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Review Article

Single nucleotide polymorphism markers with applications in aquaculture and assessment of its impact on natural populations

Roman Wenne*

Institute of Oceanology, Polish Academy of Sciences, Powstańców Warszawy 55, 81-712 Sopot, Poland

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Abstract – An increase in aquatic animal production can be achieved by extending aquaculture areas geographically, utilizing new species for culture, and using new technologies. Among new technologies useful for the increase of aquaculture production is the application of genetics and genomics. New molecular tools that benefit aquaculture have been developed. There has been a large number of experimental and review papers published concerning molecular markers and the range of their applications, including aquaculture and food product analyses. Analysis of single nucleotide polymorphisms (SNPs) has emerged as genotyping technology with wide and significant applications in aquaculture. SNPs can be used for construction of genetic linkage maps, finding quantitative trait loci (QTL) for useful traits like growth, body weight, grilsing, thermal and low oxygen tolerance, resistance to stress and diseases, mapping sex determination loci and identification of progeny in selection and chromosome manipulation experiments, assessment of genomic selectionand marker assisted selection in aquaculture. Genome-wide association studies (GWAS) facilitate the finding associations between SNPs and a trait in related or unrelated specimens. However, many traits are complex and can be controlled by number of QTL. Genotyping by genome reduction complexity sequencing emerged as an efficient and applicable technology in genomic selection. Identification of genes, sequences and nucleotides (substitutions) directly influencing phenotypic variations opens the possibility of marker-assisted selection for desirable characters in culture. SNP and QTL associations can be enhanced using genome editing technology. Examples of successful applications of SNPs in aquaculture of fish, crustacean and mollusk species, representing most geographic areas, and ecological risks assessment are reviewed.

Keywords: Aquaculture and mariculture / identification of escapees / SNP / QTL / resistance to pathogens / genomic selection / gene editing

1 Introduction

Exploitation of living marine and freshwater resources is an important source of food for human population worldwide. Global aquatic production has been increasing substantially for over 60 years and reached 167.2 million tonnes in 2014, of which 55.86% was capture fisheries production (FAO, 2016). However, aquaculture has hugely increased over the last 25 years and shows a higher potential for future development in comparison with capture fisheries. Further increases in production will be achieved by extending aquaculture areas geographically (finding new areas suitable for aquaculture industry), employing new species for culture, and using new technologies. A technology developed in recent years and useful for increasing aquaculture production and improving the protection of biodiversity is the application of genomics (McAndrew and Napier, 2010; Abdelrahman et al., 2017; Macqueen et al., 2017). New Generation Sequencing (NGS) has enabled the assembly of genomes of an increasing a number of species, and the characterization of number of genes in some cultured species has been followed by the characterization of their gene pools. This has, in turn, lead to functional studies of genes relevant to the goals of aquaculture. Genotyping by sequencing (GBS) techniques have laid the foundation for advances in aquaculture genetics and breeding (Robledo et al., 2017). Genome complexity reduction has facilitated the discovery of a large number of molecular markers, especially single nucleotide polymorphism (SNP). A range of techniques have been used for SNP discovery. The smaller scale methods include SSCP and heteroduplex analyses, random shotgun, direct polymerase chain reaction (PCR) product sequencing and expressed

*Corresponding author: rwenne@iopan.gda.pl

sequence tags (ESTs) (Liu and Cordes, 2004). Large scale SNP discovery enabled with high throughput sequencing platforms NGS and whole genome sequencing in fish has been reviewed more recently (Abdelrahman et al., 2017; Kumar and Kocour, 2017). SNP have been used for the identification of brood stocks, traits and strains in aquaculture. SNP can be applied to finding candidate genes of traits and quantitative trait loci (QTL) useful in aquaculture (Oyarzún et al., 2013; Yáñez et al., 2015). QTL are genomic regions associated with phenotypic variation for a specific trait, which can be significant for aquaculture, such as growth, skin pigmentation, body shape, color of meat, age of maturity (grilsing), thermal tolerance, lipid metabolism and resistance to stress and diseases.

Selective breeding of farmed animals for economically important quantitative traits has high potential for increasing aquaculture production. In classic selection schemes best linear unbiased prediction (BLUP) is applied to assess the selection candidates based on the phenotypes of relatives without the use of genetic markers (Boichard et al., 2016). In order to reinforce phenotypic based selection QTL markers were developed with the intended applications in marker assisted selection (MAS). The identified QTL for economically useful traits in aquaculture have been summarized recently (Abdelrahman et al., 2017). Linkage analysis to detect QTL includes family and progeny data (Rabier et al., 2016). Segregation of QTL has been studied within family. MAS can be successful if significant variance explained by a QTL (association) is not overestimated and linkage disequilibrium between marker and QTL persists throughout the population. Alternatively, large number of markers covering whole genome can be used for estimation of breeding value (Meuwissen et al., 2001). Genotyping with high density markers can shorten generation phase. Genome-wide association studies (GWAS) seek to find associations between SNPs and traits in unrelated specimens. However, many traits are complex and can be controlled by number of QTL. Genomic selection (GS) involves prediction of breeding values of selection candidates using high density markers irrespective of significance in their association studies. GS relies on the assumption that some QTL are in strong linkage disequilibrium with molecular markers (SNPs). Finding functional implications of particular SNP will enable genetic engineering by the incorporation of single nucleotides or short sequences (Dunham et al., 2014). Such alterations can make alleles in aquaculture more alike to the alleles of specimens with desirable characteristics: resistance to infections, growth or meat condition. Comprehensive use of biotechnology in aquaculture is outlined in the paper (FAO, 2017).

2 Comparison of wild and hatchery stocks: effects of escapees

One of the ecological risks of aquaculture is the deliberate or unintentional release of farmed fish to the natural environment. Hatchery reared fish are products of strong selection for traits of interest within a species. When released, they can hybridize with naturally born individuals and compromise the genetic integrity and fitness of natural populations. Population genomic analyses of early-phase Atlantic salmon (*Salmo salar*) revealed only a slight loss of genetic diversity in domesticated strains (Makinen et al., 2015). Genetic differences between farmed and wild Atlantic salmon in Norway were studied using a 7K SNP-chip (Karlsson et al., 2011). A diagnostic panel of only 60 SNPs out of 7000 SNPs was constructed and successfully identified farmed escapees. The genetic impact of gene flow caused by the straying of hatchery released fish on wild populations of Atlantic salmon in the Gulf of Finland, Baltic Sea, over 16 years, 1996–2012 was assessed with a panel of 1986 SNPs (Ozerov et al., 2016). Introgression changed the genetic composition of wild populations, increased genetic diversity and lowered genetic divergence. Highly diverged genome regions in an aquaculture strain (Saint John River) in comparison with its wild founder population (Tobique River, Canada) were identified with a 6K SNP array (Liu et al., 2017b). Some outlier loci at these regions were near QTL for growth, appetite, maturity, or disease resistance, which exhibited the effects of strong artificial selection in hatchery stocks. In order to develop a high-density SNP, taking genome duplication and across-continent genetic variation of complex traits in Atlantic salmon into account, de novo SNP discovery and validation was performed using specimens from Chilean, European and North American populations, including fish from wild and farmed origins (Yáñez et al., 2016). A 200K SNPs array can be used for assessment of gene flow from farmed stocks to wild salmon populations worldwide.

Temporal changes in the genetic structure of the threatened wild Atlantic salmon Magaguadavic River population, Bay of Fundy, Canada was studied using 112 SNPs (Bourret et al., 2011). A substantial decline in numbers of returning fish over the last two decades was noted. Wild and farmed individuals caught entering the river in 1980–2005, were genotyped. SNP genome scans identified a temporal decrease in candidate loci potentially under directional selection. This was indicated that farmed escapees had introgressed with wild Magaguadavic salmon resulting in significant change in the genetic integrity of the native population, including possible loss of adaptation to wild conditions. Historical and contemporary samples from 20 populations in Norway were genotyped with a panel of SNP markers differentiating farmed and wild Atlantic salmon (Glover et al., 2013). Five populations exhibited significant temporal genetic changes and became more similar to a pool of farmed fish with time, strongly suggesting introgression from escaped farmed fish. The remaining 15 populations displayed weak or non-significant temporal genetic changes. The among-population level of divergence decreased with time. The level of cumulative introgression has been population-specific, and was not solely dependent on the frequency of escapees observed in the population. It has been suggested that such demographic processes in the native population as spawning success and survival of the offspring influence the relative success of farmed salmon in the wild (Heino et al., 2015). Hatchery released and native extirpated salmon populations were identified in Poland using an Atlantic salmon array (Pocwierz-Kotus et al., 2015; Bernas et al., 2016). Understanding of the hybridization dynamics between wild salmon and aquaculture escapees requires discrimination of different hybrid classes (Pritchard et al., 2016). Using the Atlantic salmon array, a set of 200 SNPs differentiating an Atlantic salmon stock from Teno River, Norway and escapees was identified. Both the complete set of SNPs and smaller subsets

could reliably assign individuals to different hybrid classes up to the third hybrid (F3) generation.

Analysis of 3781 SNP markers from *Salmo trutta* SNP-array, in wild and hatchery populations of brown trout from the Lake Savalen, Norway demonstrated significant genetic differences related to human-mediated and natural selection in growth, an important fitness-related trait (Linlokken et al., 2017). An Atlantic salmon derived SNP-array was also used for the genotyping of two populations of Southern Baltic Sea trout *S. trutta* m. *trutta* and a diagnostic panel of 39 SNPs was selected for further population genetic analyses and identification of changes related to stocking (Drywa et al., 2013; Pocwierz-Kotus et al., 2014; Wenne et al., 2016b, Wenne et al., 2016c). Large numbers of SNP markers obtained with NGS was used for genome-wide diversity assessment of wild Mediterranean brown trout *S. trutta* populations and from Atlantic and Mediterranean hatchery-reared strains in southern France that had used for stocking (Leitwein et al., 2016). Reduced polymorphism and pronounced heterozygote deficiency in hatchery strains compared to wild populations was found, which implied negative effects of stocking in wild populations. However, studies of genetic structure and diversity of populations of Chum Salmon *Oncorhynchus keta* using 52 SNP markers revealed eight regional groups, indicating the persistence of the historical genetic structure in extant populations in Japan despite the execution of a hatchery program for about 120 years (Sato et al., 2014).

Application of GBS allowed for the identification of 4275 SNP loci of blue catfish, *Ictalurus furcatus*, of which a multiplex of 64 SNPs was used for genotyping (Li et al., 2014). An admixture was observed between native and culture populations. A total of 5243 high-quality SNP markers was detected with NGS technique in marine bivalve, the black-lip pearl oyster *Pinctada margaritifera* from Fiji Islands (Lal et al., 2016). Significant population genetic differentiation, including outliers, was found among 3 wild populations and evidence of a genetic bottleneck in the hatchery population. No differences between wild populations from Japan and cultured stocks in China of Sea Cucumber, *Apostichopus japonicas* were found using 51 SNPs (Dong et al., 2016).

3 Linkage maps

Linkage maps show positions of genetic markers on chromosomes. The large number of SNP discovered and the development of SNP array enabled the construction of high density maps, such as for Atlantic salmon (*S. salar*) using up to 96 000 SNP (Houston et al., 2014; Tsai et al., 2016b) and, rainbow trout (Rexroad et al., 2008; Palti et al., 2015a). Linkage maps for male and female Atlantic salmon were constructed based on SNPs (Moen et al., 2008; Lien et al., 2011; Gonen et al., 2014). Differences between male and female recombination rate were assessed. The linkage map was helpful in physical mapping of the salmon genome. An integrated linkage map for Chinook salmon (*Oncorhynchus tshawytscha*) using 14 620 SNP loci mapped, 286 salmon scaffolds, and 11 728 ESTs were created (McKinney et al., 2016). Genome regions with increased divergence between populations were found, and candidate fitness related genes such as stress response, growth and behavior were identified. Thermotolerance QTL co-occurred with several candidate genes including HSP70.

A high-density genetic linkage map was generated for channel catfish, *Ictalurus punctatus* and integrated with a physical map by application of genotyping of families with the 250K SNP array (Liu et al., 2011; Li et al., 2015). Over 50 000 SNPs were placed on this linkage map, which covered 90% (867) Mb of the catfish genome. The estimated genetic size was 3505.4 cM and a resolution of 0.22 cM for the sex-averaged genetic map. The integrated map facilitated the catfish genome assembly, QTL mapping and positional cloning of genes responsible for economically useful traits. A high-density interspecific genetic linkage map for hybrid channel catfish (*I. punctatus*) and blue catfish (*I. furcatus*) was also constructed (Liu et al., 2016). Over 26 000 SNPs were mapped to 29 linkage groups. Less than a thousand revealed significant deviation from the expected Mendelian ratio and were grouped in 2 major genomic blocks. Strong selection against the blue catfish female alleles was suggested as an explanation.

A genetic map for common carp (*Cyprinus carpio*) was constructed with 8487 SNP markers from gene coverage 50 linkage groups and spanning 3762.88 cM (Laghari et al., 2014; Xu et al., 2014; Liu et al., 2017a). 217 microsatellites and 336 SNP markers were selected to analyze the genomic DNA of 68 individuals derived from a group of F2 hybrids of mirror carp, *C. carpio* (Li et al., 2011). A genetic linkage map was constructed and 14 QTL were identified for body weight. A backcross common carp family, with 86 progeny, was used to construct a genetic map for preliminary QTL mapping. Fourteen QTL associated with body weight, body length and condition factor were detected on ten linkage groups. For common carp, a total of 978 microsatellite and 3899 SNP markers were assigned to construct the genetic map, which comprised 50 linkage groups (Jin et al., 2015a). Ten QTL were found to be associated with eye diameter and twenty QTL were found to be related to eye cross. A dense SNP-based linkage map was constructed using interspecific cross between two closely related cyprinid species in Japan: river-dwelling *Gnathopogon elongatus* and lake-dwelling *G. caerulescens* (Kakioka et al., 2013). Based on 1622 RAD-tag markers, a linkage map spanned 1390.9 cM with average marker distance of 0.87 cM. High-density genetic linkage maps for orange-spotted grouper *Epinephelus coioides* were generated using multiplexed shotgun genotyping method (You et al., 2013). The sex-averaged map contained a total of 4608 SNPs, which covered 1581.7 cM, with average distance between SNPs of 0.34 cM. Physical and linkage maps for yellowtail (*Seriola quinqueradiata*), an important species in fish aquaculture in Japan was constructed using SNP obtained from NGS results and synteny with four model fish species was analyzed (Aoki et al., 2015). A double digest RAD (ddRAD)-based genetic linkage map was generated for the Japanese eel *Anguilla japonica* (Kai et al., 2014). The map for female spanned 1748.8 cM, whereas the map span for males was 1294.5 cM. A total of 2672 SNP markers provided anchor points to 1252 scaffolds covering 151 Mb.

Genetic linkage maps were constructed also for some other species important for aquaculture, as gilthead sea bream, *Sparus aurata* (Tsigenopoulos et al., 2014); Asian seabass, *Lates calcarifer* (Wang et al., 2015a; Sun et al., 2017); mandarin fish, *Siniperca chuatsi*(Sun et al., 2017); turbot,

Scophthalmus maximus(Wang et al., 2015b); Japanese flounder, *Paralichthys olivaceus* (Castaño-Sánchez et al., 2010; Shao et al., 2015); large yellow croaker, *Larimichthys crocea* (Ao et al., 2015); black tiger shrimp, *Penaeus monodon* (Baranski et al., 2014); Pacific white shrimp, *L. annamei* (Du et al., 2010); Pacific abalone, *Haliotis discus hannai* (Qi et al., 2010); South African abalone, *Haliotis midae* (Vervalle et al., 2013) and silver-lipped pearl oyster, *Pinctada maxima* (Jones et al., 2013). Linkage maps of commercial fish and shellfish have been listed in other review papers (Wenne et al., 2007; Yue, 2014; Abdelrahman et al., 2017).

4 Growth traits

Growth is the most economically important trait in many selection programs in aquaculture, therefore there have been numerous studies on the subject. The source populations used for creation of aquaculture stocks differ in their ecological characteristics. European and North American lineages of Atlantic salmon (*S. salar*) differ in phenotypic characteristics, including rate of growth. In order to understand genetic background of these differences, large ($N = 300$) backcross families were created and were genotyped for 129 SNPs (Boulding et al., 2008). 79 significant associations were found between SNP markers and quantitative traits including QTL for parr growth and condition index linked to the sex-determining locus. Genetic mapping of QTL for body-weight in Atlantic salmon in a Mainstream Canada broodstock program was performed using a 6.5K SNP array (Gutierrez et al., 2012). Parents and progeny were genotyped. Genome-wide significant QTL ($\alpha = 0.05$) was linked to 6 chromosomes, QTL ($\alpha = 0.01$) to several chromosomes and a suggestive QTL ($\alpha = 0.05$) associated with body-weight was identified. These QTL were suggested as candidates for use in marker-assisted selection. GWAS for growth traits was performed in juvenile Atlantic salmon farmed in Scotland, UK, using a high density, 132K SNP array (Tsai et al., 2015c). After quality check, the results of genotyping of 622 fish (534 offspring, 28 sires and 60 dams) with 111 908 SNPs were chosen for the analyses. The heritability for weight and length traits was 0.5 and 0.6 respectively. Both traits were polygenic. There was little effect QTL on a few chromosomes. A possible positional candidate gene could be a SNP in the retinoic acid-induced protein 2 gene on chromosome 17. However, SNP associations found in more than one population are more likely to be reflecting real QTL in salmon (Tsai et al., 2015b).

A significant association between a SNP allele and early growth in Arctic charr, *Salvelinus alpinus*, in Canada was found for the locus containing the growth hormone-releasing hormone and pituitary adenylate cyclase-activating polypeptide genes (GHRH/PACAP2) (Tao and Boulding, 2003). SNP markers located in candidate genes involved in growth were detected in turbot by integrating next generation sequencing and growth-related QTL mapping (Robledo et al., 2016). Muscle and liver transcriptome from 18 individuals was sequenced and a total of 20 447 genes and 85 344 SNPs were found. Forty-three SNPs on growth-related genes were selected based on QTL co-localization in a wild Atlantic population. SNPs in growth hormone gene of large yellow croaker *L. crocea* was correlated with growth traits (Ni et al., 2012).

High-throughput GBS was used to detect and map a few thousand SNPs in haploid Chinook salmon, *O. tshawytscha* (Everett and Seeb, 2014). This map was used to detect QTL related to temperature tolerance and body size in families of diploid Chinook salmon. 3534 SNPs in 34 linkage groups were mapped. Four QTL for temperature tolerance and one QTL for body size were detected. A linkage map for brook charr (*Salvelinus fontinalis*) in Canada consisted of 266 SNPs and 81 microsatellites (Sauvage et al., 2012). Sixty-four growth-related and 4 stress-related QTL were found across 18 of the 40 linkage groups. QTL of little-effect and a larger effect were identified. QTL for growth were found in F2 generation of crossed wild specimens of the Asian seabass (barramundi) *L. calcarifer* originating from 4 countries Thailand, Indonesia, Malaysia and Singapore (Xia et al., 2013). For individuals kept in one tank and differing in growth, SNPs in candidate genes were genotyped using sequencing. Twenty one significant QTL were identified. QTL mapping revealed a SNP associated with growth in the intestinal fatty acid (FA) binding protein (IFABP-a) gene. NGS of transcriptome from fast and slow growing largemouth bass *Micropterus salmoides* showed that a few metabolic pathways could be associated with muscle growth (Li et al., 2017b). Putative SNPs were selected and genotyping of 17 SNPs in 340 individuals revealed three SNPs associated with growth in genes: phosphoenolpyruvate carboxykinase 1, FOXO3b, and heat shock protein beta-1.

Twenty-two SNPs were identified as associated with growth in 778 individuals representing 40 families of rainbow trout using RNA-Seq whole-transcriptome (Salem et al., 2012). A group of female fish selected for improved growth and unselected genetic cohorts (10 fish from 1 full-sib family each) were compared and allelic imbalances were identified. Some SNPs were clustered into genes of metabolic energy production pathways and were considered suitable candidates for genetic selection. Transcriptome profiles were compared between fast and slow-growing rainbow trout across seasonal gradients (Danzmann et al., 2016). Slow-growing fish had elevated creatine kinase, TSC2 n and p53 expression levels. Large fish displayed a reaction similar to resistance physiology with elevated cytoskeletal gene component expression and glycogen metabolism cycling along with higher PI3K levels as well as lipid metabolic gene expression elevated, in particular the G0S2 switch gene. Twenty-three out of 26 gene families with previously reported significant SNP-based growth differences were confirmed as having significant expression differences. However, seasonal changes in gene expression were greater than differences associated with fish size.

In studies of aquacultured invertebrates, a high-resolution genetic linkage mapand QTL identification were performed using the RAD technology in the Kuruma prawn, *Marsupenaeus japonicas* (Lu et al., 2016). QTL, 129 for high-temperature tolerance overlapped with linked SNPs, and 4 growth-related were located in regions between contiguous SNPs. Twenty eight SNP markers at 23 candidate genes potentially associated with growth were found in an improved giant freshwater prawn, *Macrobrachium rosenbergii* culture line in Vietnam (Jung et al., 2014). SNP polymorphism at vitellogenin receptor (PmVtgr) associated with reproduction-related phenotypes (gonadosomatic index and ovarian weight) of the giant tiger shrimp *P. monodon* were found (Klinbunga et al., 2015). The expression of X-box binding protein 1

(PmXbp1) during ovarian development in wild *P. monodon* broodstock and association between its SNP and growth-related parameters were observed: expression of genotype A (corresponding to a T/T349 SNP) was significantly greater than that of juveniles carrying pattern B (corresponding to a T/C349 SNP) (Prasertlux et al., 2015). The growth-related genes were screened using paired-end sequencing technology in the swimming crab *Portunus trituberculatus* in China (Lv et al., 2015b). One growth-associated SNP was identified, which was located in hemocyanin as a result of association analysis.

A SNP associated with scallop growth for both the shell and soft body was identified in the insulin-like growth factor binding proteins IGFBP gene in a bivalve, Yesso scallop, *Patinopecten yessoensis* (Feng et al., 2014). A SNP in the 3' UTR (c. 1815C>T) of the transforming growth factor beta (TGF-beta) gene was potentially negatively associated with both scallop *Chlamys farreri* growth and Tgfbr1 expression (Guo et al., 2012).

5 Sex determination in fish

Sex determination systems are extremely diverse in fish. In many species, sex can be reversed during the course of a life and can depend on environmental conditions and social interactions. Females and males can differ in growth rate, which has implications for aquaculture. Sex manipulation is commonly practiced in aquaculture for example in Nile tilapia, *Oreochromis niloticus* (Mair et al., 1991; Garcia et al., 2016; Sansuwan et al., 2017), (Calhoun and Shelton, 1983), gilthead sea bream, *S. aurata* (Loukovitis et al., 2012), European sea bass, *Dicentrarchus labrax* (Martinez et al., 2014) and turbot, *S. maximus* (Robledo et al., 2015). Early sexual maturation (grilsing) retards growth, increases production times and affects flesh quality in aquaculture. A 6.5K SNP array was used to genotype approximately 3300 fishes from the Atlantic salmon, *S. salar* Cermaq (Mainstream) Canada broodstock program (Gutierrez et al., 2015). The analysis of results revealed identification markers showing a significant association with growth, grilsing and late sexual maturation. Candidate genes linked to these genetic markers, were identified and some were connected with developmental processes. In order to overcome problems associated with early sexual maturation as in males in Tasmanian Atlantic salmon, sex-reversed females have been crossed with normal females to produce all female stock (Eisbrenner et al., 2014). The results of a TaqMan 64 SNP genome-wide scan indicated that the sex-determining gene in two Scottish Atlantic salmon families was positioned on chromosome 6, but in lineages in the SALTAS breeding program of Canadian origin this gene was found to be located at three loci. This confirmed genomic differences between different geographic lineages of salmon populations.

Twenty-six gene families involved in reproduction and sex determination were identified from testicular and ovarian transcriptomes and a number of SNP markers for further study were discovered in Amur sturgeon, *Acipenser schrenckii* (Jin et al., 2015b). The wreckfish hapuku (*Polyprion oxygeneios*) is not externally sexually dimorphic and need over 5 years to reach sexual maturity in captivity, this hinders broodstock management (Brown et al., 2016). Combined and sex-specific linkage maps were constructed based on 1575 SNP markers. A major sex-determining locus, heterogametic in males, and several markers in strong linkage disequilibrium were mapped. PCR assays were developed for two of these markers. In the rock bream *Oplegnathus fasciatus*, sequence analysis revealed 19 male-specific SNPs, which enabled the development of 3 SNP markers (Xu et al., 2013). Mapping the sex determination locus in the Atlantic halibut (*Hippoglossus hippoglossus*) using sequencing was performed (Palaiokostas et al., 2013a). A linkage map was constructed based on 5703 SNP markers and 7 microsatellites creating 24 linkage groups, equivalent to chromosome pairs in this species. A major sex determining locus was mapped to linkage group 13. Ten SNPs with significant association with phenotypic sex were tested with 97% success rate. Sex-associated DNA markers to fast track progeny testing will help to implement monosex female halibut production for an immediate improvement in productivity.

A high-density SNP based linkage map for European sea bass (*D. labrax*) was constructed with 6706 SNPs on 24 linkage groups, and putative sex-determining QTL were detected in 4 groups (Palaiokostas et al., 2015). The polygenic sex determination hypothesis in sea bass was confirmed. A linkage map with 3280 informative SNP markers was constructed, and a major sex-determining region in Nile tilapia, *O. niloticus* was identified explaining almost 96% of the phenotypic variance (Palaiokostas et al., 2013b). For 2 SNPs showing the highest association, in family and population data, all females were homozygous whereas males were heterozygous with 7 exceptions. These few male fish exceptions possessed the homozygous genotype expected of females – XX males. Appearance of sex reversal can be caused by elevated temperature. In aquaculture of half-smooth tongue sole, *Cynoglossus semilaevis*, some female fish reverse to pseudomales, which increases maintenance costs due to lower growth rate of males (Jiang and Li, 2017). A polymorphic SNP correlated with sex reversal was found. Genetic females with this SNP's allele A do not reverse into phenotypic males. Unraveling thesex reversal mechanisms can substantially improve female ratio in management of aqua-cultured stocks. Production of monosex female stocks is beneficial for commercial purposes since females grow faster and mature later than males. Developing sex-associated markers can shorten the time of monosex female production and decrease the costs of farming.

6 Resistance to pathogens

Similarly to other agricultural activities, aquaculture causes epidemiological threats and can enhance invasions of pathogens in natural waters and to new geographic areas. SNP analysis in salmonid bacterial pathogen *Renibacterium salmoninarum* causing kidney disease showed its intercontinental propagation associated with fish movements (Brynildsrud et al., 2014). The identified closely-related isolates linked to neighboring fish farms, most probably formed part of single outbreaks. It was demonstrated that a subgroup of *R. salmoninarum* isolated from Norway and the UK represented an introduction to these areas ~40 years ago. This example demonstrated the promise of SNP genotyping technology for

analysis of genetic relationships in veterinary and environmental microorganisms. A comparison of genome regions in *Vibrio harveyi* and related species with the shrimp pathogen *V. harveyi* (CAIM 1792) demonstrated its higher similarity to those of other *V. harveyi* strains than to those of the other closely related species *V. owensii*, *V. rotiferianus* and *V. campbellii* (Espinoza-Valles et al., 2015). The SNP trees showed that *V. harveyi* is the most conserved of the four species studied, and *V. campbellii* may be divided into at least three subspecies. SNPs have been used in studies of other fish pathogens, as salmon louse *Caligus rogercresseyi* (Copepoda: Caligidae). High-throughput SNP discovery and transcriptome expression profiles of *C. rogercresseyi* lead to the identification of pathways involved in resistance to antiparasitic agents, which is highly useful for investigating the susceptibility or resistance to chemical treatments (Nunez-Acuna et al., 2014). A genomic region strongly linked to pesticide emamectin benzoate resistance was defined in salmon louse using SNP-array (Besnier et al., 2014). A spread of this resistance was human-induced. Atlantic salmon introduced to aquaculture in Chile turned out to be susceptible to bacterial pathogen *Streptococcus phocae* subsp. *salmonis*, whereas rainbow trout was resistant (Salazar et al., 2016). Diseases have caused great losses in the aquaculture industry and substantial efforts have been undertaken with the aim to reduce susceptibility of farmed animals and prevent the spread of pathogens.

7 Viral diseases

Viral diseases are an important threat to the fish farming industry. The genetic background of resistance to some viral diseases have been reported in fish (Moen, 2010). Fifty segregating SNP markers linked to a major QTL were found to affect resistance to infectious pancreatic necrosis virus (IPNV) in pedigreed Atlantic salmon (*S. salar*) from a commercial breeding program in Scotland using RAD-sequencing (Houston et al., 2012). A QTL in Norwegian salmon for IPNV resistance was initially identified with microsatellite markers (Moen et al., 2009). This QTL has been employed in marker-assisted selection in two breeding companies in Norway and Scotland, which resulted in 75% reduction in the number of IPN-outbreaks (Moen, 2010; Moen et al., 2015). This QTL has been located on the SNP-based linkage map and identified as the epithelial cadherin (*cdh1*) gene. A SNP was found within the *cdh1-1* gene as the significant determinant of the resistance of Atlantic salmon individuals to IPNV. A functional involvement of epithelial cadherin protein in internalization of the IPNV was reported for the first time, as similar to bacteria and fungi. The resistance and susceptibility to grass carp reovirus (GCRV) in individuals and cell lines was associated with SNPs identified by comparative transcriptome analysis (Liao et al., 2017). GBS revealed SNPs associated with viral nervous necrosis disease (VNN) in Asian seabass (Wang et al., 2017).

In order to find SNPs useful for breeding common carp (*C. carpio*) resistant to disease caused by cyprinid herpesvirus 3 (CyHV-3), 11 candidate genes were amplified and sequenced (Kongchum et al., 2010). The utility of the identified SNP markers was evaluated in one full-sib family and results revealed that 20 markers from 9 loci segregated in a disomic and Mendelian pattern and would be applicable for linkage analysis. Infectious diseases such as koi herpesvirus (KHV) and *Aeromonas hydrophila* have caused world-wide massive mortality of common carp. Differential resistance to these diseases has been observed and programs for common carp genetic resistance and improvement of survival rates are needed in aquaculture. Interleukin-1b (IL-1b) is a key component in innate immunity and the inflammatory response. SNP variation was found at 13 positions of the interleukin-1β gene of bighead carp (*C. pellegrini*) and five strains of common carp (*C. carpio*) in China and can be helpful in understanding resistance to these diseases (Jia et al., 2015).

8 Bacterial diseases

Bacterial cold water disease (BCWD) induces mortality in many salmonid farms. In order to identify SNP markers associated with resistance to this disease and spleen size in rainbow trout in Leetown, West Virginia, USA a total of 298 offspring from the two half-sib families challenged with bacteria *Flavobacterium psychrophilum* were genotyped with Restriction-Site Associated DNA Sequencing (RAD-seq) (Liu et al., 2015b). Using GWAS, 18 SNPs associated with resistance to the BCWD and 20 SNPs associated with spleen size were identified. Linkage-based QTL mapping revealed three significant QTL for the BCWD resistance. The SNP markers facilitated fine mapping to identify positional candidate genes for BCWD resistance in rainbow trout. Selective genotyping of SNPs from *Sbf*I RAD associated DNA sequencing data were used to validate major QTL affecting BCWD resistance already detected in two families of rainbow trout, to increase density of markers in the QTL regions and to detect new QTL thanks to the higher marker density of the genome scan. Some QTL previously detected in microsatellite scans were validated and new QTL were found with SNPs using selective genotyping of SNPs from *Sbf*I RAD associated DNA sequencing data (Palti et al., 2015b). Location of candidate genes in the vicinity of two Omy8 QTL may suggest the existence of potential linkages between immune and stress responses in rainbow trout. The identified OTL can be useful for marker assisted selection. Another important bacterial disease affecting salmonids is piscirickettsiosis. 2601 Atlantic salmon (*S. salar*) smolts, the progeny of 40 sires and 118 dams from a breeding population in Chile were experimentally challenged with *Piscirickettsia salmonis* by means of intraperitoneal injection and genotyped with a 50K SNP array (Correa et al., 2015). Candidate genes including interleukin receptors and fucosyltransferase were found to be physically linked with the 5 SNPs significantly associated with the resistance trait.

Leukocyte cell-derived chemotaxin-2 (LECT2) is an important protein of the innate immune system for defense against bacterial infection. LECT2 gene was cloned, characterized, and its expression in response to a challenge with a pathogenic bacteria *V. harveyi* was studied in tissues of Asian seabass, *L. calcarifer* (Fu et al., 2014a). The LECT2 transcript was up-regulated in the kidney, spleen and liver. Three SNPs in the LECT2 gene were found to be associated with resistance to the big belly disease of Asian seabass and may be useful for selection programme in aquaculture. Enteric septicemia of

channel catfish (ESC) is caused by bacteria *Edwardsiella ictaluri*. Genotyping of several hundred fish with the catfish 250K SNP array was undertaken and was helpful in identification of genomic regions associated with ESC disease resistance (Zhou et al., 2017). Several QTL associated with resistance to ESC were identified. A SNP associated with the *nck1* gene, upregulated after ESC challenge was found.

Nine QTLs formed two main clusters for *Vibrio anguillarum* disease resistance of Japanese flounder (*P. olivaceus*) from Yantai, China (Shao et al., 2015). Synteny analysis of the QTL regions on the genome assembly revealed 12 immune-related genes including 4 strongly associated with disease resistance. The lipopolysaccharide-binding protein (LBP) gene is involved in the acute-phase immunologic response to bacterial infections. Its expression was differentiated in response to challenges of Mozambique tilapia *Oreochromis mossambicus* from Singapore, with two bacterial pathogens *Streptcoccus agalactiae* and *Aeromonas hydrophila* (Fu et al., 2014b). Associations were found in two SNPs at the LBP gene with the resistance to *A. hydrophila*. The mast cell protease 8 (MCP-8) gene expression was enhanced in intestine, kidney, spleen and liver in tilapia, after a challenge, and three SNPs identified in the MCP-8 gene were significantly associated with resistance to *S. agalactiae* (Fu et al., 2014c). These SNP markers may facilitate selection of tilapia resistant to the bacterial disease. After a challenge with the same bacterial pathogen, expression of duodenase-1 gene was up-regulated significantly in the intestine, liver and spleen in hybrid tilapia, *Oreochromis* spp. (Shen et al., 2015). Four SNPs were significantly associated with the resistance to *S. agalactiae*. One SNP was associated with growth traits. After a challenge, the expressions of the two genes Gadd45a1 (growth arrest and DNA damage 45 A) and Gadd45a2 were up-regulated in the spleen, kidney, liver and intestine (Shen et al., 2016a). The two Gadd45a genes may play an important role in resistance to *S. agalactiae*. Ten SNP markers were identified in the two Gadd45a genesin tilapia. A resource stock of grass carp was constructed consisting of specimens susceptible and resistant to hemorrhagic septicemia caused by *A. hydrophila* (Shen et al., 2016b). In the complement component C7 gene, 6 SNPs were found and the 425 C>T polymorphism may be a significant molecular marker for resistance to *A. hydrophila*. A TLR22 homologue gene was identified and characterized from grass carp *Ctenopharyngodon idella* (Su et al., 2012). Its expression in the spleen was significantly up-regulated post-injection of grass carp reovirus (GCRV). Six SNPs were detected in the gene sequence, butonly 417 G/T was significantly associated with the resistance of grass carp to GCRV.

Nine SNPs were discovered through direct sequencing of newly characterized interferon regulatory factor 2 gene from resistant and susceptible to *Aeromonas hydrophila*stock of freshwater mussel *Hyriopsis cumingii* (Wang et al., 2013). Only one SNP was significantly associated with resistance/susceptibility. The distribution of three SNPs in C-type lectin gene (CTL) in susceptible and resistant stocks of the swimming crab *P. trituberculatus* was identified, according to the survival time after *Vibrio alginolyticus* challenge (Hao et al., 2015). The non-synonymous SNP E4-205C/T, C to T transition resulting in a Threonine to Isoleucine substitution at position 152 in the peptide of CTL protein, showed significant difference between the two stocks. The T/T genotype was shown to be associated with increased resistance. In the anti-lipopolysaccharide factor gene, sixteen SNPs were significantly associated with resistance/susceptibilityof the swimming crab to *V. alginolyticus* of which most were located in introns and noncoding exons, while two synonymous and one nonsynonymous SNP were in coding exons (Li et al., 2013a). Toll gene expression in green mud crab, *Scylla paramamosain* was up-regulated after infection with *V. parahemolyticus* (Lin et al., 2012). Two hundred and twenty SNPs in the leucine-rich repeats (LRRs) domain were found including one SNP c.1372A>G with potential pathogen-resistant activities. To study crab *Eriocheir sinensis* immunogenetics, newly hatched larvae were experimentally challenged with a mixture of three pathogens: Gram-positive bacteria *Micrococcus luteus*, Gram-negative bacteria *V. alginolyticus* and fungi *Pichia pastoris* (Cui et al., 2013). Numerous genes identified in transcriptome were associated with immune pathways: Toll, immune deficiency, janus kinase-signal transducers and activators of transcription and mitogen-activated protein kinase, tumor necrosis factor receptor associated factor 6 (TRAF6), fibroblast growth factor, protein-tyrosine phosphatase and JNK-interacting protein 1 (JIP1). A cathepsin B gene of the Chinese shrimp *Fenneropenaeus chinensis* was characterized (Li et al., 2013b). A challenge test revealed the responses of FcCB in different tissues to white spot syndrome virus (WSSV) infection. The FcCB gene expressions after WSSV challenge in the gill, hepatopancreas and muscle was up-regulated, suggesting that FcCB might be involved in the immune response. Three SNPs were identified involving C/T transitions. A SNP genotype distribution in resistant and susceptible shrimps was obtained using a high-resolution melting method. However, no differences were observed in thefrequency of genotype C-984T between the two groups.

A genetic basis of monogenean fluke ectoparasite *Benedenia seriolae* disease resistance in yellowtail (*Seriola uinqueradiata*) was studied by using the linkage map with microsatellite and 142 SNP markers (Ozaki et al., 2013). Two QTL regions were found that contributed to Benedenia disease resistance.

9 Stress response

The quality of aquaculture production and fish welfare can be improved by the understanding of genetic fundamentals of stress responses. Twenty six SNP markers associated with cortisol response to crowding in rainbow trout were identified using GWAS (Liu et al., 2015a). Mapping revealed two QTL on chromosomes, of which a putative serine/threonine protein kinase gene was identified on Omy12. Its expression was changed in the liver in response to handling and under duress stress.

Hypoxia is an adversely operating environmental factor on fish survival, development and growth. To further understand molecular functions of an essential hypoxia sensor, Fih-1 was studied in a cyprinid fish, Wuchang bream *Megalobram aamblycephala* (Zhang et al., 2016). Three associated SNPs were found by correlation analysis in hypoxia-sensitive and hypoxia-tolerant groups. Six SNPs were detected in a cDNA sequence of a highly conserved and multifunctional

endoplasmic reticulum chaperone (CRT) protein gene and one SNP was associated with the salt tolerant trait in fish *P. trituberculatus* (Lv et al., 2015a).

Studies of transferrin gene resulted in finding amino-acid changes in the coded protein caused by SNPs in surviving and non-surviving Nile tilapia (*O. niloticus*) siblings kept in saltwater. An expression study indicated up-regulation of transferrin when tilapias were exposed to saltwater, which suggested its involvement in saltwater tolerance (Rengmark and Lingaas, 2007).

To study the molecular mechanism of cold tolerance, TCP-1-eta homolog gene cDNA was obtained from Whiteleg shrimp *Litopenaeus vannamei* and was sequenced (Yin et al., 2011). TCP-1-eta gene expression depended on temperature. A SNP genotype was identified as significantly related to cold tolerance among individual shrimps. SNP identification by transcriptome sequencing and candidate gene-based association analysis was performed for heat tolerance in the bay scallop *Argopecten irradians* (Du et al., 2014). SNP all-53308-760 T/C showed a significant difference in allele frequency between the heat-susceptible and heat-resistant groups. A significand difference in allele frequency at this locus was also observed between natural populations. These results suggest that SNP all-53308-760 T/C may be related to the heat tolerance. The expression level of all-53308 was negatively correlated with heat tolerance of the bay scallop. SNP polymorphism in the promoter region of metallothionein 1 and heat shock protein 90 genes was reported as associated with heat tolerance of bay scallop *Argopecten irradians* (Yang et al., 2013; Yang et al., 2015).

10 Domestication and Genomic Selection

Domestication of most cultured fish is very weakly advanced in comparison with terrestrial farmed animals and can be accelerated by application of genomic selection. Selective breeding of Atlantic salmon has been carried out intensively in Norway since the 1970s (Gjedrem, 2012). The genetic differentiation between three domesticated strains of Atlantic salmon *S. salar*, and populations of their wild conspecifics in Canada and North Europe was found to be low. The domesticated strains also harbored similar levels of genetic diversity compared to their wild conspecifics (Makinen et al., 2015). In the study of the same strains of Atlantic salmon, ten genomic regions were indicated as exhibiting signs of directional selection (Vasemagi et al., 2012). Most of the identified candidate regions were small, up to a few centimorgans in the female Atlantic salmon linkage map. The Cermaq Atlantic salmon broodstock population ('Mowi' strain from Norway) farmed since the mid 1980s in British Columbia, Canada was compared with four wild populations from Norway using genotyping with a 6.5K SNP array (Gutierrez et al., 2016). Forty four markers were identified as outliers, and were associated with molecular functions that could be related to selection for growth, response to pathogens and environmental stressors, and with an undesirable early sexual maturation – grilsing trait, that is economically important traits and domestication. A 200K SNP custom array can be applied for carrying genomic selection in breeding programmes and genetic studies in wild populations (Yáñez et al., 2016). An Atlantic salmon 15K SNP chip was evaluated as a potential genomic tool for application in a Tasmanian Atlantic salmon (*S. salar*) breeding population and was found useful for carrying within-family selection (Dominik et al., 2010). Genetic diversity and frequencies of alleles in Tasmanian Atlantic salmon was lower than observed within European populations as revealed by analysis with 218 132 SNPs array (Kijas et al., 2016). In contrast to the European Atlantic salmon, the strength of observed LD was high at short distances and remained above background for marker pairs separated by chromosomal distances of hundreds of kb.

A large number of SNPs identified withNGS were used for analysis of domestication and artificial selection effects at the genome level by identification of the signatures of selection in channel catfish, *I. punctatus* in North America (Sun et al., 2014). One SNP per 116 bp was found in the channel catfish genome. The domestic and wild populations differed in allele frequencies at 407 861 SNPs. Eleven genes in 23 genomic regions with putative selective sweeps (excess of homozygosity) were found in analysis of annotations of these SNPs against the genetic map. Genes with known function related to aquaculture performance of traits under selection were identified, among them hypoxia-inducible factor 1-beta (HIF-1b) important for response and tolerance to low oxygen levels, the transporter gene ATP-binding cassette sub-family B member 5 (ABCB5). The reference catfish genome has been published (Liu et al., 2016). The identified large number of SNPs was used for 250K SNPs mapping on the linkage map and development of high-density (690K) SNP arrays for genomic studies of cultured traits in catfish (Zeng et al., 2017).

Response to selection at the genomic level was also studied in invertebrates, including the second generation of a breeding programme of blue mussel (*Mytilus galloprovincialis*) in Australia (Nguyen et al., 2014). To assist the reconstruction of a pedigree from families, a panel of 179 SNPs was developed. In the second generation, heritability of total weight, shape and meat yield were estimated. The selection response was up to 10%, indicating that further genetic gains can be achieved through a family-based breeding programme. Recently, SNPs have been used also in studies of *Mytilus* from other geographic regions (Kijewski et al., 2009; Vera et al., 2010; Zbawicka et al., 2012; Wennerstrom et al., 2013; Zbawicka et al., 2014; Pino-Querido et al., 2015; Wenne et al., 2016a; Jilberto et al., 2017).

GS can considerably increase genetic gain in traits of interest and is suitable for analysis of polygenic traits. GS can be used to enhance existing salmon-breeding family-based schemes by incorporation of within family breeding values estimated with low density genotyping (Lillehammer et al., 2013). Alternatively to QTL and between-family genetic variation, due to the complex genetic architecture, application of a whole genome-enabled selection turned out to be a better strategy for improving rainbow trout genetic resistance against BCWD (Vallejo et al., 2016). GS was based on using high-density SNP genotype data and phenotypic records in order to compute genomic estimated breeding values (GEBVs). Individual fish representing 10 families from the first generation of the National Center for Cool and Cold Water Aquaculture (NCCCWA, USA) BCWD resistant breeding line were genotyped with the rainbow trout 57K SNP array and using restriction-site associated DNA (RAD) sequencing. The RAD genotyping platform had similar

predictive ability to GEBVs in comparison with those from the chip platform. A more thorough study of the farmed rainbow trout was carried out on larger number of specimens and full-sib families, and the GEBV based breeders mating design for progeny testing (Vallejo et al., 2017). The accuracy prediction of genomic-enabled breeding values from three GS models: single-step genomic best linear unbiased prediction (ssGBLUP), weighted ssGBLUP (wssGBLUP), and BayesB was twice that of the P-BLUP model EBV. The proportion of the phenotypic variance explained by SNPs significantly associated with resistance to salmon rickettsial syndrome (SRS) caused by *P. salmonis* was found to be low (Correa et al., 2015). Therefore GS was used in further attempts to improve genetic resistance to SRS (Bangera et al., 2017). The GBLUP method for application in the GS evaluation and optimization of SNP density may reduce costs of genotyping.

Sea lice *Lepeophtheirus salmonis* and *C. rogercresseyi* are an ectoparasitic copepod infecting salmon and rainbow trout respectively in northern and southern hemispheres. In addition to inflicting substantial economic losses to farmed and wild fish, both species can be vectors for other pathogens. Resistance of Atlantic salmon to sea lice has been found as polygenic (Tsai et al., 2016a). A comparison of genomic selection methods was performed for *C. rogercresseyi* resistance based on genotyping with an SNP array (Correa et al., 2017). Atlantic salmon 2404 individuals from 118 families were challenged and genotyped using 37K SNPs. Prediction accuracy of EBV for *C. rogercresseyi* resistance increased with increasing density of SNPs selected from the panel used for genotyping. The accuracy prediction for at least 500 SNPs was higher than pedigree-based BLUP methods. The best results were obtained with 10K SNPs using G-BLUP and Bayesian methods.

11 Traceability of aquaculture production

The successful use of SNPs in the identification of species, populations, aquaculture stocks and parentage assignments has lead to their positive evaluation for traceability in fisheries and wildlife forensics (e.g. Atlantic cod *Gadus morhua* and sole *Solea solea* (Bylemans et al., 2016)), aquaculture (e.g. Atlantic salmon *S. salar* in Norway, (Hayes et al., 2005)), and sea and freshwater wild and farmed food products including caviar (e. g. sturgeon, Ogden et al., 2013). DNA markers can be used to trace aquaculture species as market products to farm of origin in case of disease or toxin detection. The Atlantic salmon industry involves 3 tiers: nucleus specimens, multiplier herd, and commercial fish. The number of SNPs required for correct assignment of market place fish to full sib families on a single farm was up to 400, to multiplier individuals (parents) it was 74 and to nucleus individuals, was 200. SNPs have been used for species identification of food products as tuna (Kitaoka et al., 2008) and food product origin, including sturgeon caviar origin (Jenneckens et al., 2001; Ogden et al., 2013).

12 Aquaculture food product quality analyses

Aquaculture is a growing food production industry and the nutritional value of marine products, rich in micronutrients and containing high levels of n −3 FAs, compares favorably with meat from farm animals (Gjedrem et al., 2012). The quality of aquaculture products depends on harvest traits suchas body weight traits, flesh color and fat percentage and composition. In order to study the genetic basis for growth and fillet traits suchas weight and flesh color in farmed Atlantic salmon (*S. salar*), offspring with trait records were genotyped for the SNPs (Tsai et al., 2015a). Genome-wide significant QTL affecting several growth-related traits were identified on 4 chromosomes. The traits were polygenic and QTL affected the weight of several components of the harvested fish. Comparison of QTL regions in this and other studies suggests that harvest trait QTL is population-specific. Therefore, the application of marker or genomic selection for improvement in these traits can be more effective when the discovery population is closely related to the selection candidates, e.g. within-family genomic selection. In a study, it was found that a SNP variation in the 5′flanking region of the myostatin gene can be associated with harvest trait (growth) in Atlantic salmon (Penaloza et al., 2013). An Atlantic salmon array containing 5650 genome-wide distributed SNPs was used to identify genetic variation affecting fillet fat content and fillet firmness traits in farmed Norwegian Atlantic salmon (Sodeland et al., 2013). Validation of results from GWAS was performed by estimation of variance components for chromosomes based on SNPs. Results from GWAS and genome partitioning suggested that genetic variation affecting fillet fat content is located on chromosomes 9 and 10, and that genetic variation affecting fillet firmness on chromosomes 3 and 11. An array with a larger number of SNPs (38 107) was used in GWAS analysis for fillet yield, body weight, head-off carcass weight, and fillet weight in a pedigreed rainbow trout stock selected for improved growth performance (Gonzalez-Pena et al., 2016). SNP polymorphism was studied for 875 fish from full-sib families in three generations. Panels of 20 adjacent SNPs were created and used in the GWAS analysis. A few panels were found to explain very low level of variance indicating a polygenic nature of the studied traits. A majority of the identified SNPs were mapped to genes, and the gene network was considered to be involved in differentiation of growth and fillet yield in rainbow trout. A genome-wide scan revealed 4 QTL affecting flesh fat content for common carp *C. carpio* (Kuang et al., 2015). Polymorphism of SNPs in the lipoprotein lipase, an enzyme which catalyzes the oxidation of triglycerides into glycerin and FA, was associated with 2 different feeding preferences of wild and aquacultured mandarin fish *S. chuatsi*, this can be helpful in further domestication processes (Yang et al., 2011).

Fish oils are the most common source of source of n – FAs and their intake is negatively related to human cardiovascular disease risk (Fernandes et al., 2012; Tur et al., 2012). Marine organisms are a well established source of n – 3 PUFA. The primary producers of lipids and FAs enriched with n – 3 PUFA are bacteria, phytoplankton, algae and diatoms, which are grazed by zooplankton, pelagic and benthic animals, including filtrators such as marine bivalves and crustaceans, fish and marine mammals. Marine bivalve lipids have been well characterized (Baptista et al., 2014; Jarzebski et al., 1986a; Jarzebski and Wenne, 1990; Jarzebski et al., 1986b; Polak et al., 1987; Wenne and Polak, 1989; Wenne and Styczynska-Jurewicz, 1987). Long-chain FA-CoA ligases (ACSLs) play crucial roles in FA metabolism. A significant increase in

expression of ACSL1 level in a starvation experiment indicated its important role in metabolism and energy supply and storage in hepatopancreas in the clam *Meretrix meretrix* (Dai et al., 2015). Two exon SNPs and 6 intron SNPs were found in this gene by direct sequencing. Five of these SNPs and haplotypes were significantly associated with growth traits. Replacement fish meal and fish oil by soybean protein and algal meal from *Schizochytrium limacinumin* diets for giant grouper *Epinephelus lanceolatus* demonstrated that fillet FA profile of fish reflected dietary composition and was significantly affected by the lipid source (García-Ortega et al., 2016). However, possible association of SNPs with FA biosynthesis and composition have been reported for agriculture plants (Ben et al., 2017; Li et al., 2017a; Qu et al., 2017) and animals (Cosenza et al., 2017; van Son et al., 2017; Zhu et al., 2017), and very rarely in fish. A genome-wide scan for QTL affecting FA level in flesh (fillets), including n – 3 polyunsaturated FAs (PUFA) was performed in an Asian seabass *L. calcarifer* F-2 family containing 314 offspring (Xia et al., 2014). High percentages of n – 3 PUFA, especially C22:6 and C20:5 were observed in the flesh. All family members were genotyped using 22 SNPs, and microsatellites. QTL for total n − 3 PUFA content in flesh, QTL for C18:0b and C22:6 were found. EcoRI-NlaIII based GBS of a few hundred individuals of large yellow croaker *L. crocea* resulted in finding 69 845 SNP markers distributed along the entire genome (Xiao et al., 2016). The association of 39 significant SNPs was found with the content of eicosapentaenoic acid and docosahexaenoic acid in the muscle. SNP markers were mapped to functional genes involved in lipid digestion, absorption, and metabolism, such as apolipoprotein B, carnitine O-acetyltrasferase, oxysterol binding protein 10 andpalmitoyl-protein thioesteraes 2 Gene.

13 Conclusions

Analysis of SNPs has emerged as a genotyping technology with wide and significant applications in aquaculture. SNPs can be used for construction of high-density and high-resolution genetic linkage maps, finding QTL for useful traits like growth, body weight, morphological characters, grilsing, thermal and low oxygen tolerance, resistance to stress and diseases, mapping sex determination loci and identification of progeny in selection and chromosome manipulation experiments and assessment of genomic selectionin aquaculture. SNPs are used for identification of region-selective sweeps (containing genes) in the genome, which are related to useful traits for aquaculture. SNPs are useful also to identify genes, sequences and nucleotides (substitutions) directly influencing phenotypic variations, thus opening the possibility of marker assisted selection for desirable characters/traits in culture. If a sufficiently large number of SNPs is discovered and used, mutations in genes associated with a trait can be identified. The identified genotypes can be used in marker assisted selection. A large number of SNPs used in a study is feasible for analysis of polygenic (complex) traits and facilitates the finding of genotypes useful for aquaculture.

Re-sequencing of genomes of several individuals belonging to the same species gives the possibility to obtain from dozens of thousands to dozens of millions SNPs (Abdelrahman et al., 2017; Yue and Wang, 2017). However, this approach is still expensive and time-consuming. SNPs associated with traits of choice (phenotypes) can be identified by using complexity reduction strategies through NGS such as RNA-seq, GBS (Elshire et al., 2011), multiplexed shotgun genotyping (Andolfatto et al., 2011) and restriction-site associated DNA sequencing (RAD-seq). Moreover, several RAD variants was developed with differences in the protocol: the original RAD (mbRAD) (Miller et al., 2007; Baird et al., 2008), ezRAD (Toonen et al., 2013), ddRAD (Peterson et al., 2012) and 2bRAD 2b-RAD (Wang et al., 2012); for details see review (Davey et al., 2013; Andrews et al., 2016). SNP genotyping can be performed on low or massive scale depending on the defined aims of research. Such methods as matrix-assisted laser desorption ionization time of flight (MALDI-TOF) mass spectrometry, Taqman allelic discrimination, real-time (quantitative) PCR and microarray or gene chips have been used in many studies related to aquaculture (Liu and Cordes, 2004). These methods have been improvedand their yield increased. Arrays with thousands or hundreds of thousands of SNPs have become a new high throughput genotyping tool. Usually, a large number of SNP loci is needed for evaluation of differences and changes in aquacultured stocks and estimation of genome wide linkage disequilibria. Strength of linkage disequilibria and genome size determine number of SNPs on array needed for GWAS and discovery of QTLs. Most of these assayed loci however are not informative, but it is now possible to identify several tens rather than hundreds of polymorphic and diagnostic SNP loci and subsequently use them for cost effective genotyping or few SNPs strongly associated with targeted economically useful trait. In case of complex traits, genomic selection is more feasible. Genotyping bygenome-reduction complexity sequencing can be recommended as an efficient and applicable technology in genomic selection.

In recent years, new methods of genetic engineering have been developed, which enable more precise characteristication and altering of gene function. Such technologies as zinc-finger nucleases, transcription activator-like effector nucleases and clustered, regularly interspaced, short palindromic repeats (CRISPR)–CRISPR-associated (Cas) systems (CRISPR/Cas9) have emerged as new tools for potential improvement of aquacultured fish (Cui et al., 2017; Li and Wang, 2017). The CRISPR/Cas9 gene editing technology has been used to generate lines of site directed mutated cell lines of Chinook salmon *O. tshawytscha* (Dehler et al., 2016) and can be used for determination of SNP function and QTL assessment (Macqueen et al., 2017). However, these technologies can be potentially used in highly developed large scale aquaculture systems.

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