

Genome Based Research in Aquaculture

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GENOME BASED RESEARCH IN AQUACULTURE

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ABSTRACT

Genome -based technologies are being instigated to manipulate the structure and function of the genome and to identify the genes of interest for genetic modification of economically important species. Genome editing technologies have also been designed for genetic manipulation of aquaculture species to increase production and quality with minimum investment costs. DNA marker technologies are the most widely used genome technologies. DNA fingerprints are used to construct physical maps while genetic maps are based upon meiotic recombination. BAC fingerprinting is the commonly used method for physical mapping. Next- generation sequencers revolutionized science and allowed the de-novo whole genome sequencing. QTL mapping has made it possible to identify the genes responsible for a particular trait. Government involvement and better training of aquaculturists are direly needed to reinforce the practical implications of genome- based technologies.

Keywords: BAC finger printing, genome editing, microsatellite markers, QTL mapping, SNPs.

INTRODUCTION

Aquaculture Genomics

Aquaculture is a recent rather rapidly developing field of agriculture, having great economic and cultural significance. Seafood marks 20% of the animal protein intake by the world population while in China, aquaculture marks the production of 50% of consumed seafood (Ruane et al., 2016).

Aquaculture genomics officially started in the 1990s, marked by the first Aquaculture genomics workshop held in 1997 in Dartmouth, Massachusetts, United States of America. The workshop aimed to commence genomic research on six species including: Oysters, Shrimps, Tilapia, Salmonids, Catfish, and Striped bass.

Sustained production of any species depends upon the understanding of biology, ecology, reproduction, nutrition, physiology, genetics and genomics. All these fields of research are unified by

understanding the genome of a particular species. The draft whole-genome sequences provide better insights to enhance the production and quality in various agricultural sectors. Whole-genome sequencing has been done for oysters, shrimp, tilapia, rainbow trout, catfish, Atlantic salmon, and striped bass.

Traditional Biotechnologies for Aquaculture

i. Selective Breeding

It involves the selection of individuals with desirable traits to enhance the production and quality of farmed animals. The traits considered for aquaculture species include: faster growth rate, disease resistance, increased tolerance to abiotic factors, sexual maturation, and feed conversion efficiency. In late the 1960s, selective breeding programs of Atlantic salmon were developed in Norway (Gjedrem and Baranski, 2010). The techniques used in selective breeding

include: strain selection, hybridization, cross-breeding and within-strain selection. This is usually done by measurement of traits in selected individuals and pedigree analysis (Gutierrez and Houston, 2017).

Selective breeding programs have been carried out for almost 60 species which include: Atlantic salmon, tilapia, common carp, grass carp, rainbow trout, silver carp, sea bream, channel fish, European seabass, rohu, yellowtail, Asian seabass, Pacific and eastern oyster, shrimps, scallops and pearl oysters (Gjedrem and Baranski, 2010). Genetically improved stocks are rarely used for aquaculture with less than 10 percent production by genetically modified species (Gjedrem and Robinson, 2014).

ii. Polyploidy

In polyploidy, the individuals have extra chromosome sets (Dunham, 2011). Triploid organisms have three pairs of homologous chromosomes and are commonly observed in wild populations. Triploidy can also be introduced in cultured organisms by forcefully retaining the second polar body (Chourrout, 1980; Lou and Purdom, 1984). The second polar body is retained by the application of extreme temperature, hydrostatic pressure and chemical shocks immediately followed by fertilization (Dunham, 2011). In rainbow trout, application of high pH and calcium to egg or sperm can induce triploidy (Ueda et al., 1988). Triploidy affects all of the traits considered while planning to culture a particular species.

Triploid fish can also be produced from tetraploid fish (Chourrout et al., 1986). Tetraploids are produced by restricting the first cleavage of the embryo by applying hydrostatic pressure. In rainbow trout, tetraploids do not grow normally as compared to diploid controls. Mating of these tetraploid males with diploid females results in triploid progeny that grows normally and has a high survival rate (Chourrout et al., 1986).

iii. Gynogenesis

In gynogenesis, the inheritance of genetic material to the embryo occurs from the female parent. Sperms are inactivated by exposure to UV radiations and these inactivated sperms induce the process of development without the contribution of the paternal genome. Sperms from closely associated but distinct species lessen the risk of actual fertilization, in case if the process of sperm inactivation is not properly done (Suwa et al., 1994). The diploid state can be retained by inhibiting the first cleavage or by retaining the second polar body.

Gynogenesis is induced for the production of a population with similar genetic makeup (Arai, 2001). These clonal lines can be used for genome studies as in channel catfish, doubled haploid clonal line was used to study the whole genome (Waldbieser et al., 2010; Liu et al., 2016b). Gynogens have been produced for species such as ayu (Taniguchi et al., 1996), amago salmon (Kobayashi et al., 1994), and hirame (Yamamoto, 1999). Gynogens are mainly used for research purposes.

iv. Androgenesis

Androgens are produced by the exposure of eggs to UV radiation. Production of androgens is tricky than the production of gynogens because irradiated eggs have a low survival rate (Scheerer et al., 1986). Blocking the first cleavage is the only way to recover diploidy (Dunham, 2011).

Androgens are produced to get clonal lines, mono-sex populations or to study sex-determining mechanisms (Dunham, 2011). Heterogametic male results in the production of population with an equal proportion of males and females while a homogametic male will produce 100 percent YY male progeny. Mating of YY males with XX females will result in all male population (Parsons and Thorgaard, 1985). The mono-sex culture

of males is of significant interest as males of many species have a faster growth rate as compared to females.

v. *Sex Reversal*

Most of the species used in aquaculture are sexually dimorphic with a different growth rate in males and females. Production of mono-sex populations of individuals having a higher growth rate is of great significance in aquaculture. Hormonal treatment is the commonly used method for sex reversal. Genotypic sex gets determined at fertilization time while phenotypic sex is established later on. Phenotypic sex of cattle fish establishes on the 19th day following fertilization.

Hormones used for sex reversal are androgens and estrogens which are administered at a critical period for sex determination. Androgens are mostly the testosterone derivatives and these are used for the production of male mono-sex populations (Yamazaki, 1983; Dunham, 1990). The most widely used androgen for sex reversal is 17-methyltestosterone (Dunham, 1990). 3-estradiol is widely used for producing mono-sex populations of females (Yamazaki, 1983; Dunham, 1990). Hormones are usually administered by bath soaking (Yamazaki, 1983; Donaldson and Hunter, 1982), along with feed (Shelton et al., 1981), or by implantation (Boney et al., 1984). The method used for hormonal administration depends upon the development and growth of the species (Dunham, 2011).

vi. *Gene Transfer*

It is the process by which a foreign gene is transferred into an organism. The gene is transferred after a proper understanding of its function. After extensive studies, the function of growth hormone gene was well understood and then it was introduced into mice. Transgenic mice showed a remarkable increase in growth performance, about 2.5

times higher than the controls (Palmiter et al., 1982).

Techniques used for gene transfer into fish include microinjection (Zhu et al., 1985) and electroporation (Inoue et al., 1990). Goldfish is the first fish species in which gene transfer was successfully demonstrated (Zhu et al., 1985). Other transgenic fish species include Rainbow trout (Chourrout et al., 1986), Channel catfish (Dunham et al., 1987), Nile tilapia (Brem et al., 1988) and Northern pike (Gross et al., 1992).

DNA Marker Technologies

Allozyme Markers

Allozymes are the enzymes produced by the genes present on a single locus (Kucuktas and Liu, 2007). Allozymes are the type I markers because their function is known (Liu and Cordes, 2004). Allozymes are the allelic forms of an enzyme encoded by alleles on the same locus (Hunter and Markert, 1957; Parker et al., 1998; Carvalho, 2004).

Genetic diversity in natural fish populations is mostly studied by the use of allozyme electrophoresis. Allozyme data is usually used by the fisheries sector but this data is also used for the development of aquaculture as both these fields cannot be separated (Dunham, 2004). The uses of allozyme electrophoresis in aquaculture include: inbreeding analysis, parentage analysis and identification of stock (Liu and Cordes, 2004).

Restriction Fragment Length Polymorphism Markers (RFLP)

Restriction fragment length polymorphism (RFLP) markers are the first markers (Botstein et al., 1980). In the 1980s, it was the most common method for studying genetic variations. Restriction enzymes are used to digest DNA, separation of fragments is done agarose gel electrophoresis followed by Southern blot (Southern, 1975) for the visual display

of fragments having different lengths (Liu et al., 2007). RFLP can also be analyzed by PCR amplification.

The application of RFLP is limited because it can detect only larger changes in DNA fragments ignoring point mutations. After all agarose gel electrophoresis has low resolution.

Mitochondrial DNA Markers

The evolutionary rate of mitochondrial DNA is higher than the nuclear genome due to which mtDNA is polymorphic in a species. D-loop of mtDNA is highly polymorphic so it can be used for genetic analysis of a population (Liu, 2007a).

The analysis of mitochondrial markers is usually done by PCR or RFLP (Liu and Cordes, 2004). Maternal inheritance, high polymorphism and short size of mtDNA make RFLP a suitable method for a population (Liu and Cordes, 2004; Okumuş and Çiftci, 2003; Billington, 2003). In striped bass (*Morone saxatilis*), addition or deletion is exhibited at Xba I restriction site which can be analyzed by performing PCR followed by the digestion of DNA fragment by restriction enzyme (Ravago et al., 2002). Analysis of mtDNA is a powerful tool for studying genetic diversity in populations (Avisé, 1995).

Genetic variations have been studied (using mtDNA) in the following aquaculture species: striped bass (Wirgin and Maceda, 1991; Garber and Sullivan, 2006), Walleye (Merker and Woodruff, 1996), channel catfish (Waldbieser et al., 2003), salmonids (Nielsen et al., 1998; Crespi and Fulton, 2004), red snapper (Pruett et al., 2005) and bluegill (Chapman, 1989).

DNA Barcoding

In DNA barcoding, a small molecular marker from the 5' end of mitochondrial cytochrome oxidase I (COI) gene is used (Hebert et al., 2003; Tavares

and Baker, 2008). This method is used to differentiate closely related species (Dawnay et al., 2007) and in molecular systematics (Hardman, 2005).

The application of DNA barcoding in aquaculture includes species identification to avoid seafood fraud which includes the replacement of lower value species with higher value species for profit (Wong et al., 2011; Wong and Hanner, 2008).

RAPD Markers

Random amplified polymorphic DNA (RAPD) is PCR-based, firstly developed in 1990. It uses a single primer to amplify unknown regions of DNA (Welsh and McClelland, 1990; Williams et al., 1990). RAPD markers are produced after the amplification of bands from closely related species (Liu et al., 1998; Liu, 2007b).

Microsatellite Markers

These are the repeatedly found 1-6 base-pair sequences in the genome. In most fishes, microsatellites can be found at a frequency of one microsatellite per 2-10 kb of DNA fragment. The most common microsatellites are the dinucleotide among which AG and AC repeats are abundant. AT-rich types are relatively more common as compared to GC-rich repeat types in trisatellites and tetrasatellites. Penta and hexanucleotide microsatellites are less frequent and less important (Tóth et al., 2000).

Microsatellites are commonly associated with the non-coding region of the genome (Metzgar et al., 2000). The coding region of the genome contains only 10-15 percent microsatellites (Moran, 1993; Edwards et al., 1998; Serapion et al., 2004). The Presence of dinucleotide microsatellites results in the frameshift mutation in protein-coding sequences. Due to high polymorphism, microsatellites are extensively used for pedigree analysis, kinship and genetic analysis of fish stocks.

SNP Markers

Single nucleotide polymorphism (SNP) is due to alteration in the position of an allele at a given locus. SNP results in a very minute change in alleles because the length of the fragment is same and most common base substitutions occur from A to G or C to T. Remote technologies are required to identify such minute differences. Affymetrix Axiom genotyping technology is usually used for the analysis of SNP arrays.

Illumina-based RNA sequencing has been used to identify SNP markers from catfish (Liu et al., 2011). An aggregate of 8.4 million SNPs have been recognized in four aquaculture and one wild population of channel catfish (Sun et al., 2014). The frequency of SNPs in the catfish genome is one SNP per 93 base pairs (Liu et al., 2016b). SNPs have also been identified in the genome of common carp (Xu et al., 2012), rainbow trout (Palti et al., 2015a), pearl oyster (Jones et al., 2013) and Atlantic salmon (Yáñez et al., 2016).

Genome Mapping Technologies

Genome mapping involves the splitting of the genome into smaller pieces to identify the relationship between the genomes. Physical mapping and genetic linkage mapping are the two methods used in genome mapping.

Genetic Linkage Mapping of Aquaculture Genomes

Genetic maps are usually formed by the isolation of DNA from blood or tissue samples and then marker patterns are analyzed. Markers that are located in close proximity on the chromosomes are inherited together. Recombination is likely to occur when markers are located far away from each other. Genetic distance in

centiMorgan (cM) is assigned based on recombination frequency.

Mapping population and genetic markers are developed for constructing genetic maps. The co-segregation of closely located markers is used to reconstruct the order of these markers. In this way, markers are recorded in parents and each of the individuals in progeny. The sequences that differ between the two parents are used as markers and their genes are illustrated by characteristics that can be differentiated among two parents. Their linkage with other markers is then calculated and gene loci are bracketed with nearest markers.

All the genetic markers are assigned a linkage group (LG) and co-segregated markers belong to similar linkage group. Distances between linkage groups are described by the recombination fraction. Genetic linkage mapping is suitable for F2 hybrids because of the segregation of traits and markers. F1 generation can also be used for mapping when the parents are heterozygous for loci. Microsatellites and SNP markers are used to construct genetic maps because these are abundant in the genome. The number and types of markers have been identified for a variety of aquaculture species; some are described in table 1.

Physical Mapping of Aquaculture Genomes

Physical maps are constructed by smashing the genome into tiny fragments which are reassembled and their overlapping path is used to predict physical distance. Genome fragmentation is usually done by restriction enzymes or sonication. Isolation of these fragments is done with the help of electrophoresis and their migration pattern (DNA fingerprint) helps to identify the DNA stretch present in a clone.

Table 1. Genetic linkage maps for some aquaculture species

Species	Number and type of marker
Asian seabass (<i>Lates calcifer</i>)	790 microsatellites and single SNP (Wang et al., 2011).
Atlantic salmon (<i>Salmo salar</i>)	5650 SNPs (Lien et al., 2011).
Brown trout (<i>Salmo trutta</i>)	288 microsatellites and 13 allozymes (Gharbi et al., 2006).
Catfish (<i>Ictalurus punctatus</i>)	54,342 SNPs (Li et al., 2015).
Common carp (<i>Cyprinus carpio</i>)	732 microsatellites (Zhang et al., 2013).
Grass carp (<i>Ctenopharyngodon idella</i>)	279 microsatellites and SNPs (Xia et al., 2010b).
Japanese flounder (<i>Paralichthys olivaceus</i>)	1375 microsatellites (Castaño-Sánchez et al., 2010).
Pacific oyster (<i>Craasostrea gigas</i>)	1,166 microsatellites and SNPs (Hedgecock et al., 2015).
Rainbow trout (<i>Oncorhynchus mykiss</i>)	2,226 microsatellites and SNPs (Guyomard et al., 2012).
Scallop (<i>Mizuhopecten yessoensis</i>)	169 microsatellites (Li et al., 2012).
Sea bream (<i>Sparus aurata. L</i>)	321 microsatellites, expressed sequence tags and SNPs (Tsigenopoulos et al., 2014).
Shrimp (<i>Penaeus monodon</i>)	3959 SNPs (Baranski et al., 2014).
Tilapia (<i>Oreochromis mossambicus</i>)	525 microsatellites (Lee et al., 2005).
Yellowtail (<i>Seriola quinqueradiata & Seriola lalandi</i>)	217 microsatellites (Ohara et al., 2005).
European seabass (<i>Dicentrarchus labrax</i>)	162 microsatellites (Chistiakov et al., 2005).

Physical mapping is done by cloning DNA fragments in cloning vectors like Bacterial Artificial Chromosome (BAC). 100-200kb long DNA fragments are being cloned and the number of BAC vectors used depends upon the length of genome. BAC clones are then overlapped to get an ordered entire genome of the organism. Contigs are the overlapping restriction patterns where the DNA fragments realign to form a physical map. Fluorescence methods are used for finger printing of BAC clones (Ding et al., 2001; Luo et al., 2003). Fingerprint data is then transformed into data set by Finger Printed Contigs (FPC) software (Soderlund et al., 2000). Physical maps have been established for the following aquaculture species: Atlantic salmon (*S. salar*) (Ng et al., 2005), Tilapia (*O. mossambicus*) (Katagiri et al., 2005), Channel catfish (*I. punctatus*) (Xu et al., 2007), Rainbow trout

(*O. mykiss*) (Yniv Palti et al., 2009), Common carp (*C. carpio*) (Xu et al., 2011), Asian seabass (*L. calcarifer*) (Xia et al., 2010a) and Scallop (*M. yessoensis*) (Zhang et al., 2011a).

Radiation Hybrid Mapping

Radiation hybrid (RH) mapping uses a concept that irradiation induces chromosome break between two markers if the distance between them is large but if the distance between markers is small, they will be co-retained in the hybrids. In RH mapping, the co-retention of markers in the hybrid cell lines is calculated and is represented by Θ which can be 0 (markers always co-retained) or 1 (random co-retention of markers). Map functions are then used to convert this raw value into centirays (CR) - RH map unit. Radiation hybrid panels are used for screening of markers from many hybrid cell lines in a

single panel to generate chromosome maps of high resolution (Walter et al., 1994). RH mapping has been performed for only a few aquaculture species: Zebrafish, European seabass and Gilthead seabream (Senger et al., 2006; Sarropoulou et al., 2007; Guyon et al., 2010).

Optical mapping

In optical mapping, a single DNA molecule is used to construct whole-genome restriction maps (Schwartz et al., 1993). Restriction endonucleases are used to digest the DNA fragment, fluorescent dye is then used for visual representation to record the length of fragments. These ordered restriction fingerprints of the genome are referred to as an optical map.

Genome Sequencing Technologies

i. First-generation DNA sequencers

Chain-termination gene sequencing uses di-deoxyribonucleotides which stop DNA synthesis upon their addition into fragment (Sanger et al., 1977). In the early 1980s, automated sequencers based upon Sanger sequencing method, were developed. ABI 3700 or 3730 are the first generation sequencers that can sequence 96 samples per run with 500-800 bp in each sample.

ii. Second-Generation (Next Generation) Sequencers

Roche 454 Genome Sequencer FLX system (launched in 2005) and Solexa (Illumina) sequencing platform (launched in 2006) marked the onset of second-generation sequencing. 454 technology has been used for the sequencing of the following aquaculture species: Atlantic salmon, Atlantic cod, rainbow trout, crucian carp, scallops and catfish (Salem et al., 2010; Hou et al., 2011; Star et al., 2011; Liao et al., 2013). Sequencing errors associated with

pyrosequencing resulted in limited use of 454 technology.

iii. Third Generation DNA Sequencers

Single-molecule sequencing (SMS) and real-time sequencing are usually done in third-generation sequencers (Heather and Chain, 2016). Single molecule real time platform from Pacific biosciences is currently used third generation technology. In PacBio sequencers, 50,000- 100,000 reads can be generated per flow cell. Upto 40kb genome sequences can be read with each flow. There are 10 percent chances of errors in PacBio sequencing due to the formation of consensus sequences. Nanopore DNA sequencing is another third-generation sequencing platform but its use is limited.

Genetic Analysis Techniques

i. Traits considered for aquaculture

The genetic analysis of aquaculture species is used to identify the genetic basis of production traits and to use this information in breeding programs. This information is important for strain selection for breeding programs. The traits considered while selecting any species for aquaculture are growth rate, disease resistance; feed conversion efficiency, robustness, tolerance to abiotic factors, reproductive traits etc.

ii. Quantitative trait locus (QTL) mapping in aquaculture species

Multiple genes control specific traits in aquaculture species and QTL mapping helps to identify the genes that control a particular trait. QTL analysis for various aquaculture species has been conducted with remarkable progress. QTL studies for aquaculture species are shown in table 2.

Genome Editing Techniques

i. Zinc Finger Nuclease (ZFN) Technology

Genome editing involves the process of making changes to specific portions of the genome. ZFN technology involves cutting down target DNA in vivo at specific sites by the use of zinc finger protein along with its FokI endonuclease domain (Kim et al., 1996). The zinc finger recognizes the nucleotide triplet. Genome editing of culture cells has been done by using this technology (Bibikova et al., 2002; Townsend et al., 2009; Provasi et al., 2012).

ii. TALEN

Transcription activator-like effector nucleases (TALEN) are the engineered enzymes used to cut DNA at specific sites. They can bind at any site on DNA and binding with cleavage domain results in the cutting of DNA at specific sites (Boch et al., 2009). Double strand breaks (DSB) are generated in target DNA which is reconstructed by homologous recombinations or non-homologous end joining (NHEJ). NHEJ causes additions or deletions which are then used for gene knockout.

iii. CRISPR/Cas 9

CRISPR are the clustered regularly interspaced short palindromic repeats in the bacterial DNA. Cas proteins are the nucleases that cut DNA and are associated with CRISPR. It is a bacterial immune mechanism against pathogens. It was first used for genome editing in 2012 and is used for modifying the genome of various species such as zebrafish (Jao et al., 2013).

Hurdles in the Practical Application of Genome-Based Technologies in Aquaculture

Major provocation in the application of genomic research in aquaculture include the dissociation of genomics from breeding programs, limited skill and expertise in bioinformatics, computational limitations for the analysis of large data sets, funding limitations for aquaculture, disparity in genomic research in the world, ethical, legislative and regulatory issues.

CONCLUSION

The use of second-generation sequencers has not only revolutionized science but has also reduced sequencing costs due to which molecular research has extended to various aspects. These technological advances have made it possible to recognize the genes that account for economically important traits of organisms. Genome editing technologies have unfolded novel ways for further genetic manipulation of aquaculture organisms. However, limited skills and expertise in computer science and bioinformatics are the basic challenges faced by aquaculture researchers. The application of novel technologies to aquaculture is also limited due to the dearth of aquaculture industries. Government involvement and a change in the training of the next generation of scientists are necessary for the practical implications of genome- based research.

Table 2: QTL studies for aquaculture species.

Species	Traits
Arctic charr (<i>Salvelinus alpinus</i>)	Body weight and age of sexual maturity (Moghadam et al., 2007; Küttner et al., 2011).
Arctic charr (<i>S. alpinus</i>)	Tolerance to salinity (Norman et al., 2011).
Asian seabass (<i>L. calcarifer</i>)	Growth (Wang et al., 2011).
Asian seabass (<i>L. calcarifer</i>)	Resistance to viral nervous necrosis disease (Liu et al., 2016a).
Asian seabass (<i>L. calcarifer</i>)	Omega-3 fatty acid (Xia et al., 2014).
Atlantic salmon (<i>S. salar</i>)	Body-weight and condition (Reid et al., 2005).
Atlantic salmon (<i>S. salar</i>)	Adaptive traits (Boulding et al., 2008).
Atlantic salmon (<i>S. salar</i>)	Resistance against pancreatic necrosis virus (Moen et al., 2009; Gheyas et al., 2010).
Atlantic salmon (<i>S. salar</i>)	Resistance against anaemia (Moen et al., 2007).
Atlantic salmon (<i>S. salar</i>)	Delayed sexual maturity (Gutierrez et al., 2014).
Catfish (<i>I. punctatus</i>)	Columnaris disease resistance (Geng et al., 2015).
Coho salmon (<i>Oncorhynchus kisutch</i>)	Hatch timing, growth, length and weight (McClelland and Naish, 2010).
Common carp (<i>C. carpio</i>)	Muscle fiber (Zhang et al., 2011b).
Common carp (<i>C. carpio</i>)	Growth rate (Boulton et al., 2011).
Common carp (<i>C. carpio</i>)	Maneuverability (Laghari et al., 2014).
Eastern oyster (<i>Crassostrea virginica</i>)	Resistance to diseases (Yu and Guo, 2006).
European seabass (<i>D. labrax</i>)	Growth (Louro et al., 2016).
Gilthead sea bream (<i>S. aurata</i>)	Growth and sex determination (Loukovitis et al., 2011).
Gilthead sea bream (<i>S. aurata</i>)	Pasteurellosis resistance (Massault et al., 2011).
Gilthead sea bream (<i>S. aurata</i>)	Skeletal abnormalities (Negrín-Báez et al., 2015).
Japanese flounder (<i>P. olivaceus</i>)	Resistance against vibrio anguillarum (Wang et al., 2014).
Large yellow croaker (<i>Larimichthys crocea</i>)	Growth (Ye et al., 2014).
Pacific oyster (<i>Crassostrea gigas</i>)	Growth (Guo et al., 2012).
Pacific oyster (<i>Crassostrea gigas</i>)	Summer mortality resistance (Sauvage et al., 2010).
Rainbow trout (<i>O. mykiss</i>)	Temperature tolerance (Perry et al., 2005).
Rainbow trout (<i>O. mykiss</i>)	Life history (Leder et al., 2006).
Rainbow trout (<i>O. mykiss</i>)	Spawning time (Colihueque et al., 2010).
Rainbow trout (<i>O. mykiss</i>)	Osmoregulation capabilities (Bras et al., 2011).
Rainbow trout (<i>O. mykiss</i>)	Resistance to whirling disease (Baerwald et al., 2011).
Rainbow trout (<i>O. mykiss</i>)	Rate of development (Easton et al., 2011).
Rainbow trout (<i>O. mykiss</i>)	Growth (Wringe et al., 2010).
Rainbow trout (<i>O. mykiss</i>)	Smoltification (Nichols et al., 2008).
Rainbow trout (<i>O. mykiss</i>)	Resistance to <i>Flavobacterium psychrophilum</i> (Vallejo et al., 2014).
Rainbow trout (<i>O. mykiss</i>)	Cold water bacterial disease resistance (Palti et al., 2015b).
Rainbow trout (<i>O. mykiss</i>)	Response to crowding stress (Rexroad et al., 2013).
Rainbow trout (<i>O. mykiss</i>)	Sex determination (Cnaani et al., 2007).

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