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MARKER-ASSISTED SELECTION IN FISH: A REVIEW

ABSTRACT

10 The important economical traits like body growth, resistance to diseases, meat quality, etc.
11 highly influence the profitability of the food animals including fishes. The main target of
12 every selective breeding programme is to produce improve offspring for these traits.
13 However, improvement of performance traits through traditional phenotype-based selection
14 needs several generations to optimise these characters. Marker-Assisted Selection (MAS) is a
15 type of indirect method of selection of better performing breeding individuals. MAS is
16 beneficial when the traits are difficult and expensive to measure and low heritability and
17 recessive traits. MAS facilitate the exploitation of existing genetic diversity in breeding
18 populations and can be used to improve desirable traits in livestock. MAS depends on
19 identifying the link between a genetic marker and Quantitative traits loci (QTL). The distance
20 between marker and target traits determines the association of the marker with the QTL.
21 After identifying the markers linked to QTL, they can be used in the selective breeding
22 programme to select the brooders having better genetic potential for the targeted trait.
23 Improvement of performance traits through MAS is fast and more accurate and allows us to
24 understand the genetic mechanism affecting performance traits.

25

26 **Keywords:** Marker-Assisted Selection, Quantitative traits loci, genetic diversity, trait

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1.0 INTRODUCTION

30 Marker-Assisted Selection (MAS) is a type of biotechnology that uses molecular
31 genetic markers as a criteria for selecting a desired traits (Ashraf, 2012). Marker Assisted
32 Selection (MAS) is indirect selection process where a trait of interest is selected not based on
33 the trait itself but on a marker linked to it (Ribaut and Ragot 2007).

34 MAS is considered a “revolutionary” approach to traditional tree breeding as it allows
35 breeders to select individuals based on their genotypes, rather than being restricted to
36 phenotypic characteristics (Boopathi *et al.*, 2013).

37 Sax (1923) was the first to show how genetic factors influencing quantitative traits can be
38 identified using markers.

39 Recently MAS become very popular method of indirect selection for production of
40 the genetically improved offspring’s in aquaculture breeding programme. As most of the
41 performance traits such as growth or disease resistance are controlled by multiple genes and
42 therefore inherited as quantitative traits, analysis of their associated quantitative trait loci
43 (QTL) is an essential part of aquaculture genomics (Liu and Cordes, 2004). QTLs are largely
44 unknown genes that affect performance traits (such as growth rate and disease resistance) and
45 these are important to breeders.

46 MAS in a breeding context involves scoring indirectly for the presence or absence of
47 a desired phenotype or phenotypic component based on the sequences or banding patterns of
48 molecular markers located in or near the genes controlling the phenotype. The sequence
49 polymorphism or banding pattern of the molecular marker is indicative of the presence or
50 absence of a specific gene or chromosomal segment that is known to carry a desired allele
51 (Brumlop and Finckh, 2011).

52 Marker-assisted selection method (MAS) or genome-wide marker-assisted selection
53 method (G-MAS) was not widely used in aquaculture, but nowadays its use is increasing due
54 to its ease of use and quicker than traditional phenotype-based selection. Now it becomes a
55 fertile field of research for the aquaculture researchers to discover novel genetic marker that
56 can be used to link with the QTLs in selective breeding programmes (Hauser *et al.*, 2011;
57 Dichmont *et al.*, 2012; Abdul-Muneer, 2014).

58 In order to manage individual species effectively, identification of different species
59 from a mixed catch becomes important. DNA markers are widely being accepted not only to
60 obtain information about gene flow and allele frequencies in aquaculture practices but also to
61 identify hybrids. The majority of the markers, which are used in inter- and intra-specific
62 disparity, include RAPD for species and sub-species identification done in tilapia (Bardakci
63 and Skibinski 1994), and iso-enzyme used in intraspecific variations in Sparidae species
64 (Alarcón and Alvarez 1999). Similarly, Nijman *et al.*, (2003) reported the use of mtDNA
65 markers as an important tool in rapid detection of hybridization between species and
66 subspecies of livestock.

67 Markers tend not to have any biological effect, but rather can be thought of as notable and
68 constant points of reference within the genome (Guimaraes, Ruane, Scherf, Sonnino, and
69 Dargie, 2007). Markers can be found within the desired gene or, more commonly, linked to a
70 gene determining a trait of interest (Brumlop and Finckh, 2011; Guimaraes *et al.*, 2007).
71 Unlike genetic engineering, MAS does not alter the original DNA (Vogel and Van Aken,
72 2009); instead it uses genetic marker to identify naturally-occurring genetic variations among
73 individuals, with the intent of selecting those with the best potential to meet desired criteria
74 and objectives.

75 Marker Assisted Selection (MAS) provides several other benefits to breeders, in that
76 it can select for genes that demonstrate low heritability, have recessive alleles, and are
77 difficult, expensive, or time exhaustive to determine phenotypically (Boopathi, 2013a;
78 Brumlop and Finckh, 2011; Xu and Crouch, 2008). MAS also allows for gene pyramiding or
79 combining multiple genes within the same breeding line, while having fewer unintentional
80 losses and fewer selection cycles (Boopathi, 2013a; Xu and Crouch, 2008).

81 Furthermore, MAS may be viewed by the public with more support than genetic engineering
82 as breeders are not manually manipulating the genes, and thus all offspring inheritance occurs
83 naturally (Vogel and Van Aken, 2009). It is also believed that genetic markers may be
84 important in the assessment, conservation and use of diversity in germplasm and varieties
85 (Brumlop and Finckh, 2011).

86 Molecular marker maps have been constructed for a number of aquaculture species,
87 e.g. tilapia, *Clarias*, giant tiger prawn, kuruma prawn, Japanese flounder and Atlantic salmon,
88 although their density is generally low (Nichols *et al.*, 2003). As many preferred traits are not
89 observed until maturity, MAS eliminates this waiting period by allowing for the early
90 selection of desired genotypes at the seedling stage (Yanchuk *et al.*, 2002).

91 The desirable phenotypic variations in the performance traits of fishes are used to
92 increase the aquacultural yield, improve incomes of farmers and enhances food security
93 through selective breeding by choosing better-performed individuals. However, phenotype-
94 based selection needed considerable time to optimise the traits, so researchers are now
95 moving from phenotype based selection to genotype-based selection. The lacking of a
96 molecular marker is the main limiting factor for the realization of genotype based selection
97 potentials in fishes. However, with the advent of DNA-based genetic markers in the late
98 1970s and now the ease of the marker discovery through the next generation sequencing
99 allowed the researchers to identify large numbers of markers spreads throughout the genome

100 of any species of interest. The markers are used to detect linkage with the traits of interest,
101 thus allowing MAS finally to become a reality (Peterson *et al.*, 1990). This paper aim to
102 provide information regarding the technical aspect of MAS and the current application in
103 fisheries and Aquaculture in other to increase high quality production within a period of time.

104 **2.0 Marker Assisted Selection**

105 Incorporation of marker information into breeding programs in aiding identification
106 and selection of superior individuals has been widely studied (Bernardo, 1994; Han *et al.*,
107 1997; Xie and Xu, 1998; Romagosa *et al.*, 1999; Ayoub *et al.*, 2003; Jordan *et al.*, 2003).

108 Molecular markers in aquaculture and fisheries have been used for over 50 years
109 (Ryman and Utter, 1987; Liu and Cordes, 2004) and their use has steadily increased over the
110 last two decades (Park and Moran, 1994; Chauhan and Rajiv, 2010; Dichmont *et al.*, 2012;
111 Abdul-Muneer, 2014).

112 An important factor in MAS is the accuracy of estimating the genetic effects related to
113 the trait of interest. In contrast to genetic engineering (GE), MAS does not alter the original
114 DNA. Rather, it identifies whether the desired trait(s) are being expressed, so that individuals
115 with the best potential can be selected (Andersson, 2001).

116 Molecular marker analysis allows the identification of genome segments, so called
117 Quantitative Trait Loci (QTL), contributing to the genetic variance of a quantitative trait and
118 thus to select superior genotypes as these loci (Cannai *et al.*, 2003). Allelic variation in
119 genetic markers can be linked to the variation in traits of economic interest, and thus the
120 marker provides DNA level information on the inheritance of the traits.

121 The practical use of markers in selection can be roughly divided into three classes:

- 122 1) Removing genetic disorders,
- 123 2) Marker breeding value-selection, and
- 124 3) Genomic selection.

125 **2.4 MAS versus Phenotypic Selection**

126 Marker-Assisted Selection (MAS) will probably never replace Phenotypic Selection
127 (PS) entirely. There is no general pattern by which it can be predicted whether MAS or PS
128 will be more useful. Empirical comparisons of MAS and PS for increasing gain from
129 selection have been made in several studies. The outcomes of these studies are conflicting. In
130 some studies MAS is reported to be more effective/efficient than PS (e.g. Yousef and Juvik
131 2001; Abalo *et al.*, 2009) while other studies considered the two methods equal (e.g. Van
132 Berloo and Stam 1999; Willcox *et al.*, 2002; Hoeck *et al.*, 2003; Moreau *et al.*, 2004). In a

133 third group of studies PS proved to be more effective/efficient than MAS (e.g. Davies *et al.*,
134 2006; Wilde *et al.*, 2007) and in other comparisons the effectiveness/efficiency of MAS and
135 PS varied within the same study, depending on the populations or on the trait selected for
136 (e.g. FlintGarcia *et al.*, 2003b; Robbins and Staub 2009).

137 **2.5 Limitations of MAS**

- 138 • Cost
- 139 • Requirement of technical skill
- 140 • Automated techniques for maximum benefit

141 **2.6 Advantages of MAS**

142 In addition to the cost and time savings described above, for a number of breeding
143 scenarios, MAS methods are likely to offer significant advantages compared with
144 conventional selection methods. These scenarios assume the availability of markers for
145 multiple traits and take into consideration the advantages of MAS under optimum situations
146 (Dreher *et al.*, 2002; Dudley, 1993).

- 147 1. Gene stacking for a single trait: MAS offers potential savings compared with
148 conventional selection when it allows breeders to identify the presence of multiple
149 genes/alleles related to a single trait, and the alleles do not exert individually
150 detectable effects on the expression of the trait.
- 151 2. Early detection: MAS offers potential savings compared with conventional selection
152 when it allows alleles for desirable traits to be detected early, well before the trait is
153 expressed and can be detected phenotypically. This benefit can be particularly
154 important in species that grow slowly.
- 155 3. Heritability of traits: Up to a point, gains from MAS increase with decreasing
156 heritability. However, due to the difficulties encountered in QTL detection, the gains
157 are likely to decline beyond a certain threshold heritability estimate.

158 **2.7 Disadvantages of MAS**

159 Perhaps the greatest disadvantage of MAS is the time and financial investment
160 required
161 to develop markers that are widely applicable for traits of agronomic importance.
162 Often a marker developed in one or a few related genotypes will not work for
163 other genotypes in a breeding scheme due to allelic effects. Furthermore, development of
164 markers, particularly for QTL, is complicated by epistatic interactions and the critical need
165 for good quality phenotypic data.

166 **2.8 Quantitative Trait Loci**

167 In fish, several QTL studies have been published; in salmonids (Jackson *et al.*, 1998;
168 Johansen 1999; Robinson *et al.*, 1999; Sakomoto *et al.*, 1999; Marfyuniuk 2001, Ozaki *et al.*,
169 2001 Somorger 2001. Tao and Baiding 2003), in catfish (Liu *et al.*, 2003), in tilapia (Cnaani
170 *et al.*, 2003) and in silver barb (Hussain *et al.*, 2002).

171 Marker Assisted Selection (MAS) is followed by two steps, detection of molecular markers
172 associated with quantitative trait locus (QTL) and application of those markers.

173 The position of the chromosome that controls the economical important trait is termed as
174 QTL.

175 The concepts for detecting QTL were developed more than 90 years ago (Sax, 1923). In
176 aquaculture species, much effort has been applied for QTL mapping. QTLs are mapped by
177 linkage disequilibrium with molecular markers exhibiting Mendelian segregation.
178 Economically important traits are controlled by the single or group of gene.

179 The basic concept of QTL studies is to know the number and location of loci
180 associated with phenotypic traits (Mackay, 2001; Mauric io, 2001; Burt and Hocking, 2002;
181 Erickson *et al.*, 2004). Thus, candidate gene or molecular markers, resulted by QTL mapping,
182 could be used in MAS (Groenen *et al.*, 2000). QTL detection is an ongoing effort in
183 aquaculture species. More than 37 important traits have been located in about 20 aquaculture
184 species.

185 QTL mapping is the practical application of marker-assisted selection in aquaculture
186 (Al-Samarai, 2015). With rapid advancement of molecular technology, it is now possible to
187 use molecular marker information to map major quantitative trait loci (QTLs) on
188 chromosomes (e . g . , Paterson *et al.*, 1988,1991; Hilbert *et al.*, 1991; Jacob *et al.*, 1991;
189 Stuber *et al.*, 1992). Once QTL for a trait are identified, individuals can be selected for
190 breeding on the basis of marker alleles that segregate with favorable phenotypes (Lande and
191 Thompson, 1990). This strategy, known as marker-assisted selection (MAS), is particularly
192 useful for traits that cannot be measured on selection candidates directly, notably disease
193 resistance or meat quality traits (Sonesson, 2007a).

194 **2.8.1 QTL Detection for in Fish**

195 A number of genetic maps have been developed specifically to locate QTL in several
196 fish species. The first of such map was produced in Zebrafish (Postlethwait *et al.*, 1994;
197 Shimoda *et al.*, 1999), which is a non-aquacultural species. Among cultivable fish groups
198 low-density maps have been developed for salmonids (Sakamoto *et al.*, 2000; Ghabi 2001)

199 for catfish (Liu *et al.*, 2003; Poompuang and Na-Nakorn 2004) for tilapia (Kocher *et al.*,
 200 1998; Cnaani *et al.*, 2003), for Japanese flounder (Sanchez *et al.*, 2003), for red sea beam
 201 (Sakamoto *et al.*, 2003), for Oyster (Yu and Geso 2003), and for shrimp
 202 ([Http://shrimppmap.tag.csiro.au](http://shrimppmap.tag.csiro.au)).

203 **2.8.3 QTL Mapping in Fish**

204 Although in fish several studies have confirmed the existence of significant genetic
 205 variation for quantitative traits at commercial importance (Kause *et al.*, 2003) and have
 206 recognized the potential of MAS for their genetic improvement (Flint and Mott 2001). Thus
 207 far, very few QTL for production traits have been identified in fish (Sonesson 2003). Much
 208 effort is devoted to QTL mapping for growth, feed conversion efficiencies, disease resistance,
 209 fecundity, and spawning time (Dunham et al 2001).

210 Several QTL studies have been published in rainbow trout for temperature tolerance
 211 (Jackson *et al.*, 1998). Danzmann *et al.*, 199, Perry 2001), spawning time (Sakamoto *et al.*,
 212 1999; fish back et al 2000, O' Malley 2001); growth (Martynicik 2001), disease resistance
 213 (Ozaki *et al.*, 2001), and fitness traits (Somorjai 2001). Other notable QTL studies published
 214 in aquacultural fish species include: in tilapia for temperature and salinity tolerance
 215 (Streadman and Kocher 2002; Cnaan *et al.*, 2003), in catfish for feed conversion efficiency
 216 and bacterial septicaemia resistance (Liu 2003), in guppy for growth (Nakajima and
 217 Taniguchi 2002), in Atlantic salmon for infectious anemia resistance (Moen *et al.*, 2003 and
 218 in Arctic Charr for growth rates and fitness traits (Johansen 1999, Somorjai 2001).

219 In salmonids, QTL have been found related to body weight and size (Martyniuk *et al.*,
 220 2003; O'Malley *et al.*, 2003; Reid *et al.*, 2005), for colouration pattern (Streelman, Albertson
 221 and Kocher, 2003) and for one form of albinism (Nakamura *et al.*, 2001). Zimmerman *et al.*,
 222 (2005) found QTL for pyloric caeca number, a trait related to feed conversion efficiency.

223 **Table 1: QTL studies in selected aquaculture species**

Species	Traits	Reference
Arctic charr	Body weight and sexual maturation; Salinity tolerance	Küttner <i>et al.</i> , 2011
Asian seabass	Resistance against viral nervous necrosis disease Growth-related trait Omega-3 fatty acids	Wang <i>et al.</i> , 2006 Xia <i>et al.</i> , 2014

Atlantic salmo	Growth traits and flesh colour Resistance against IPN Late sexual maturation	Baranski <i>et al.</i> , 2010; Tsai <i>et al.</i> , 2014; Moen <i>et al.</i> , 2009 ; Houston <i>et al.</i> , 2008 ; 2010 Gutierrez <i>et al.</i> , 2014
Catfish	Columnaris disease resistance ESC disease resistance Hypoxia tolerance Heat stress Head size	Geng <i>et al.</i> , 2015 Wang <i>et al.</i> , 2013; Zhou <i>et al.</i> , 2017 Wang <i>et al.</i> , 2016; Jin <i>et al.</i> , 2016 Geng <i>et al.</i> , 2016
Common carp	Common carp Morphometric traits Swimming ability	Zhang <i>et al.</i> , 2011 Boulton <i>et al.</i> , 2011 Laghari <i>et al.</i> , 2014
Eastern oyster	Disease resistance	Yu and Guo, 2006
European seabass	Growth, body weight Morphometric traits and stress Response	Louro <i>et al.</i> , 2016 Massault <i>et al.</i> , 2010
Pacific white shrimp	Growth parameters	Andriantahina <i>et al.</i> , 2013
Giant tiger prawn	Disease resistance and sex determination	Robinson <i>et al.</i> , 2014
Japanese flounder	Vibrio anguillarum resistance	Wang <i>et al.</i> , 2014
Pacific oyster	Growth Resistance against summer mortality Viability	Guo <i>et al.</i> , 2012 Sauvage <i>et al.</i> , 2010 Plough and Hedgecock, 2011 Plough <i>et al.</i> , 2016
Gilthead seabream	Skeletal deformities Sex determination and body growth	Negrín-Báez <i>et al.</i> , 2015 Loukovitis <i>et al.</i> , 2011 Massault <i>et al.</i> , 2011
Rainbow trout	Growth related traits	Kocmarek <i>et al.</i> , 2015; Wringe <i>et al.</i> , 2010; Leder <i>et al.</i> , 2006.

Tilapia	Growth traits Sex	Liu <i>et al.</i> , 2014; Wang <i>et al.</i> , 2015 Palaikostas <i>et al.</i> , 2015
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225 2.8.4 QTL analysis

226 1. QTL for growth traits

227 Growth is one of the most important economic traits of all aquaculture species. Up to
 228 2012, QTL analyses have been conducted in more than 20 aquatic species (Yue *et al.*, 2014),
 229 and growth is the most popular trait studied. Wang *et al.*, (Wang *et al.*, 2006) used 380
 230 F1 Asian seabass to identify five major QTLs and 27 potential QTLs. Of them, three major
 231 QTLs for body weight, length, and body length were located at a similar linkage group 2
 232 (LG2) position with the nearby Lca287 microsatellite and accounted for 28.8%, 58.9%, and
 233 59.7% of
 234 the phenotypic variations. The other two major QTLs for body weight were located at another
 235 LG2 position. These five major QTLs have been confirmed in two other Asian
 236 seabass populations (Wang *et al.*, 2008). Further QTL fine mapping of the Asian seabass
 237 growth trait identified three candidate “growth genes” (CATHEPSIN D, KCTD15, and
 238 CSMD2) affecting body weight, body length, and total length (Wang *et al.*, 2011). The
 239 function of the *cathepsin D* gene in humans involves cell proliferation and cell growth;
 240 therefore, *cathepsin D* may also be a major “growth gene” in Asian seabass. O’Malley *et al.*,
 241 (O’Maller *et al.*, 2008) identified QTLs for body weight in rainbow trout on 10 different LGs.

242 Wringe *et al.*, (2010) used additional backcrossed families and SSR markers to
 243 confirm the O’Malley *et al.*,’s results and found several major candidate growth genes (e.g.,
 244 *GH2* and *Pax7*). Reid *et al.*, 2004 identified a QTL for body weight in two LGs (AS8 and 11)
 245 of Atlantic salmon, and reported that it was homologous to the growth QTL in rainbow trout.
 246 Houston *et al.*, (2009) identified QTLs for body weight in LG1 and LG5 of Atlantic salmon.
 247 Gutierrez *et al.*, (2012) further used a 6.5 K SNP chip to identify QTLs in six LGs at the
 248 genomic level. Cnaani *et al.*, (2004) identified a QTL for tilapia growth on LG23, which is
 249 the linkage group with the genetic sex-determining region. Song *et al.*, (Song *et al.*, 2012)
 250 used 1487 SSRs to produce a high-density genetic linkage map and successfully identified a
 251 QTL affecting body weight in LG14 of Japanese flounder.

252 Some reports have used a candidate gene approach to identify growth-related genes
 253 and molecular markers in fish. Tao and Boulding (2003) found polymorphisms in the growth
 254 hormone gene (*GH*) that were significantly associated with growth rate of Arctic charr

255 (*Salvelinus alpinus*). Li *et al.*, (2009) reported an SNP in the insulin-like growth factor-
256 (IGF)1
257 gene 5' untranslated region (UTR) of largemouth bass (*Micropterus salmoides*). Sun *et al.*,
258 (2012) reported that two SNPs in exon 3 of the myostatin (*MSTN*) gene were significantly
259 related to body weight and Fulton's factor in common carp. Liu *et al.*, (2012) also found that
260 a SNP in the *MSTN* 3' UTR was very significantly associated with total length, body length,
261 and body weight of bighead carp.

262 **2. QTL for feed conversion rate**

263 FCR is one of the most important economic traits in fish, as fish with a better FCR
264 increase profits.

265 Liu (2005) used AFLP markers to construct a catfish genetic map and found a QTL
266 associated with FCR. Zimmerman *et al.*, (2005) revealed three QTLs for the number of
267 pyloric caeca in three LGs of rainbow trout, and this is an important index associated with
268 FCR.

269 FCR studies have also been reported in common carp from the Heilongjiang Fisheries
270 Research Institute of the Chinese Academy of Fishery Sciences (Wang, 2012).

271 **3. QTL for sex determination**

272 Sex phenotype and sex determination in fish have specific evolutionary status and
273 diversity. Males and females of some species have significant differences in growth rate or
274 commercial value; therefore, monosex fish culture is a promising strategy. The sex-
275 determining (SD) loci and QTLs have been studied in a limited number of fish, such as tilapia
276 (Lee *et al.*, 2004) rainbow trout (Alfaqih *et al.*, 2009) and salmonids (Davidson *et al.*, 2009).
277 Previous studies have demonstrated that sex QTLs are located on LG1, 2, 3, 6, and 23 of
278 tilapia (Cnaani *et al.*, 2004; Lee *et al.*, 2004; Cnaani *et al.*, 2008) Eshel *et al.*, (2011) reported
279 a major candidate sex QTL that is considered the sex determining region in tilapia. Fifty-one
280 genes in this region have been annotated, and 10 have been confirmed.

281 The anti-Müllerian hormone gene is the most differentially expressed gene in male
282 and female tilapia. Sun *et al.*, (2014) recently published several sex-specific markers, and one
283 is tightly linked with the sex-determining region discovered by Eshel *et al.*, The sex-
284 determining locus in rainbow trout is located on the LG of RT10, and this locus also
285 significantly affects thermo-resistance and body length. The sex-determining regions in Artic
286 charr (Moghadam *et al.*, 2007) brown trout (Gharbi *et al.*, 2006) and Atlantic salmon (Gilbey
287 *et al.*, 2004) are located on the LGs of AC4, BT28, and AS1, respectively.

288 Woram *et al.*, (2003) compared LGs of sex-determining loci in four salmonids and
289 found that although the nucleotide sequences flanking the sex-determining loci were well-
290 conserved, the SD LGs were diverse, suggesting that the regions underwent different
291 recombination events.

292 Loukovitis *et al.*, (2011) located growth and sex-determining QTLs in gilthead sea
293 bream and showed that these two traits have similar genetic control in LG21. Martínez *et al.*,
294 (2009) located a sex QTL on LG5 of turbot and proposed a ZZ/ZW sex-determining
295 mechanism. Viñas *et al.*, (2012) also found a major sex QTL on turbot LG5. These findings
296 suggest that the sex-determining genes may occur on turbot LG5. Song *et al.*, (2012) used
297 high-density genetic maps to locate seven sex QTLs on the half-smooth tongue sole LG1f,
298 LG14f, and LG1m.

299 Additional study by Chen *et al.*, (2014) provided insight into ZW sex chromosome
300 evolution and identified sex-determining genes, such as *dmrt1* and *neurl3*.

301 **2.8.5 Factors affecting QTL analyses**

302 The power of mapping QTL can be influenced by a number of factors, such as genetic
303 properties of QTL, experiment design, environmental effects, marker density and
304 informativeness, genotyping errors and precision of trait measurement. Details about how
305 these factors influence the power of QTL mapping can be found in some very good reviews
306 (e.g. Crosses 2001; Flint and Mott 2001; Doerge 2002).

307 **2.8.6 Methods of Detecting QTL**

308 Basically, three methods are frequently used for mapping QTL and estimating their
309 effects, namely Single-Marker Association Analysis (SMAA), Simple Interval Mapping
310 (SIM) and Composite Interval Mapping (CIM) (Crosses 2001; Flint and Mott 2001; Doerge
311 2002).

312 **2.9 Current Status of Applications of MAS in Fish**

313 Molecular marker maps have been constructed for a number of aquaculture species,
314 e.g. tilapia, catfish, giant tiger prawn, kuruma prawn, Japanese flounder and Atlantic salmon,
315 although their density is generally low. Density is high for the rainbow trout, where the map
316 published in 2003 has over 1 300 markers spread throughout the genome – the vast majority
317 are AFLPs but it also includes over 200 microsatellite markers (Nichols *et al.*, 2003). Some
318 QTLs of interest have been detected (e.g. for cold and salinity tolerance in tilapia and for
319 specific diseases in rainbow trout and salmon).

320 In a recent review of MAS in fish breeding schemes, Sonesson (2003) suggested that
321 MAS would be especially valuable for traits that are impossible to record on the candidates
322 for selection such as disease resistance, fillet quality, feed efficiency and sexual maturation,
323 and concluded that MAS is not used in fish breeding schemes today and that the lack of dense
324 molecular maps is the limiting factor. Marker Assisted Selection (MAS) has become a
325 valuable tool in selecting organisms for desirable traits. MAS is expected to increase genetic
326 gain compared to traditional breeding programs and reduce the cost of progeny testing by
327 early selection. The application of MAS in breeding programmes depends on the knowledge
328 of breeders about variable marker information.

329 REFERENCES

- 330 Alarcon, J.A., Alvarez, M. C. (1999). Genetic identification Sparidae species by isozyme
331 markers. Applications to interspecific hybrids. *Aquaculture*, 173, 95-103.
- 332 Anderson, J. L., Marí, A. R., Braasch, I., Amores, A., Hohenlohe, P., Batzel, P. (2001).
333 Multiple sex-associated regions and a putative sex chromosome in zebrafish
334 revealed by RAPD mapping and population genomics. 3, 427-437.
- 335 Ashraf, M., Akram, N. A., Foolad, M. R. (Eds.). (2012). Marker-Assisted Selection in Plant
336 Breeding for Salinity Tolerance. 913, 305–333. doi:10.1007/978-1-61779-986-0.
- 337 Bardakci, F., Skibinski, D. O. F. (1994). Application of the RAPD technique in tilapia fish
338 species and subspecies identification. 73, 117–123. doi:10.1038/hdy.1994.110.
- 339 Bernardo, R. (1994). Prediction of maize single-cross performance using RFLPs and
340 Biotechnology in Agriculture and Food
341 (<http://tandfonline.com/doi/book/10.1081/EEBAF>).
- 342 Boopathi, N. M. (2013a). Marker-Assisted Selection. In Genetic Mapping and Marker
343 Assisted Selection: Basics, Practice and Benefits. 173–186. doi:10.1007/978-81-
344 322-0958-4
- 345 Brumlop, S., Finckh, M. R. (2011). Applications and potentials of marker assisted selection (
346 MAS) in plant breeding. Pp. 178. http://www.bfn.de/0502_skripten.html
- 347 Chen, J., Wang, Y., Yue, Y., Xia, X., Du, Q., Chang, Z. (2014). A novel male-specific DNA
348 sequence in the common carp, *Cyprinus carpio*. *Mol Cell Probes*. 23, 235–9.
- 349 Cnaani, A., Zilberman, N., Tinman, S., Hulata, G., Ron, M. (2004). Genome-scan analysis for
350 quantitative trait loci in an F-2 tilapia hybrid. *Mol Genet Genomics*. 272(2):162-
351 172.

- 352 Danzmann, R. G., Gharbi, K. (1994). Gene mapping in fishes: a means to an end. *Genetica*.
353 111(1-3):3-23.
- 354 Davidson, W. S., Koop, B. F., Jones, S. J. M., Iturra, P., Vidal, R., Mas, A., Jonassen, I.,
355 Lien, S., Omholt, S. W. (2009). Sequencing the genome of the Atlantic salmon
356 (*Salmo salar*). *Genome Biol* 11:403
- 357 Davies, J., Berzonsky, W., LEACH, G. (2006): A Comparison of Marker-Assisted and
358 Phenotypic Selection for High Grain Protein Content in Spring Wheat. *152*, 117-
359 134.
- 360 Dekkers, J. C. M., Hospital, F. (2002). The use of molecular genetics in the improvement of
361 agricultural populations. *Nature Revs. Genet.* 3: 22–32.
- 362 Doyle, J. J., Doyle, J. L. (1987). A rapid DNA isolation procedure for small quantities of
363 fresh leaf tissue. *Phytochem. Bull.* 19: 11–15.
- 364 Dreher, K., Khairallah, M., Jean-Marcel, R., Monis, M. (2002). Money matters (I): costs of
365 field and laboratory procedures associated with conventional and marker assisted
366 maize breeding at CIMMYT. *Molecular Breeding* I I: 221-234.
- 367 Dudley, J. W. (1993). Molecular markers in plant improvement: manipulation of genes
368 affecting quantitative traits. *Crop Sci.* 33: 660–668.
- 369 Edward, M. D., Stuber, C. W., Wendel, J. F. (1987a). Molecular markers facilitated
370 investigation of quantitative trait loci in maize. I. Numbers, genomic distribution
371 and types of gene action. *Genetics* 115: 113-125
- 372 Erickson, D. L., Fenster, C. B., Stenoien, H. K., Price, D. (2004). Quantitative trait locus
373 analyses and the study of evolutionary process. *Molecular Ecology* 13: 2505-2522.
- 374 Eshel, O, Shirak, A., Weller, J. I., Slossman, T., Hulata, G., Cnaani, A. (2011). Fine mapping
375 of a locus on linkage group 23 for sex determination in Nile tilapia (*Oreochromis*
376 *niloticus*). *Anim Genet.* 42: 222–4.
- 377 Ferguson, M. (1994). The role of molecular genetic markers in the management of cultured
378 fishes. *Reviews in Fish Biology and Fisheries*, 4(3): 351–373.
379 <https://doi.org/10.1007/BF00042909>
- 380 Flint-Garcia, S.A., Darrah, L. L., McMullen, M. D., Hibbard, B. E. (2003). Phenotypic versus
381 genomic selection in an established commercial layer breeding program. *Genetics*
382 *Selection Evolution* 45: 29.
- 383 Gharbi, K., Gautier, A., Danzmann, R.G., Gharbi, S., Sakamoto, T., Hoyheim, B., Taggart, J.
384 B., Cairney, M., Powell, R., Krieg, F., Okamoto, N., Ferguson, M. M., Holm, L. E.,

385 Guyomard, R. (2006). A linkage map for brown trout (*Salmo trutta*): chromosome
386 homeologies and comparative genome organization with other salmonid fish.
387 *Genetics* 172:2405–2419

388 Gilbey, J., Verspoor, E., McLay, A., Houlihan, D. (2004). A microsatellite linkage map for
389 Atlantic salmon (*Salmo salar*). *Anim Genet* 35:98–105

390 Gimelfarb, A., Lande, R. (1994). Marker-assisted selection and marker QTL association in
391 breeding programs. *Genetics*. 132: 1199-1210.

392 Gjedrem, T. (2009). Genetic improvement of cold-water fish species. *Aquac Res.* 31:25–33.

393 Groen, A. F., Crooijmans, R. P. M. A., Van Kampen, A. J. A., Van der Beek, S, Van der
394 Poel, J. J., Groenen, M. A. M. (2000). Microsatellite polymorphism in commercial
395 broiler and layer lines. *Proc 5th World Congr Genet Appl Livestock Prod* 21:95-98.

396 Gross, M., Schneider, J., Moav, N., Alvarez, C., Myster, S., Liu, Z., Hallerman, E., Hackett,
397 P., Guise, K., Faras, A., Kapuscinski, A. (1995). Molecular analysis and growth
398 evaluation of transgenic northern pike. *Aquaculture* 103: 253-273.

399 Guo, X., Hershberger, W.K., Cooper, K., Chew, K.K., 2012. Artificial gynogenesis with
400 Hayes, B. J., Chamberlain, A. J., Mcpartlan, H., Macleod, I., Sethuraman, L., Goddard, M. E,
401 (2007). Accuracy of marker-assisted selection with single markers and marker
402 haplotypes in cattle. *Genetics Research* 89: 215-220.

403 Houston, R. D., Bishop, S. C., Hamilton, A., Guy, D. R., Tinch, A. E., Taggart, J. B.,
404 Derayat, A., McAndrew, B. J., Haley, C. S. (2009). Detection of QTL affecting
405 harvest traits in a commercial Atlantic salmon population. *Anim Genet.* 40(5):753-
406 755.

407 Houston, R. D., Haley, C.S., Hamilton, A., Guy, D. R, Tinch, A. E., Taggart, J. B. (2009).
408 Major quantitative trait loci affect resistance to infectious pancreatic necrosis in
409 Atlantic salmon (*Salmo salar*). *Genetics*. 178:1109–15.

410 Hulata, G. (2003). Detection of a chromosomal region with two quantitative trait loci,
411 affecting cold tolerance and fish size, in an F-2 tilapia hybrid. 223(1-4):117-128.

412 Jackson, T.R., Ferguson, M.M., Danzmann, R.G., Fishback, A.G., Ihssen, P.E., O’Connell,
413 M., Crease, T.J. (1998). Identification of two QTL influencing upper temperature
414 tolerance in three rainbow trout (*Oncorhynchus mykiss*) half-sib families. *Heredity*
415 80: 143– 151.

416 Jacob, H. J., Lindpainter, K., Lincoln, S. E., Kusumi, R. K., Mao, Y. P., Ganten, D., Dzau, V.
417 J., Lander, E. S., (1991). Genetic mapping of a gene causing hypersensitive rat.
418 Cell. 67:213-224.

419 Jansen, R.C. (1993). Interval mapping of multiple quantitative trait loci. Genetics 135, 205-
420 211.

421 Jonasson, J., Stefansson, S. E., Gudnason, A., Steinarsson, A. (1999). Genetic variation for
422 survival and shell length of cultured red abalone (*Haliotis rufescens*) in Iceland.
423 *Journal of Shellfish Research* 18: 621-625.

424 Kause, A., Paananen, T., Ritola, O., Koskinen, H. (2003). Direct and indirect selection of
425 visceral lipid weight, fillet weight, and fillet percentage in a rainbow trout breeding
426 program. *Journal of Anim Sci.* 85: 3218-3227.

427 Kocher, T. D., Lee, W.J., Sobolewska, H., Penman, D., McAndrew, B. (1998). A genetic
428 linkage map of a cichlid fish, the tilapia (*Oreochromis niloticus*). *Genetics* 148:
429 1225–1232.

430 Lander, E. S., Botstein, D. (1989). Mapping Mendelian factors underlying quantitative traits
431 using RFLP linkage maps. *Genetics* 121: 185-199

432 Lee, M., Sharopova, N., Beavis, W. D., Grant, D., Katt, M., Blair, D. and Hallauer, A.
433 (2004). Expanding the genetic map of maize with the intermated B73 Mo17 (IBM)
434 population. *Plant Molecular Biology* 48: 453–461.

435 Li, J., Boroevich, K. A., Koop, B. F., Davidson, W. S. (2009). Comparative genomics
436 identifies candidate genes for Infectious Salmon Anemia (ISA) resistance in
437 Atlantic Salmon (*Salmo salar*). *Mar Biotechnol.* 13: 232-241.

438 Liu, F., Sun, F., Xia, J. H., Li, J., Fu, G. H., Lin, G. (2014). A genome scan revealed
439 significant associations of growth traits with a major QTL and GHR2 in tilapia. *Sci*
440 *Rep.* 4:7256

441 Liu, P., Li, J., He, Y. Y., Kong, J., Wang, Q. (2004). Present situation and protective
442 measures of genetic resources in *Fenneropenaeus chinensis*. *Mar. Fish Res* 25: 80–
443 85.

444 Liu, Z., Karsi, A., Li, P., Cao, D., Dunham, R. (2003). An AFLP-based genetic linkage map
445 of channel catfish (*Ictalurus punctatus*) constructed by using an interspecific hybrid
446 resource family. *Genetics* 165: 687–694.

447 Liu, Z.J., Li, P., Argue, B., Dunham, R., (1998a). Inheritance of RAPD markers in channel
448 catfish (*Ictalurus punctatus*), blue catfish (*I. furcatus*) and their F1, F2 and
449 backcross hybrids. *Anim. Genet.* 29: 58–62.

450 Liu, Z.J., Nichols, A., Li, P., Dunham, R., (1998b). Inheritance and usefulness of AFLP
451 markers in channel catfish (*Ictalurus punctatus*), blue catfish (*I. furcatus*) and their
452 F1, F2 and backcross hybrids. *Mol. Gen. Genet.* 258, 260–268.

453 Loukovitis, D., Sarropoulou, E., Tsigenopoulos, C. S., Batargias, C., Magoulas, A.,
454 Apostolidis, A. P., Chatziplis, D., Kotoulas, G. (2011). Quantitative trait loci
455 involved in sex determination and body growth in the gilthead sea bream (*Sparus*
456 *aurata* L.) through targeted genome scan. *PLoS ONE*, 6:e16599.

457 Luo, W., Zeng, C., Deng, W., Robinson, N., Wang, W., Gao, Z. (1997). Genetic parameter
458 estimates for growth-related traits of blunt snout bream (*Megalobrama*
459 *amblycephala*) using microsatellite-based pedigree. *Aquac Res.* 45:1881–8.

460 Mackay, T. F. C. (2001). The genetic architecture of quantitative traits. *Annu Rev Genet*,
461 35:303-339.

462

463 Martinez, P., Bouza, C., Hermida, M., Fernandez, J., Toro, M. A., Vera, M., Pardo, B.,
464 Millan, A., Fernandez, C., Vilas, R., (2009). Identification of the Major Sex-
465 Determining Region of Turbot (*Scophthalmus maximus*). *Genetics* 183(4):1443-
466 1452.

467 Martyniuk, C. J., Perry, G. M. L., Mogahadam, H. K., Ferguson, M. M., Danzmann, R. G.
468 (2003). The genetic architecture of correlations among growth related traits and
469 male age at maturation in rainbow trout. *Journal of Fish Biol* 63:746–764

470 Moen, T., Agresti, J. J., Cnaani, A., Moses, H., Famula, T. R., Hulata, G., Gall, G. A. E.,
471 May, B. (2004b). A genome scan of a four-way tilapia cross supports the existence
472 of a quantitative trait locus for cold tolerance on linkage group 23. *Aquaculture* 35:
473 893–904.

474 Moen, T., Fjalestad, K.T., Munck, H. and Gomez-Raya, L. 2003. A multistage testing
475 strategy for detection of quantitative trait loci affecting disease resistance in Atlantic
476 salmon. *Genetics* 167: 851–858.

477 Moen, T., Hoyheim, B., Munck, H., Gomez-Raya, L. (2004a). A linkage map of Atlantic
478 salmon (*Salmo salar*) reveals an uncommonly large difference in recombination rate
479 between the sexes. *Anim. Genet.* 35: 81–92.

480 Moghadam, H., Poissant, J., Fotherby, H., Haidle, L., Ferguson, M., Danzmann, R. (2007).
481 Quantitative trait loci for body weight, condition factor and age at sexual maturation
482 in Arctic charr (*Salvelinus alpinus*): comparative analysis with rainbow trout
483 (*Oncorhynchus mykiss*) and Atlantic salmon (*Salmo salar*). *Mol Genet Genomics*
484 277(6):647-661.

485 Moreau, L., Lamarie, S., Charcosset, A., Gallais, A. (2000). Economic Efficiency of One
486 Molecular marker assisted selection for the mall quality traits in barley. *Mol*
487 *Breeding* 3: 427-437

488 Nichols, K. M., Bartholomew, J., Thorgaard, G. H. (2003). Mapping multiple genetic loci
489 associated with *Ceratomyxa shasta* resistance in *Oncorhynchus mykiss*. *Dis. Aquat.*
490 *Org.* 56: 145–154.

491 O'Malley, K.G., Sakamoto, T., Danzmann, R. G., Ferguson, M. M. (2003). Quantitative trait
492 loci for spawning date and body weight in rainbow trout: testing for conserved
493 effects across ancestrally duplicated chromosomes. *J. Hered.* 94: 273–84.

494 Ozaki, A., Sakamoto, T., Khoo, S., Nakamura, K., Coimbra, M.R., Akutsu, T., Okamoto, N.
495 (2001). Quantitative Trait Loci (QTL) associated with resistance/susceptibility to
496 infectious pancreatic necrosis virus (IPNV) in rainbow trout (*Oncorhynchus*
497 *mykiss*). *Mol. Genet. Genomics* 265: 23–31.

498 Perry, G. M., Danzmann, R. G., Ferguson, M. M., Gibson, J. P. (2001). Quantitative trait loci
499 for upper thermal tolerance in outbred strains of rainbow trout (*Oncorhynchus*
500 *mykiss*). *Heredity.* 86: 333– 341.

501 Poompuang, S., Hallerman, E. M. (2004). Toward detection of quantitative trait loci and
502 marker-assisted selection in fish. *Rev. Fish. Sci.* 5: 253–277.

503 Park, S.O., Crosby, K. M., Huang, R., Mirkov, T. E. (1995). Identification and confirmation
504 of FAPD and SCAR markers linked to the ms-3 gene controlling male sterility in
505 melon (*Cucumis melo* L.). *Journal of the American Society for Horticultural*
506 *Sciences.* 129:819-825.

507 Paterson, A., Lander, S. E., Hevit, J. D., Peterson, S., Lincoln, S. E., Lanksley, S. D. (1988).
508 Resolution of quantitative traits into Mendelian factors by using a complete linkage
509 map of Restriction Fragment Length Polymorphisms. *Nature.* 325: 721-726

510 Peterson, B.K., Weber, J.N., Kay, E.H., Fisher, H. S., Hoekstra, H. E. (1990). Double digest
511 RADseq: an inexpensive method for de novo SNP discovery and genotyping in
512 model and non-model species. *PLoS One.* 1990;7:e37135.

513 Postlethwait, J.H., Johnson, S.L., Midson, C.N., Talbot, W.S., Gates, M., Ballinger, E.W.,
514 Africa, D., Andrews, R., Carl, T., Eisen, J.S. (1994). A genetic linkage map for the
515 zebrafish. *Science* 264, 699-703.

516 Reid, D. P., Szanto, A., Glebe, B., Danzmann, R. G., Ferguson, M. M. (2005). QTL for body
517 weight and condition factor in Atlantic salmon (*Salmo salar*): comparative analysis
518 with rainbow trout (*Oncorhynchus mykiss*) and Arctic charr (*Salvelinus alpinus*).
519 *Heredity*. 94(2):166-172.

520 Ribaut, J. M., Ragot, M. (2007). Marker-Assisted Selection to improve drought adaptation in
521 maize: the backcross approach, perspectives, limitations, and alternatives. *J Exp Bot*
522 58: 351-360.

523 Robison, B.D., Wheeler, P.A., Sundin, K., Sikka, P., Thorgaard, G.H. (2001). Composite
524 interval mapping reveals a major locus influencing embryonic development rate in
525 rainbow trout (*Oncorhynchus mykiss*). *J. Heredity* 92: 16–22.

526 Rodriguez, M.F., LaPatra, S., Williams, S., Famula, T., May, B. (2005). Genetic markers
527 associated with resistance to infectious hematopoietic necrosis in rainbow and
528 steelhead trout (*Oncorhynchus mykiss*) backcrosses. *Aquaculture* 241: 93–115.

529 Ross, P., Hall, L., Smirnov, I., Haff, L. (2011). High level multiplex genotyping by MALDI-
530 TOF mass spectrometry. *Nat. Biotechnol.* 16, 1347– 1351.

531 Ryman, N., Utter, F. (1987). *Population Genetics and Fishery Management* University of
532 Washington Press, Seattle. 420 pp.

533 Sakamoto, T., Danzmann, R. G., Gharbi, K., Howard, P., Ozaki, A., Khoo, S. K. (2000). A
534 microsatellite linkage map of rainbow trout (*Oncorhynchus mykiss*) characterized by
535 large sex-specific differences in recombination rates. *Genetics*. 155: 1331-1345.

536 Sakamoto, T., Danzmann, R.G., Okamoto, N., Ferguson, M. M., Ihssen, P. E. (1999).
537 Linkage analysis of quantitative trait loci associated with spawning time in rainbow
538 trout (*Oncorhynchus mykiss*). *Aquaculture* 173: 33–43.

539 Sakamoto, T., Danzmann, R.G., Okamoto, N., Ferguson, M.M., Ihssen, P.E. (1999). Linkage
540 analysis of quantitative trait loci associated with spawning time in rainbow trout
541 (*Oncorhynchus mykiss*). *Aquaculture* 173: 33–43.

542 Sax, K. (1923). The association of size differences with seed-coat pattern and pigmentation in
543 *Phaseolus vulgaris*. *Genetics* 8: 522-560.

544 Shimoda, N., Knapik, E.W., Ziniti, J., Sim, C., Yamada, E., Kaplan, S., Jackson, D., de
545 Sauvage, F., Jacob, H., Fishman, M.C. (1999). Zebrafish genetic map with 2000
546 microsatellite markers. *Genomics* 58, 219-232.

547 Somorjai, I.M., Danzmann, R. G., Ferguson, M. M. (2001). Distribution of temperature
548 tolerance quantitative trait loci in Arctic charr (*Salvelinus alpinus*) and inferred
549 homologies in rainbow trout (*Oncorhynchus mykiss*). *Genetics* 165: 1443–1456.

550 Sonesson, A. (2007). Within-family marker-assisted selection for aquaculture species. *Genet*
551 *Sel Evol.* 39:301–18.

552 Sonesson, A.K. (2003). A combination of walk-back and optimum contribution selection for
553 fish – a simulation study. *Genet. Sel. Evol.* 37: 587–599.

554 Song, W., Li, Y., Zhao, Y., Liu, Y., Niu, Y., Pang, R. (2012). Construction of a high density
555 microsatellite genetic linkage map and mapping of sexual and growth-related traits
556 in half-smooth tongue sole (*Cynoglossus semilaevis*). *PLoS One.*7:e52097.

557 Song, W., Pang, R., Niu, Y., Gao, F., Zhao, Y., Zhang, J. (2012). Construction of high
558 density genetic linkage maps and mapping of growth-related quantitative trait loci in
559 the Japanese flounder (*Paralichthys olivaceus*). *PLoS One.*7:e50404.

560 Spelman, R. J., Garrick, D. J. (2013). Genetic and economic responses for within-family
561 marker-assisted selection in dairy cattle breeding schemes. *Journal of Dairy Science*
562 81: 2942–2950.

563 Streelman, J.T., Kocher, T. D. (2003). Microsatellite variation associated with prolactin
564 expression and growth of salt-challenged tilapia. *Physiol. Genomics* 9: 1 –4.

565 Sun, X. W., Liang, L. Q. (2004). A genetic linkage map of common carp (*Cyprinus carpio*
566 *L.*) and mapping of a locus associated with cold tolerance. *Aquaculture.* 238:165–
567 72.

568 Tong, J. G., Sun, X. W. (2004). Genetic and genomic analyses for economically important
569 traits and their applications in molecular breeding of cultured fish. *Sci China Life*
570 *Sci.* 58:178–86.

571 Van Ooijen, J. W. (1999). Join Map 4, software for the calculation of genetic linkage maps in
572 experimental populations. Netherlands.

573 Vogel, B., Van Aken, J. (2009). Smart Breeding - Marker-Assisted Selection: A non-invasive
574 biotechnology alternative to genetic engineering of plant varieties Amsterdam, the
575 Netherlands. (p. 28).

576 Gharbi, K, Ferguson, M. M., Danzmann, R. G. (2001). Characterization of Na, K-ATPase
577 genes in Atlantic salmon (*Salmo salar*) and comparative genomic organization with
578 rainbow trout (*Oncorhynchus mykiss*). *Mol Genet Genomics* 273:474–483

579 Wang, C. M., Lo, L.C., Feng, F., Zhu, Z.Y., Yue, G.H. (2008). Identification and verification
580 of QTL associated with growth traits in two genetic backgrounds of Barramundi
581 (*Lates calcarifer*). *Anim Genet.* 39(1):34-39.

582 Wang, C.M., Lo, L. C., Zhu, Z. Y., Yue, G. H. (2006). A genome scan for quantitative trait
583 loci affecting growth-related traits in an F1 family of Asian seabass (*Lates
584 calcarifer*). *BMC Genomics*.

585 Wang, S., Meyer, E., McKay, J. K., Matz, M. V. (2012). 2b-RAD: a simple and flexible
586 method for genome-wide genotyping. *Nat Methods.* 9:808–10.

587 Weller, J. I. (2001). *Quantitative trait loci analysis in animals*. London, CABI Publishing.
588 287 pp.

589 Willcox, M. C., Khairallah, M., Bergvinson, D., Crossa, J., Deutsch, J.A., Edmeades, G.O.,
590 Gonzalez-de-Leon, D., Jiang, C., Jewell, D.C., Mihm, J.A., Williams, W.P.,
591 Hoisington, D.A. (2002). Selection for resistance to southwestern corn borer using
592 marker assisted and conventional backcrossing. *Crop Sci.* 42: 1516–1528.

593 Woram, R.A., McGowan, C., Stout, J.A., Gharbi, K., Ferguson, M.M., Hoyheim, B.,
594 Sakamoto, J., Davidson, W., Rexroad, C., Danzmann, R.G. (2003). A genetic
595 linkage map for Arctic char (*Salvelinus alpinus*): evidence for higher recombination
596 rates and segregation distortion in hybrid versus pure strain mapping parents.
597 *Genome* 47: 304–315.

598 Wringe, B., Devlin, R., Ferguson, M., Moghadam, H., Sakhrani, D., Danzmann, R. (2010).
599 Growth-related quantitative trait loci in domestic and wild rainbow trout
600 (*Oncorhynchus mykiss*). *BMC Genetics.* 11(63).

601 Xie, C., Xu, X. (1998) . Efficiency of multistage marker-assisted selection in the
602 improvement of multiple quantitative traits. *Heredity.* 80: 489-498.

603 Xu, Y., Beachell, H., McCouch, S. R. (2008). A marker based approach to broadening the
604 genetic base of rice in the USA. *Crop Sci.* 44: 1947–1959.

605 Yanchuk, A. D. (2002). The role and implications of biotechnology in forestry. *Food and
606 Agriculture Organization of the United Nations, Unasylva* (30), 18–22.

607 Yu, Z., Guo, X. (2003). Genetic linkage map of the eastern oyster (*Crassostrea virginica*)
608 Gmelin. *Biol. Bull.* 204, 327–338.

609 Yue, G. H. (2014). Recent advances of genome mapping and marker-assisted selection in
610 aquaculture. 15:376–96.

611 Zhang, Y., Wang, S., Li, J., Zhang, X., Jiang, L., Xu, P. (1992). Primary genome scan for
612 complex body shape-related traits in the common carp (*Cyprinus carpio*). *J Fish*
613 *Biol.* 82:125–40.

614 Zheng, J., Liu, J., Liu, H., Li, J., Chen, K. (2003). Sequence and structural analysis of 4SNC-
615 Tudor domain protein from *Takifugu rubripes*. *Bioinformation.* 4:127-131.

616 Zimmerman, A.M., Wheeler, P.A., Ristow, S.S., Thorgaard, G. H. (2005). Composite interval
617 mapping reveals three QTL associated with pyloric caeca number in rainbow trout,
618 *Oncorhynchus mykiss*. *Aquaculture* 247: 85–95.

619

620