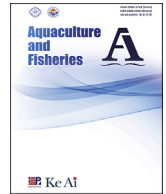




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Review article

Natural and artificial polyploids in aquaculture

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ABSTRACT

Genome polyploidy has been revealed to result in evolutionary advantages and novelties, and therefore, polyploid aquatic animals may possess excellent traits of economic interest including rapid growth, extensive adaptability and disease resistance. For this reason, numerous species of natural polyploid fishes, such as common carp, gibel carp, crucian carp, salmon, and sturgeon, were chosen as important target species for aquaculture. Many artificial polyploids have been commercially utilized for aquaculture and most of them were created from natural polyploid fishes of the Cyprinidae and Salmonidae. Thanks to the easy mass production and better economic traits in growth and flesh quality, the synthesized autopolyploids or allopolyploids from natural polyploid species in cyprinid fishes have been extensively applied to aquaculture throughout China. This review outlines polyploidy advantages and innovative opportunities, lists natural polyploid species used in aquaculture, and summarizes artificial polyploids that have been induced or synthesized, and used in aquaculture. Moreover, some main research trends on polyploid utilization and ploidy manipulation of aquaculture animals are also introduced and discussed in the review.

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Sustainable aquaculture is a highly efficient way of producing animal proteins by consuming a minimum of grain (Larsen & Roney, 2013) and has made a great contribution to world food security and human nutrition (FAO, 2016; Gui, 2015a; Naylor et al., 2000; Pauly et al., 2002; Worm & Branch, 2012). Since the 1980s, the increasing production of fishes and other aquatic products has been almost all from aquaculture production (FAO, 2016). Significantly, two kinds of polyploidy animals, including naturally evolved polyploids and artificially induced polyploids, have been widely used in global aquaculture (Arai, 2001; Gui, 2015a, 2015b; Hulata, 2001; Piferrer et al., 2009; Rothbard, 2006; Zhou & Gui, 2017). Here, we analyze the advantages of polyploids and the innovation opportunities for enhancing economic traits, outline natural and artificial polyploids used in aquaculture, review the main approaches for inducing artificial polyploids, and summarize their contributions to aquaculture in the past two decades.

1. Polyploidy advantages and innovation opportunities

Polyploids are organisms with 3 or more chromosome sets

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(genomes), and are very common among plants, in which all of the angiosperms are paleopolyploids (Bowers, Chapman, Rong, & Paterson, 2003) and about 95 percent of pteridophytes are polyploids (Grant, 1981). Based on the analysis of the *hox* gene clusters and whole genomes, vertebrates were proposed to have undergone two rounds (2R) of whole genome duplication (WGD) (Ohno, 1970) before the divergence of lamprey from the jawed vertebrates (Smith et al., 2013), resulting in an approximate chromosome number of 48 ($2N = 48$) in most diploid vertebrates. It was proposed that a third round of WGD, also known as fish-specific genome duplication (FSGD), might occur after the divergence of tetrapods and teleost fish (Amores, Catchen, Fontenot, & Postlethwait, 2011; Braasch et al., 2016; Jaillon et al., 2004; Kasahara et al., 2007; Meyer & van de Peer, 2005; Pasquier et al., 2016). Additionally, polyploidy appears to occur repeatedly in some taxonomic fish orders including Cypriniformes, Salmoniformes, Perciformes, Siluriformes, Acipenseriformes, Gymnotiformes and Characiformes (Leggatt & Iwama, 2003; Mei & Gui, 2015; Taylor, Braasch, Frickey, Meyer, & Peer, 2003; Van de Peer, Taylor, & Meyer, 2003). Analysis of the genome of extant salmonids suggests a salmonid-specific fourth whole-genome duplication occurred about 80 million years ago (Mya) (Lien et al., 2016). The common carp (*Cyprinus carpio*) was estimated from the draft genome sequence to have undergone another polyploidy event approximately 8.2 (Mya) (Xu et al., 2014). In the *Carassius* species

complex, two extra rounds of polyploidy were recently revealed by analyzing conserved DMRT1 genes. An early polyploidy event might result in a common tetraploid ancestor of *Carassius gibelio*, *Carassius auratus auratus* and *Cyprinus carpio* before 18.49 Mya, and a late polyploidy event might occur at around 0.51 Mya, and lead to the current hexaploid gibel carp (*Carassius gibelio*) (Li et al., 2014).

There are several disadvantages of polyploidy, such as the disrupting changes in cellular architecture, potential difficulties during meiosis, or epigenetic instability. Nonetheless, polyploids are usually well adapted once they pass through the bottleneck of instability, and possess 3 obvious advantages: heterosis, gene redundancy and unisexual reproduction (Comai, 2005) that might fuel evolutionary success and enrich species diversification. Polyploidization may lead to instantaneous speciation (Coyne & Orr, 2004). FSGD had been supposed as a major driving force behind the dramatic rise and rapid radiation of teleost fish because the phylogenetic timing of the FSGD followed the divergence of the “species-poor” actinopterygian lineages (44 species in 5 families) and gave origin to the “extremely species-rich” teleost fish lineages (23,637 species in 425 families) (Meyer & van de Peer, 2005). The result of polyploidization and the increased gene number provide raw material for functional divergence and innovation including gene neofunctionalization and subfunctionalization (Conant & Wolfe, 2008; Liu, Li, & Gui, 2009; Ohno, 1970; Otto, 2007).

According to their chromosomal composition and formation mechanisms, polyploids are divided into autopolyploids and allopolyploids (Comai, 2005). In autopolyploids, multiplying chromosome sets within a species occur when a chromosome set doubling, unreduced gametes or polyspermy occurs. Environmental changes, for example, a low or sudden decreases in environmental temperature, may cause polyploidy through increasing the number of unreduced gametes (Leggatt & Iwama, 2003). Intergeneric or interspecific hybridization may occasionally result in the occurrence of allopolyploidy (Piferrer et al., 2009; Song et al., 2012) which promotes heterozygosity. Some allopolyploids exhibit heterosis in their growth rate and disease resistance through integrating the beneficial economic traits from both parents, showing more vigour than their diploid progenitors (Comai, 2005).

Owing to gene redundancy from introducing an additional chromosome set, both autopolyploids and allopolyploids can be protected from deleterious recessive mutations. Significantly, gene duplicates resulting from polyploidization provide extra “degrees of freedom” to diversify gene function (Otto, 2007). Polyploidy is an ongoing process. After polyploids form, they pass through a bottleneck of instability and subsequently became new diploids or paleopolyploids through diploidization, during which the duplicated genes rapidly lose function or undergo sub-, or neofunctionalization to partition the ancestral gene functions (Comai, 2005; Otto, 2007; Scannell, Byrne, Gordon, Wong, & Wolfe, 2006; Wapinski, Pfeffer, Friedman, & Regev, 2007). In tetraploid Atlantic salmon (*Salmo salar*), large genomic reorganization seems to have been driven by bursts of transposon-mediated repeat expansions during the following rediploidization process (Lien et al., 2016). In addition, re-establishment of the genomic structure and balancing of the regulatory elements of the genome, such as epigenetic remodeling, also occur after a polyploidization event (Soltis & Soltis, 1999). By investigating the genome-specific allele expression in hybridogenetic fish allotriploid *Squalius alburnoides* complex (PAA genome), an allele-specific silencing pattern was adopted to adjust the transcription level of triploids to the diploid state (Pala, Scharf, Brito, Vacas, & Coelho, 2010). Altogether, these changes in genomic structure and gene expression in polyploids increase genome flexibility, which might provide them with variations not available in diploids and enable them to adapt to novel niches and trigger a species radiation with higher survival rates and

fitness, and also allow polyploids to pass evolutionary transitions that were previously impossible (Otto, 2007; Parisod, Holderegger, & Brochmann, 2010; Sémon & Wolfe, 2007).

Polyploids generally possess enlarged cell size. Compared to diploid counterparts, polyploid plants usually maintain the same number of cells and develop larger leaf, flower and fruit. For example, in west African *Acacia senegal* wild trees, polyploidy was revealed to confer trait superiority, especially in relation to drought stress. In the polyploid *Carassius* species complex, hexaploid *Carassius gibelio* was demonstrated to have a better growth performance and higher yield than tetraploid *C. auratus* (Zhou, Wang, Wang, & Gui, 2017). In fact, the first Chinese fish farmers chose tetraploid common carp with 100 chromosomes to culture in ponds about 3000 years ago owing to its fast growth performance and extensive adaptability. Additionally, salmon, one of the most important aquaculture fishes in the world, have also evolved from polyploid ancestors. Moreover, some polyploids are distributed across a larger ecological amplitude, and the frequency of polyploids in cold latitudes is higher than those in warmer latitudes, indicating these polyploids can withstand harsh environments. Many examples of the rapid adaptation of plant polyploids to new niches had been reported, such as allopolyploid plants in the arctic, which is one of the Earth’s most polyploid-rich areas (Comai, 2005). Hexaploid *Achillea borealis* have a fivefold fitness advantage over their tetraploid siblings in dune habitats, and neohexaploids, the first generation mutants screened from tetraploids, achieve a 70% fitness advantage via genome duplication per se (Ramsey, 2011).

In the polyploid *Carassius* species complex, hexaploid *Carassius gibelio* has a wider geographic distribution and higher frequencies in cold latitudes than the tetraploid *Carassius auratus* (Gui & Zhou, 2010; Jiang et al., 2013). In the 386 specimens of the *Carassius* species complex sampled from 4 different sites of Xingkai Lake and Suifen River in Northeast Asia, about 87.3% of individuals were identified as hexaploid *Carassius gibelio* and were ubiquitously distributed, whereas the tetraploid *Carassius auratus* existed only in the Russian reach of the Suifen River. Significantly, the genetic diversity of hexaploids is much higher than that of tetraploids (Jiang et al., 2013), indicating ecological or evolutionary benefits afforded by polyploidy and the multiple reproduction modes of hexaploid *Carassius gibelio*.

Additionally, polyploidy is associated with the formation of unisexual species, although the association mechanism is still unclear (Comai, 2005). In the analyzed 179 insect and vertebrate polyploids, about 60 percent of polyploids (106) reproduce by unisexual reproduction (Otto, 2007), which facilitates species expansion in the absence of sexual mates. Recently, Choleva et al. (2012) reconstructed the evolutionary route from sexuality to polyploid clonality by performing a series of crossing experiments between 2 sexual species of spined loach (*Cobitis taenia* and *C. elongatoides*), and provided clear proof that gynogenesis might be directly triggered by interspecific hybridization and polyploidy is a consequence of clonal reproduction in *Cobitis* fish. It has been assumed that unisexual species will be short-lived on an evolutionary timescale because they lack genetic recombination to generate genetic variation, and/or because they accumulate deleterious mutations known as Muller’s ratchet. However, some of the exceptional cases, such as the hexaploid *Carassius gibelio* which can reproduce by gynogenesis (Jiang et al., 1983), demonstrate the ecological and evolutionary success of unisexual species (Gui & Zhou, 2010; Avise, 2015). How to remove Muller’s ratchet effect (the accumulation of deleterious mutations) and how to obtain genetic diversity to adapt to changing environments are the two basic biological puzzles in evolution of unisexual species. In natural populations of the polyploid *Carassius* species complex, a lot of hexaploid clones and a minor but significant portion of hexaploid

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