

Comparative Genomics of Fish: Insights into Evolutionary Processes

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Abstract Comparative genomics provides a powerful tool for understanding evolutionary processes, particularly in the diverse and ecologically significant group of fish. This study explores the evolutionary significance of fish genomics, highlighting the diversity of fish genomes and their key evolutionary milestones through comparative analyses with other vertebrates. Utilizing advanced genome sequencing techniques, bioinformatics tools, and comprehensive genomic databases, this study identifies gene family expansions, adaptive evolution, and evolutionary innovations within fish genomes. A case study on the evolution of antifreeze proteins in Antarctic fish illustrates the broader implications of these findings for understanding adaptation. This study also reveals critical evolutionary processes such as speciation, convergent evolution, and horizontal gene transfer. Looking forward, the integration of emerging technologies and interdisciplinary approaches in fish comparative genomics holds significant potential for advancing our understanding of evolutionary biology and informing conservation efforts.

Keywords Comparative genomics; Fish evolution; Gene family expansion; Antifreeze proteins; Speciation

1 Introduction

Comparative genomics is a field of biological research in which the genomic features of different organisms are compared. This approach allows scientists to identify similarities and differences in the DNA sequences of various species, providing insights into their evolutionary relationships and the functional elements of their genomes. By comparing the genomes of different species, researchers can uncover conserved sequences that have been maintained throughout evolution, as well as lineage-specific adaptations that have arisen in response to unique environmental pressures (Fertin and Rusu, 2011; Sarropoulou and Fernandes, 2011).

Fish represent a highly diverse group of vertebrates, making them an ideal subject for evolutionary studies. Teleost fish, in particular, are the second most well-characterized group of vertebrates in terms of genomic data, with high-quality draft genome sequences available for several model species such as *Danio rerio* (zebrafish), *Gasterosteus aculeatus* (stickleback), *Oryzias latipes* (medaka), *Takifugu rubripes* (fugu), and *Tetraodon nigroviridis* (tetraodon) (Negrisolo et al., 2010). The diversity within and among fish species, such as the salmonid fishes, provides a rich context for studying genetic polymorphisms important in adaptation and speciation (Elmer, 2016). Additionally, the availability of recently sequenced genomes for various fish species, including those native to New Zealand, further enhances the potential for comparative genomic studies to reveal evolutionary patterns and processes (Papa et al., 2022).

This study utilizes comparative genomics to gain a deeper understanding of the evolutionary processes that have shaped the genomes of fish. By analyzing the genomic data from both model and non-model fish species, this study identifies conserved genomic regions and lineage-specific adaptations; addresses unresolved taxonomic issues among teleost fish and to explore the influence of various factors on phylogenetic tree topology. Ultimately, this study aims to provide new insights into the genetic mechanisms underlying the diversity and adaptation of fish species, contributing to a broader understanding of vertebrate evolution.

2 Evolutionary Significance of Fish Genomics

2.1 Diversity of fish genomes

Fish genomes exhibit remarkable diversity, both in terms of size and composition. This diversity is largely driven by the presence and variation of transposable elements (TEs), which can constitute a significant portion of the

genome. For instance, the TE content in fish genomes ranges from 5% in pufferfish to 56% in zebrafish, with a positive correlation between genome size and TE content (Shao et al., 2019). This variation in TE content and genome size highlights the unique evolutionary trajectories of different fish species and underscores the importance of TEs in shaping fish genomes.

2.2 Evolutionary milestones in fish genomes

Fish genomes have undergone significant evolutionary changes, including whole-genome duplications (WGDs) that have played a crucial role in their diversification. The teleost fish, for example, experienced a third round of WGD at the base of their lineage, which has contributed to their extensive gene repertoire and functional diversity (Braasch et al., 2015). Additionally, the phylogenetic relationships among fish species have been shaped by these genomic events, with most major fish lineages being established before the end of the Cretaceous period, over 65 million years ago (Hughes et al., 2018). These evolutionary milestones have provided fish with the genetic toolkit necessary for adaptation to a wide range of environments, including extreme conditions (Wang and Guo, 2019).

2.3 Comparative analysis with other vertebrates

Comparative genomics between fish and other vertebrates reveals both conserved and lineage-specific genomic features. For example, while some TE superfamilies are widespread across vertebrates, fish genomes are particularly dominated by DNA transposons, unlike mammalian genomes which are shaped predominantly by non-LTR retrotransposons (Chalopin et al., 2015). Furthermore, fish genomes exhibit a higher degree of synteny conservation than previously thought, with large syntenic chromosome segments being maintained across different fish species and even other vertebrates (Mazzuchelli et al., 2012). This conservation is evident in the strong chromosomal synteny observed among cichlid species and other vertebrates, suggesting that despite the plasticity of fish genomes, certain genomic regions have remained stable throughout evolution.

In summary, the comparative genomics of fish provides valuable insights into the evolutionary processes that have shaped their genomes. The diversity of fish genomes, the significant evolutionary milestones they have undergone, and their comparative analysis with other vertebrates all contribute to our understanding of vertebrate evolution and the unique adaptations of fish.

3 Methodologies in Fish Comparative Genomics

3.1 Genome sequencing techniques

Genome sequencing is a fundamental methodology in fish comparative genomics, enabling the detailed analysis of genetic material across different species. High-throughput sequencing technologies, such as next-generation sequencing (NGS), have revolutionized the field by allowing the rapid and cost-effective sequencing of multiple genomes. For instance, the sequencing of over 50 ray-finned fish genomes has provided extensive genetic resources for understanding divergence, evolution, and adaptation in fish genomes. Additionally, targeted high-throughput sequencing has been employed to study specific gene families, such as the insulin-like growth factor axis in salmonid fish, offering high-resolution evolutionary insights (Lappin et al., 2016). The generation of chromosome-level genome assemblies, termed "chromosome," is also emphasized as a key component for enabling large-scale conserved synteny analyses (Braasch et al., 2015).

3.2 Bioinformatics tools and techniques

Bioinformatics tools and techniques are crucial for analyzing the vast amounts of data generated by genome sequencing. These tools facilitate the alignment, annotation, and comparison of genomic sequences. For example, phylogenetic tests designed to trace the effect of whole-genome duplication events on gene trees have been applied to investigate fish evolution using genome-wide data from 144 genomes and 159 transcriptomes (Hughes et al., 2018). RNA sequencing (RNA-seq) is another powerful bioinformatics approach that has significantly advanced our understanding of fish transcriptomes, aiding in the mapping and annotation of dynamic transcriptomes and providing insights into biological processes such as development and adaptive evolution (Qian et al., 2014). Additionally, comparative cytogenetic mapping using BAC clones and fluorescence in situ hybridization has been integrated with genomic data to identify conserved synteny and genome regions in cichlid fish (Mazzuchelli et al., 2012).

3.3 Comparative genomics databases

Comparative genomics databases are essential for storing, organizing, and accessing genomic data from multiple fish species. These databases enable researchers to perform comparative analyses and identify orthologous genes and genomic regions across different species. For instance, a comprehensive phylogenomic database of ray-finned fishes has been compiled, providing genome-scale support for phylogenetic relationships and resolving contentious nodes in fish phylogeny. The Fish-T1K project has generated a large database of fish transcriptomes, integrating them with published fish genomes for potential applications in functional verification, molecular breeding, and drug development (Bian et al., 2019). Additionally, databases such as Ensembl and COSMIC have been utilized to match sequenced fish genomes with cancer gene information, facilitating comparative studies of cancer-related gene copy number variation in fish (Baines et al., 2022).

By leveraging these methodologies, researchers can gain deeper insights into the evolutionary processes that shape fish genomes, enhancing our understanding of their biology and informing practical applications in areas such as conservation, aquaculture, and medicine.

4 Key Findings in Fish Comparative Genomics

4.1 Gene family expansions and contractions

Gene family expansions and contractions play a significant role in the adaptive evolution of fish. For instance, the study on vertebrate gene family size revealed that gene families in *Danio rerio* (zebrafish) had undergone substantial expansions, likely due to genome-wide duplication events in their ancestors, followed by contractions due to gene fractionation (Meng and Yang, 2019). Additionally, the whale shark genome study highlighted a major increase in gene families at the origin of jawed vertebrates, independent of genome duplication, suggesting that gene family expansions are crucial for vertebrate evolution (Tan et al., 2021). Furthermore, the 14-3-3 gene family in various fish species showed dynamic evolution characteristics, with recombination events accelerating their evolution (Cao and Tan, 2018).

4.2 Adaptive evolution in fish

Adaptive evolution in fish is driven by various genomic mechanisms. The study on whitefish (*Coregonus ssp.*) demonstrated that relaxed purifying selection is driving the high nonsynonymous evolutionary rate of the *NADH2* gene, which may be associated with adaptive divergence and speciation (Jacobsen et al., 2016). Similarly, the analysis of cancer-related gene duplications in fish revealed that higher numbers of tumor suppressor genes are correlated with longer lifespans, suggesting that these genes play a role in adaptive evolution by providing genetic defenses against oncogenic processes (Baines et al., 2022). Additionally, orphan genes in bony fish have been implicated in adaptive evolution, contributing to traits such as fin and tail development and kidney physiology.

4.3 Evolutionary innovations in fish genomes

Fish genomes exhibit several evolutionary innovations that contribute to their adaptability and diversity. The study on salmonid fishes, particularly charr (*Salvelinus*), highlighted the use of genomic tools to identify genetic polymorphisms important in adaptation and speciation, revealing the genetic mechanisms behind the diversity of salmonid fishes (Elmer, 2016). The whale shark genome study also discovered a new toll-like receptor (TLR29) and multiple copies of NOD1, indicating novel immune system adaptations in chondrichthyan fish. Moreover, the comparative cytogenetic analysis of *Pyrrhulina* species revealed the presence of a multiple X1X2Y sex chromosome system and the dynamics of repetitive DNA, contributing to karyotype divergence and evolutionary innovations in these small-sized fish (Moraes et al., 2019).

4.4 Comparative genomics and phylogenomic approaches

Comparative genomics and phylogenomic approaches are essential for understanding the evolutionary relationships among fish species. The study on model fish species used robust phylogenetic frameworks to reconstruct genome-level evolution, revealing common features conserved across genomes and identifying lineage-specific characteristics (Negrisolo et al., 2010). This approach is crucial for resolving taxonomic issues and understanding the evolutionary history of teleost fish. Additionally, the comparative analysis of gene family size across vertebrates provided insights into the evolutionary patterns of gene family size changes, highlighting the importance of comparative genomics in studying vertebrate evolution.

By integrating findings from multiple studies, we gain a comprehensive understanding of the evolutionary processes shaping fish genomes, from gene family dynamics to adaptive evolution and genomic innovations. These insights are crucial for advancing our knowledge of fish biology and evolution.

5 Case Study: Evolution of Antifreeze Proteins in Antarctic Fish

5.1 Background and importance

Antarctic fish have evolved unique adaptations to survive in the extreme cold of the Southern Ocean, where temperatures can drop below the freezing point of seawater. One of the most critical adaptations is the development of antifreeze proteins (AFPs) and antifreeze glycoproteins (AFGPs), which prevent the formation of ice crystals in their bodily fluids. These proteins are essential for the survival of these fish in sub-zero temperatures and represent a fascinating example of evolutionary ingenuity under extreme selective pressures (Lee et al., 2011; Cheng and Xuan, 2020).

5.2 Genomic insights into AFP evolution

Recent genomic studies have provided significant insights into the evolution of AFPs in Antarctic fish. Long-read sequencing has enabled the generation of high-quality genome assemblies, revealing the complex genomic regions associated with AFPs. For instance, the genome of the Antarctic eelpout, *Ophthalmolycus amberensis*, showed unique evolutionary patterns in the hemoglobin and AFP loci, highlighting the role of transposable elements in their evolution (Figure 1) (Hotaling et al., 2022). Additionally, the independent evolution of AFPs in various fish lineages, such as the notothenioids and codfishes, underscores the diverse genetic mechanisms that have given rise to these proteins. In notothenioids, AFPs evolved from an extant gene, while in codfishes, they arose de novo from non-coding DNA, demonstrating the power of comparative genomics to uncover these evolutionary processes (Xuan et al., 2019; Bista et al., 2022).

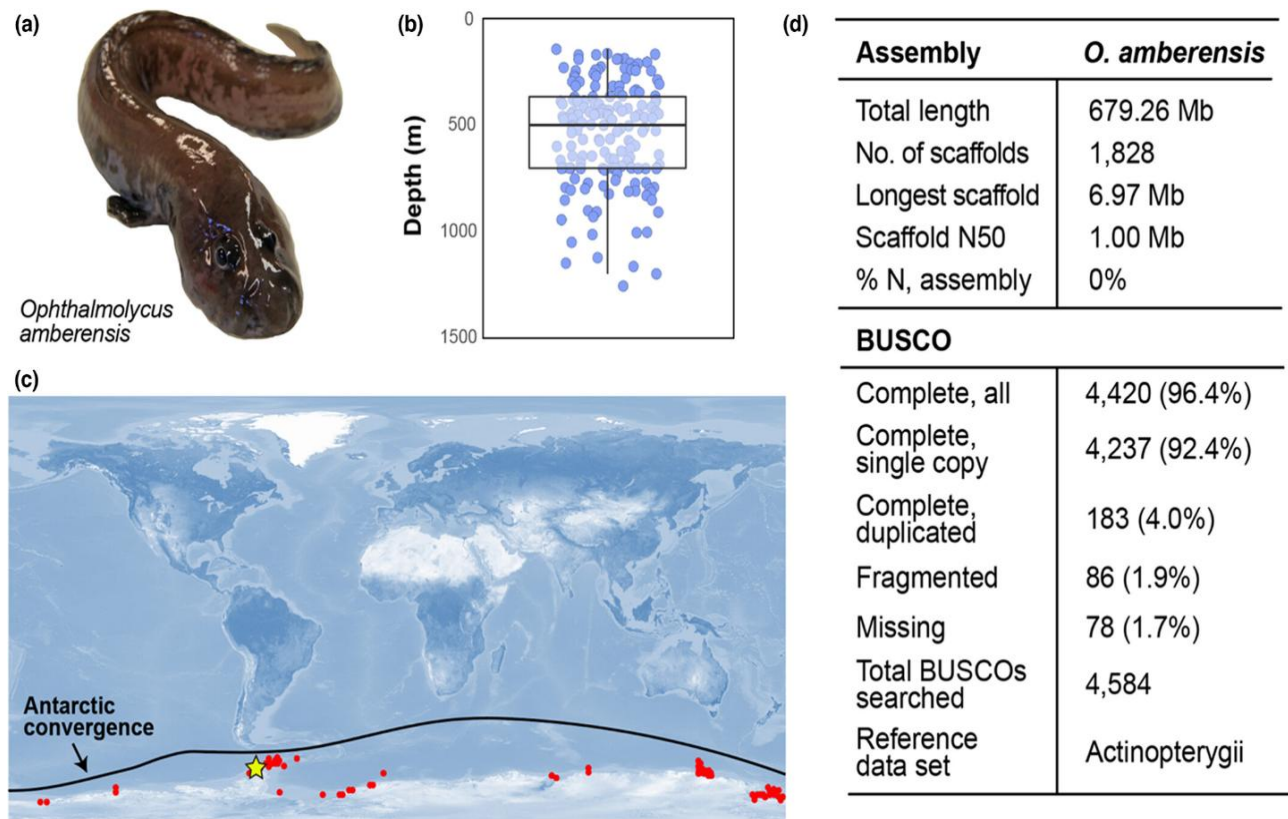


Figure 1 (a) An Antarctic eelpout, *Ophthalmolycus amberensis*, sampled from the Gerlache Strait on the West Antarctic peninsula. (b) Depth records (n=168 records) for *O. amberensis*. (c) the distribution of *O. amberensis* from AquaMaps (<https://www.aquamaps.org/>). Red circles represent sampling localities and the dark line indicates the Antarctic convergence (or Antarctic polar front). A yellow star denotes where the specimens used in this study were collected. (d) Assembly and BUSCO (benchmarking universal single-copy orthologs; Simão et al., 2015) statistics for the *O. amberensis* genome assembly (Adopted from Hotaling et al., 2022)

The study of Hotaling et al. (2022) provides a comprehensive overview of the Antarctic eelpout, *Ophthalmolycus amberensis*. This species, found primarily around the Antarctic Peninsula, lives at various depths, as indicated by the box plot. The map shows its distribution, concentrated around the Antarctic convergence. The genome assembly data reveals a high-quality draft genome with excellent completeness, as shown by the BUSCO analysis, indicating a well-covered genomic assembly. This information is crucial for understanding the genetic basis of adaptation to extreme environments in Antarctic fish.

5.3 Broader implications for understanding adaptation

The study of AFPs in Antarctic fish has broader implications for understanding adaptation to extreme environments. The evolution of AFPs is a clear example of how new genes can arise and confer significant survival advantages. This knowledge enhances our understanding of molecular evolution and the innovative processes by which new genes can develop, from gene duplication to de novo gene birth (Baalsrud et al., 2017). Furthermore, the presence of AFPs in distantly related fish species suggests convergent evolution, where similar environmental pressures lead to the development of analogous adaptations (Graham et al., 2013). These findings not only shed light on the evolutionary history of Antarctic fish but also provide valuable insights into the mechanisms of adaptation and survival in extreme conditions, which can be applied to other organisms facing similar environmental challenges (Cziko et al., 2014; Shin et al., 2014; Rivera-Colón et al., 2023).

6 Evolutionary Processes Unveiled by Fish Genomics

6.1 Speciation and genomic divergence

Fish genomics has provided significant insights into the processes of speciation and genomic divergence. For instance, the study of Lake Whitefish species pairs (*Coregonus clupeaformis*) has revealed that speciation can occur with gene flow, driven by both demography and selection. This research demonstrated that secondary contact between post-glacial populations led to heterogeneous genomic differentiation, influenced by linked selection and introgression (Rougeux et al., 2016). Similarly, the genomic analysis of neotropical cichlid fishes (*Amphilophus* spp.) highlighted that sympatric speciation is facilitated by polygenic architectures, which promote rapid and stable speciation even in the presence of gene flow (Figure 2) (Kautt et al., 2020). Additionally, the study of *Labrus bergylta* showed that strong reproductive isolation can occur between sympatric color morphs, driven by divergent selection associated with phenotypic variation (Casas et al., 2021).

The study of Kautt et al. (2022) illustrates the evolutionary dynamics of the Midas cichlid species complex in Nicaraguan lakes. It showcases the species' colonization and diversification over time, highlighting how different environmental conditions in various crater lakes have driven morphological and genetic divergence. The t-SNE analysis in the bottom right corner reveals clear genetic clustering by lake and species, emphasizing the distinct evolutionary paths taken by these cichlids. This suggests a strong role of geographic isolation and local adaptation in shaping the diversity of this species complex.

6.2 Convergent evolution in fish

Convergent evolution, where different species independently evolve similar traits, is another fascinating aspect revealed by fish genomics. In cichlid fishes from Lake Victoria, parallel evolution of male nuptial coloration has been observed, with blue and red-backed species evolving repeatedly in different ecological niches. This phenomenon, termed "hybrid parallel speciation", suggests that admixture-derived alleles were targeted by divergent selection, facilitating new speciation events (Meier et al., 2018). Furthermore, the study of replicate ecomorphs in cichlid adaptive radiations demonstrated that strong functional phenotypic differentiation is associated with clear genomic divergence, even in young species pairs, indicating a modest but significant extent of convergent evolution (McGee et al., 2016).

6.3 Horizontal gene transfer in fish

Horizontal gene transfer (HGT) is a process where genes are transferred between different species, and it has been well-documented in bacteria and invertebrates. However, recent research has provided the first reliable evidence of HGT from marine bacteria to fishes. This study identified a functional gene transferred to teleost fishes, which is expressed and regulated developmentally, suggesting that HGT can significantly influence vertebrate evolution

by altering the genetic and metabolic repertoire of fishes (Sun et al., 2015). This discovery underscores the potential of HGT to contribute to the evolutionary processes in vertebrates, expanding our understanding of genetic exchange across different domains of life.

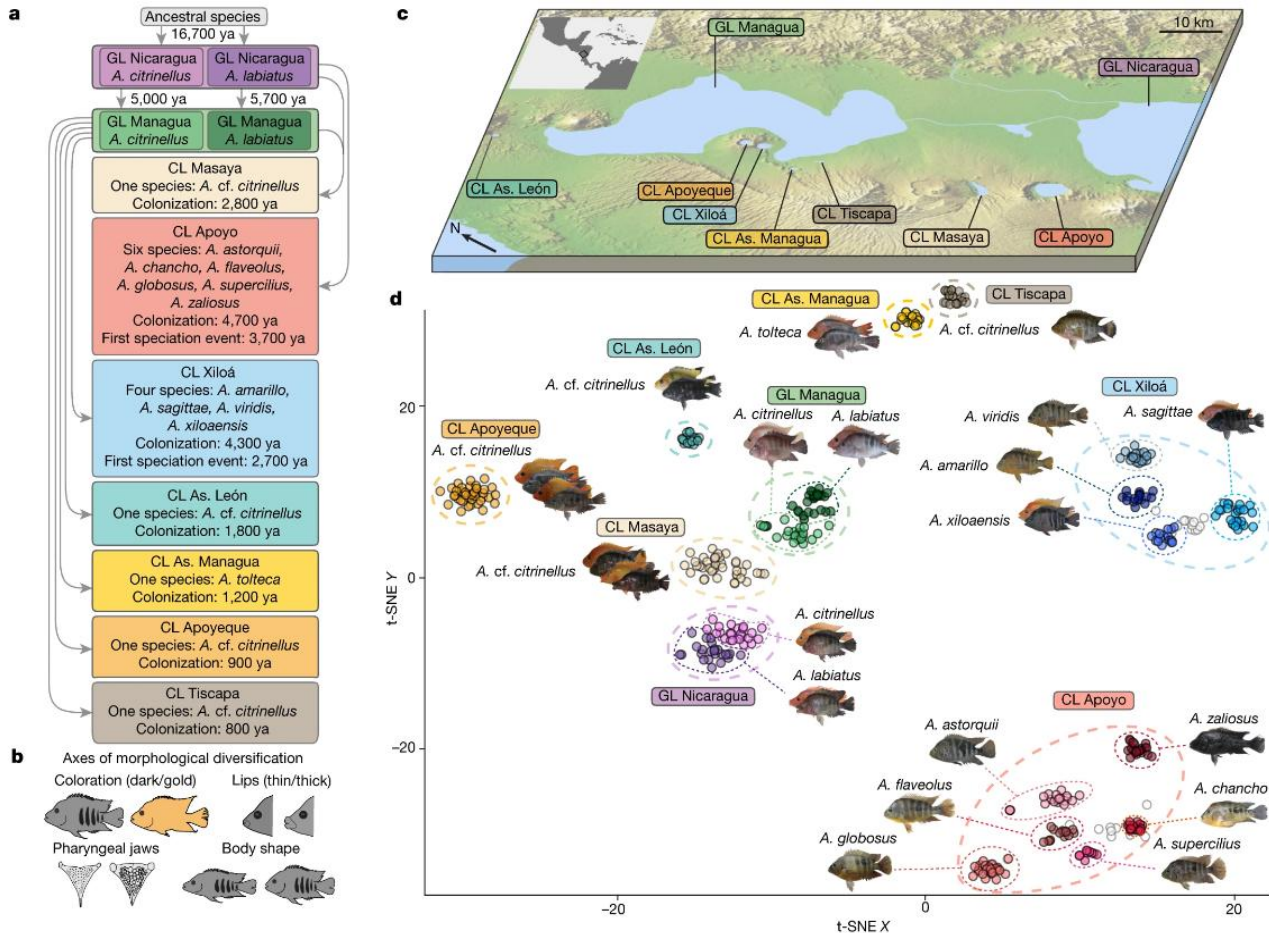


Figure 2 Evolutionary relationships among all members of the Midas cichlid species complex (Adopted from Kautt et al., 2020)
 Image caption: a, Simplified demographic history with colonization and first sympatric speciation times (in years ago, ya) inferred from model-based coalescent simulations. b, Major phenotypic axes that have been suggested to contribute to population divergence and speciation in Midas cichlid fishes. c, Map of the Nicaraguan great lakes (GL) and crater lakes (CL) (image credit: NASA/JPL/NIMA). d, Dimensionality reduction (t-SNE) of whole-genome genotype data reveals clustering by lake and described species (two species in GLs Nicaragua and Managua, six species in CL Apoyo, and four species in CL Xiloá). Representative specimens are shown for each species and lake population, with dark/gold and thin- or thick-lipped morphs. White circles represent individuals of mixed ancestry (Adopted from Kautt et al., 2020)

7 Future Directions in Fish Comparative Genomics

7.1 Emerging technologies and their potential

The field of fish comparative genomics is poised to benefit significantly from emerging technologies. Advances in next-generation sequencing (NGS) have already transformed our ability to generate high-quality genomic data for a wide array of fish species, including both model and non-model organisms. The vast amount of genomic data generated by NGS requires sophisticated bioinformatics tools for analysis and interpretation (Li, 2024). The development of chromosome-level genome assemblies, termed "chromonomes," is particularly promising as it enables large-scale conserved synteny analyses, which are crucial for accurate orthology detection and understanding genome connectivity (Braasch et al., 2015). Additionally, the application of ancient DNA (aDNA) techniques to fish genomics is opening new avenues for investigating evolutionary processes and ecological dynamics over historical timescales (Oosting et al., 2019). These technological advancements are expected to continue driving the field forward, providing deeper insights into the genetic basis of biodiversity and adaptation in fish.

7.2 Integrating comparative genomics with other disciplines

Integrating comparative genomics with other scientific disciplines such as cytogenetics, ecology, and evolutionary biology can offer a more holistic understanding of fish genomes. For instance, combining cytogenetic mapping with genomic data has proven effective in identifying conserved synteny and understanding chromosomal evolution in cichlid fishes (Mazzuchelli et al., 2012). Similarly, the integration of ecological genomics with comparative transcriptomics allows researchers to study genome-environment interactions in natural settings, providing valuable insights into how fish species adapt to their environments (Krabbenhoft and Turner, 2017). Furthermore, the use of phylogenomic approaches to resolve evolutionary relationships among fish species can enhance our understanding of lineage-specific characteristics and evolutionary history (Negrisol et al., 2010). These interdisciplinary approaches are essential for addressing complex questions in fish biology and evolution.

7.3 Conservation implications

The insights gained from fish comparative genomics have significant implications for conservation efforts. Genomic tools can help identify genetic diversity and adaptive potential within fish populations, which is critical for developing effective conservation strategies. For example, understanding the genetic basis of phenotypic traits and population divergence can inform the management of marine fish populations and their resilience to environmental changes (Hemmer-Hansen et al., 2014). Additionally, the application of genomics in fisheries management can enhance our ability to trace the origin of processed samples, enforce regulations, and anticipate the effects of climate change on fish stocks (Valenzuela-Quiñonez, 2016). By integrating genomic data with conservation practices, we can better protect and manage fish biodiversity in the face of ongoing environmental challenges.

In summary, the future of fish comparative genomics lies in the continued development and application of emerging technologies, the integration of genomics with other scientific disciplines, and the translation of genomic insights into conservation practices. These efforts will not only advance our understanding of fish evolution and adaptation but also contribute to the sustainable management and preservation of fish species worldwide.

8 Concluding Remarks

The comparative genomics of fish has provided significant insights into evolutionary processes, revealing both conserved and unique genomic features across different species. Studies have demonstrated the utility of comparative genomics in resolving phylogenetic relationships among model fish species, despite some challenges with alignment methodologies and noncoding sequences. The analysis of whole-genome sequences has shed light on the evolutionary patterns of diversification and adaptation, particularly in New Zealand fish species, highlighting the correlation between genome size and repeat elements, as well as the impact of assembly contiguity on genic features.

Furthermore, comparative genomics has been instrumental in understanding the connectivity of evolutionary processes, integrating macro- and micro-evolutionary scales to elucidate the influence of life history traits and historical demography on genetic connectivity. The integration of cytogenetics and genomics has also revealed conserved synteny and chromosomal evolution in cichlid fishes, challenging the notion of high rates of chromosomal rearrangements in fish genomes.

In salmonid fishes, genomic tools have facilitated the study of genetic polymorphisms and their role in adaptation and speciation, with a focus on the insulin-like growth factor axis and the evolutionary implications of whole-genome duplication. The study of cichlid fish genomics has provided novel insights into adaptive radiation and the genomic features underlying explosive diversification. Additionally, the application of modern molecular cytogenetic techniques has elucidated the karyotype evolution and neo-Y chromosome formation in small-sized fish species.

Comparative genomics will continue to play a crucial role in future evolutionary studies by providing a framework for understanding the genetic basis of adaptation, speciation, and diversification. The ability to transfer

knowledge from model species to non-model species will enhance our understanding of economically and evolutionarily important fish species. As genomic technologies advance, the integration of high-resolution sequencing and cytogenetic mapping will further refine our understanding of chromosomal evolution and the mechanisms driving genome organization.

Future research should focus on improving alignment methodologies and developing robust algorithms for analyzing noncoding sequences to overcome current limitations in phylogenomic studies. Additionally, the continued exploration of genome duplication events and their evolutionary consequences will provide deeper insights into the adaptive potential of fish species. By standardizing comparative genomic approaches across diverse taxa, researchers can better understand the ecological and evolutionary determinants of genetic connectivity and inform conservation and management policies.

In summary, comparative genomics offers a powerful toolset for unraveling the complexities of fish evolution, providing a comprehensive understanding of the genetic and genomic underpinnings of biodiversity. The ongoing integration of genomic data with ecological, morphological, and behavioral studies will pave the way for new discoveries and applications in evolutionary biology.

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Conflict of Interest Disclosure

Author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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