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What role for genomics in fisheries management and aquaculture?

Roman Wenne[1,a], Pierre Boudry[2], Jakob Hemmer-Hansen[3], Krzysztof P. Lubieniecki[4], Anna Was[5] and Antti Kause[6]

[1] Department of Genetics and Marine Biotechnology, Institute of Oceanology, Polish Academy of Sciences, Powstańców Warszawy 55, 81-712 Sopot, Poland
[2] IFREMER Laboratoire de Génétique et Pathologie, 17390 La Tremblade, France
[3] Danish Institute for Fisheries Research, Department of Inland Fisheries, Vejlsøvej 39, 8600 Silkeborg, Denmark
[4] Department of Molecular Biology and Biochemistry, Simon Fraser University, 8888 University Dr., Burnaby, BC, V5A 1S6, Canada
[5] Molecular Ecology Research Group, Galway-Mayo Institute of Technology, Galway, Ireland
[6] MTT Agrifood Research Finland, Biotechnology and Food Research, Biometrical Genetics, 31600 Jokioinen, Finland

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Abstract – The development and application of genomics has been facilitated in a number of fields by the availability of new methodologies and tools, such as high throughput DNA sequencing and complementary DNA (cDNA) microarrays. Genomic tools are already used in research on commercially important fish and shellfish species. Thousands of expressed sequence tags (EST) are now available for some of these species, and the sequencing of complete genomes of tilapia, cod, salmonids, flatfishes, sea bass and Pacific oyster has been proposed. Microarray technology through simultaneous analysis of the expression of thousands of genes allows the identification of candidate genes involved in the function of multiple physiological, morphological and behavioural traits of interests in organisms and populations from different environments. This paper reviews the current development of genomic technologies, and pinpoints their potential beneficial applications as well as implications for fisheries management and aquaculture.

Key words: Genomics / Genetics / Fisheries / Mariculture / Quantitative trait loci / Fish / Oyster

Résumé – Quel rôle pour la génomique dans la gestion des pêches et de l'aquaculture ? Le développement et l'application de la génomique ont été facilités dans un certain nombre de domaines par la disponibilité de nouveaux outils et de nouvelles méthodes, tels que le séquençage d'ADN à haut débit et les puces à ADN (« microarrays »). Les outils de la génomique sont déjà développés sur les espèces de poissons et d'invertébrés d'importance commerciale. Des milliers d'étiquettes, marqueurs de séquence exprimée (EST) sont désormais disponibles pour quelques unes de ces espèces et le séquençage du génome complet de tilapia, de la morue, de salmonidés, de poissons plats, du bar, et de l'huître creuse sont demandés. La technologie des puces à ADN, au travers d'analyse simultanée de l'expression de milliers de gènes, permet l'identification de gènes candidats impliqués dans les multiples fonctions physiologiques, morphologiques et comportementales chez les organismes et les populations d'environnements variés. Cet article présente la synthèse de récents développements de ces technologies du génome, et met en évidence leurs applications potentielles ainsi que les implications dans la gestion des pêches et de l'aquaculture.

1 Introduction

It is well recognised that fisheries catches have reached a plateau in recent years. Due to the high demand for fish and shellfish on the global market, aquaculture production contributes an increasing amount to the food supply. Management of exploited wild stocks is undergoing systematic improvement. Results of population genetic investigations have recently been incorporated as a useful tool in stock identification in addition to morphological, biological and physiological traits. The aquaculture industry has expanded especially in South America and Asia, from where aquaculture products are also exported world-wide. Simultaneously, industry practices should be sustainable and marine biodiversity should be maintained. Genomics tools combined with the already well-established aquaculture and fisheries management practices can serve as a novel framework for such developments. Genomics is a field of science that deals with the structure, function and evolution of genomes. Many current DNA and

[a] Corresponding author: RWenne@iopan.gda.pl

RNA-based studies fall into this field, even if they are often not strictly part of it. Genomics often simply implies the use of high throughput DNA- or RNA-based methods. It comprises comparative, functional and environmental genomics. Comparative genomics examines whole genomes, their gene content, gene order, structure, evolution and taxonomy. Functional genomics investigates the biochemical and physiological role of gene products and their interactions on a large or small scale. Environmental genomics encompasses studies of molecular variation in natural or artificial populations of different taxa and their response to environmental conditions such as temperature or pollutants. One of the main efforts in genomics has been to obtain high numbers of large pieces of genome sequences and to assemble them into full chromosomal sequences. Another goal has been to study the expression of thousands of genes using techniques such as microarrays or other high throughput expression RNA profiling (i.e. transcriptomics). The analysis of the immense amount of data generated by such approaches often requires the use of specific computerised methods, or "bioinformatics". The knowledge of genomics opens new perspectives for the biotechnology of marine organisms, with implications for fisheries and aquaculture.

2 Sequencing and analyses of genomes

Sequencing of genomes facilitates the development of a variety of DNA-based genetic markers that can be used for the management of wild and cultured populations. Expressed Sequence Tags (EST) are obtained by sequencing complementary DNA (cDNA) libraries. Such libraries can be obtained from tissue specific libraries or generated by Suppressive Subtractive Hybridization (SSH). EST databases for various important marine species have been established (e.g. in Atlantic salmon *Salmo salar*: http://web.uvic.ca/cbr/grasp/ and oyster *Crassostrea gigas*: http://www.ifremer.fr/GigasBase/) and most sequences are submitted to databases (http://www.ncbi.nlm.nih.gov/Genbank/, http://www.ncbi.nlm.nih.gov/sites/entrez, http://compbio.dfci.harvard.edu/tgi/). EST are the first step towards obtaining full-length cDNA and gene sequences. Sequencing of whole fish and shellfish genomes contributes not only to the understanding of vertebrate and invertebrate evolution but also to environmental genomics and aquaculture (Crollius and Weissenbach 2005; Cossins and Crawford 2005). Full genome sequences are now available for a few model fish species such as zebrafish *Danio rerio* (http://www.sanger.ac.uk/Projects/D_rerio/), fugu *Takifigu rubripes* (http://www.fugu-sg.org/), puffer fish *Tetraodon nigroviridis* (http://www. genome.gov/11008305), medaka *Oryzias latipes* (http://dolphin.lab.nig.ac.jp/medaka/index.php) and stickleback *Gasterosteus aculeatus*: (http://www.genome.gov/12512292). To date, only one commercially important fish – *Tilapia* (Cichlid Genome Consortium, http://hcgs.unh.edu/cichlid/) has obtained funding for sequencing; however, knowledge of the genome sequences of other commercially important species is critical for an efficient identification of economically important genes and polymorphisms. Recently, international collaborative initiatives have been undertaken with the aim of obtaining full or partial genomic sequences of commercially important fish and shellfish species such as salmon and rainbow trout (cGRASP, www.cgrasp.org), cod (www.codgene.ca), sea bass *Dicentrarchus labrax* (Chini et al. 2006) and the Pacific oyster *Crassostrea gigas* (Hedgecock et al. 2005). Full genome sequences can be based on the sequencing and assemblage of bacterial artificial chromosomes (BAC) containing DNA fragments of the whole target genome, or using shotgun approaches. BAC libraries are available for Atlantic salmon (Thorsen et al. 2005), rainbow trout *Oncorhynchus mykiss* (Palti et al. 2004), sea bass (Whitaker et al. 2006), channel catfish *Ictalurus punctatus* (Quiniou et al. 2003) and oysters *Crassostrea virginica* and *C. gigas* (Cunningham et al. 2006), and they have been used to construct physical maps (e.g. salmon, Ng et al. 2005; sea bass, Volckaert et al. 2006 and channel catfish, Quiniou et al. 2007).

3 Fisheries

3.1 Discrimination of wild populations

Population genetic research has contributed substantially to our understanding of how fish and shellfish species are genetically structured into reproductively isolated populations throughout their distributions. Such knowledge is of major importance for fisheries management because local populations are often considered worth conserving due to their unique contribution to the genetic diversity of the species, which may allow them to sustain productivity in changing environments (e.g. Hilborn et al. 2003). In addition, local populations are often adapted to local environmental conditions and are therefore characterised by unique morphological, physiological and life history traits that have a genetic basis and are therefore of conservation interest. Moreover, such populations are often of great economic interest. However, the actual genetic basis of quantitative traits remains largely unknown, because their analysis has, until recently, been logistically difficult and time consuming to conduct in most species. Thus, the identification of local adaptations in natural populations has recently been highlighted as worthy of special attention in the years to come (e.g. Moritz 2002; van Tienderen et al. 2002; ICES 2006).

Many fish and shellfish populations have been over exploited or reduced by changes in local environments. These populations are endangered and some indigenous populations are already extinct (e.g. Dulvy et al. 2003; Reynolds et al. 2005), and hence there is an urgent need for knowledge on the basic population structure of many species. Various genetic markers have been used in order to identify and characterise populations. Studies using markers such as allozymes, mitochondrial (mt) DNA polymorphism, microsatellites, restriction fragments length polymorphism (RFLP) and recently, amplified fragments length polymorphism / random amplified polymorphic DNA (AFLP/RAPD) have successfully demonstrated significant genetic differences between populations of many species. However, these markers represent only a small fraction of the total genomic polymorphism. Furthermore, they are mostly believed to be selectively neutral, and have thus mainly been used to draw inferences about the interplay of gene flow, genetic drift and historical processes, thereby limiting inferences about local adaptations in the species under

study. Single nucleotide polymorphisms (SNP) is a new class of genetic markers with powerful applications in population genetics (Morin et al. 2004). It will be very helpful in managing natural and captive populations in the future. SNP can be identified in inter-individual comparison of genomic DNA sequences (e.g. Smith et al. 2005a) or sequences derived from EST (e.g. Hayes et al. 2007). Thus, both coding and non-coding DNA sequences can be used to identify SNP and several recent studies have used some of these approaches for initial SNP identification in species of relevance to fisheries and aquaculture (e.g. salmon, Ryynänen and Primmer 2006; Hayes et al. 2007; rainbow trout, Smith et al. 2005a and Arctic charr *Salvelinus alpinus*, Tao and Boulding 2003). Currently, highly informative (i.e. highly divergent) SNP can be used to discriminate between natural populations of both salmon (e.g. Smith et al. 2005b) and Atlantic cod (Stenvik et al. 2006).

Newly developed techniques enable screening for polymorphisms throughout the genome. Screening for many more loci will open new possibilities in population genetic research, moving to population genomics (Luikart et al. 2003). Global gene expression can be examined through the use of microarray techniques, enabling the simultaneous analysis of thousands of genes. Different expression levels can be observed in specimens originating from different localities and differing in functional traits (Rise et al. 2004a). Microarrays have been developed for a number of fish and shellfish species such as salmonids (Rise et al. 2004a; von Schalburg et al. 2005a), killifish *Fundulus* (Oleksiak et al. 2002), carp *Cyprinus carpio* (Gracey et al. 2004), zebrafish (Ton et al. 2002), catfish (Li and Waldbieser 2006), medaka (Kimura et al. 2004), European flounder *Platichthys flesus* (Williams et al. 2003), Japanese flounder *Paralichthys olivaceus* (Kurobe et al. 2005), mussel *Mytilus galloprovincialis* (Venier et al. 2006) and Pacific oyster (Lang et al. 2006). However, even if arrays have not been developed for a species, reliable estimates of gene expression may still be achieved through alternative measures such as cross species hybridization (Renn et al. 2004) or the use of non-array based quantification of gene expression, such as cDNA-AFLP or differential display (Breyne et al. 2003; Venkatesh et al. 2005). It should be noted that gene expression analyses essentially measure expression phenotypes. The degree of heritability of gene expression traits has rarely been assessed, but is often assumed (Gibson and Weir 2005). For these measures to be used to illustrate population genetic differences, the environment needs to be controlled to rule out environmental effects on gene expression. Therefore, analyses of global gene expression require common garden approaches. Still, if properly designed such studies have great potential to disclose the genetic basis of adaptations in local populations of fish and shellfish (e.g. Whitehead and Crawford 2006; Larsen et al. 2007)

Genome scans are another important group of genomic tools applying the screening of a high number of markers to cover the entire genome of a species under study (e.g. Luikart et al. 2003; Storz 2005). Genome scans allow for the identification of outlier loci that are potentially under selection or linked to a locus under selection (i.e. hitch-hiking selection, Maynard Smith and Haigh 1974), thereby facilitating detection of the genetic basis of local adaptation in natural populations. Outliers can be detected using model based (e.g. Beaumont and Nichols 1996) or model free (e.g. Schlötterer 2002; Kauer et al. 2003) methods. Conclusions with respect to outlier status of particular loci will often be considerably strengthened, if signals of selection are supported by several different analytical approaches as well as different pairwise population comparisons (e.g. Vasemägi et al. 2005; Bonin et al. 2006). Allozymes, microsatellites and AFLP have been used in genome scans in non-model species (e.g. Storz and Dubach 2004; Vasemägi et al. 2005; Bonin et al. 2006), but SNP will also be very useful for these approaches (see e.g. Akey et al. 2002). A major advantage of genome scans is that they can be applied to natural populations, thereby increasing the number of species for which such approaches are possible.

3.2 Future applications in management and conservation of natural populations

Genomics offers new and exciting possibilities for conservation genetics in several ways. First of all, the number of neutral genetic markers available will increase for most species. This will likely improve estimates of the effects of demographic processes, such as population declines and bottlenecks, effective population sizes, identification of wild and farmed individuals etc. (Morin et al. 2004; Kohn et al. 2006). It may also result in increased statistical power to detect minute levels of population structuring and to assign individuals of unknown origin to known baseline populations, for instance in mixed stock analyses (see e.g. Manel et al. 2005). In addition, the identification of outlier loci in genome scans offer new possibilities to identify informative markers which are suited for the specific question raised in each management scenario (see e.g. Banks et al. 2003; Beacham et al. 2004; Smith et al. 2005b).

Another, and very promising, application of genomics in relation to conservation is the detection of the genetic basis of local adaptation. Given that we know very little about this in most species of fish and shellfish, such knowledge will greatly improve our ability to manage genetic diversity in natural populations. The fact that genomic resources can sometimes be transferred between closely related species means that many species of fish and shellfish will effectively become "genome enabled" in the coming years (Storz and Hoekstra 2007), facilitating studies of the genetic basis of local adaptation.

3.2.1 Case study using Atlantic salmon

Atlantic salmon is one of the species of relevance to both fisheries management and aquaculture, where genomic resources are building up rapidly. Hence this species could serve as an important case study to demonstrate the resources that may become available in other species in the near future, as well as the potential applications of these resources. Genomic approaches in Atlantic salmon have targeted both RNA and DNA levels of variation. For instance, a salmonid microarray containing cDNA representing 16 006 genes has been developed. The genes spotted on the array have been carefully selected from Atlantic salmon and rainbow trout EST databases.

This array will serve as an important resource for genetic, physiological and ecological studies as well as many other fields of salmonid research (von Schalburg et al. 2005a). Gene expression patterns determined either for target genes or using microarrays have already been used to investigate the salmonid immune response, several disease processes and disease resistance (Lindenstrom et al. 2003, 2006; Rise et al. 2004b; Sigh et al. 2004; Bridle et al. 2006a,b; Fast et al. 2006; Martin et al. 2006; Purcell et al. 2006). Moreover, they have been used to survey the genes involved in the maturation and development of the rainbow trout ovarian and testicular tissues (von Schalburg et al. 2005b, 2006; Bonnet et al. 2007), to examine brain gene expression profiles in male salmon with different life history strategies (Aubin-Horth et al. 2005a,b), to carry out toxicogenomic profiling of hepatic tumour promoters in rainbow trout (Tilton et al. 2006), to investigate the response of the rainbow trout transcriptome to model chemical contaminants (Koskinen et al. 2004) and to study gene expression in atrophying muscle (Salem et al. 2006). Microarrays have also been applied to discriminate between farmed and wild Atlantic salmon using genome wide transcription profiles. Thus, similar transcription profiles characterised farmed strains from Norway and Canada and suggested adaptation via gene expression to common captive environments (Roberge et al. 2006).

The DNA level has been targeted through markers such as microsatellites and SNP. For example, Vasemägi et al. (2005) used EST linked microsatellites in a genome scan of natural populations of Atlantic salmon and identified a number of outlier loci potentially under selection and it has been shown that these markers can be used in other salmonids (Ng et al. 2005). SNP have been identified through different approaches. For example, five populations of chinook salmon *Oncorhynchus tshawytscha* from Pacific North America were surveyed for SNP at 19 loci by sequencing (Campbell and Narum 2007). Of these 13 were chosen for Taqman assays (5' exonuclease assays) out of 58 SNP. Similarly, 1195 SNP have been identified from EST and 121 of these have been characterised by pedigree analysis. As a result of the genome duplication that took place in common ancestor of extant salmonids 25–120 millions years ago (MYA), it has been estimated that up to 15–20% of salmonid loci have functional duplicates. Therefore, when identifying putative SNP in the Atlantic salmon EST database, it is important to be able to distinguish between true SNP (i.e., those corresponding to alleles at a single locus) and paralogous sequence variants (PSV; i.e., sequence differences between duplicate loci), (Wright J.J., Simon Fraser University, Burnaby, BC, Canada, pers. comm.; Hayes et al. 2007).

SNP with known locations on a linkage map can be used to identify QTL, which can subsequently be genotyped in natural populations. An example of such research is Atlantic salmon in which 4 full sib families (backcrossed F1 males to a female from European and American parental populations) were used to identify SNP for known QTL. The identified SNP in traits under selection will be genotyped in endangered wild Atlantic salmon to demonstrate genetic differences in functional traits among these endangered salmon populations and may help in their conservation (Boulding E.G., University of Guelph, Canada, pers. comm.).

The examples outlined above illustrate the immense potential that genomics has to improve both fisheries management and aquaculture. Particularly the last case shows how the two fields could be integrated through the availability of genomic resources, with considerable potential to advance conservation efforts in the species.

4 Aquaculture

4.1 Using genomic information in aquaculture breeding

4.1.1 Constructing DNA pedigrees

In breeding programmes, information on family relations of individuals is used when estimating genetic parameters (heritabilities and genetic correlations) and breeding values for traits, and when optimising selection and mating in order to avoid inbreeding. Similarly, pedigrees are useful in the management of conservation programmes and wild populations (e.g. when controlling inbreeding, Wilson and Ferguson 2002). In addition to physical individual tagging, pedigrees can be determined using DNA markers. This procedure is quite straightforward using microsatellites. Typically 10–20 variable genetic markers are needed to assign >95% of individuals to single pairs of parents (e.g. Vandeputte et al. 2006). To do this, one needs tissues samples from both potential parents and their offspring, and several freely available softwares exists for parental assignment (reviewed by Jones and Ardren 2003). Physical individual markers are useful when large facilities exist where family groups can be held separately until fish are large enough to be individually tagged. For instance, in salmonid breeding programs fish are typically held in hundreds of family tanks until they are individually tagged at a weight of approximately 50g (Kause et al. 2005). Using DNA pedigrees is useful in many aquaculture breeding and conservation programmes when individual tagging is difficult or when facilities for family tanks do not exist. Three examples of using DNA pedigrees are presented below: walk-back selection, estimation of genetic parameters, and conservation programmes.

Walk-back selection refers to a selection programme where a group of superior individuals are first selected, and then only the selected animals are genotyped for family relations. Using the established pedigree, only those superior animals that are not too closely related are used in matings (Doyle and Herbinger 1994; Sonesson 2005). This is an improved mass selection scheme to obtain genetic improvement while simultaneously controlling for inbreeding. This is cost-effective because only some hundreds of individuals among the potentially (tens of) thousands of individuals reared need to be genotyped. This is especially useful for species for which no extensive resources are available, or for new species whose reproduction cannot be fully controlled. Furthermore, there are studies showing that microsatellite markers are useful for determining the effective number of parents and their individual reproductive success (e.g. Boudry et al. 2002), and level of inbreeding in mass selection scheme in the Nile tilapia *Oreochromis niloticus* (Komen H., Animal Breeding and Genetics Group, Wageningen University, The Netherlands, pers. comm.) and

the flat oyster, *Ostrea edulis* (Launey et al. 2001). A full population can be genotyped for parental analysis, which allows one to estimate heritabilities and genetic correlations to traits of interest. Such an approach has been used on common carp (Vandeputte et al. 2005).

Likewise, DNA pedigrees are useful in conservation programmes of wild fish and shellfish, especially when aiming at controlling inbreeding. Microsatellite genotyping in the induced mass spawns of lion-paw scallop *Nodipecten subnodosus* demonstrated that some parents contribute a much higher percent to the progeny than expected (Petersen J.L., Genomic Variation Laboratory, University of California Davis, Davis, CA USA, pers. comm.). Similarly, the impact of hatchery practices on the genetic variability of progenies can be monitored (Taris et al. 2006). That is, when the effective population size is reduced and inbreeding can decrease hatchery stocks. Microsatellite genotyping can be also useful in assessment of introgression to/from a natural population. Mutli-plexing (i.e. simultaneous PCR amplification) of microsatellites (e.g. Taris et al. 2005) and SNP-based parentage assignment (Rengmark et al. 2006; Anderson and Garza 2006) are now greatly facilitating these types of studies.

4.1.2 Marker assisted selection

Marker assisted selection (MAS) refers to a selection procedure which is improved using information from genetic markers. Allelic variation in genetic markers can be linked to the variation in traits of economic interest, and thus the marker provides DNA level information on the inheritance of the traits. MAS is especially useful for traits that are difficult to breed using traditional means. Such traits can be costly or difficult to record (e.g. feed efficiency, disease resistance, concentration of omega-3-acids), they may require slaughtering of individuals (e.g. fillet quality, body composition), may be from only one sex (e.g. caviar production), or they cannot be directly recorded from breeding candidates (e.g. sea performance when breeding candidates are held at a fresh water breeding station). Moreover, MAS can be used early in life to breed for traits that are expressed later in life (e.g. caviar production, maturity age), allowing one to cull the population to save feed and management costs (e.g. Martinez et al. 2005).

The practical use of markers in selection can be roughly divided into three classes: 1) removing genetic disorders, 2) marker breeding value-selection, and 3) genomic selection. These three methods differ in the complexity of computational selection tools needed and requirements of the genomic data. Recessive genetic disorders, determined by a simple Mendelian one-locus method can be effectively removed from a population using a gene test done on a small tissues sample. Individuals carrying a deleterious allele are culled, and no computationally demanding selection tools are needed. Such tests are in practical use in terrestrial farm animals (e.g. Sironen et al. 2006). Marker breeding values of individuals can be estimated by combining information on phenotypes and a single or several QTL segregating within a pedigreed population (Fernando and Grossman 1989). When estimating breeding values, genetic variation can be explained by the QTL effect(s) and the remaining polygenetic parts. For a QTL to be useful here, a genetic marker needs to be located very close to the actual gene, i.e., within less than 1 centi Morgan (cM). If this is not the case, then it is unlikely that the QTL will be applicable across the whole population, and the linkage between the marker and the gene will be broken down by recombination during the next few generations. Thus, QTL fine mapping is needed for the QTL to be practically useful. Marker breeding values are used in dairy cow selection, e.g., in France and Germany (Hayes et al. 2006a).

Genomic selection refers to selection directed on allelic variation identified across the whole genome. Allelic variation at thousands of loci as well as their effects on economic traits can be estimated, and genomic breeding values can be thus estimated (Meuvissen et al. 2001). After the effects of the alleles have been established, no phenotypic information on animals is needed in selection. The use of SNP analysis is the most promising method for such whole-genome analysis. Using current technology, variation in tens of thousands of SNP can be simultaneously estimated. For this method to be effective however, Hayes et al. (2006a) suggested that 10–20 QTL need to be found for each trait and up to 30 000 SNP may be needed to obtain a dense enough marker map. Methods to perform such analyses, together with genomic selection tools, are currently under development. Thousands of putative SNP have been detected in Atlantic salmon (Hayes et al. 2007). Sauvage et al. (2007) reported a very high level of DNA polymorphism in the Pacific oyster (i.e. one SNP every 60 bp in coding regions and one every 40 bp in non-coding regions).

4.1.3 Linkage maps and QTL in aquatic species

Linkage maps are needed for mapping major chromosome regions influencing phenotypic traits (i.e. QTL). Examples of published linkage maps for several major aquaculture species are given in Table 1. The list is illustrative rather than an exhaustive list of linkage maps. For most of the marker maps, the average distance between markers is 2–15 cM. An average marker distance of 20 cM would be suitable for the location of a QTL to a correct chromosome arm. A useful feature is that the male maps are often shorter than the female maps. Thus, the initial QTL mapping revealing chromosomes harbouring QTL can be more easily performed using male parents. Fine mapping of QTL positions, in turn, is more effectively performed using female parents (Hayes et al. 2006b). For fine mapping, a marker distance of 1 cM or less is needed.

A variety of markers have been used for identification of populations and strains in the wild and in aquaculture with the aim of improving management. These markers can be used for construction of high-resolution genetic linkage maps and search for QTL, and finally to MAS (Liu and Cordes 2004; Sarropoulou et al. 2005a; Senger et al. 2006; Silverstein et al. 2006; Montano-Perez et al. 2006). Table 2 presents an illustrative list of QTL studies performed on several aquaculture species. Two observations can be made from these studies. First, most of the studies are on growth-related traits, followed by disease resistance traits. Only a few studies exist for quality or feed utilisation traits. MAS will be especially useful for disease and quality traits. Second, most of the studies on aquatic species have not progressed to fine-mapping. Consequently, a

Table 1. A sample of published linkage maps on aquaculture species. If two values are given for a parameter, the first refers to the male and the second to the female map.

Species	Latin name	Number and type of markers in a map	Map length (cM)	Number of linkage groups	Average distance between markers (cM)	Reference
Vertebrate						
Sea bream	*Sparus aurata*	198[1]	1242	26	9.7	Franch et al. (2006)
Sea bass	*Dicentrarchus labrax*	162[1]	567 / 906	25	3.5 / 5.6[a]	Chistiakov et al. (2005)
Atlantic salmon	*Salmo salar*	251 / 230[1,2]	103 / 901	31 / 33	0.41 / 3.9[a]	Moen et al. (2004a)
		50[1]	n.a.	15	n.a.	Gilbey et al. (2004)
Rainbow trout	*Oncorhynchus mykiss*	476[1–6]	2628	31	5.6[a]	Young et al. (1998)
		1314[1–10]	4359	30	7.4	Nichols et al. (2003b)
		903[1]	2750	31	3.0[a]	Guyomard et al. (2006)
		209[1,6–8]	~ 1000	29	4.8[a]	Sakamoto et al. (2000)
Brown trout	*Salmo trutta*	279 / 242[1,7]	346 / 912	35 / 43	1.2 / 3.8[a]	Gharbi et al. (2006)
Pink salmon	*Oncorhynchus gorbuscha*	22[7]	n.a.	8	n.a.	Matsuoka et al. (2004)
Arctic charr	*Salvelinus alpinus*	301[1,2,8]	390 / 992	46	n.a.	Woram et al. (2004)
Tilapia	*Oreochromis niloticus*	162[1,2]	704	30	4.3[a]	Kocher et al. (1998)
Tilapia	*O. niloticus* × *Oreochromis aureus*	545[1,8]	1311	24	2.4[a]	Lee et al. (2005)
Tilapia	*O. niloticus* × *O. aureus* × *O. mossambicus*	214 / 62[1,2]	1632 / 514	24 / 14	7.6 / 8.3[a]	Agresti et al. (2000)
Common carp	*Cyprinus carpio*	268[1,6]	4111	50	15.3[a]	Sun and Liang (2004)
Channel catfish	*Ictalurus punctatus*	418[2]	1593	44	3.8[a]	Liu et al. (2003)
		262[1]	1958	32	8.7	Waldbieser et al. (2001)
Walking catfish	*Clarias macrocephalus*	134[2]	2037	31	17.1	Poompuang and Na-Nakorn (2004)
Japanese flounder	*Paralichthys olivaceus*	231 / 304[1,2]	741 / 670	25 / 27	8.0 / 6.6	Coimbra et al. (2003)
Ayu	*Plecoglossus altivelis*	178[1,2]	1660	36	11.7	Watanabe et al. (2004)
Invertebrate						
Pacific oyster	*Crassostrea gigas*	96 / 119[2]	758 / 1031	10 / 11	8.8 / 9.5	Li and Guo (2004)
		88 / 86[1]	616 / 771	11 / 12	8.0 / 10.4	Hubert and Hedgecock (2004)
Eastern oyster	*Crassostrea virginica*	114 / 84[1,2,10]	647 / 904	12 / 12	6.3 / 12.6	Yu and Guo (2003)
Blacklip abalone	*Haliotis rubra*	102 / 98[1]	621 / 766	17 / 20	7.3 / 9.8	Baranski et al. (2006)
Pacific abalone	*Haliotis discus hannai*	94 / 119[1,2,6]	1366 / 1774	19 / 22	18.2 / 18.3	Liu et al. (2006)
		167 / 160[1]	702 / 888	18 / 19	4.7 / 6.3	Sekino and Hara (2007)
Blue mussel	*Mytilus edulis*	116 / 121[2]	825 / 863	14 / 14	8.1 / 8.0	Lallias et al. (2007b)
European flat oyster	*Ostrea edulis*	137 / 149[2]	471 / 450	9 / 10	4.9 / 4.2	Lallias et al. (2007a)
Zhikong scallop	*Chlamys farreri*	197 / 166[2]	1631 / 1504	20 / 19	9.2 / 10.2	Li et al. (2005)
Sea urchin	*Strongylocentrotus nudus*	194[2]	2988	24	17.1	Zhou et al. (2006)
Sea urchin	*Strongylocentrotus intermedius*	199[2]	2615	23	15.4	Zhou et al. (2006)
Kuruma prawn	*Penaeus japonicus*	129[2]	1276	44	15.0	Moore et al. (1999)
		227 / 125[2]	1781 / 1026	43 / 31	9.7 / 10.9	Li et al. (2003)
Black tiger shrimp	*Penaeus monodon*	63[2]	1412	19	22	Wilson et al. (2002)
White shrimp	*Penaeus vannamei*	182 / 212[2]	2116 / 2771	47 / 51	15.6 / 17.1	Pérez et al. (2004)
Chinese shrimp	*Penaeus chinensis*	194 / 197[2]	1738 / 2191	36 / 35	11.0 / 13.5	Li et al. (2006b)

n.a. - Not available.

Types of genetic markers used: [1]- Microsatellites; [2]- AFLP Amplified fragment length polymorphism; [3]- VNTR Variable number of tandem repeats; [4]- SINE Small interspersed nuclear element; [5]- Minisatellites; [6]- RAPD Randomly amplified polymorphic DNA; [7]- Allozymes; [8]- SNP Single nucleotide polymorphism; [9]- RFLP Restriction fragment length polymorphism; [10]- SSCP Single strand conformation polymorphism.

[a] - Calculated as: map length / number of markers.

Table 2. A sample of published quantitative trait loci QTL studies in aquaculture species.

Species	Latin name	Traits studied	Reference
Vertebrate			
Atlantic salmon	*Salmo salar*	Infectious salmon anaemia	Moen et al. (2004b)
		Infectious pancreatic necrosis virus, furunculosis, infectious salmon anaemia	Kjoglum et al. (2005)
		Furunculosis, infectious salmon anaemia	Grimholt et al. (2003)
Atlantic salmon/Rainbow trout/ Arctic charr	*Salmo salar/Oncorhynchu mykiss/Salvelinus alpinus*	Body weight, condition factor	Reid et al. (2005)
Coho salmon	*Oncorhynchus kisutch*	Fillet colour	Araneda et al. (2005)
Rainbow trout	*Oncorhynchus mykiss*	Hatching time, embryonic length, weight	Martinez et al. (2005)
		Embryonic development rate	Robison et al. (2001)
		Development rate	Sundin et al. (2005)
		Body length, thermotolerance	Perry et al. (2005)
		Growth, condition factor, maturity age	Martyniuk et al. (2003)
		Spawning time	Sakamoto et al. (1999)
		Length, pyloric caeca, no of scales	Nichols et al. (2004)
		Pyloric caeca	Zimmerman et al. (2005)
		Thermotolerance	Jackson et al. (1998); Danzmann et al. (1999)
		Infectious pancreatic necrosis virus	Ozaki et al. (2001)
		Infectious hematopoietic necrosis	Rodriquez et al. (2004)
		Ceratomyxa shasta resistance	Nichols et al. (2003a)
		Killer-cell activity	Zimmerman et al. (2004)
		Albinism	Nakamura et al. (2001)
Arctic charr	*Salvelinus alpinus*	Growth rate	Tao and Boulding (2003)
Tilapia	*Oreochromis mossambicus* × *O. aureus*	Innate immunity, response to stress, growth	Cnaani et al. (2004)
Tilapia	*Oreochromis niloticus* × *Sarotherodon galilaeus* male × *O. mossambicus* × *O. aureus* female	Thermotolerance	Moen et al. (2004c)
Common carp	*Cyprinus carpio*	Cold tolerance	Sun and Liang (2004)
Japanese flounder	*Paralichthys olivaceus*	Lymphocystis disease resistance	Fuji et al. (2006)
Asian seabass	*Lates calcarifer*	Body weight, length, condition factor	Wang et al. (2006)
Invertebrate			
Eastern oyster	*Crassostrea virginica*	*Perkinsus marinus* resistance	Yu and Guo (2006)
European Flat oyster	*Ostrea edulis*	*Bonamia ostreaea* resistance	Lallias et al. (2007a)
Pacific abalone	*Haliotis discus hannai*	Shell, muscle, gonad, digestive gland and gill weight	Liu et al. (2007)
Kuruma prawn	*Penaeus japonicus*	Body weight, length	Li et al. (2006a)
Blue shrimp	*Litopenaeus stylirostris*	Infectious hypodermal and hematopoietic necrosis virus resistance	Hizer et al. (2002)

lot of effort must be focused on this area, in order for genomic studies to be useful in practical breeding programmes.

Studies of large scale gene expression using microarrays containing clones from cDNA libraries are helpful in the discovery of candidate genes for particular/multifactorial traits (Sarropoulou et al. 2005b). However, the challenge is to find between-individual variation in gene expression that could be exploited in selective breeding. By simply knowing that a certain gene is expressed or not is not enough, the gene must also display alternative gene variants that can be selected. Moreover, gene expression is tissue and time specific, inducing methodological challenges for the development of general selection tools. Hedgecock et al. (2007) recently reported transcriptomic analysis of growth heterosis in larvae using megacloning and massively parallel signature sequencing (MPSS) in the Pacific oyster *Crassostrea gigas*. Microarrays have been produced (Lang et al. 2006; Jenny et al. 2007) and are currently under development to study summer mortality following SSH approaches (Huvet et al. 2004; Saavedra and Bachère 2006).

4.1.4 Identification of sex determining factors

The understanding of sex determination systems is one of the most sought after aspects of genomics in finfish aquaculture. Aquaculture farmers often prefer to farm only one of the sexes, because of its superior characteristics (Kause et al. 2003). Moreover, production of sterile animals (e.g. using triploidy) will enable further reduction of risks related to escape effects of farmed animals on natural marine populations. Males are the heterogametic sex in Atlantic salmon and Arctic charr *Salvelinus alpinus*. Several microsatellite markers are linked to the sex-determining factor (SEX) in the linkage analysis (Woram et al. 2003; Artieri et al. 2006; Fujiki K. and Kwitkowski C.N., Simon Fraser University Burnaby, B.C. Canada pers. comm.). BAC or fosmid clones positive for these microsatellites were isolated from libraries. Fluorescence in situ hybridisation (FISH) was used to identify their positions on chromosomes. Fosmids, BACs and BAC-ends sequences were used for the identification of the SEX candidate genes. Despite the great recent progress in this area, the SEX factor(s) continues to be elusive in salmonids as well as in many other fish and shellfish species.

4.1.5 Cost-benefit analyses

The development and extensive use of genomic tools in selection are resource demanding. Consequently, a cost-benefit analysis would be useful for determining the advantage of using genomic tools. Break-even cost of genotyping depends on the efficiency of marker assisted selection (MAS, relative to traditional selection), the duration until the selected loci are fixed, the size of the producer level and costs of genotyping, as shown by the analysis of pig enterprise by Hayes and Goddard (2004). Likewise, breeders should determine in advance how MAS can be most effectively used. For instance, should all individuals be genotyped, should individuals be genotyped early in life or at maturity, should only pre-selected breeding candidates be genotyped, could within-family selection be effective, and what are the economical benefits and practical constraints of the alternative selection strategies. To date, no such studies have been performed in aquatic species.

4.2 Cultured fish and shellfish health

Genomics can help to overcome problems related to infectious diseases by better understanding host defence systems and identifying QTL or candidate genes. Aquaculture productivity is reduced by various pathogens. Examples of genomics based studies include oomycete *Saprolegnia parasitica* (Torto-Alalibo et al. 2005), a bacterial agent of cold-water disease *Flavobacterium psychrophilum* (Soule et al. 2005) and a parasitic protozoan ciliate *Ichthyophthirius multifiliis*, the agent of the white spot disease through virulent factors (Abernathy et al. 2007). The acute phase response following infection of catfish with *Edwarsiella ictaluri*, causing enteric septicaemia, was studied by high density in situ oligonucleotide microarray (Peatman et al. 2007). Numerous acute phase proteins were upregulated and many pathogen recognition receptors and chemokines were differentially expressed in the liver. These results were confirmed with real-time PCR. A candidate gene approach was employed to find markers associated with disease resistance in which 28 microsatellites located near and within the immune genes were developed (Karsi A., Mississippi State University USA, pers. comm.). Several microsatellites were associated with resistance and susceptible phenotypes. These markers have been incorporated in the catfish linkage map, which will facilitate finding resistance QTL and will help in development of MAS programmes. Cytokines are important immune system regulators in fish, and genomics and proteomics can help to develop vaccines and immunostimulants for aquaculture (Savan and Sakai 2006). Bao et al. (2007) identified 26 chemotactic cytokine genes, sequenced them and studied their expression in catfish.

Whirling disease, caused by *Myxobolus cerebralis*, strongly affects American hatcheries and certain natural populations of rainbow trout. A European hatchery Hofer strain exhibits almost complete resistance to this pathogen. Microarray technology was used to study differences in global gene expression between resistant and susceptible rainbow trout strains (Baerwald M.R., University of California, Davis USA, pers. comm.). Several candidate genes were discovered that indicate genetic mechanisms of resistance to whirling disease in fish. To pinpoint these genetic mechanisms of resistance, rainbow trout full sib families under hatchery conditions were exposed to the bacterial pathogen *Yersinia ruckeri*, which causes enteric red mouth disease and to *Flavobacterium psychrophilum* (Palti Y., NCCCWA-ARS-USDAKearneysville, USA, pers. comm.). Linkage disecquilibrium and the resistance to the pathogens was assessed by genotyping using microsatellites linked to the four major histocompatibility (MH) genomic regions, to toll-like receptor genes and to the two copies of tumour necrosis factor superfamily 13b. Knowledge of the base-line MH sequence variation in the broodstock and its association/linkage disequilibrium with resistance to specific pathogens is useful in monitoring loss of MH variability and the potential increase in susceptibility to other pathogens that are not part of the selective breeding. Atlantic salmon

T-cell receptor alpha/delta genes exhibit vast diversity for antigen recognition (Yazawa et al. 2007). Differences in susceptibility to infectious hematopoietic necrosis virus were studied with microarray technology between four salmonid species (*Salmo salar*, *Oncorhynchus nerka*, *O. keta* and *O. kisutch*). The observed differences were related to species-specific differences in viral ability to enter cells, and possibly to effectiveness in taking control over cellular mechanisms rather than from strength of the host immunological response (Miller K. and Traxler G., Pacific Biological Station Fisheries and Oceans, Nanaimo, Canada, pers. comm.).

Examples of related studies in cultured invertebrates involve activated protein kinase (AMP) and other elements of the immune system in peneid shrimps and Pacific oyster (*Crassostrea gigas*, Bachère et al. 2004). In oysters, the availability of animals selected to improve their resistance against diseases can greatly contribute to the identification of genes or proteins involved in defence mechanisms (e.g. summer mortality in *C. gigas*: Huvet et al. 2004; *Martelia sydneyi* in *Saccostrea glomerata*: Newton et al. 2004). Another pathogen of shrimp is the white spot syndrome virus, which can be controlled by the anti-viral immunity of injected double stranded (ds)RNA molecules and single stranded (si)RNA (Westenberg et al. 2005).

4.3 Alternative feed

Functional genomics can contribute to the production of new kinds of feed for cultured fishes. Two such examples are the possibility of production of novel feed sources (such as plant based protein for carnivorous fish) and terrestrial transgenic plant (e.g. soybean or rapeseed) as feed. The use of traditionally marine feed components for aquaculture faces lower availability of marine resources. These marine components can be replaced by terrestrial vegetable ingredients, as oils. However, the quality of vegetable oils needs to be improved in order to meet nutritional demands of farmed fish (Opsahl-Ferstad et al. 2003). Transgenic plants with increased amounts of some fatty acids in seeds, and with possibility of their extension into longer, marine – similar fatty acids can improve quality of vegetable oils for use as fish feed. Present evidence indicates that in salmonids, novel plant-based feed sources may induce only weak genotype-by-diet interactions that would need special attention from fish breeders (Quinton et al. 2007). However, novel feed ingredients may have deleterious effects on quality or biological efficiency of aquatic species, and it is a challenge to develop the feed and the hatchery animals further. Moreover, genomic approaches could also contribute to a better understanding of lipid pathways and synthesis of long chain polyunsaturated fatty acids, facilitating the selection of genotypes that produce a good performance when feed a low fish oil or protein diet.

5 Conclusion

- The implementation of genomic approaches should be encouraged in the fields of fisheries and aquaculture by supporting the development of genomic resources, such as BAC libraries, fine scale linkage maps, EST databases and expression profiling.
- Open access web-based resources, joining available genomic data (EST, mapping data, BAC fingerprinting and annotation) should be developed in order to favour integrated collaborations.
- Studies of local adaptations in the wild and hatchery populations should incorporate genomic approaches to further understand the footprints of selection at a genome wide level.
- The potential of molecular marker assisted selection and the domestication process in aquaculture species should be further explored, benefiting from the development of new genomic resources and computational and analytical tools.
- Current QTL studies have used sparse linkage maps. Thus, we do not have DNA markers that are located close enough to the actual gene that would allow their use in practical breeding programmes. Consequently, there is a need for denser genetic maps for aquaculture species.
- Most of the QTL studies are on growth related traits, and to a lesser extent on disease resistance traits. More QTL studies are needed on body composition, fillet/product quality, and feed efficiency.
- SNP data provide attractive possibilities for genomic selection. Genomic methods for SNP data analysis need further development.
- Alternative strategies of using genomic information in broodstock selection need to be assessed, and their cost-effectiveness needs to be evaluated.

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