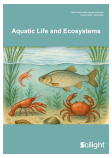
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Review

Research Progress on the Regulatory Mechanisms of Circadian Rhythms in Fish and Their Applications in Aquaculture

Yuzhuo You [1,2,3,4,5,6], Guo Yu [7] and Zhengyi Fu [1,2,3,4,5,*]

[1] Hainan Fisheries Innovation Research Institute, Chinese Academy of Fishery Sciences, Sanya 572024, China
[2] South China Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences, Guangzhou 510300, China
[3] Key Laboratory of Efficient Utilization and Processing of Marine Fishery Resources of Hainan Province, Sanya Tropical Fisheries Research Institute, Sanya 572018, China
[4] Hainan Engineering Research Center for Deep-sea Aquaculture and Processing, Sanya Tropical Fisheries Research Institute, Sanya 572018, China
[5] International Joint Research Center for Conservation and Application of Fishery Resources in the South China Sea, Sanya Tropical Fisheries Research Institute, Sanya 572018, China
[6] College of Fisheries and Life Sciences, Dalian Ocean University, Dalian 116023, China
[7] Hainan Branch of Hefei Herun Technical Services Co., Ltd., Haikou 570105, China
* Correspondence: zhengyifu@163.com

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Abstract: Circadian rhythms constitute an endogenous timekeeping system that fish have evolved to anticipate the alternation of light and darkness, and their molecular basis centers on the rhythmic expression of core clock genes. Teleosts display a markedly decentralized organization, in which multiple brain regions and peripheral tissues harbor endogenous, directly photoreceptive oscillators; consequently, fish rhythms are highly sensitive and plastic with respect to environmental factors such as light, temperature, salinity, dissolved oxygen and feeding. Advances in multi-omics, gene editing and live imaging have substantially deepened understanding of fish circadian biology, including the functional dissection of clock genes, the characterization of tissue-specific expression profiles, and the characterization of interactions between the clock and metabolism, immunity and reproduction. Against this background, chrono-aquaculture—the scheduling of farming practice to match the endogenous rhythms of the cultured species—has emerged as a promising framework for improving production efficiency and animal welfare while reducing environmental load. Nevertheless, important challenges remain, including a pronounced reliance on a small number of model species, limited understanding of multi-factor interactions, and a persistent gap between laboratory findings and large-scale application. This review synthesizes the molecular regulatory networks of fish circadian rhythms, the mechanisms through which environmental factors act, physiological and behavioral rhythms, and their application in aquaculture, and discusses key bottlenecks and future directions, with the aim of supporting both fish chronobiology and precision aquaculture management.

Keywords: circadian rhythm; diel rhythm; clock genes; environmental factors; chrono-aquaculture

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1. Introduction

Circadian rhythms are endogenous timekeeping systems that organisms have evolved to anticipate the periodic changes in light caused by the Earth's rotation. They free-run with a period close to, but generally not equal to, 24 h, and can be entrained and phase-reset by external zeitgebers such as light, temperature and feeding [1–4]. By contrast, a diel rhythm is the 24-h pattern of variation displayed by an organism under a light–dark (LD) cycle. Such a pattern may be driven by an endogenous clock, by the direct action of light and darkness, or by both, including masking effects. Distinguishing between the two requires evidence from free-running under constant conditions, entrainment and phase resetting by zeitgebers, and explicit tests for masking [5]. Circadian rhythms are not a passive response to external stimuli but an active timing mechanism driven by a highly conserved molecular oscillator network [6]. In vertebrates, a transcription–translation feedback loop centered on core clock genes, including *clock*, *bmal1*, *per*, and *cry*, constitutes the molecular core of the circadian clock [7]. These genes and their encoded proteins form a self-sustaining oscillation through reciprocal activation and repression, which in turn regulates the rhythmic expression of a vast array of clock-controlled genes, thereby imposing temporal organization on critical life processes including cell proliferation and differentiation, energy metabolism, immune defense, behavioral patterns, and adaptive responses to environmental challenges [8]. Therefore, circadian rhythms constitute a fundamental biological basis for maintaining internal homeostasis and enhancing environmental adaptability, and their integrity and stability are directly linked to individual growth, survival, and reproductive performance [9].

In the evolutionary lineage of vertebrates, fishes occupy a critical position bridging the study of fundamental biological mechanisms and ecological adaptation. The circadian clock system in fishes not only retains a core molecular framework largely conserved with mammals but has also evolved distinct lineage-specific characteristics [10]. Unlike mammals, which rely on the suprachiasmatic nucleus (SCN) as the single master pacemaker, the circadian system of teleost fish exhibits a pronounced "decentralized" organization, wherein multiple brain regions and peripheral tissues harbor endogenous, directly photosensitive oscillators. Consequently, their circadian regulation is more sensitive and exhibits greater plasticity in response to environmental changes [11]. Furthermore, as aquatic poikilotherms, fish experience body temperature and metabolic states that are directly influenced by ambient environmental conditions. Consequently, factors such as temperature, dissolved oxygen, and salinity often exert stronger modulatory effects on their circadian system compared to those observed in terrestrial homeotherms [12,13]. This not only establishes fish as an important model for understanding the evolution and environmental adaptation of vertebrate circadian rhythms, but also underscores the necessity of fully accounting for species-specific ecotypes and life-history variations in related research.

In natural aquatic ecosystems, circadian rhythms are crucial for the survival and reproductive success of fish [14]. Precise circadian regulation enables fish to anticipate predictable daily environmental changes and to execute critical life activities—including foraging, predator avoidance, reproduction, and migration—within the most favorable temporal windows [13]. Photoperiod is the most critical zeitgeber driving the daily rhythmic expression of clock genes in fish, capable of inducing the upregulation of specific genes—such as *cry1a* and *per2*—thereby synchronizing and resetting cellular physiological rhythms [15]. However, fish do not rely solely on light signals. Temperature also plays a critical regulatory role in circadian rhythms. Studies have demonstrated that, even in the absence of light, temperature cycles alone are sufficient to induce rhythmic expression of clock genes such as *per4* in zebrafish (*Danio rerio*) embryos and primary cells [16]. More notably, feeding behavior in fish can act as an independent zeitgeber. Although the central clock is primarily entrained by the photoperiod, peripheral clocks can be independently reset by scheduled feeding times. This regulatory paradigm was first demonstrated in zebrafish [17]. Through the integration of environmental cues such as light, temperature, and feeding with the endogenous circadian clock, circadian rhythms orchestrate highly ordered temporal variations in physiological processes—including metabolism, endocrine signaling, immunity, and behavior—and synchronize behavioral patterns such as feeding, locomotion, reproduction, and sleep, thereby maintaining physiological homeostasis and behavioral regularity in dynamic environments [18,19]. Normal circadian rhythms optimize nutrient digestion and absorption, energy allocation and utilization, and immune surveillance, thereby comprehensively enhancing the environmental adaptability of fish [20].

However, modern anthropogenic activities are continuously reshaping the temporal ecological environment of fish and imposing compounded stress on their circadian systems. Under intensive aquaculture conditions, fish are frequently subjected to prolonged exposure to highly artificial environments characterized by high stocking densities, continuous or irregular photoperiods, random feeding schedules, and fluctuating water quality [21,22]. These conditions differ markedly from the natural zeitgeber regime to which fish are adapted, and can desynchronize the rhythm system from natural light–temperature cycles, leading in turn to metabolic imbalance,

immune suppression and heightened stress responses [23,24]. Previous studies have demonstrated that circadian disruption can induce phase shifts or amplitude attenuation in parameters associated with the hypothalamic–pituitary–interrenal (HPI) axis, thereby abolishing the normal time-dependent responses of fish to stressful events. Moreover, circadian disruption impairs the coordination between feeding and digestive rhythms, leading to reductions in feed intake, feed conversion efficiency, and overall growth performance [23,25–27]. More notably, such desynchronization effects can persist throughout the entire life history, increasing the risks of embryonic hatching failure, reduced larval survival, and disease outbreaks, thereby exerting sustained impacts on aquaculture production and population recruitment [14].

In parallel, wild fish populations face increasingly severe disruption of their rhythms. Artificial light at night in coastal and inland waters is altering the light environment for a large number of species: even illumination as low as 1 lux is sufficient to suppress the nocturnal rise in melatonin in European perch (*Perca fluviatilis*), indicating that light pollution can act directly on endocrine output without necessarily altering the oscillator itself; if sustained, however, it may further shift the phase and amplitude of the rhythm [28]. In addition, temperature anomalies, extreme weather events, altered dissolved oxygen distribution and chemical pollution—all associated with global environmental change—can affect the circadian system of fish [23,29–31]. However, most of the available evidence remains at the level of diel rhythms; whether these changes originate in the oscillator itself requires confirmation from free-running and phase-resetting experiments under constant conditions. Anthropogenic stressors rarely act in isolation; they typically superimpose on natural light and temperature cycles, producing complex interactive effects whose consequences are difficult to assess comprehensively at present. Understanding the regulatory mechanisms of fish circadian rhythms and how they respond to environmental stress is therefore not only a fundamental question in biology but also of pressing importance for ecological conservation and fisheries management.

In recent years, the rapid advancement of molecular biology, multi-omics technologies, and gene editing has substantially broadened the depth and scope of fish circadian rhythm research. Significant progress has been made in elucidating the functions of core clock genes, mapping regulatory pathways, characterizing tissue-specific expression profiles, and deciphering the crosstalk between the circadian clock and metabolic, immune, and reproductive systems [32–34]. Against this backdrop, the concept of "chrono-aquaculture"—an approach that optimizes aquaculture management based on circadian regulation—has gradually emerged. Its core principle lies in aligning husbandry practices with the endogenous biological rhythms of cultured species, thereby simultaneously achieving multiple objectives, including enhanced production, improved product quality, reduced stress, and lower resource consumption [35]. Nevertheless, current research still exhibits three prominent limitations. First, studies remain heavily concentrated on a limited number of model organisms or commonly farmed species, such as zebrafish, nile tilapia (*Oreochromis niloticus*), and rainbow trout (*Oncorhynchus mykiss*), whereas knowledge regarding commercially valuable fish species and those with specialized ecotypes remains conspicuously lacking [12,36]; Second, single-factor experiments continue to predominate, and mechanistic insights into the interactive effects of multiple environmental variables remain relatively limited [37]; Third, the translation of optimal laboratory-derived parameters to large-scale aquaculture settings lacks systematic validation, and replicable, broadly applicable technical protocols for circadian-based management have yet to be established [38].

This article is a narrative review that aims to integrate evidence across three levels—molecular mechanisms, ecological adaptation, and aquaculture applications—rather than to address a single focused question; therefore, a standardized systematic review search and screening protocol was not adopted. Literature was retrieved primarily from Web of Science, PubMed, and CNKI. Search terms combined circadian, diel, clock gene, and zeitgeber with fish, teleost, and aquaculture, as well as combinations of the terms for "circadian rhythm", "biological clock", "diel rhythm", and "zeitgeber" with those for "fish" and "aquaculture". The search was conducted up to November 2026, with backward citation searching for early classic studies such as the cloning of the Clock gene in zebrafish. Literature was selected based on topical relevance and strength of evidence: priority was given to studies providing evidence from constant light/constant dark free-running conditions, zeitgeber entrainment, or *in vitro* oscillation; studies reporting only phenotypic observations under light–dark cycles are identified in the text with respect to their level of evidence.

Against this background, the review first defines the conceptual boundaries of circadian rhythms, diel rhythms and masking, together with the criteria used to distinguish them. It then examines progress in fish circadian research along four thematic strands—molecular regulatory networks, environmental regulation, physiological and behavioral rhythms, and aquaculture application—and identifies the key issues that remain, including the imprecise demarcation between rhythm types, a strong reliance on a small number of model species, limited understanding of environmental interactions, and a weak link between research and industry. Finally, in light of

the move toward greener, more precise and more intelligent aquaculture, the review outlines priorities for future research, with the aim of providing a theoretical reference for studies of fish chronobiology and for precision aquaculture management.

2. Core Molecular Mechanisms and Regulatory Networks of Fish Circadian Rhythms

2.1. Composition and Evolutionary Characteristics of Core Clock Genes

The core clock gene family in fish comprises the positive regulators *clock* and *bmal1*, along with the negative regulators of the period family (*per1*, *per2*, *per3*) and the cryptochrome family (*cry1*, *cry2*, *cry3*). The proteins encoded by these genes interact to form a stable molecular oscillator that drives the generation and maintenance of circadian rhythms [39]. Although this molecular framework is highly conserved across vertebrates, teleost fishes have undergone lineage-specific whole-genome duplication events, resulting in unique features in the composition and evolution of their clock genes [40]. From an evolutionary perspective, the common ancestor of vertebrates underwent two rounds of whole-genome duplication, whereas teleost fishes experienced an additional, lineage-specific whole-genome duplication event early in their evolution. This event provided abundant genetic raw material for biological innovation [41]. Comparative genomic analyses indicate that lobe-finned fishes (Sarcopterygii) and basal ray-finned fishes (Actinopterygii) retain only two copies of the clock gene—*clock1* and *clock2*—whereas teleosts, owing to the teleost-specific third round of whole-genome duplication (3R), generally possess three copies: *clock1a*, *clock1b*, and *clock2*. Moreover, certain teleost lineages exhibit species-specific duplications of *clock2* [42]. Sequence variation in the clock protein is primarily concentrated in the N-terminal region and the polyglutamine (poly Q) tract. Notably, *clock1* and *clock2* have undergone distinct evolutionary trajectories across different fish lineages, suggesting that these two paralogs may have undergone subfunctionalization or neofunctionalization [41,42]. Functional divergence is also evident within the *cry* gene family. Studies have revealed that *cry1* and *cry2* proteins play distinct roles in the circadian regulation of fish: *cry2* is primarily involved in the rhythmic regulation of the central oscillator, whereas *cry1* plays a predominant role in sustaining rhythmicity in peripheral tissues [43]. Light can drive circadian rhythms in various tissues by modulating the expression levels and post-translational modifications of *cry1*, *cry2*, and *Clock* proteins, and such regulation exhibits pronounced tissue-specific differences [44]. Furthermore, *per2*, a key light-responsive clock gene, is considered to play a central role in the transmission of photic signals to the central circadian clock. Studies in zebrafish have demonstrated that *per2* contributes to the maintenance of tissue-specific expression of rhythmic genes and regulates both circadian behavior and the circadian rhythm of the cell cycle in larvae [45]. Evolutionary studies of cavefish (*Astyanax mexicanus*) provide a unique natural experiment for understanding how light signals shape the circadian clock. Research has revealed that the *per2* gene in cavefish harbors aberrant splice variants, with the most abundant transcript encoding a truncated *per*2 protein. Owing to a transposon insertion, this truncated protein is predominantly localized to the cytoplasm, in stark contrast to the distribution pattern of its zebrafish ortholog, which is present in both the nucleus and the cytoplasm [46]. This finding indicates that, during evolution in complete darkness, mutations have occurred at multiple levels of the circadian light-signaling pathway—from opsin-based photoreceptors to nuclear effectors—underscoring the profound selective pressure exerted by the environment on shaping the circadian clock system. Taken together, teleosts retain a vertebrate-consistent topology in the core loop, whereas the copy redundancy generated by the 3R event provided raw material for remodeling regulatory connections: what is conserved is the logic of who represses whom; what varies is which copy, in which tissue, and at which phase executes that logic. This pattern of a conserved framework with variable execution is both a starting point for understanding interspecific differences in fish rhythms and a prerequisite for judging whether temporal parameters can be extrapolated across species.

2.2. Molecular Operation of the Transcription–Translation Feedback Loop

The core molecular mechanism underlying fish circadian rhythms is a self-sustaining transcription–translation feedback loop composed of positive and negative regulatory elements. In the positive limb of the loop, the *clock* and *bmal1* proteins form a heterodimer that binds to E-box elements in the promoter regions of target genes, thereby activating the transcription of negative regulators such as *PER* and *CRY*, as well as a broad array of clock-controlled genes [47]. Upon reaching a critical threshold in the cytoplasm, the *PER* and *CRY* proteins form complexes that translocate into the nucleus, where they repress the transcriptional activity of the CLOCK-BMAL1 heterodimer, thereby shutting down their own expression. Subsequently, both proteins are degraded via the ubiquitin–proteasome pathway, relieving the repression and allowing CLOCK-BMAL1 to reinitiate transcription, thus commencing the next cycle of approximately 24 h. This interlocked feedback mechanism constitutes the core circadian oscillator (Figure 1) [7]. Zebrafish, as a model organism for investigating this

mechanism, have provided crucial experimental evidence. The zebrafish clock gene exhibits pronounced circadian rhythmic expression in multiple tissues, including the brain, eye, pineal gland, kidney, and heart. Moreover, cultured explants of these tissues can sustain autonomous oscillations *in vitro*, providing the first demonstration that multiple organs in vertebrates harbor independent, self-sustaining circadian oscillators [48]. Further studies have revealed that zebrafish possess two BMAL paralogs, *zfbmal1* and *zfbmal2*, both of which can heterodimerize with clock to regulate circadian rhythmicity. However, these two paralogs exhibit differential expression patterns across tissues, suggesting that peripheral clocks possess independent regulatory capacity [49]. Importantly, a further regulatory layer is superimposed on the core loop: rather than replacing the CLOCK–BMAL1–PER/CRY oscillator, these factors set its phase and output in a cell type- or tissue-specific manner. In recent years, novel circadian regulatory factors have been continuously identified, substantially enriching the molecular network of fish circadian rhythms. Recent studies have revealed that AMH (Anti-Müllerian hormone) signaling is essential for maintaining circadian homeostasis in zebrafish. AMH regulates the molecular clock oscillation in the pituitary in a cell type-specific manner, enabling the precise output of circadian signals and thereby maintaining rhythmic coherence at both the tissue and systemic levels. Mechanistically, AMH binds to its receptors, *bmpr2a* and *bmpr1bb*, triggering the phosphorylation and nuclear translocation of SMAD1/5/9. These activated *Smads* subsequently bind to specific cis-regulatory elements—including *E/E'-boxes*, *RREs* (ROR response elements), and *CREs* (cAMP response elements)—to modulate the expression of clock genes [50]. This breakthrough reveals a novel molecular mechanism of endocrine–circadian clock interplay, offering new perspectives for understanding the neuroendocrine regulation of vertebrate circadian rhythms. In addition, *roraa* in zebrafish has been shown to be expressed rhythmically, and its knockout impairs circadian function, manifesting as reduced expression of core clock genes and disrupted behavioral rhythms. Mechanistic studies have shown that Roraa directly regulates *per2* transcription through the RORE element, and that *roraa* deficiency markedly alters the expression of lipid metabolism-related genes, indicating that Roraa acts as a key link between circadian and metabolic regulation [34]. The fish rhythmic network can therefore be summarized as a layered structure comprising a conserved core and lineage-specific modulatory layers: what is conserved is the CLOCK–BMAL1–PER/CRY feedback topology; what is lineage-specific is the type of modulatory connection exemplified by Amh setting the phase of the pituitary oscillator through Smad1/5/9, and by Roraa regulating *per2* through RORE and linking the clock to lipid metabolism. The significance of this distinction is that rhythm abnormalities arising from knockout of modulatory-layer genes should not be equated with disruption of the core oscillator.

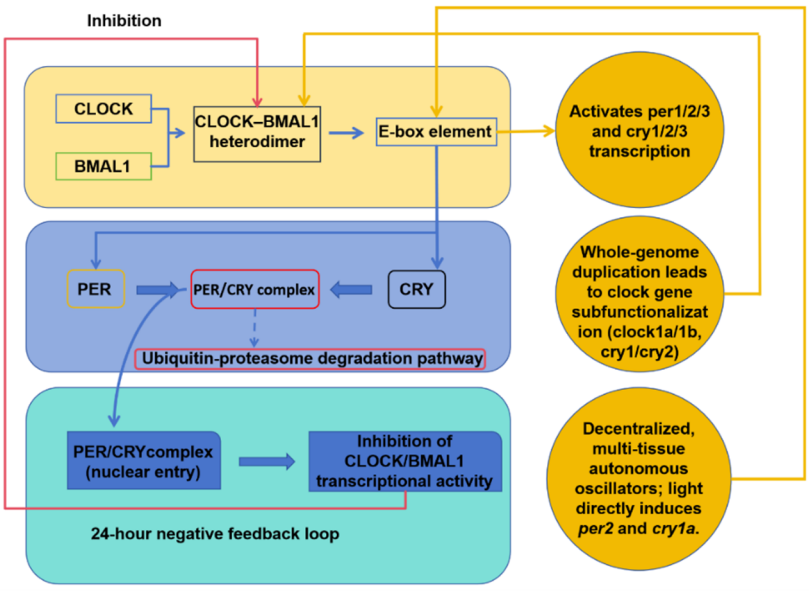


Figure 1. Schematic representation of the core clock gene transcription–translation negative feedback loop in fish.

2.3. Tissue-Specific Expression Profiles of Clock Genes

Clock gene expression in fish is tissue-specific and forms part of the molecular basis for environmental adaptation. In common carp (*Cyprinus carpio*), for example, core clock genes are highly expressed in the brain, pituitary and retina and display diel rhythms under LD cycles: *clock* and *bmal* are expressed at higher levels during the night, *per* peaks around the light–dark transitions, and *cry* shows tissue- and subtype-specific patterns. Even

under continuous light, retinal clock genes continue to oscillate autonomously, indicating that this tissue possesses an endogenous oscillatory capacity that does not depend on light [51]. Six core clock genes (*Per1–3* and *Cry1–3*) have been cloned from goldfish (*Carassius auratus*), showing approximately 90% sequence identity with their zebrafish orthologs. qPCR revealed that all six are rhythmic in the retina, whereas only *Per2–3* and *Cry2–3* are rhythmic in the liver and gut, with phases and amplitudes that differ markedly from those in the retina. This suggests that different tissues respond differently to zeitgebers and that exogenous cues such as feeding may contribute to the regulation of peripheral clocks [52]. This finding also supports the use of goldfish as a model for studying tissue-specific circadian oscillators in teleosts. In the mandarin fish (*Siniperca chuatsi*), clock gene expression profiles differ markedly between fast and slow muscle fibers: *nr1d2* and *per3* are arrhythmic in slow muscle, and *cry2/3* and *tim* are arrhythmic in fast muscle, whereas most clock genes are highly expressed during the dark phase in slow muscle and peak during the light phase in fast muscle. Myogenic regulatory factors are significantly correlated with clock gene expression, suggesting that circadian regulation may contribute to the temporal control of muscle growth through myogenic genes [53]. This finding is relevant to understanding the chronobiological regulation of muscle development in fish and identifies a potential target for optimizing growth management through rhythm-based interventions in aquaculture. However, not all peripheral tissues of fish possess autonomous clocks. In atlantic cod (*Gadus morhua*), fast muscle showed no rhythmicity under *in vitro* culture, suggesting that its peripheral clock may not be autonomous and may instead depend on input from the central clock or from other peripheral signals [54]. This finding reveals interspecific differences in the capacity for autonomous regulation of peripheral circadian clocks among fish species, highlighting the need for caution when extrapolating conclusions derived from model organisms such as zebrafish to other fish taxa.

A gradient emerges across these four species: visually related, directly photoreceptive tissues such as the retina generally retain autonomous oscillation in isolated preparations or under continuous light, whereas the autonomy of metabolic tissues—liver, gut and skeletal muscle—varies markedly. Hepatic and intestinal rhythms in goldfish depend on exogenous cues such as feeding for their phase, and fast muscle of atlantic cod loses rhythmicity entirely after isolation. Tissue specificity therefore extends beyond expression profiles to the degree of autonomy: the more directly a tissue is regulated by light, the less its oscillation depends on central input. The term "peripheral clock" is consequently not homogeneous; at least two classes can be distinguished—photo-autonomous clocks (retina, pineal) and centrally or feeding-dependent clocks (liver, gut, fast muscle). These observations also argue for caution when extrapolating findings from model species such as zebrafish to other fish.

It should be noted that the evidence for autonomous retinal oscillation in carp derives from continuous light, and that for cod from isolated culture, both of which bear directly on endogeneity, whereas the comparisons in goldfish and mandarin fish were made under LD cycles and thus represent diel-level evidence, the endogeneity of which remains to be confirmed by free-running experiments under constant darkness or light.

2.4. Coordinated Regulatory Network of Central and Peripheral Circadian Clocks

Unlike mammals, which rely on the SCN as a single central pacemaker, teleosts possess a decentralized circadian system. Studies using *per3*-luc transgenic zebrafish have shown that endogenous, directly photoreceptive circadian oscillators are present in multiple brain regions; light induces *c-fos* expression, and brain oscillations persist under constant darkness. Not all nuclei in the zebrafish brain are, however, both light-sensitive and rhythmic—some are neither—indicating that circadian regulation is considerably more complex than previously recognized [11]. In Japanese flounder (*Paralichthys olivaceus*), *per2* in the SCN shows a diel rhythm, with higher expression during the day than at night under LD cycles, suggesting that the SCN may serve as a central pacemaker. This pattern differs markedly among species: in zebrafish, no clear *per2* rhythm is detectable in the SCN, and the redundant pacemaking capacity of multiple brain regions may compensate for the absence of a single dominant SCN. The role of the SCN in fish circadian regulation may therefore depend on the species' lifestyle and ecological niche. In flounder, rhythmic *per2* expression is also present in the pineal gland and pituitary, indicating that multiple central structures may contribute jointly to rhythm regulation [55]. Peripheral clocks are regulated by central signals but can also be synchronized directly by local environmental cues. In nile tilapia, *clock1*, *bmal1a*, *cry2a*, *per1b* and *cry5* in the brain all show diel rhythms whose phases are unaffected by feeding time, whereas the phases of *clock1* and *cry5* rhythms in the liver can be significantly shifted by feeding during the dark phase [56]. These results indicate that light dominates the synchronization of central clocks, whereas feeding time specifically regulates peripheral clocks, the two forming a hierarchical regulatory network that is both coordinated and independent. In goldfish, scheduled feeding induces food anticipatory activity (FAA), a behavior that is endogenous and persists under continuous light. In the brain, *per1* expression depends strictly on the photoperiod and is unaffected by feeding time, whereas in the liver the phase of the *per1* rhythm can be significantly advanced by feeding during

the dark phase; under continuous light, scheduled feeding suppresses the hepatic *per1* rhythm, further supporting a dual-control model of central light synchronization and peripheral feeding synchronization [57]. It should be noted that, among the evidence cited above, only the zebrafish brain data (constant darkness) and the goldfish FAA data (continuous light) bear directly on endogeneity, whereas the expression profiles of the flounder SCN and the tilapia brain derive mainly from observations under LD cycles; their pacemaker status and endogeneity therefore require confirmation through persistence under constant darkness and through phase-resetting experiments.

The fish pineal gland is a key hub linking the light environment to endocrine rhythms. It converts photoperiodic information into the rhythmic release of melatonin, which exhibits a conserved pattern of higher levels at night and lower levels during the day across the fish species studied, making it a key signaling molecule for characterizing the relationship between environmental photoperiod and circadian regulation [58]. In the fish pineal gland, core clock genes—*bmal1*, *per1*, *per2*, *per3*, *cry1* and *cry2*—together with *aanat2*, which encodes the rate-limiting enzyme for melatonin synthesis, are all expressed, constituting a complete and functionally autonomous local oscillator [59]. Unlike other brain regions, the pineal gland is simultaneously a photoreceptor, an oscillator and an endocrine output organ; this triple identity makes it the most consistently weighted central node in the decentralized architecture of fish. Studies in Atlantic salmon (*Salmo salar*) have shown that, in parr under LD cycles, clock genes in the pineal gland and brain, together with plasma melatonin and cortisol, all display diel rhythms; after smoltification induced by continuous light, however, these rhythms disappear, indicating that developmental stage and light history strongly modulate pineal function [60]. It should be noted that the disappearance of rhythms under continuous light may reflect either arrest of the oscillator or merely the loss or masking of the output rhythm because the zeitgeber signal is absent; distinguishing between these possibilities requires transfer to constant darkness or experiments on isolated tissue. In Atlantic salmon, the expression of *Clock*, *Bmal1*, *Per2* and *Cry2* in the brain is photoperiod-dependent. Under long-day conditions, *Clock*, *Bmal1* and *Per2* exhibit no significant diel rhythmicity, whereas the phase of *Cry2* expression is delayed relative to short-day conditions [61]. A comparison of melatonin synthesis and clock gene regulation between teleost fish and mammals indicates that the photoperiod-dependent regulation of circadian rhythms is largely conserved among vertebrates, although species-specific differences exist [59].

In summary, rhythm regulation in teleosts is not a unidirectional hierarchy from center to periphery but is better described as a three-tiered structure: multiple directly photoreceptive brain regions, together with the pineal gland, form a set of parallel central pacemakers whose relative weight varies with species ecology (the flounder SCN shows a clear *per2* rhythm, whereas zebrafish display redundancy across multiple brain regions); peripheral tissues form semi-autonomous oscillators driven by light and feeding cues; and endocrine signals such as melatonin and cortisol act as coupling channels between the two (Figure 2). The widely cited model of central light synchronization with peripheral feeding synchronization is thus the typical expression of this structure under natural photoperiods and regular feeding; when photoperiod or feeding schedules are disrupted, the relative weight of the two shifts.

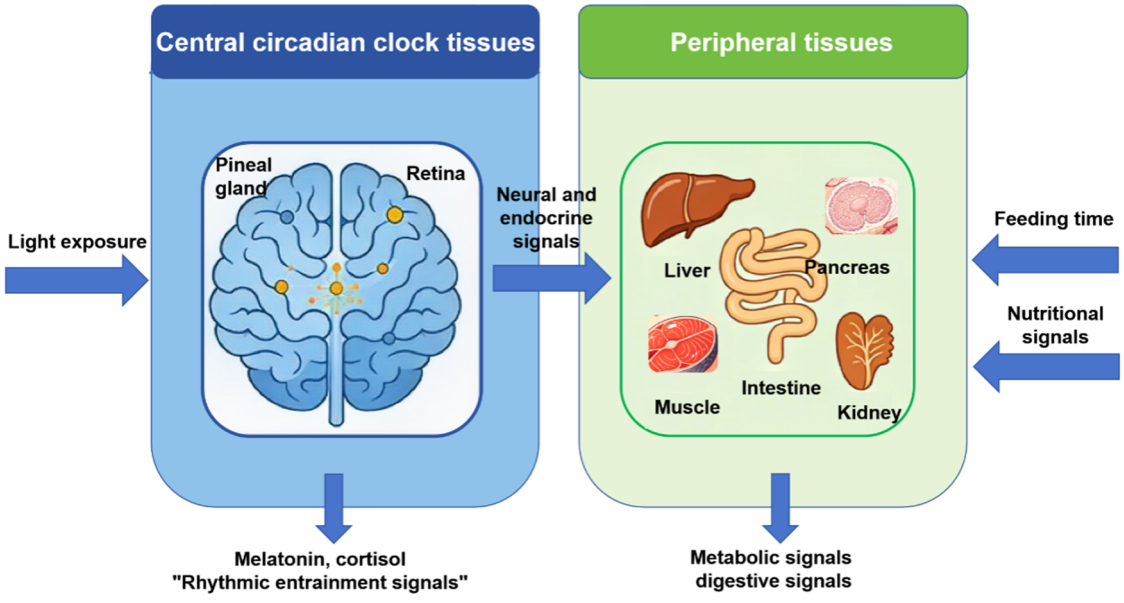


Figure 2. Multilayered Coordinated Regulatory Model of Central and Peripheral Circadian Clocks in Teleost Fish.

2.5. Characteristics of Core Clock Genes in Nocturnal Fish

Current research on fish clock genes is highly concentrated on diurnal model species such as zebrafish, whereas the rhythmic molecular architecture of nocturnal fishes may exhibit distinct tissue-specific phasing and regulatory logic [62]. Pleuronectiformes, which are predominantly benthic and nocturnal, provide a key model for dissecting this divergence. In the Senegalese sole (*Solea senegalensis*), a typical nocturnal flatfish, *Per1*, *Per2*, and *Clock* display daily rhythmic expression in the retina, optic tectum, and liver, yet the phases in the retina and liver are completely opposite [62,63]. This phase-reversal pattern suggests that the central photoreceptive regions and peripheral metabolic tissues of nocturnal fishes may be driven by light and feeding time, respectively. Thus, the division of labor among tissue-specific zeitgebers is conserved in nocturnal species, although their phase output is reshaped by an overall shift in activity timing. The tissue distribution of *Per3* further reveals a localized feature of central clock regulation in nocturnal fishes: this gene exhibits robust daily oscillations in the retina and optic tectum but lacks rhythmic expression in the diencephalon and cerebellum, indicating that central clock gene regulation is not brain-wide but concentrated in nuclei directly related to visual processing [62]. Studies on the Japanese flounder further reveal a key difference between nocturnal flatfishes and zebrafish at the pacemaker level. In the flounder SCN, *per2* displays a day-high/night-low diel expression, whereas the zebrafish SCN lacks a clear *per2* rhythm, suggesting that the SCN may serve as a circadian pacemaker in some nocturnal teleosts [55,64]. Further analysis of peripheral tissue (caudal fin) showed that *per1*, *per2*, and *cry1* maintain daily rhythms *in vivo*, but rapidly lose rhythmicity upon *ex vivo* culture. Cortisol (but not melatonin) significantly upregulates the expression of these three genes, implying that peripheral clock oscillations in nocturnal flatfishes may depend on continuous input from the SCN–pituitary–adrenal axis rather than cell-autonomous oscillations [64]. Research on the turbot (*Scophthalmus maximus*) provides complementary evidence from a light-driven perspective. Under a light-dark cycle, *clock1*, *per1*, *per2*, and *cry1* exhibit rhythmic expression in both the hypothalamus and the eye. However, after transfer to constant darkness, the rhythms of *per2* and *cry1* disappear in the hypothalamus, whereas all four gene rhythms are maintained in the eye [65], indicating brain-region heterogeneity in the light dependence of the central clock in nocturnal flatfishes, with visual tissues possessing stronger autonomous oscillatory capacity.

In summary, the core clock genes of nocturnal flatfishes do not run in reverse; rather, within a conserved framework they undergo a triple rearrangement—increased SCN weighting, localized central output, and greater dependence of peripheral clocks on hormonal input—that reconfigures phase relationships among tissues rather than producing a global phase shift. In this sense, the degree of decentralization in fish may itself be a function of ecological type; given that most available evidence comes from observations under LD cycles, extrapolating conclusions from diurnal species such as zebrafish to nocturnal farmed fish still requires careful validation.

3. Environmental Regulation of Fish Circadian Rhythms

3.1. Photoperiod: Multilevel Regulation by the Primary Zeitgeber

As the principal zeitgeber driving the fish circadian system, the photoperiod transmits light signals to the clock through the retino-hypothalamic pathway and deep-brain photoreceptors, thereby synchronizing the phase of central and peripheral clocks and exerting a profound influence on fish physiology, behavior and gene expression [66]. For example, photoperiod markedly alters the diel rhythms of serum melatonin, cortisol, glucose and electrolytes in the common dentex (*Dentex dentex*). Melatonin increases during the dark phase, but this rhythm is not sustained under constant darkness, suggesting that melatonin output depends largely on the light–dark transition rather than on a self-sustained oscillator. The cortisol peak shifts from night to day with photoperiod, and the glucose peak lags 4 h behind it, indicating that cortisol and glucose are involved in the regulation of carbohydrate metabolism, whereas electrolytes reflect ion balance [67]. In European sea bass (*Dicentrarchus labrax*), clock genes and key genes of the brain–pituitary–gonadal axis share conserved co-regulatory structures in their promoters, and their expression is strongly regulated by photoperiod; long photoperiods suppress *npas2* and several *gnrh* and *kiss* receptors. If the dentex results show that photoperiod can alter the phase of endocrine output, the sea bass results indicate that this regulation acts further upstream: before any measurable endocrine or morphological change in the reproductive axis, photoperiod has already altered the transcription of the relevant genes through clock genes—an observation with practical implications for aquaculture [68]. The molecular window for photoperiodic control of the spawning season may therefore open earlier than previously assumed.

Continuous light is a common management practice in aquaculture, but its effects on the rhythm system require careful evaluation. Under a normal photoperiod, clock genes, melatonin and related transcriptional and stress genes in Atlantic salmon display diel rhythms, whereas continuous light abolishes the rhythms of most clock genes and nuclear transcription factors and exerts opposite effects on clock gene expression in the pineal gland and liver, indicating that light can influence clock gene expression across tissues; its long-term consequences for

fish welfare nevertheless remain to be clarified [69]. It is important to distinguish between two possibilities: the disappearance of rhythms under continuous light may result from arrest of the oscillator, or it may reflect merely the loss or masking of the output rhythm when the zeitgeber signal is absent; telling these apart requires transfer to constant darkness or experiments on isolated tissue. The effects of light intensity and spectral composition also warrant attention: artificial light at night at an intensity as low as 1 lux is sufficient to suppress the nocturnal rise in melatonin in European perch, indicating that light pollution can act directly on endocrine output [28]. In cultured starry flounder (*Platichthys stellatus*), juveniles reared at low light intensity (15 lux) gained significantly more weight than those at high intensity (2500 lux); high intensity markedly reduced daily feed intake and specific growth rate [70]. This indicates that light intensity management concerns not only rhythms but also production performance directly. It follows that the three components of light act at different levels: photoperiod sets phase (entrainment); intensity determines the thresholds for melatonin suppression and feeding activity (direct effects and masking); and spectral composition influences the efficiency with which signals are transmitted through deep-brain photoreceptors. The three are not parallel "lighting conditions" but act on timing, output and input, respectively. This also explains why "light adjustment" in practice often yields inconsistent results: changing intensity produces effects that are immediate but transient, whereas only changing the period produces lasting phase shifts.

Photoperiod control is therefore the most reliable and most readily implemented means of rhythm management in aquaculture. In practice this involves setting the photoperiod according to the natural light preferences of the target species and avoiding continuous light or continuous darkness; minimizing light leakage at night, which can disrupt the melatonin rhythm; and optimizing light intensity, since excessively high levels may suppress feeding rather than stimulate physiological function.

3.2. Temperature: A Distinctive Circadian Regulatory Cue in Ectothermic Animals

For fish, which are ectotherms, temperature is not only a physiological factor governing metabolic rate but also an important zeitgeber independent of photoperiod; its regulation of rhythms operates mainly at two levels, phase synchronization and amplitude modulation, and affects the period only when it exceeds the range of temperature compensation [71]. In zebrafish, locomotor activity rhythms are primarily entrained by the photoperiod; however, under constant dim light, temperature cycles can also independently serve as zeitgebers to entrain activity rhythms, whereas under constant temperature, these rhythms are free-running. Temperature also affects overall activity levels and the degree of diurnality [72]. In the absence of light, temperature cycles can entrain the rhythmic expression of clock genes in zebrafish. Temperature can selectively alter the basal expression levels of certain clock genes, and the regulation of *per4* appears to be independent of the E-box. In addition, the core circadian clock exhibits temperature compensation. Temperature can also modulate the amplitude of transcriptional rhythms and regulate E-box-driven circadian oscillations by affecting the expression, phosphorylation, and activity of the CLK protein [16]. Ectothermic animals can be effectively entrained by small diel temperature cycles of only 1–2 °C, and the phase response curve to temperature pulses is similar to that induced by light pulses. When light and temperature cycles are in phase, circadian rhythms become more stable and exhibit higher amplitudes; when they are out of phase, the resulting phase is determined by the relative strength of the two cues. At the molecular level, temperature can directly regulate the synthesis and degradation of clock proteins, indirectly influence the circadian clock through changes in membrane properties, ionic balance, second messengers, and phosphorylation pathways, and also alter clock phase by modulating melatonin rhythms. [73]. Temperature plays a decisive role in the establishment of circadian rhythms during early development. Using transgenic reporter fish lines, studies have shown that under complete darkness, zebrafish require temperature cycles during early developmental stages to establish stable gene-expression rhythms and cell-cycle rhythms. Moreover, after the onset of somitogenesis, the expression of *zfper1b* can be directly regulated by abrupt temperature shifts [71]. This finding has important implications for larval fish culture, indicating that even before the onset of first feeding, appropriate temperature cycles can serve as zeitgebers to facilitate the establishment of endogenous rhythms in the absence of photoperiodic cues. In the context of climate change, the effects of temperature on fish circadian rhythms have attracted increasing attention. A study on arctic char (*Salvelinus alpinus*) showed that under the naturally shortening photoperiod of late summer, diel fluctuations in hepatic transcript levels were markedly attenuated in the low-temperature group (8 °C), whereas rhythms were stronger in the high-temperature group (15 °C). Different core clock genes exhibited distinct temperature responses, with some showing elevated expression levels and enhanced rhythmicity at 15 °C, thereby revealing potential molecular mechanisms by which fish may adapt to climate warming [74]. Other studies have further shown that cold stress can markedly affect the molecular circadian machinery and endocrine system of zebrafish. Specifically, it

downregulates the expression of *gh1* and its receptor, *igf1* and its receptor, as well as multiple clock genes; elevates cortisol levels while reducing the expression of its receptor; and simultaneously upregulates *aanat2*, a key gene involved in melatonin synthesis in the brain. These changes are particularly closely associated with the growth axis and the melatonin axis [75]. Whether temperature can act as a zeitgeber independent of photoperiod under natural conditions remains unclear. Laboratory studies suggest that it can, but in nature light and temperature cycles are usually coupled, and whether the two act synergistically or whether one takes precedence remains unresolved [76,77]. In addition, the molecular sensor underlying temperature compensation has not yet been identified, which remains one of the central unresolved questions in the field of circadian biology [78].

In summary, temperature acts in three distinct ways: as a zeitgeber, a regular 1–2 °C temperature cycle can entrain rhythms under constant darkness or constant temperature and produces a phase–response curve similar to that of light pulses; as a modulator, temperature alters rhythm amplitude and metabolic rate without necessarily shifting phase—the difference in amplitude between 8 and 15 °C in Arctic char is a case in point; and as a stressor, acute or sustained deviation from the optimal temperature suppresses clock gene expression and activates the stress axis, as illustrated by the downregulation of *gh1*/*igf1* and the rise in cortisol under cold stress. What separates the three is not the magnitude of the temperature change but whether the signal is regular and whether it is accompanied by a phase shift. It follows that temperature entrainment demonstrated in the laboratory is often overridden or weakened by photoperiod in natural and cultured settings, and that fluctuations in tank water temperature are mostly passive and irregular, so their effects are more likely to fall into the modulatory or stress category than into entrainment.

3.3. Salinity: Mechanisms of Circadian Reprogramming in Euryhaline Fish

Salinity is a key environmental factor affecting physiological homeostasis in fish, and for euryhaline species inhabiting estuaries and coastal waters in particular, fluctuations in salinity constitute a recurring endocrine and osmoregulatory challenge that can also act as an environmental signal on the rhythm system [20,79]. Studies indicate that the effects of salinity on fish rhythms depend on stress intensity: low-salinity stress did not eliminate the diel rhythms of turbot but instead remodeled them, through phase shifts or the emergence of 48–72 h infradian oscillations, thereby maintaining homeostasis in the absence of obvious oxidative damage [20]. Salinity can also act directly on the output of the fish clock. In rainbow trout, increasing water salinity significantly enhances nocturnal melatonin synthesis in the pineal gland, an effect mediated by upregulation of *aanat2* expression and AANAT activity and independent of light, indicating that salinity can bypass the photoperiod and directly modulate the endocrine output of the rhythm system [80]. It should be noted that direct modulation of output is not equivalent to entrainment: whether a signal qualifies as a zeitgeber depends on its capacity to shift the phase of a rhythm and to maintain a stable phase relationship, which requires validation by phase–response experiments. In juvenile spotted sea bass (*Lateolabrax* sp.), transfer from seawater to low salinity and to freshwater significantly reduced oxygen consumption, yet oxygen consumption continued to show a free-running rhythm of approximately 23.2–23.3 h even under constant darkness, with peaks still occurring before sunset [81]. Because this result provides a free-running period measured under constant darkness ($\tau \approx 23.2$–23.3 h, shorter than 24 h), it can be directly classified as an endogenous circadian rhythm; its theoretical significance is that salinity change mainly alters metabolic rate rather than disrupting the core oscillator. The rhythm system of euryhaline fish therefore appears to tolerate salinity fluctuations well. Rain-induced changes in estuarine salinity and turbidity can induce a phase reversal of the activity rhythm in yellowfin bream (*Acanthopagrus australis*): fish are diurnally active and occupy shallow water between rain events, but become nocturnally active and move to deeper water after rain, and the diurnal rhythm is restored once conductivity and turbidity return to previous levels [82]. This suggests that estuarine factors such as salinity and turbidity can modulate the phenotypic plasticity of fish activity rhythms; whether the reversal reflects clock phase resetting or a direct effect of turbidity and light, however, remains to be distinguished under constant conditions. The naked carp (*Gymnocypris przewalskii*) of Lake Qinghai feeds during the day and drinks at night, and its intestinal ion transport and osmoregulatory functions show pronounced diel rhythms, an adaptation to a highly saline–alkaline environment [83]. For euryhaline cultured species, an abrupt change in salinity does not necessarily disrupt the core rhythm immediately, but it may alter metabolic rate; during salinity adjustment, feeding schedules should therefore be adjusted in parallel to avoid a mismatch between metabolic peaks and feeding troughs.

In summary, the effects of salinity on the rhythm system fall into three categories, none of which constitutes entrainment in the strict sense: first, changes in the phase and amplitude of rhythms (the phase shift and 48–72 h infradian oscillations observed in turbot under low salinity); second, direct modulation of output without involving the oscillator (the upregulation of melatonin synthesis in the rainbow trout pineal gland); and third, remodeling of

rhythms as a stressor under extreme salinity (the adaptation of naked carp to highly saline–alkaline water). What these share is a common mechanism: salinity acts primarily by altering osmotic pressure and ion balance, and thereby cellular metabolic state, which in turn affects the amplitude and phase of the oscillator indirectly; unlike light and temperature, it does not provide predictable temporal information. Except in tidal estuarine environments where salinity follows a stable daily cycle, salinity is therefore better regarded as a modulator than as a zeitgeber of rhythms.

3.4. Hypoxia and Dissolved Oxygen: Bidirectional Interactions Between the Circadian Clock and Hypoxia Signaling Pathways

Hypoxia is a common environmental stressor in aquaculture, particularly under high-density culture conditions and during periods of elevated summer temperature. Recent studies have revealed bidirectional interactions between hypoxia signaling pathways and the circadian system, a mechanism of considerable importance for understanding stress responses in cultured fish. Hypoxia can markedly suppress the rhythmic amplitude of *per1* in zebrafish and abolish their diel locomotor rhythm. Chromatin immunoprecipitation (ChIP) assays have confirmed that hypoxia-inducible factor 1 alpha (Hif-1α) can directly bind to the E-box element of *per1* and regulate its transcription. Conversely, the circadian clock can in turn regulate the expression of hypoxia-related genes and the accumulation of Hif-1α protein, while Hif-1α accumulation itself also exhibits circadian rhythmicity [84]. The Hif signaling pathway is closely interconnected with the circadian clock and cellular redox signaling, making zebrafish an ideal model for investigating the underlying mechanisms of this interaction [85]. Under extreme conditions, temperature and salinity stress disrupt rhythms in different ways: prolonged high temperature can cause the collapse of diel rhythms in turbot, reflected in the loss of diel rhythms in SOD (Superoxide Dismutase) and ALT (Alanine Aminotransferase), persistently elevated ACP (Acid Phosphatase) indicating an inflammatory response, suppressed T3 and accumulation of malondialdehyde, leading to oxidative damage and metabolic suppression; low-salinity stress, by contrast, causes only remodeling of rhythms, indicating that the two stressors act through distinct mechanisms [20]. This suggests that the combined effects of multiple stressors deserve particular attention: hypoxic events are frequent in hot seasons, and because temperature stress has already reduced the redundancy of the rhythm system, maintaining stable dissolved oxygen levels is of practical value in limiting the combined burden. In Antarctic icefish (*Notothenia neglecta*) held at 0 °C, oxygen consumption, muscle oxygen content and swimming behavior all show diel rhythms [86]. Juvenile lake sturgeon (*Acipenser fulvescens*) show a diel rhythm in metabolic rate, peaking at dawn; their standard metabolic rate remains unaffected at 30% air saturation, indicating that the species is an oxyregulator, whereas maximum forced metabolic rate declines as oxygen saturation falls [87]. Whether the suppressive effect of hypoxia on the circadian clock is mediated directly by HIF-1α acting on clock genes, or indirectly through metabolic stress, remains unclear. Current evidence suggests that both contribute, but their relative contributions and the extent of interspecies variation remain unresolved; moreover, the mechanisms by which the rhythm system adaptively remodels under chronic hypoxia have yet to be investigated.

In summary, the relationship between hypoxia and the rhythm system is not one of zeitgeber and entrainment but of stress and interference: HIF-1α binds directly to the E-box of *per1* and suppresses its amplitude, constituting a molecular interference pathway, while the clock in turn regulates the accumulation of HIF-1α, so that stress intensity itself varies with time of day—implying that a hypoxic event of the same severity may cause different degrees of damage depending on when it occurs. This bidirectionality has direct management implications: dissolved oxygen management should not aim merely at staying above a threshold, but should also consider when oxygen is most likely to fall below that threshold and when hypoxia carries the greatest cost.

3.5. Feeding and Nutritional Signals: Independent Zeitgebers for Peripheral Circadian Clocks

In fish, brain clock gene rhythms are strictly regulated by photoperiod and are unaffected by feeding time, whereas the phases of core clock genes such as *per1*, *clock1* and *cry5* in peripheral tissues such as the liver and gut can be shifted markedly by scheduled feeding; under continuous light, scheduled feeding still drives rhythmic expression of peripheral clocks, directly supporting the model of central light synchronization with peripheral feeding synchronization [17]. Unlike mammals, in which rhythmic regulation is dominated by the SCN of the hypothalamus, teleost fish possess a decentralized circadian system in which feeding, as a non-photic zeitgeber, can entrain the rhythms of peripheral tissues independently of the photoperiod. This creates a dual-layer regulatory framework together with the central clock and directly drives the expression of clock genes in peripheral organs, thereby reshaping metabolic and behavioral rhythms [57,88]. Feeding time can serve as a potent zeitgeber that induces FAA in fish. This behavior is endogenous in nature and can be stably maintained even under continuous

light, making it a key behavioral hallmark of feeding entrainment in fish [89]. Studies in goldfish have shown that FAA is driven by an endogenous timing system and can be entrained by periodic feeding, while also being influenced by the lighting regime. When photic and feeding-related zeitgeber signals conflict, the influence of the feeding cue gradually becomes more prominent [90]. Zebrafish, as a model species, provided the first direct evidence for this mechanism: their locomotor rhythm is primarily regulated by the photoperiod, whereas feeding rhythms can be reset independently by feeding time. The phases of these two rhythms are dissociated from one another, supporting a multi-oscillator model of circadian regulation [91]. Studies have shown that glucocorticoid (GC) signaling is a key pathway mediating feeding entrainment of the circadian clock. Using wild-type and *gr*$^{-/-}$ mutant zebrafish, studies have demonstrated that light-induced synchronization of behavior and clock gene expression is unaffected by glucocorticoid receptor (GR) deficiency; however, feeding-induced entrainment of the circadian clock is markedly attenuated or even abolished in the mutants, accompanied by disrupted expression of metabolism-related clock genes [92]. These findings confirm that the GC–GR signaling pathway is involved in the regulation of the circadian clock by feeding rhythms. Feeding rhythms also exhibit marked species specificity and plasticity, with substantial differences in the feeding-entrainment windows between diurnal and nocturnal fish species. In medaka (*Oryzias latipes*), the circadian rhythm of aggressive behavior can be rapidly resynchronized to feeding time [93]. Studies in channel catfish (*Ictalurus punctatus*) have shown that scheduled feeding significantly alters the peak time and amplitude of *per* gene rhythms in both brain and liver, suggesting that feeding can influence metabolism by regulating clock gene transcription [94]. Studies in European sea bass have confirmed that feeding time can act as a potent zeitgeber, synchronizing both central and peripheral circadian rhythms as well as epigenetic rhythms in the liver [95]. Feeding time is one of the most practical circadian management strategies in aquaculture. Key principles include maintaining a fixed daily feeding schedule, avoiding rhythm disruption and stress caused by random feeding, and setting feeding windows according to the natural feeding habits of the target species. Diurnal fish should preferably be fed during the light phase, whereas nocturnal species may be fed during the dark phase. A single scheduled feeding event per day is often sufficient to establish a stable feeding rhythm, without the need for excessively increasing feeding frequency. In aquaculture systems with limited light cues, precisely timed feeding can help maintain the homeostasis of peripheral circadian clocks and compensate for insufficient photic entrainment [17,96]. Light, temperature and feeding are established zeitgebers capable of entraining fish rhythms, whereas salinity acts mainly as a modulator and dissolved oxygen mainly as a stressor, altering the phase and amplitude of rhythms; together these two classes of signal shape the environmental response profile of fish rhythms (Figure 3).

In summary, feeding can rank alongside light as a zeitgeber because the two act at different levels of the signaling hierarchy: light, acting through the retina and deep-brain photoreceptors, sets central phase, whereas feeding, acting through metabolic state and glucocorticoid signaling, acts directly on peripheral tissues, so that each can set phase without mutual interference. This also explains why scheduled feeding can still re-establish peripheral rhythms under continuous light: the temporal information for peripheral clocks is then supplied by feeding rather than by light. This yields a testable prediction: in metabolically active tissues (liver, gut, muscle), sensitivity of phase to feeding time should exceed sensitivity to light, whereas the reverse should hold for visually related tissues.

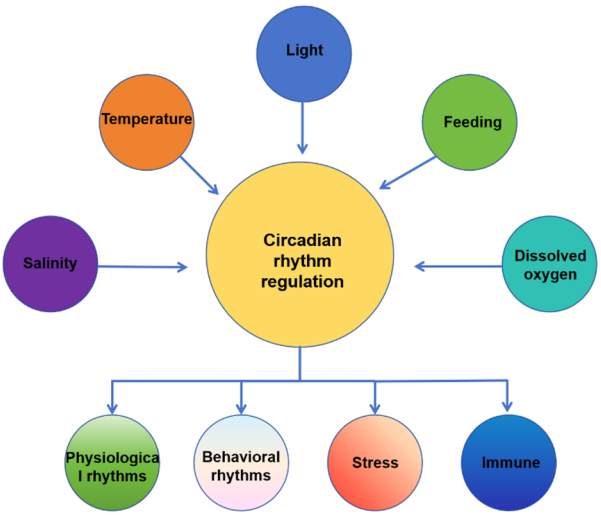


Figure 3. Regulation of fish circadian rhythms by major environmental factors.

4. Physiological and Behavioral Characteristics of Circadian Rhythms in Fish

4.1. Rhythms of Metabolism, Endocrine Function, and Immunity

The circadian system regulates metabolic enzymes, transporters and hormone signaling pathways through rhythmic clock gene expression, participating in fish metabolic regulation at the levels of carbohydrate, lipid and protein metabolism; glucose homeostasis in particular shows a pronounced daily fluctuation. In red drum (*Sciaenops ocellatus*), long photoperiods have been shown to improve growth and feed utilization, and the thyroid hormone T4 rhythm free-runs under continuous dim light, persisting in the absence of a periodic zeitgeber and thus meeting the criterion for free-running rhythms; this provided the first evidence for an endogenous circadian rhythm of thyroid hormone in fish, suggesting that activation of the hypothalamic–pituitary–thyroid axis is regulated by the fish's own clock [97]. Studies have shown that key genes of hepatic lipid metabolism in gilthead sea bream (*Sparus aurata*) display pronounced diel rhythms under LD cycles, with peak times differing among genes; feeding time has little effect on their phase, and some genes remain rhythmic under constant darkness. This indicates that hepatic lipid metabolism in this species is driven by an endogenous oscillator and is synchronized mainly by the LD cycle rather than by feeding time [98]. Eighteen clock genes have been identified in peripheral tissues of Atlantic cod, some of which are maternally transmitted during early development; most are widely expressed across tissues, and myogenic genes are significantly correlated with clock gene expression, indicating that peripheral clocks can regulate muscle physiology [99]. Endocrine rhythms are a core output of the fish circadian system and span multiple levels, including the HPI and hypothalamic–pituitary–gonadal (HPG) axes. In Senegalese sole, genes of the HPI axis and plasma cortisol show pronounced diel rhythms, with peak times differing among components; moreover, cortisol levels differ significantly when acute stress is applied at different times of day, providing the first demonstration of a diel rhythm in HPI axis endocrine activity and of a time-of-day effect on the stress response [100]. Along the growth axis, *pacap*, *gh* and *igf1* in Senegalese sole all peak in the second half of the dark phase, whereas *igf1r* peaks in the middle of the light phase; GH injection at mid-dark most strongly suppressed pituitary *gh* expression and promoted hepatic *igf1* expression, confirming that the effects of GH vary with time of day [101]. With respect to immune rhythms, the circadian system likewise exerts pronounced control over immune function. In medaka, the core clock proteins CLOCK and BMAL1 bind directly to the E-box of the *tnf-α* gene and drive its transcription in a circadian manner; the intensity of the fish immune response is time-dependent, with LPS stimulation inducing the highest *tnf-α* expression during the subjective night and the lowest during the day [102]. This finding is of theoretical importance for understanding the temporal strategy of immune defense in fish and provides a potential basis for optimizing vaccination timing—vaccination during the phase of highest immune responsiveness may confer stronger protection [103]. The existence of metabolic and endocrine rhythms suggests that feeding time should be matched to peaks in metabolic activity in order to improve feed conversion efficiency [104]. The effects of hormone treatment are time-dependent, and selecting the optimal time of administration can improve efficacy and reduce side effects [105].

In summary, metabolic, endocrine and immune rhythms are not independent clock outputs but share a common upstream phase framework: their phases are set by photoperiod and feeding time, and they differ mainly in amplitude and in the response thresholds of downstream effectors. Thyroid hormone and hepatic lipid genes remain rhythmic under continuous dim light or constant darkness, indicating that their phase is provided by an endogenous oscillator, whereas the time-of-day effects seen in cortisol, GH and *tnf-α* reflect effector differences superimposed on this framework. This has a direct practical implication: the "optimal time" for drug administration or vaccination should not be expressed in clock hours but in zeitgeber time (ZT) or relative to feeding time; otherwise it is neither comparable nor transferable across photoperiods and feeding regimes.

4.2. Rhythms of Feeding and Locomotor Behavior

Feeding behavior and locomotor activity are the most direct behavioral outputs of circadian rhythms in fish and are also among the easiest parameters to monitor and manipulate in aquaculture management. Feeding rhythms in fish exhibit a high degree of species specificity and can generally be classified as diurnal, nocturnal, or crepuscular feeding patterns. Notably, the phases of feeding and locomotor rhythms may be independent of one another, a phenomenon that highlights the multi-oscillator organization of the fish circadian system [106]. In rainbow trout, feeding behavior under a light–dark cycle is mainly concentrated during the light phase and is characterized by two prominent peaks: a light-induced onset peak after lights-on and an endogenous anticipatory peak before lights-off. In contrast, locomotor rhythms show marked behavioral divergence according to vertical distribution in the water column, with bottom-dwelling individuals displaying diurnal activity and surface-dwelling individuals exhibiting nocturnal activity [107]. These results indicate that rainbow trout possess an endogenous circadian clock regulating daily rhythms, and that its principal pacemaker is not located in the pineal

gland, a conclusion that differs markedly from earlier melatonin-based interpretations. This finding has important implications for aquaculture management: even within the same species, individuals occupying different water layers may exhibit opposite activity rhythms, and therefore the vertical distribution of fish within the culture system should be taken into account when optimizing feeding schedules. Goldfish exhibit high plasticity in both feeding and locomotor rhythms, with pronounced individual variation, and may display diverse patterns including diurnal activity, nocturnal activity, or a dissociation between the timing of activity and feeding. Under light–dark (LD) conditions, activity is biased toward the daytime whereas feeding is more evenly distributed; under constant darkness, locomotor activity and feeding exhibit free-running rhythms of 25.3 h and 24.4 h, respectively, with independent phases, reflecting the high adaptive plasticity of their circadian system [108]. This plasticity may be one of the key factors enabling goldfish, as a highly adaptable species, to survive across a wide range of environments. Similarly, juvenile pink salmon (*Oncorhynchus gorbuscha*) display both circadian rhythmicity and marked individual variation in swimming activity: under 12L:12D, 68% of individuals were diurnal and the remainder nocturnal; in constant light and constant temperature, about half maintained an endogenous activity rhythm for up to 10 days, whereas the other half showed no rhythm. Mean swimming speed increased significantly with light intensity, indicating a positive phototactic response; after a phase delay of the LD cycle, most individuals resynchronized within a single cycle, indicating a strong capacity for re-entrainment [109].

In summary, behavioral rhythms carry two kinds of information at once: they reflect the phase of the endogenous oscillator, and they also incorporate immediate inputs such as light and feeding. Behavior is therefore both the most accessible index of rhythmicity and the most easily misread. Across the three species, differences between individuals and between species lie mainly in amplitude and phase rather than in the presence or absence of an underlying mechanism: the diurnal preference of goldfish can shift as a whole, pink salmon individuals can be either endogenous or arrhythmic, and rainbow trout diverge by depth within a single population. It follows that when behavior is used to judge whether a species is "rhythmic", both the observation conditions and the proportion of rhythmic individuals must be reported; otherwise "rhythmic versus arrhythmic" becomes merely a function of how the samples were taken.

4.3. Rhythms of Sleep, Reproduction, and Shoaling Behavior

Sleep is a key behavioral phenotype of circadian rhythmicity in fish, although its definition and detection remain challenging. Fish sleep is generally characterized by reduced activity, an elevated arousal threshold, species-specific posture, and rebound effects following deprivation. In the three-spot wrasse (*Halichoeres trispilus*), stable locomotor rhythms are maintained under light–dark cycles as well as under constant light and constant darkness. Pineal melatonin exhibits a conserved rhythm with high levels at night and low levels during the day, and functions to suppress locomotion and respiration while promoting sleep. At the same time, *per1*, *per2*, *bmal1*, and *cry1* in the brain show circadian rhythmic expression, suggesting that clock genes regulate endogenous locomotor rhythms and, together with melatonin, coordinately mediate sand-burrowing sleep behavior and the sleep–wake cycle [110].

Most fish species exhibit seasonal reproduction, and many also display diel spawning rhythms. Studies have shown that zebrafish maintained under a 14L:10D photoperiod spawn during the daytime, with a spawning peak occurring approximately 3 h after lights-on. Their locomotor activity is also diurnal and reaches its maximum after lights-on but before spawning. Nocturnal feeding does not alter the spawning rhythm, although it reduces the proportion of daytime activity to 49.6%. Under continuous light, locomotor activity becomes free-running with a period of 22.3 h, and the spawning rhythm remains synchronized with it, peaking at CT3 [111]. Taken together, zebrafish possess endogenous circadian rhythms of both spawning and locomotor activity. These two rhythms are phase-aligned and both are entrained by the photoperiod, whereas only locomotor activity is modulated by feeding time. In medaka maintained under a 16L:8D photoperiod and subjected to five scheduled feeding regimes, the circadian rhythm of aggressive behavior was found to be rapidly resynchronized to feeding time and remained stable even after 3 days of starvation. In contrast, spawning and courtship rhythms were regulated solely by the light–dark cycle and were unaffected by feeding time [93]. This indicates that fish can use different zeitgebers to synchronize different behavioral rhythms in a differentiated manner. The finding highlights the complexity of behavioral rhythm regulation: not all behaviors respond to the same zeitgeber, and the rhythms of different behaviors may be controlled by different oscillators or may differ in their sensitivity to the same zeitgeber signal. Such differences are not randomly distributed but are related to the ecological function of the behavior: reproductive behaviors (spawning, courtship) are tightly locked to photoperiod, ensuring that the reproductive window matches seasonal and thermal conditions; feeding-related behaviors (aggression, feeding) can be remodeled by feeding time, improving the efficiency of energy acquisition; and locomotor and shoaling activities

are modulated by both light and internal state. In other words, the zeitgeber sensitivity of a behavior reflects its degree of constraint within the temporal niche—the stronger the constraint (as in reproduction), the less the behavior can be rewritten by non-photic signals; the weaker the constraint (as in shoaling), the more readily it degrades into an immediate response to the light environment. Shoaling behavior is likewise regulated by photoperiod. In zebrafish, mean shoaling time is significantly higher during the light phase than during the dark phase, but this diurnal difference disappears under continuous light or darkness, indicating that it is driven directly by the LD cycle as an environmental signal rather than by an endogenous circadian rhythm [112,113]. This conclusion has important methodological implications: not all observed diel differences arise from endogenous circadian rhythms; some may simply reflect the direct masking effects of light.

4.4. Individual Differences and Circadian Plasticity

Circadian rhythms in fish are not fixed traits; rather, they exhibit pronounced individual variation and circadian plasticity within populations. This not only represents an important strategy for adaptation to variable environments but also has significant implications for aquaculture management. Within the same population, some individuals display stable rhythmicity, whereas others exhibit weakly rhythmic or arrhythmic phenotypes, and the phase, period, and activity patterns of these rhythms can be dynamically adjusted in response to environmental cues [114]. For example, marked individual differentiation in feeding rhythms has been observed within groups of rainbow trout. Under a light–dark cycle, feeding occurs predominantly during the daytime, and endogenous rhythmicity can still be maintained under continuous light. Although social hierarchy and leader-initiated feeding behavior are present within the group, no significant differences in growth performance have been found between dominant and subordinate individuals, suggesting that circadian variation is manifested more as diversity in behavioral strategies than as differences in growth outcomes [115]. Gilthead seabream larvae display pronounced circadian plasticity during ontogeny. Behavioral rhythms persist under constant light, although the phase of peak activity shifts progressively with age and converges on the typical light–dark pattern by approximately 60 days post-hatch. Upon transfer from constant light to a light–dark cycle, clock gene expression is rapidly re-entrained, indicating that the circadian system remains highly adaptable throughout larval development [116]. Recent field and aquaculture studies have further confirmed that individual variation in fish chronotypes is both widespread and stable. High-throughput tracking of wild fish has shown that even under the same environmental conditions, individuals still exhibit consistent differences in diel activity patterns, and the expression of chronotype phenotypes can be modulated by temperature, wave conditions, and social interactions [117]. At the same time, fish circadian rhythms are closely associated with personality-related behaviors, with late chronotypes typically exhibiting greater aggression and exploratory tendency. This suggests that the circadian system and behavioral syndromes jointly shape adaptive strategies [118]. Circadian plasticity is particularly pronounced in estuarine and euryhaline fish, which can rapidly reverse their activity phase in response to fluctuations in environmental factors such as salinity and turbidity, thereby coping with drastic environmental change [82]. Mechanistically, individual differences and plasticity in circadian rhythms arise from the decentralized multi-oscillator circadian system of fish, in which central and peripheral oscillators can respond independently to different zeitgebers, such as light, feeding, and temperature, thereby enabling the independent temporal regulation of diverse behavioral and physiological rhythms [119]. This modular mode of regulation enables fish to maintain both circadian stability and flexibility in complex environments, and it also provides a theoretical basis for “rhythm-adaptive management” in aquaculture. Ignoring individual differences in chronotype and applying a uniform management strategy may lead to circadian disruption in some individuals, increased stress, and reduced feed utilization efficiency. In contrast, refined management that takes circadian diversity into account can effectively improve aquaculture performance and animal welfare [120].

These sources of variation can therefore be separated into three categories, each with different management implications. First, individual chronotypes are stable differences among individuals within a population at a single point in time, possibly arising from genetic or early developmental factors; managing them requires either grouping animals by chronotype or tolerating diversity. Second, developmental plasticity is the adjustment of phase within an individual as it ages (for example, gilthead sea bream larvae approach the adult rhythm by about 60 days post-hatch); managing it requires resetting parameters according to developmental stage. Third, environmentally induced plasticity (for example, the reversal of activity phase after rainfall) is a short-term response to an abrupt perturbation; management should allow time for recovery rather than adjust long-term protocols on the basis of such events. Conflating the three makes it easy to mistake individual differences for unreliable parameters, or developmental plasticity for population divergence. (The species, experimental conditions and types of evidence for endogenous rhythmicity for each study are summarized in Table 1.)

Table 1. Grading of evidence for endogenous rhythmicity in fish rhythm studies.

Species	Life Stage	Experimental Conditions	Zeitgeber/Treatment	Endpoint (Tissue/Behavior)	Endogenous Evidence	Key Findings	References
Free-running (period measurable)							
Goldfish (*Carassius auratus*)	Adult fish	12L:12D; DD light pulse	Light; demand feeding	Locomotor activity; feeding	Rhythms persisted under constant darkness: locomotor period 25.3 h, feeding period 24.4 h	Individuals showed different preferences, and locomotor and feeding phases could be dissociated	[108]
Sea bass (*Lateolabrax* sp.)	Juvenile fish	DD; salinity 31.5‰→15‰ 31.5‰→0‰	Abrupt salinity drop	Oxygen consumption rate	Rhythms persisted under constant darkness (approximately 23.3 h)	Oxygen consumption decreased but the rhythm persisted; it weakened after 8–10 d.	[81]
Zebrafish (*Danio rerio*)	Adult fish	14L:10D; LL; ZT3/Z7 dark pulse	Light; night feeding; dark pulses	Spawning; locomotor activity	Under constant light, the locomotor period was 22.3 h and spawning was synchronized; a brief dark pulse shifted the spawning peak.	Both rhythms were in phase and synchronized by light; only locomotor activity was affected by feeding.	[111]
Persistence under constant conditions							
Common carp (*Cyprinus carpio*)	Adult fish	LL; DD	Light	Brain, pituitary, retina: *clock*, *bmal*, *per*, *cry*	Rhythms persisted under constant light/constant darkness; retinal clock was unaffected by light	*Clock*, *bmal* peaked at lights-off, *per* peaked at lights-on; *cry* showed no consistent pattern.	[51]
Turbot (*Scophthalmus maximus*)	Adult fish	LD; DD; LL; timed feeding	Light; feeding	Multiple tissues: *clock1*, *per1*, *per2*, *cry1*; locomotor activity, FAA (food-anticipatory activity)	Genes remained rhythmic, but behavior was arrhythmic.	Genes were endogenous, whereas behavior depended on light; FAA was present under constant light but absent under constant darkness.	[65]
Autonomy in isolated tissue							
Atlantic cod (*Gadus morhua*)	Adult fish	*In vitro* (cells; 5-d explants); varying light	Light (*in vitro*)	White muscle: *arntl2, clock*, *cry2*, *per2a*, *nr1d1*	Most genes were arrhythmic; only clock remained rhythmic.	Indicates a non-autonomous peripheral clock; light alters *cry2*, *per2a* levels without inducing rhythms	[54]
Japanese flounder (*Paralichthys olivaceus*)	Adult fish	*In vivo*: LD → DD; *in vitro*: fin culture	Light; cortisol; melatonin	Caudal fin: *per1*, *per2*, *cry1*	Rhythms persisted *in vivo* but disappeared *in vitro*.	It depends on the SCN–pituitary–adrenal axis; short light exposure upregulates *per2* and *cry1*.	[64]
LD-only observations							
Goldfish (*Carassius auratus*)	Adult fish	LD	Light	Retina, liver, and intestine: *Per1–3*, *Cry1–3*	LD-only observations	All retinal genes were rhythmic; in the liver and intestine, only some were rhythmic, with different phases.	[52]
Japanese flounder (*Paralichthys olivaceus*); Greater Amberjack (*Seriola dumerili*); Japanese medaka (*Oryzias latipes*)	larval fish	LD	Light	SCN, pineal gland, pituitary, habenula	LD-only observations	SCN: *per2* expression is higher during the day than at night in Japanese flounder; rhythmic expression is observed in greater amberjack but not in Japanese medaka. In Japanese flounder, *per2* expression is rhythmic in the pineal gland and pituitary but arrhythmic in the habenula.	[55]
Senegalese sole (*Solea senegalensis*)	Adult fish	LD	Light	Retina, optic tectum, diencephalon, cerebellum, liver	LD-only observations	The retina and liver were in opposite phase; Per3 was rhythmic in only two regions.	[62,63]

Table 1. *Cont.*

Species	Life Stage	Experimental Conditions	Zeitgeber/Treatment	Endpoint (Tissue/Behavior)	Endogenous Evidence	Key Findings	References
Constant conditions and masking							
Zebrafish (*Danio rerio*)	Adult fish	LD, reversed LD, DD, LL (10 d each)	Light	Shoaling	No difference under constant light or constant darkness.	Shoaling increased with the light period and had no endogenous component.	[112,113]
Molecular or genetic causation							
Zebrafish (*Danio rerio*)	Adult fish	*Roraa* knockout/overexpression	Genetic manipulation	Behavioral rhythms, core clock genes, lipid metabolism genes	Knockout attenuated it, whereas overexpression had the opposite effect	Roraa regulates *per2*; lipid metabolism genes were altered.	[34]

Note: LD, light–dark cycle; LL, constant light; DD, constant darkness; ZT, zeitgeber time; FAA, food anticipatory activity. "*In vitro* culture" comprises cell culture and tissue explant culture. Rows are arranged by evidence type, in the following order: free-running, persistence under constant conditions, autonomy in isolated tissue, LD-only observations, constant conditions and masking, and molecular or genetic causation. The table is a representative rather than exhaustive summary of the literature.

5. Optimization of Aquaculture Management Based on Circadian Rhythms

Light is the most important zeitgeber in fish and also the most practical environmental variable to manipulate in aquaculture. Appropriate adjustment of photoperiod, light intensity, and spectral composition helps stabilize the central circadian clock, enhance rhythmic amplitude, and further improve growth performance and feed utilization efficiency [121]. Previous studies have shown that moderately prolonging the dark phase or maintaining complete darkness at night can enhance antioxidant capacity and increase the expression of immune-related genes in cultured fish [122]. The optimal range of light conditions also differs markedly among fish with different ecological types. Nocturnal or benthic species generally adapt better to lower light intensities and shorter photoperiods, whereas diurnal species often exhibit superior production performance under moderate photoperiods [123]. In industrial aquaculture systems, the use of dynamic light intensity and spectral regimes that mimic natural variation may not only help maintain circadian stability but also optimize both energy efficiency and production performance [124]. Therefore, light-environment regulation should shift from a "one-size-fits-all" approach to "species-specific parameter optimization", and should be designed in coordination with feeding schedules to improve the overall effectiveness of circadian management [125,126].

Scheduled feeding is one of the most readily applicable circadian-management strategies in aquaculture practice. A stable feeding schedule can induce FAA and promote better temporal coordination among digestive enzyme secretion, intestinal absorption, and energy metabolism, thereby improving feed conversion efficiency and reducing the water-quality burden caused by uneaten feed [127]. Because feeding time can act as a non-photic zeitgeber that independently entrains peripheral circadian clocks, precise scheduled feeding to optimize metabolic rhythms often has greater management value than simply increasing feeding frequency in fish with a multi-oscillator circadian system [17,128]. From a practical production perspective, long-term and stable feeding windows should be established according to the natural feeding habits of the target species, the imposed photoperiod regime, and patterns of environmental fluctuation, rather than relying on randomized feeding strategies.

Stress and welfare management based on circadian rhythms represents an important direction for improving the stability of intensive aquaculture. The key lies in identifying time-of-day differences in stress sensitivity, physiological tolerance, and recovery capacity in fish, and in scheduling high-stress procedures—such as harvesting, grading, transport, anesthesia, and vaccination—during periods when responses are weaker and recovery is faster, while avoiding resting phases or other sensitive windows. Existing studies have shown that operations such as salinity fluctuation, anesthetic treatment, and crowded transport all exhibit clear time-of-day effects; when combined with rhythm-disrupting factors such as continuous light and irregular feeding, these procedures may further exacerbate cortisol elevation, immune suppression, and the accumulation of chronic stress [129–133]. Therefore, aquaculture management should focus not only on the intensity of a given operation, but also on its temporal dimension, so as to achieve simultaneous improvements in production efficiency and animal welfare.

It should be emphasized that the three groups of measures differ in the strength of the evidence supporting them, and that management should rank them accordingly while taking their interactions into account. Photoperiod and feeding time are supported by evidence of entrainment and phase resetting and can therefore be treated as "timing parameters" that can be set directly; stress-timing management rests mainly on time-of-day effects, in which the same operation produces different outcomes at different times, and is therefore a matter of "scheduling"; whereas

recommendations on spectrum and light intensity derive largely from comparisons of production performance and have not yet been linked directly to rhythm mechanisms, so they are better regarded as "optimization parameters" rather than "essential parameters". When the two classes of zeitgeber conflict, available evidence suggests that the weight of the feeding signal in peripheral tissues increases over time; peripheral metabolic management should therefore prioritize a stable feeding schedule, whereas reproductive and central objectives should continue to rely primarily on photoperiod. Taken together, these strategies constitute an optimized chrono-aquaculture framework centered on matching the phase of the cultured species' rhythms and its dependence on zeitgebers (Figure 4). The main interventions, their parameter settings and effects are summarized in Table 2.

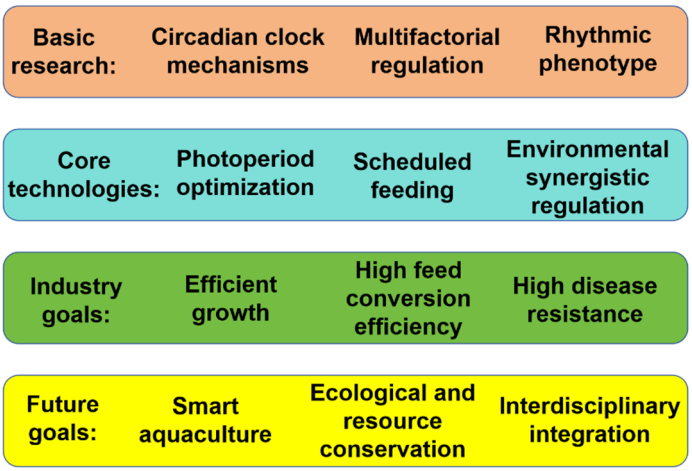


Figure 4. Optimization Framework for "Chrono-Aquaculture" Management Based on Fish Circadian Rhythms.

Table 2. Rhythm-based aquaculture enhancement measures and their effects.

Measure	Target Species	Key Parameters	Effect	Evidence Type	Reference
Reduced light intensity	Starry flounder (*Platichthys stellatus*)	low 15/medium 500/high 2500 lux	Low light: weight gain 44.0 g; high light: 32.4 g; no difference in cortisol.	Production performance + physiological indicators	[70]
Increased feeding frequency	Flathead grey mullet (*Mugil cephalus*)	1, 2, and 10 meals per day (feeding rate 3%)	10-meal group 0.80 g > 2-meal group 0.70 g > 1-meal group 0.63 g	production performance + physiological indicators	[104]
Daytime scheduled feeding	Rainbow trout (*Oncorhynchus mykiss*)	light-phase feeding, dark-phase feeding, and random feeding × LL/LD, 3 months	Light-phase feeding alleviated oxidative damage, whereas random or dark-phase feeding exacerbated it	physiological indicators	[122]
Control of nighttime light leakage	European perch (*Perca fluviatilis*)	avoid nighttime light exposure	maintained the nocturnal rise in melatonin	physiological indicators	[28]
Timing of anesthesia procedures	Tambaqui (*Colossoma macropomum*)	eugenol anesthesia administered separately during the day and at night	Recovery was slower at night: 5–7 min vs 1–2 min during the day	physiological indicators	[130]
Scheduling high-stress procedures outside the rest phase	Nile tilapia (*Oreochromis niloticus*) tench (*Tinca tinca*)	a stress test every 4 h	Stress was most pronounced during the rest phase (the dark phase in tilapia and the light phase in tench)	behavioral indicators	[131]
Allowing recovery periods between multiple procedures	Rainbow trout (*Oncorhynchus mykiss*)	stacking of crowding, transport, and exposure, etc.	A single procedure increased the rate by 8–9 times/min, whereas stacked procedures increased it by 25 times/min; recovery took approximately 4 d	physiological indicators	[132]
Avoiding shift-work-style Lighting	Turquoise killifish (*Nothobranchius furzeri*)	"5+2" shift-work lighting, 8 weeks	Activity amplitude and rhythmicity index decreased; clock gene expression was altered	rhythm indicators	[133]
Timing of hormone administration	Golden shiner (*Notemigonus crysoleucas*)	injections administered separately in the early and late light phase	Gonadotropin was effective only when administered early; prolactin was inhibitory only when administered early	physiological indicators	[105]
Feeding during the light phase	European seabass (*Dicentrarchus labrax*)	feeding at the midpoint of the light phase (ML) and the midpoint of the dark phase (MD)	The ML group maintained intact rhythms; in the MD group, only a few genes retained rhythmicity	rhythm indicators	[95]

Table 2. *Cont.*

Measure	Target Species	Key Parameters	Effect	Evidence Type	Reference
Photoperiod manipulation	European seabass (*Dicentrarchus labrax*)	different photoperiods (including continuous light)	Photoperiod regulates clock genes and reproductive axis genes; continuous light suppressed *gnrh1* and *kiss2*	molecular indicators	[68]
Setting temperature cycles during the embryonic stage	Zebrafish (*Danio rerio*)	constant darkness + temperature cycles (48–72 hpf)	Temperature cycles are a prerequisite for establishing self-sustained rhythms; acute temperature changes can regulate *per1b*	molecular/developmental indicators	[71]

Note: ML, feeding at the midpoint of the light phase; MD, feeding at the midpoint of the dark phase. Only measures with clear evidence of enhancement are listed in the table.

6. Key Issues in Current Research on Fish Circadian Rhythms

Although substantial progress has been made in the study of fish circadian rhythms with respect to molecular mechanisms, environmental responses, and aquaculture applications, the field as a whole still faces several fundamental challenges that constrain its further development [18].

First, the conceptual boundary between sleep and circadian rest in fish remains unclear. Although several criteria have been proposed, including reduced activity, elevated arousal threshold, species-specific posture, and sleep homeostasis [134,135], most studies still infer sleep primarily from changes in activity levels, with insufficient validation based on multiple complementary indicators [136]. This not only reduces the comparability among different studies, but also increases the likelihood that simple light avoidance or inactive behavior may be misinterpreted as an endogenous sleep-like state [137].

Second, reliance on model species remains a major structural limitation in current research. Zebrafish have long dominated this field because of their advantages in genetic manipulation, short reproductive cycle, and transparent larvae [138]. However, fishes comprise an extremely diverse group with complex ecological types, and circadian systems may differ substantially among species inhabiting different environments [5,139]. Moreover, circadian phenotypes obtained under laboratory-domesticated conditions may show systematic biases relative to those expressed in natural environments [140,141]. Therefore, if a small number of model species continue to be used as proxies for the entire diversity of fishes, it will be difficult to accurately reveal the ecological adaptability and evolutionary diversity of fish circadian rhythms [117].

Third, research on the interactions among multiple environmental factors remains clearly insufficient. In natural waters and aquaculture environments, variables such as light, temperature, dissolved oxygen, and salinity often fluctuate in concert, and their combined effects cannot be simply regarded as the linear sum of single-factor responses. At present, understanding remains limited regarding the decoupling of light and temperature, the interactions between hypoxia and circadian pathways, the chronic effects of artificial light at night, and the mechanisms underlying multiple-stressor interactions [142–144]. This limitation directly constrains the extrapolation of current findings to real ecological and production settings.

In addition, there remains a clear methodological gap between laboratory-based mechanistic studies and field monitoring of circadian phenotypes. Existing molecular assays and behavioral tracking techniques offer high temporal resolution, but they are mostly implemented under controlled conditions. By contrast, field studies have long been constrained by difficulties in individual identification, insufficient synchronous recording of environmental variables, and the complexity of data processing [114,145,146]. More importantly, no unified standard has yet been established for interpreting how field-obtainable indicators, such as spatial position and activity depth, correspond to circadian state [147]. This means that many mechanisms established under laboratory conditions remain difficult to validate effectively in natural environments.

Finally, cross-level integrative research remains insufficient. At present, there is still a lack of a systematic framework linking molecular oscillations, individual behavior, and population-level ecological consequences [148]. For example, how polymorphisms in core clock genes influence individual chronotype differentiation, and how circadian variation in turn affects population dynamics through resource competition, predator–prey interactions, and host–parasite relationships, remain insufficiently understood [149]. If an integrative framework cannot be established from molecules to individuals, and further to populations and aquaculture systems, research on fish circadian rhythms will be unlikely to translate into truly effective tools for ecological conservation and fisheries management.

From an industrial perspective, a substantial translational gap still exists between basic research and aquaculture practice. Although photoperiod manipulation and scheduled feeding have already demonstrated considerable application potential, on-farm management of lighting, feeding, stocking density, and stress control

still relies heavily on empirical rules and lacks support from species-specific circadian parameters. Moreover, it remains insufficiently evaluated whether the optimal circadian regimens identified under laboratory conditions can function reliably in large-scale and dynamic aquaculture systems. Future efforts should focus on establishing quantifiable, verifiable, and broadly applicable circadian-management parameter systems for key cultured species, and on promoting their integration with intelligent equipment and real-time monitoring technologies [95].

Overall, the major bottlenecks in current research on fish circadian rhythms are mainly reflected in the lack of unified conceptual criteria, insufficient taxonomic coverage, weak understanding of multifactor interaction mechanisms, lagging field-monitoring technologies, and an incomplete pathway for industrial translation. To achieve substantive breakthroughs in the future, coordinated advances will be required in the establishment of standardized criteria, the expansion of research to non-model fish species, cross-scale integrative studies, and scenario-based application validation. Such efforts will help drive the field beyond mere "mechanistic elucidation" toward broader "ecological interpretation" and "practical application in aquaculture".

7. Conclusions and Perspectives

Overall, research on fish circadian rhythms is moving beyond the analysis of individual molecular mechanisms toward a new stage characterized by multidimensional ecological integration and coordinated advancement of industrial applications. Future basic research should place greater emphasis on non-model economically important fish species and fishes inhabiting special environments, with the aim of systematically elucidating the plastic responses of circadian rhythms under combined stress conditions such as high temperature, low salinity, and hypoxia, as well as their coupling with important traits including growth, metabolism, stress resistance, and immunity [150]. At the same time, it is necessary to further refine the criteria for defining rhythmic phenotypes of sleep, rest, and stress-related behaviors in fish, and to promote mechanistic investigations into the core circadian network and its downstream effects under conditions involving the coupling of multiple environmental factors [29]. At the methodological level, technologies such as miniaturized sensors, acoustic telemetry, machine learning, and underwater intelligent recognition will provide important support for the in situ, long-term, and non-invasive monitoring of circadian rhythms in fish [145]; The integration of multi-omics and epigenetic approaches will also help identify key molecular targets involved in circadian regulation [95]. At the aquaculture application level, species-specific circadian parameter databases should be established for major cultured fish species, and technical protocols should be developed for photoperiod optimization, precision feeding, stress-timing management, and coordinated regulation under multiple environmental factors. These strategies should also be deeply integrated with intelligent lighting systems, precision feeding technologies, and real-time physiological monitoring platforms [20,131]. It can be anticipated that, with the further integration of basic research and industrial needs, "chrono-aquaculture" will evolve from a conceptual proposal into a verifiable and scalable management model, thereby providing a new chronobiological pathway for the high-quality and sustainable development of aquaculture.

Author Contributions

Y.Y.: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing—original draft preparation, Visualization. G.Y.: Conceptualization, Methodology, Formal analysis, Investigation. Z.F.: Software, Validation, Resources, Writing—review and editing, Supervision, Project administration, Funding acquisition. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement

The original contributions presented in the study are included in the article. Further inquiries can be directed to the corresponding authors.

Conflicts of Interest

Guo Yu is employed by the Hainan Branch of Hefei Herun Technical Services Co., Ltd. The remaining authors declare no conflicts of interest.

Use of AI and AI-Assisted Technologies

During the preparation of this work, the authors used ChatGPT, developed by OpenAI, to assist with language polishing and to improve the readability and scientific writing style of the manuscript. After using this tool, the authors carefully reviewed, edited, and revised the relevant content to ensure the accuracy, originality, and integrity of the manuscript. The authors take full responsibility for the content of the published article.

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