [55].

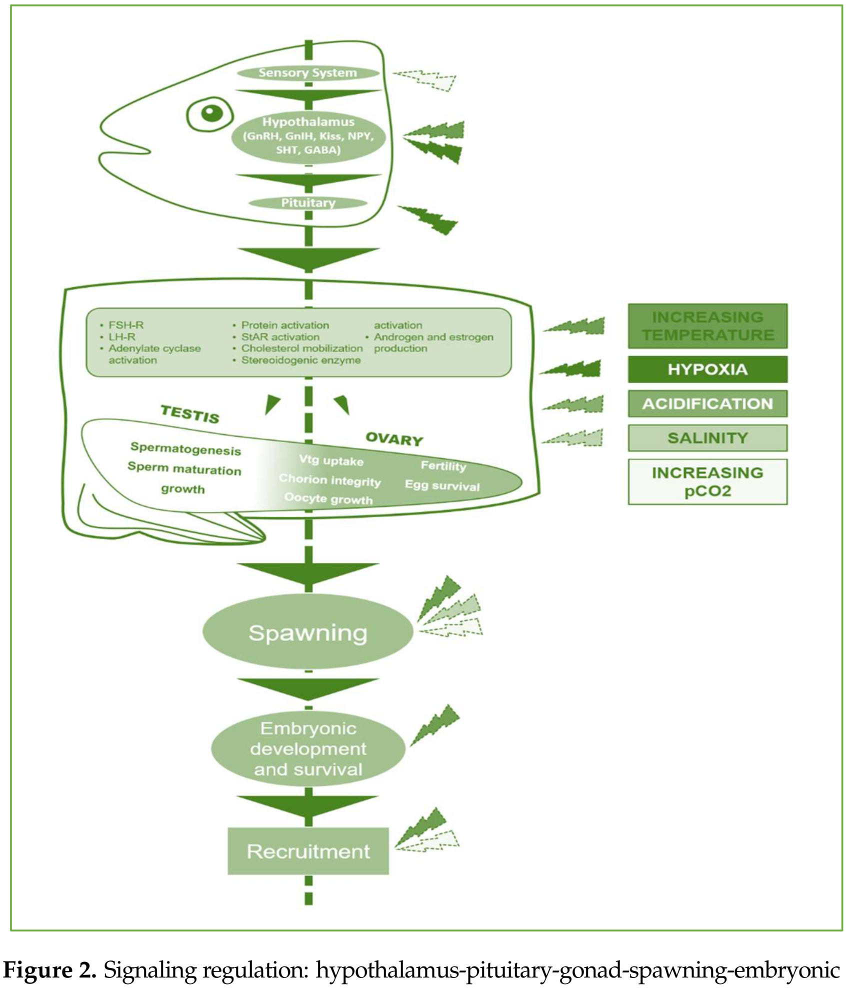

Figure 2. Signaling regulation: hypothalamus-pituitary-gonad-spawning-embryonic development altered by abiotic factors. Abbreviations: GnRH, gonadotropin releasing hormone; GnIH, Gonadotropin-inhibitory hormone; Kiss, kisspeptin; NPY, neuropeptide Y; SHT, somatotropin, GABA, gamma-aminobutyric acid.

4. Climate Change and Solutions towards Sustainability

The average global temperature has increased by 0.74 °C in the last 100 years [56]. Scientists are working to manage fisheries and aquaculture at appropriate spatial and temporal scales, using an integrative approach to limit the impact of climate change on fish reproductive biocomplexity [2]. Biocomplexity is a study of the complex structures and behaviors arising from dynamic, non-linear interactions of active biological agents, with a hierarchical structure that integrates control processes and feedback mechanisms. Researchers have linked several different elements in an effort to formulate an understanding of the complex natural environment of the fishery and its use. These elements include knowledge of the fishing area used by the fishermen, and their knowledge of the biology and ecology of specific species, as well as their local ecological knowledge (LEK) based on studies of ethnobiology, ethnoecology, and ethnotaxonomy of fish. Understanding these factors is very important, and crucial to the process of moving fishery and aquaculture systems towards improved management and sustainability [13,57]. Additionally, understanding how various environmental factors interact to govern the reproductive axis in fish is also crucial for understanding and forecasting ecological phenomena relating to fish populations, as well as for potential applications in the management of captive fish breeding [36,57].

Climate vulnerability assessments should be conducted as part of a future fisheries management framework, according to studies in recent years [58,59]. Adaptation planning on the cusp of climate change can provide a rapid appraisal approach to understanding vulnerabilities. In recent years, the fish baskets approach has gained enormous importance as a participatory framework for carrying out climate profiling and data-limited assessments that adapt to changes in stock status, to increase the number of fisheries that can implement multispecies management to improve their performance [60]. Yang and colleagues [61] proposed a hierarchical framework to analyze the relationships between fish spawning and abiotic factors, which are intricately linked to species-specific ecology. According to the simulated studies of large, protected areas, such as marine reserves, can preserve mobile stocks and significantly boost stock sizes, preventing the environmental harm caused by declines in fish populations below carrying capacity [62]. Highly migratory species can be successfully managed through the implementation of fishing quotas, prohibitions on fishing during the mating season, the creation of marine protected areas (MPAs) and overall catches in these significant areas, or the restriction of certain gear types (such as bottom trawling in sensitive habitats). The recruitment of larvae from unfished offshore areas would also boost inshore stock enhancement, even for non-mobile species [63]. We must adopt new economic thinking to attain long-term objectives [64]. To lessen the strain on migratory species, local markets must be formed to maximize the economic potential of fresh, local fish as a premium product [65].

It is critical to monitor long-term demographic responses to climate change to protect vulnerable fish populations. The rate of climate change frequently outpaces the average rate of evolutionary change [66]. Recent meta-analyses suggest that species with adaptive phenotypic responses may be evolving too slowly to keep pace with climate change [67,68]. Therefore, monitoring numerous responses, and comprehending their limitations, is essential for efficient resource management and endangered species preservation [19].

However, distinguishing the effects of climate change from the effects of poor management is difficult because, for example, recruitment failure can be caused by both poor environmental conditions and a small spawning stock size. It was also reported that sustained overfishing, plus inappropriate size selectivity of the main fishing gears, have caused the decline in spawning stock biomass [11]. Since calculating the size of fish populations is exceedingly challenging, aquaculture research using virtual population analysis (VPA) is only used to anticipate fish stock size [69] and estimate the most commercially fished stocks [70]. Fish provides high-quality protein, which is in increasing need as the human population rises. The River Ranching Program was created to encourage financially and environmentally responsible sustainable use and conservation of fishing resources. This program supports sustainable fisheries, the preservation of biological diversity, the evaluation of ecosystem services, the reduction of habitat degradation, and the enhancement of social and economic benefits. Additionally, utilizing a cluster or area-based approach, it will assure the improvement of traditional fisheries, trade, social protection of inland people, and environmental sustainability. The development of adaptation techniques, such as the breeding of climate-resilient or saline-resistant species, could benefit from research on predictive modelling, and supercomputing tools [71]. Temperature increases above the ideal range of tolerance can be controlled by better feeding and selective breeding [72,73]. The developmental stage of the gonads at the time of hormonal therapy, the type of hormonal therapy, the potential stress caused by hormonal manipulation, and the latency period between hormonal stimulation and stripping for inexpensive in vitro fertilization, should all be considered when choosing a spawning induction procedure [74]. The survival of eggs and the growth of the embryos are strongly influenced by parental fitness and maternal nutritional fitness, according to earlier research [75]. Rather than relying on the success of fertilization and the survival of embryos, a biostatistical method employing the fry survival rate has been shown to be a significant criterion to estimate fish output [76]. A more comprehensive approach, including multispecies and ecosystem analyses, would allow for more accurate predictions of the effects of climate change on fish recruitment [77]. An ecosystem approach to fisheries (EAF) emphasizes interactions between ecosystem elements and the human system, to achieve sustainable development in fisheries and aquaculture by emphasizing holistic, integrated, and participatory processes [12]. As a pilot program that may be used on a large scale, community-based periodic training, awareness raising, and information dissemination on trending adaption measures are recommended [78,79], that may help to uplift the production and livelihood of stakeholders as a process to prevent ecological harm [80]. An inventory of ecological information and biological attributes of various fish species, particularly diet and reproduction and their correlation, is needed for successful management [81]. Aquaculture is becoming the last resort to meet the present and larger consumption rates of a growing population, and to withstand the impacts of climate change on potential fisheries production. For this reason, aquaculturists need to develop adaptive strategies to maintain productivity in containment, in order to manage the fisheries resources sustainably. In the following sections we have attempted to summarize first, the biotechnological detection of antioxidants and fertility rates that are useful for the assessment and awareness of reprotoxicity risk, using a non-invasive and non-lethal approach [7,82,83]; then, the assisted reproduction using xenotransplantation and surrogacy [84,85]; and finally, the nutrigenomics programs [86,87] that may contribute effectively to counteract the fish reproductive risk posed by climate change.

4.1. Non-Invasive and Non-Lethal Antioxidative Defense Monitoring and Sustainability

Temperature influences biochemical reactions and metabolic rates, having an impact on the amount of energy available for growth, foraging, and reproduction. As a result, understanding the physiological and molecular responses used by fish to cope with ocean warming is essential. In the eco-physiology field, the health of wild and cultured fish has been monitored with several parameters such as the oxidative stress and the resulting physiological response [83,88]. The oxidants' overexpression, specifically reactive oxygen species (ROS), is considered harmful to cells, since they cause DNA damage in the form of single-strand scission, base deletions, mutations, and degradation, as well as peroxidation of cell membrane fluidity, all leading to apoptosis. Indeed, antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), glutathione peroxidases (GPXs), glutathione reductase (GR), and many others are the most important components of the antioxidative defence mechanisms in fish [89,90]. These physiological responses are closely dependent on how fish use antioxidants to counteract oxidative stress due to rising temperatures. As a consequence, measurements of antioxidative biomarkers may detect the presence of some environmental stressor more quickly and specifically, allowing an early estimation of the damage [7,91]. Strategies that minimize harm to the animals, thereby facilitating the benefits of animal experiments, were formally established by the Council of the European Communities with the Directive 86/609/EEC [92]. At the time of its composition, it partially contained concepts about ethical standards for the regulation and review of animal experimentation covering the 3Rs principle: Replacement, Reduction, and Refinement [93]. Non-invasive procedures adhere to the 3Rs principle, which can be applied to large numbers of specimens and also can be used for repeated assessments without negatively impacting the population of the selected biological species. The redox skin biopsy status evaluation is based on an epithelial cells removal procedure which does not require animal sacrifice, avoiding ethical issues. It provides the adequate biological material needed for biochemical and molecular antioxidative assays, extensively used on several organisms [82,94,95]. In fish, the skin is covered and protected by the Skin Mucus Layer (SML). It is a complex secretion composed of several compounds such as cytokines, peptides, lysozyme, lipoprotein, lectins, and proteases. This layer plays an important role in immune functions, reproduction, excretion, respiration, ionic and osmotic regulation, and protection against microorganisms (see [96] for review). Thus, in fish, the skin biopsy used for SML detection consists of gently scraping the body surface with a sterile spatula [97,98] (Figure 3A). This is a method that has been validated on numerous fishes such as the Atlantic salmon *Salmo salar* [97], the rainbow trout *Oncorhynchus mykiss* [94], the walking catfish *Clarias batrachus* [99], the Arctic char *Salvelinus alpinus*, the brook trout *Salvelinus fontinalis*, the koi carp *Cyprinus carpio*, the striped bass *Morone saxatilis*, the haddock *Melanogrammus aeglefinus*, the atlantic cod *Gadus morhua* and hagfish *Myxine glutinosa* [100], the dusky splitfin *Goodea gracilis* [98,101], and the chapultepec splitfin *Girardinichthys viviparous* [102]. This method allows quantification of ROS and detection of the activity of antioxidant enzymes such as SOD, CAT, and GPx. It also enables an assessment of the oxidative damage biomarkers such as ThioBarbituric Acid Reactive Substances (TBARS) for lipid oxidation and for protein oxidation. Non-invasive methods cannot always be used in toxicological studies and in environmental assessments. In fact, other strategies that do not involve specimen euthanasia are applied, and referred to as non-lethal methods. In fish biology, plasma sampling is a widely used technique for investigating health and physiology. Several plasma sampling techniques have been developed, including cannulation [103–105], gill and heart punctures [106,107], and caudal puncture [108,109]. This latter method provides a quick, easy, and relatively non-lethal method for obtaining a blood sample. In fact, a common practice is to insert a heparinized needle syringe, or a needle and heparinized vacutainer, into the ventral surface midline of the caudal peduncle posterior to the anal fin (see [110] for review) (Figure 3B).

Studies on fish plasma have been performed investigating stress-induced changes using glutathione peroxidase and α-tocopherol as biomarkers [111], and provide estimates of antioxidative damage by detecting Super Oxide Dismutase (SOD) and Gonad Stimulating Hormone (GSH) activities [112], as well as Catalase (CAT) and Glutathione-S-Transferase (GST) activities [99]. The plasma studies not only assess the potential for temperature to affect gametogenesis, by showing how gonadal steroids testosterone (T) and 11-ketostestosterone (11KT) are higher in fish exposed at higher temperature [113], but they also investigate determination of the sexual cycle and spawning season using sex steroids biomarkers such as androgens, 17 α-hydroxyprogesterone, and 17 β-estradiol [114]. Additionally, other parameters such as egg quality and fry survival rate may be used as non-invasive methods for determination of the optimal fertilization success [69]. In fact, these two parameters are influenced by temperature, physiological antioxidative defense, endocrine status, and diet [115,116]. Other intrinsic factors, including maternal age and genetics, also have an impact on egg quality and, indirectly, on the survival rate of the fry [117–119].

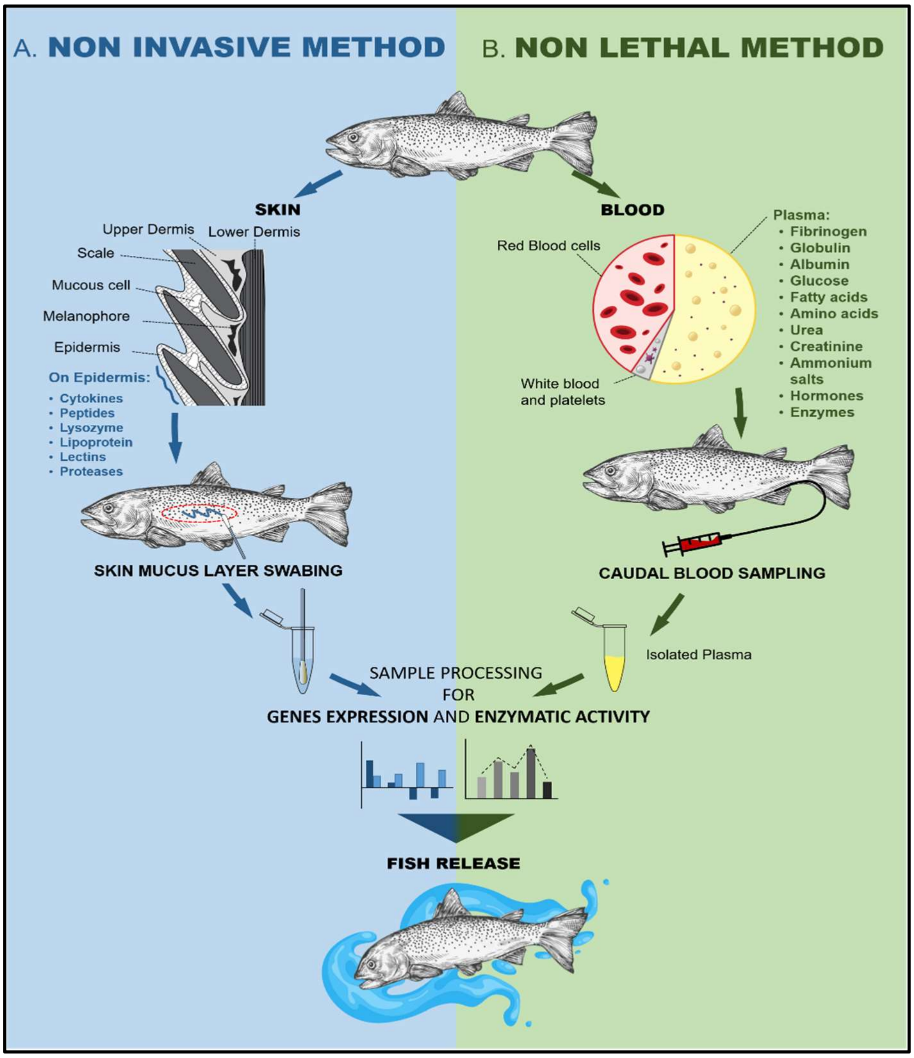

Figure 3. Non-invasive and non-lethal methods used to detect antioxidative biomarkers. (**A**) Non-invasive method concerning fish skin epidermis, which consists in gently scraping the body surface with a sterile spatula followed by sample processing for gene expression and enzymatic activity. (**B**) Non-lethal method concerning blood plasma obtained by heparinized needle syringe into the ventral surface midline of the caudal peduncle posterior to the anal fin, followed by sample processing for gene expression and enzymatic activity.

Monitoring these responses in farmed fish populations is less cost-effective and more cumbersome compared to simply monitoring temperature or other general indicators of population health such as growth or disease incidence. Taking action when these measures fall outside the limits of tolerance allows risk prediction and preventative damage control, therefore leading to improvements in the sustainability of aquaculture in the face of climate change. Furthermore, applying novel solutions to practical problems is mainly achieved through experimentation.

There is a scarcity of studies using sophisticated methods to investigate climate-driven responses in fish. Therefore, it is essential to conduct more species-specific and environmentally realistic studies to understand future climate change-induced fish ecophysiologies. It is also necessary to select a broader range of stressors and model fish species to understand unexpected outcomes under different climate scenarios. Additional research on non-lethal endpoints to trace stress events in fish is also required. No studies exist which implement a comparative-collective approach to investigating fish stress responses along with life cycles, feeding strategies, or behavioral responses under diverse culture conditions or regimes. So, other than the growth and disease incidence, it is also important to understand the stress response in fishes under climate change conditions. Hence, we have discussed the technological advances of these procedures, and their potential to better handle these studies in a changing climate scenario.

4.2. Assisted Reproduction

The approach to protecting declining fish populations through in situ conservation, is the highest priority under this climate change scenario. Hence, scientists have recommended ex situ conservation as an effective means to derive functional gametes to conserve and propagate these valuable germlines through captive breeding [85,120,121].

The development of surrogate broodstock via germ cell transplantation, which produces millions of fish gametes with desirable qualities like growth, disease resistance, fecundity by using just one donor without immune-rejection, is one of the most promising methods for ex situ conservation. Surrogate broodstock technology thus enables (1) transplanting donor germ cells from a single selected fish with superior traits into many recipient fish, to produce offspring with superior genetic traits in an efficient and reliable manner; (2) the process of producing gametes for a species with a long generation period from gametes from a recipient species with a short generation time, which shortens the time needed to breed fish; and (3) the long-term implantation of cryopreserved germ cells from desirable species or strains as genetic resources; (4) the mass production of genetically sterile fish through the transplantation of germ cells from a donor fish that is sterile due to a mutation in the somatic cells into normal recipients that do not have this mutation.

This process could be accomplished by three distinct developmental stages, embryonic, hatchling, and adult stage, and could be transplanted by the following methodologies including (1) blastomere transplantation from embryo to embryo [122] (Figure 4A), (2) differentiated primordial germ cell (PGC) transferred from embryo to embryo [123] (Figure 4A); (3) differentiated PGC transplanted from larvae to embryo and larvae [124] (Figure 4B), (4) spermatogonial transplantation in larvae [125] (Figure 4C), (5) spermatogonial transplantation from adult to adult, and [126], (6) oogonia transplantation [127] (Figure 4D).

Researchers have successfully achieved surrogacy in fish by using a micro injector to implant donor germ cells into the peritoneal cavities of freshly hatched larvae. This procedure can be carried out before recipient fish go through the sex determination stage, allowing the hatchlings to produce the xenogenic donor derived offspring when they reach adulthood [124,128,129]. Isolation of spermatogonial cells from juveniles of one species is another practical approach for xenogeneic germ cell transplantation (GCT) in sexually competent fish. The pejerrey *Odontesthes bonariensis*, whose spermatogonial cells were surgically transplanted into the gonads of the sexually mature Patagonian pejerrey *O. hatcheri*, was used in earlier experiments to examine the possibilities of this recently developed technology [130]. Lacerda and colleagues [84] performed a successful transplant in phylogenetically distant donor and recipient species of PGCs from goldfish (*Carassius auratus*) and loach into zebrafish blastulae, to produce donor sperm. Intraperitoneal transplantation of germline stem cells using surrogate broodstock has been successfully employed in *Takifugu rubripes* [131], *Nibea mitsukurii* [132], and *Scomber japonicus* [133]. Morita and colleagues [134] described that mating between males and females with superior traits may become impossible, due to varying time of maturity, when group spawning of the ensuing surrogate parent fish may lead to fertilization involving eggs and sperm generated from donors with superior traits.

With the aid of primordial germ cells, spermatogonia, and oogonia, the cryo-banking technique is a “silver bullet” for preserving the priceless genetic resources of fish gametes [135]. When cryopreserved germ cells were injected into the body cavities of allogeneic or xenogeneic recipients who had undergone triploidization or endogenous germ cell ablation, the transplanted germ cells began to migrate toward the recipient’s genital ridges, where they eventually were integrated. For cyprinid species, it is already known how to implant gonadal PGCs into freshly developed larvae; transplant migration-stage PGCs into the blastodisc of blastula embryos; and cryopreserve entire embryos bearing migrating PGCs [123,136,137] for identification of a cell-surface protein [138].

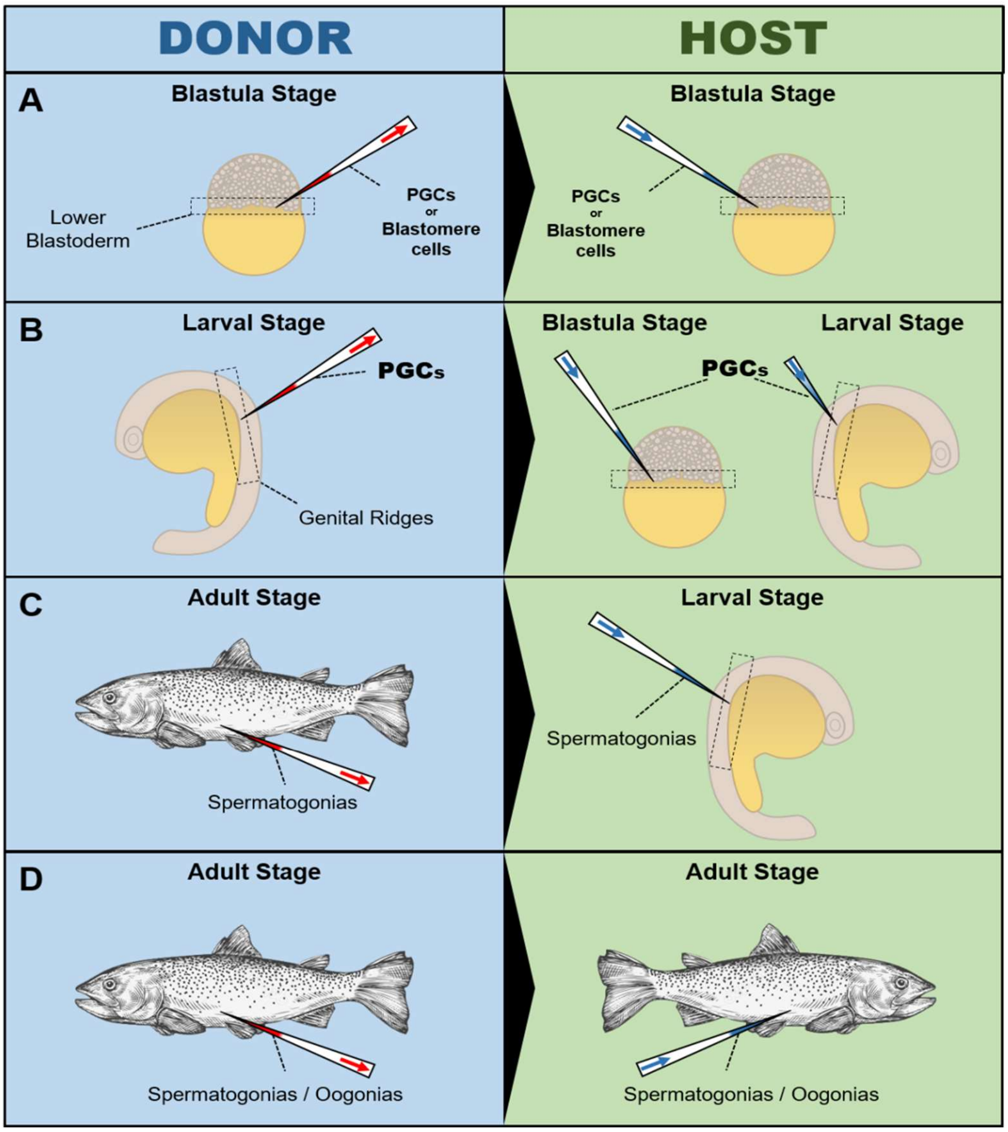

Figure 4. Germ cell transplantation. (**A**), Blastomere/differentiated primordial germ cells (PGCs) transplantation from embryo to embryo. (**B**), Differentiated PGCs transplanted from larvae to embryo and larvae. (**C**), Spermatogonial transplantation from adult to larvae. (**D**), Spermatogonials/Oogonias transplantation from adult to adult.

In recent decades, the use of DNA markers for the selection of individual fish with superior traits has made it possible to identify target phenotypes more quickly and easily [139]. The combination of genome-based selection and surrogate broodstock technology during the transplantation of germline stem cells, may represent a major advance for fish breeding in the future [140]. Studies have also demonstrated that freezing immature human testicles in liquid nitrogen can be used to permanently freeze germline stem cells within the testis without affecting survival rates [127,135,141]. The development and use of future reproductive technologies are greatly influenced by sociopolitical issues. The advances in reproductive technology, and their use, are still plagued by a great deal of ambiguity due to the expense and unpredictability of the approval procedures for legalizing these technologies [142]. To date we have no evidence that assisted reproduction is economically feasible to implement at a significant scale for aquaculture, compared to the cultivation of new species or new varieties tolerant to changes in temperature regimes; but we know that species presently farmed for food have advantages, such as extraction of marine drugs.

In any case, completion of the life cycle in captivity is a critical milestone in farming of any animal. The primary aim behind captive breeding and rearing of new species or new varieties, is to increase seed production and begin the process of domestication. A species cannot be considered a reasonable candidate for mass production until seedstock availability is secured and genetic selection is possible. Assisted reproduction technologies help take advantage of sexually dimorphic growth, and overcome problems with growth performance and flesh quality associated with sexual maturation and genetic containment. The primary benefit of assisted reproduction is that, particularly when gonadal tissue is available, it is not necessary to spawn the threatened species in captivity, which is often challenging. This process offers a unique and adaptable method for the storage and subsequent reintroduction of important genetics into a population, which could be hugely beneficial to the conservation of fish. Considering that conservation programs often require thousands of new individuals to be produced over many years to successfully support dwindling populations, the application of germ cell surrogacy is arguably better suited to support large-scale fish conservation efforts than the other methods. So, we have to consider the trade-off between the economic viability and a pure culture line.

4.3. Nutrigenomics

Fish reproductive functional physiology is highly regulated by nutritional status, including nutritional supplements and environmental stress [143]. Climate changes cause increased physiological stress on cultured stock, and the long-term effects resulting from climate change are altered reproductive cycles and vulnerability to diseases. Nutrigenomic approaches are the most effective and sustainable methods of dealing with these challenges while also allowing both accurate measurement of physiological changes, as well as providing health benefits to the fish. Modern nutrigenomic strategies help us to use specific gene expression patterns to evaluate the effects of nutrition on key metabolic processes relating to reproductive performance by addressing some of the limitations in reproductive performance [144]. Fish health is based on their immunity, which is composed of two main components; the innate immune response, which is the first line of defence against infection, and the adaptive immune response, characterized by a specific antigen recognition. Fish immunity can be trained by changes in environmental factors and pathogens. In fact, in innate immune cells, metabolic and epigenetic changes can be induced by certain microbial ligands capable of binding to specific pattern recognition receptors. This increases responsiveness upon secondary stimulation and even protects against a subsequent infection, especially in broodfish (Figure S1). Nutrition strongly affects the interplay between innate and adaptive immunities, affecting the cell-mediated immunity, phagocyte function, cytokine production, and mucosal secretory antibody response [86]. Well known transcriptomics studies have highlighted the effects of different dietary treatments on specific genes, that can be targeted via nutritional intervention to improve brood fish performance [145]. When the expression pattern of genes in response to the dietary level of a nutrient is utilized as a response criteria, along with the functional components (immunostimulants, antioxidants, pre- and pro-biotics), nutrigenomics can aid research in defining nutrient requirements and the development of specialized feeds for brood fish under a changing climate scenario [87]. Additionally, with a changing environment, the role of micronutrients, which depend on the physiological state of the fish, such as the reproductive season and environmental stress, might vary from nutrient to nutraceutical. Broodstock nutrition affects egg quality and larval survival. With the expression of the effector genes, the physiological effects of various nutraceuticals remain to be well investigated [146]. However, it should be echoed that great care must be taken in the analysis of generated data sets, as well as in the use of biomarkers for complexity caused by climate change, with regards to the reproductive physiology of fish. Data should be generated properly and following a consistent methodology, for example, using the spatial transcriptomics approach (Figure 5). Spatial transcriptomics is a technology used to spatially resolve RNA-seq data, and thereby all mRNAs, in individual tissue sections. This technique allows for gene activity measurements and mapping in tissue samples. Tissue samples are prepared on glass slides and, by means of tissue-domain oligo primers, genes are encoded. Finally, the data are analyzed and gene clusters are associated with tissue domains.

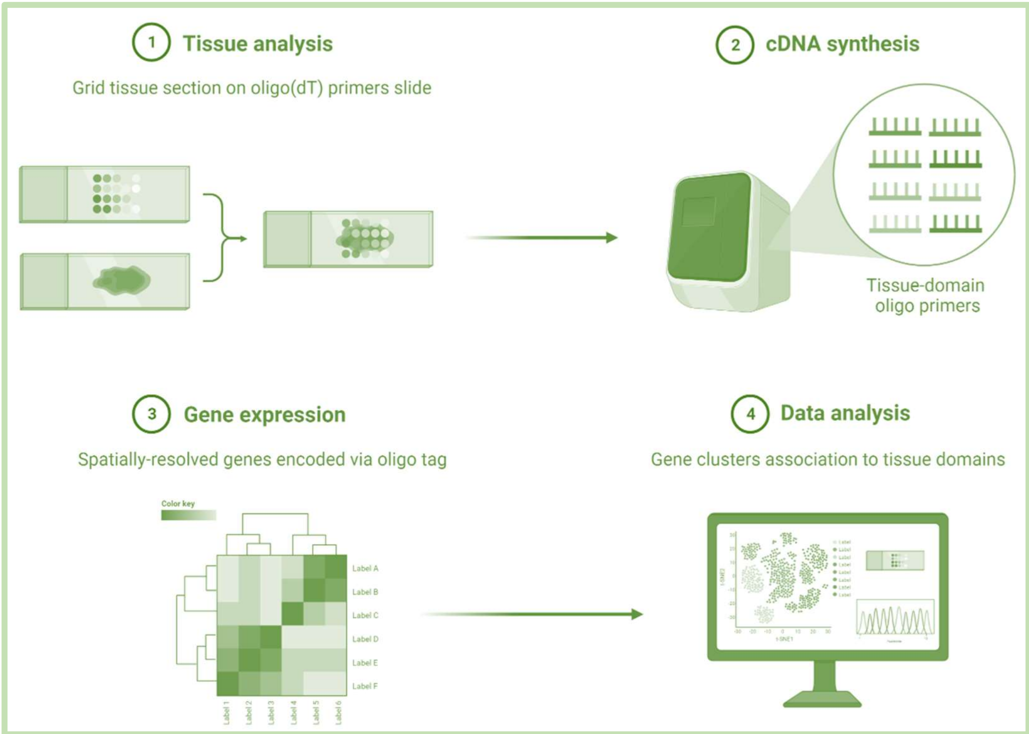

Figure 5. Spatial transcriptomics: schematic approach for fish sustainability programs.

As biological processes are rarely monogenetic, the predictive value of specific biomarkers may be undermined by the actions of many hundreds or thousands of different genes and environmental and/or nutritional history. Based on the available information it is clear that the power of nutrigenomics technology is able to handle all aspects of reproduction in aquaculture production, its sustainability, and economic viability, including the effects of climate change. Dietary and nutritional mitigation measures could be a promising option to manage thermal stress. However, this research area is understudied among diverse fish species groups. A wide range of studies, with a range of supplementary ingredients, is required to understand nutritional measures as a mitigation option to combating climate change-induced thermal stress.

5. Conclusions

Climate change has generated a great amount of interest in thermal eco-physiology, since temperature is such an extremely important factor in aquatic environments. Fish are poikilothermic and are unable to regulate their body temperature. Sexual reproduction in fish is strongly reliant on specific environmental cues that trigger and regulate sexual maturation, breeding, and offspring survival. The environmental stochasticity, combined with disturbance of breeding grounds, may negatively impact reproduction and endanger successful breeding and survival in fish in fisheries as well as in aquaculture.

Technological advancements using non-invasive and non-lethal monitoring, along with assisted reproduction and nutrigenomics in aquaculture systems, should provide a rapid and innovative appraisal approach towards the establishment of useful protocols for the sustainability of fish resources.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/w15040725/s1, Figure S1. Fish Immunity and trained immunity in response to infection.

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