

1 **A systematic review and meta-analysis of genetic parameters for complex quantitative**  
2 **traits in aquatic animal species**

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9

10 **Abstract**

11 A systematic review and meta-analysis of genetic parameters underlying inheritance and complex  
12 biological relationships for quantitative traits are not available for aquatic animal species. I  
13 synthesised and conducted a comprehensive meta-analysis of the published information from 1985  
14 to 2017 on heritability, common full-sib effects and genetic correlations for quantitative characters  
15 of biological importance (growth, carcass and flesh quality, disease resistance, deformity and  
16 reproduction) for aquaculture species. A majority of the studies (73.5%) focussed on growth related  
17 traits (body weight), followed by those on disease resistance (15.9%), whereas only a limited number  
18 of studies (10.6%) reported heritability estimates for carcass and flesh quality, deformity or  
19 reproduction characteristics. The weighted means of heritability for growth (weight, food utilisation  
20 efficiency, maturity) and carcass (fillet weight and yield) traits were moderate. Resistance against  
21 various bacteria, virus and parasites were moderately to highly heritable. Across aquatic animal  
22 species, the weighted heritability for a range of deformity measures and reproductive traits  
23 (fecundity, early survival) was low and not significantly different from zero. The common full-sibs ( $c^2$ )

24 accounted for a large proportion of total variance for body traits but it was of smaller magnitude in  
25 later phase of the growth development. The  $c^2$  effects however were not significant or in many cases  
26 they were not reported for carcass and flesh quality attributes as well as survival and deformity. The  
27 maternal genetic effects were not available for all traits studied especially for reproductive and early  
28 growth characters. Genetic correlations between body and carcass traits were high and positive,  
29 suggesting that selection for rapid growth can improve fillet weight, a carcass trait of paramount  
30 importance. Body weight, the most commonly used selection criterion in aquatic animals, showed  
31 non-significant genetic correlation with disease resistance, likely because both positive and negative  
32 genetic associations between the two types of traits. Interestingly the genetic associations between  
33 growth and reproductive performance (fecundity) and fry traits (fry weight, fry survival) were  
34 favourable. To date, there are still no published data on genetic relationships of carcass and flesh  
35 quality with disease resistance or reproductive performance in any aquaculture species. Additionally,  
36 the present study discussed new traits, including functional, immunological, behavioural and social  
37 interaction as well as uniformity that are emerging as potential selection criteria and which can be  
38 exploited in future genetic improvement programs for aquatic animals.

39 *Keywords:* Meta-analysis, heritability, genetic correlations, quantitative traits, growth, disease  
40 resistance

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86 **I. INTRODUCTION**

87 Quantitative genetic parameters (heritability, maternal and common full-sib effects, phenotypic and  
88 genetic correlations) provide information needed for development of breeding objectives, design of  
89 selection strategies as well as assessment of selective breeding genetic improvement programs.  
90 Across aquatic animal species, heritability and trait correlations are often estimated in experimental  
91 populations prior to selection in order to examine genetic characteristics of new traits before closed  
92 nucleus breeding populations are initiated (Nguyen 2016; Olesen et al. 2003). As part of the process  
93 of monitoring selective breeding programs, the genetic parameters are re-estimated to ensure the  
94 continued response of traits under selection (i.e., selection criteria) and to predict possible changes  
95 in correlated characters to refine the breeding strategy. A large number of studies have reported  
96 heritabilities, maternal and common environmental effects and genetic correlations for traits of  
97 economic importance (e.g., body weight and survival) in important aquaculture species such as  
98 salmonids (Atlantic salmon, rainbow trout), carps, tilapias, shrimps, molluscs and newly cultured  
99 species (section 2.1 below). By contrast, genetic inheritance of flesh quality, behaviour and fitness-  
100 related traits is not well documented, although a few recent studies shown heritable additive  
101 genetic variations in sexual maturity, deformity and survival (Thoa et al. 2016), social interactions,  
102 and behavioural response characteristics (Drangsholt et al. 2014). Genetic correlations between  
103 growth performance and traits of commercial importance, such as flesh and eating quality,  
104 reproduction, fitness and functional adaptation traits, are not well understood. It is thus not possible  
105 to make any prediction of correlated changes in these traits to selection for high growth, a trait of  
106 paramount importance in almost all genetic enhancement programs for aquaculture species. On the  
107 other hand, measuring realised correlated response in these traits to selection is costly and time-  
108 consuming and an issue that remains unresolved because it requires multigenerational in-depth  
109 pedigree data to assess the changes with confidence (Hamzah et al. 2014b; Nguyen et al. 2010a).  
110 The possible changes on one trait to selection for another can be predicted from the knowledge of  
111 genetic and phenotypic correlation estimates.

112 While there is a paucity of published information in the literature to aid our understanding of  
113 genetic inheritance for commercial traits, especially those that are difficult to measure, a growing  
114 number of attempts has been made to develop systematic breeding programs for new species,  
115 including marine finfishes (Knibb et al. 2016) or spiny rock lobsters of high economic value (Nguyen  
116 et al. 2018a). As a first step to start genetic breeding programs for a new species, simple questions  
117 that breeders often ask is which traits they should select for, whether these traits are heritable and  
118 can respond to selection, and whether there are any consequences of selection on other characters  
119 of commercial interest. When the breeding program proceeds, expansion of the breeding goals also  
120 requires accurate estimates of genetic parameters for candidate traits. To obtain a reliable set of  
121 heritability and genetic correlations for new traits, rigorous experimental designs with reasonable  
122 family structure and sample size (Lynch and Walsh 1998) should be used. Taking these issues  
123 collectively, there is a need for a systematic review and meta-analysis of the published literature to  
124 guide decisions on future design and development of genetic improvement programs for aquatic  
125 animal species. Such a study has not been conducted for aquatic species, and weighted values of  
126 heritability and estimated correlations for commercial characters are currently not available.

127 The aim of this study, thus, was to synthesise information about inheritance and relationships  
128 among quantitative traits of economic importance in aquaculture species. Further, I also discussed  
129 the experimental design (i.e., sample size) required to obtain reliable genetic parameter estimates as  
130 well as proposing future directions to dissect genetic architecture of complex traits, especially novel  
131 characters that are emerging as potential selection criteria in selective breeding programs for  
132 aquaculture species.

133

## 134 **II. MATERIALS AND METHODS**

### 135 1. Search strategy, selection criteria and traits

136 A systematic search of public electronic databases (PubMed, ISI Web of Knowledge, CABI and Google  
137 Scholar) using five keywords: “heritability, genetic parameters, correlations, variance and covariance  
138 components and aquaculture species” was undertaken to identify studies published in international,  
139 peer-reviewed journals from 1985 to 1<sup>st</sup> March 2017. Published work prior to 1985 on genetic  
140 variation in quantitative traits in fish and shellfish was reviewed by Gjedrem (1983) and Gjerde  
141 (1986). In this study, a total of 1,120 records was identified from the databases. They were selected  
142 for inclusion in this review following the PRISMA (the Preferred Reporting Items for Systematic  
143 reviews and Meta-Analyses) protocol (Moher et al. 2009) (Supplementary file 1). Initially, their  
144 abstracts were screened, 260 duplicate or irrelevant records (i.e., papers on human, plant or  
145 terrestrial farmed animals or those did not report genetic parameter estimates) were excluded. The  
146 remaining 860 articles were examined for their full text, and 304 records were further excluded on  
147 the basis of the following criteria: 1) studies with less than 15 families due to their low statistical  
148 power to obtain reliable genetic parameter estimates (see Section 2.4), 2) reports with negative  
149 heritability or genetic and phenotypic correlations out of parameter space (-1 to 1), 3) studies  
150 published in languages other than English, 4) obviously irrelevant literature (i.e., papers on aquatic  
151 animals other than aquaculture species or those that reported traits that were not examined in this  
152 review), and 5) non-peer reviewed materials or project reports. After the assessment, 556 articles  
153 were assessed by studying their full texts and only 300 articles were eligible for inclusion in the  
154 review (256 references were discarded, mainly due to 1-5 as above). Our final screening also  
155 removed eight articles. A final list of 292 articles was used in our meta-analysis (full list of the  
156 references is given in Supplementary file No.2).

157 The dataset was then extracted from these (292) papers that included name of authors (references),  
158 Latin name of species, common species name, data records (observations), numbers of sires and  
159 dams (family), mating design, analytic methods, age of the animal, basic statistics for traits (mean,  
160 standard deviation and coefficient of variation), genetic parameters (heritability, common full-sib

161 effects, phenotypic and genetic correlations) and their associated standard errors reported for traits  
162 of commercial importance.

163 Traits were grouped in six broad categories: 1) growth-related traits (body weight and feed  
164 utilisation efficiency), 2) carcass (fillet weight and fillet yield) and flesh quality (pH, colour, fat  
165 content) traits, 3) reproductive characteristics (sexual maturity, female weight before or after  
166 spawning, fecundity, fry weight, fry survival), 4) diseases resistance (virus, bacteria, parasite or  
167 others), and 5) fitness traits, mainly morphological deformity and survival during grow-out.

168

## 169 2. Meta-analysis

170 Firstly, I derived standard errors ( $s$ ) for heritability and common full-sib effects for studies in which  
171 they were not reported. The theoretical  $s$  can be calculated based on the heritability estimate,  
172 number of offspring per sire and number of sires (Falconer and Mackay 1996). It can be also  
173 calculated approximately as  $32h^2/n$  where  $n$  is the number of data records (Koots et al. 1994).  
174 Alternatively, the SE of the heritability and common full-sib estimates for these studies were  
175 calculated by dividing weighted mean standard deviation ( $SD_w$ ) by the square root of the number of  
176 records in the estimate, using Equation 1 (Borenstein et al. 2011).

$$177 \quad SD_w = \left[ \frac{\sum_{i=1}^y s_i^2 n_i}{\sum_{i=1}^y n_i} \right]^{0.5} \quad [1]$$

178 where  $s$  is the standard error and  $n$  is the number of records for the  $i^{\text{th}}$  estimate ( $i=1,2,3\dots y$ ).

179 Correlations among the three methods were greater than 0.9; hence only results based on the  
180 number of data records (Equation 1) are used in this study. I then weighted each estimate of a  
181 parameter from studies by their sample size or the inverse of variance. Both of the weighting  
182 methods gave similar weighted mean heritability for growth or reproductive traits, but the standard

183 errors from the latter method (the inverse of the variance) were smaller than those from the former.  
184 Therefore, weighted means for basic statistics (trait mean, SD, CV) for all traits were derived using  
185 sample size as weight. On the other hand, weighted mean heritability and common full-sib effects  
186 were obtained using the inverse of the variance as weight (Akanno et al. 2013; Safari et al. 2005).  
187 To calculate the weighted mean estimate of phenotypic and genetic correlations between traits,  
188 Fisher's Z transformation was applied to remove the dependency of the variance on the estimate  
189 (Equation 2), with the standard error calculated in Equation 3. The weighted mean phenotypic and  
190 genetic correlations ( $r_w$ ) were back-transformed using Equation 4,

$$191 \quad Z = \log \left[ \frac{1+r}{1-r} \right]^{0.5} \quad [2]$$

$$192 \quad SE_Z = \sqrt{1/(n-3)} \quad [3]$$

$$193 \quad r_w = \frac{e^{2z} - 1}{e^{2z} + 1} \quad [4]$$

194 where  $r$  is the correlations,  $n$  is number of records for phenotypic correlations or number of families  
195 for genetic correlations and  $z$  is the weighted mean for the Z transformed correlations.

196

197 **Heterogeneity:** Heterogeneity among studies was assessed using three different statistical tests:  $Q$ ,  
198  $H$  and  $I$ . The  $Q$  statistic (Cochran 1954) tests the null hypothesis that the true parameter estimate is  
199 the same in all studies vs. the alternative that at least one of the estimates differs. It approximately  
200 has a Chi-square distribution with  $k-1$  degrees of freedom where  $k$  is the number of parameter  
201 estimates. The statistic  $H$  different from one indicated heterogeneity of studies. In addition, the  
202 inconsistency index  $I^2$  statistic (ranging from 0 to 100%), which is defined as the percentage of  
203 observed between-study variation that is due to heterogeneity rather than chance, was also used.  
204 Significant heterogeneity was determined by  $P < 0.1$  or  $I^2 > 50\%$ . Although heterogeneity was not



205 significant for the majority of traits, random model was used to derive the weighted mean for the  
206 parameter estimate (see section on random model).

207 Publication bias (small study effect): To assess the effect of publication bias, the Begger's funnel plot  
208 and Egger regression asymmetry test were used. The funnel plot visually displays the standard error  
209 of the parameter estimate of each study against its log value. The Egger test determine whether the  
210 intercept deviated significantly from zero and an asymmetric plot indicate possible publication bias,  
211 and the degree of asymmetry was tested using Egger's test ( $P < 0.05$  indicated significant publication  
212 bias)(Egger et al. 1997). Sensitivity analysis was performed by excluding studies with z-value greater  
213 than 3 (one study at a time) to assess the influence of the individual study on the overall results.

214

215 3. Estimation of weighted means of genetic parameters (heritability, common full-sib effect  
216 and correlations)

217 The weighted means of genetic parameters were obtained from a random effect model (Equation 5)  
218 in the metaphor package (Viechtbauer 2010). This model accounted for between- and within- study  
219 variation. Restricted maximum likelihood analysis was conducted in ASReml (Gilmour et al. 2009) to  
220 determine the relative contributions of between- and within-study variation to the weights

221 
$$y_i = \mu + r_i + e_i \quad [5]$$

222 where  $y_i$  is the estimate of a parameter in the  $i^{th}$  study,  $\mu$  is the mean (weighted mean of the  
223 estimates),  $r_i$  is the random term to account for variation between studies and  $e_i$  is the error term  
224 (within-study variation). The components of  $r_i$  and  $e_i$  are assumed to be normally distributed with  
225 means of zero and variances of  $r_i^2$  and  $V$ , respectively. For heritability and common full-sib effects,  $V$   
226  $= \sigma_e^2 / w_i$  where  $w_i = 1 / (\sigma_r^2 + r_i^2)$ . The  $V$  for genetic correlations is  $V = \sigma_e^2 / (n - 3)$  where  $n$  is the number  
227 of sires. The 95% confidence interval for the estimates was calculated from  $V$ , with those for genetic  
228 correlations being back transformed using equation 4.

229

#### 230 4. Calculation of statistical power

231 I considered a simplest sib design in which  $N$  sires are each mated to  $n$  unrelated dams. A further  
232 assumption was that the sire variance and error term was normally distributed. Power calculation of  
233 this design for variance component estimation followed the formula given by Lynch and Walsh  
234 (1998, page 887) as:

$$235 \Pr \left[ F_{N-1, N(n-1)} > \frac{F_{N-1, N(n-1), (1-\alpha)}}{1 + nh^2 / (1 - 4h^2)} \right] \quad [6]$$

236 where  $N$  is number of sires. Each is mated with  $n$  dams. Alpha ( $\alpha$ ) is a chosen significance level (5, 1  
237 or 0.1%) and  $h^2$  is the heritability for the trait in question.  $F$  is the test statistic having  $N$  degrees of  
238 freedom for the numerator and  $N(n-1)$  for the denominator.

239 I modelled four options with different numbers of sires and dams to calculate statistical power: 1) 8  
240 sires and 16 dams, 2) 15 sires and 30 dams, 3) 30 sires and 60 dams, and 4) 45 sires and 90 dams.  
241 The ratio of males to females was based on the design of several breeding programs, although  
242 mating of one male to two females was not always successful. These parameters were used to  
243 calculate statistical power to detect a significant heritability at a probability of 95% or 99% ( $\alpha = 0.05$   
244 or 0.01) (Equation 6).

245

### 246 III. RESULTS

#### 247 1. Characteristics of the data

248 Characteristics of the studies reviewed here are presented in Table 1. The species considered  
249 included salmonids, carps, tilapias, crustaceans and molluscs (species composition is given in Table  
250 1). A number of recent studies have been conducted in freshwater and marine finfishes and they  
251 were classified as other fishes, including yellowtail kingfish, Atlantic charr, Asian and European

252 seabasses, seabream, common sole, yellow perch, flounder and turbot. Five major groups of traits  
253 were examined, namely growth-related traits, carcass and flesh quality, disease resistance,  
254 reproductive performance and fitness-related traits (mainly deformity and survival).

255 The average sample size (number of individuals) of the studies included in this review ranged from  
256 3,296 to 27,933 (Table 1). The average number of sires and dams (or number of families) across  
257 populations were 199 and 264, respectively. A majority of the studies applied single-pair mating  
258 (with a hierarchical nested mating design with a ratio of one male to 2 females) or incomplete  
259 (rectangular) factorial mating by set (e.g. male 1 mated with females 1 and 2, male 2 with females 2  
260 and 3, and so on to male  $n$  with female 1 and  $n$ ). Mass spawning also was practised for some species,  
261 mainly in new aquaculture species including yellowtail kingfish, seabream, abalone and blue mussel,  
262 where microsatellite DNA markers were used for parentage assignment. There is an increasing trend  
263 in the number of studies that have used DNA markers for parentage assignment and pedigree  
264 construction. Conventionally, individual identification in fish involved use of Passive Integrated  
265 Transponder (PIT) tags, whereas visible implant elastomer (VIE) (or visible implant alphanumeric) in  
266 combination with eye tags were used in crustacean species. A wide array of testing environments  
267 during grow-out were used, predominantly ponds or cages. Only three studies employed  
268 recirculating or intensive culture systems.

269 With the pedigree information available in almost all studies (96.9%), Restricted Maximum  
270 Likelihood (REML) method applied to a single or multiple trait mixed model was performed to  
271 estimate genetic parameters. Some studies reported realised heritability from selection experiments  
272 (1.5%). A small proportion of the  $h^2$  estimates was also obtained from conventional intraclass  
273 correlation analysis (only three studies).

274

275 2. Summary statistics

276 Body weight is frequently recorded in selective breeding programs for aquaculture species ( $n = 193$ ).  
277 There is a growing interest regarding genetic improvement for disease resistance ( $n = 55$ ). Only a  
278 limited number of studies investigated flesh/eating quality attributes ( $n = 18$ ), reproduction traits  
279 ( $n = 9$ ) and morphological deformity ( $n = 11$ ) in aquaculture species. Limited samples sizes were  
280 observed for quality, reproductive and fitness-traits, mainly because they are expensive or difficult  
281 to measure. The coefficients of variation for reproductive traits were substantially larger than  
282 growth and carcass/flesh quality characteristics (results not tabulated). The mean and standard  
283 deviations are trait-, population-, or environment-specific because market weights of aquaculture  
284 species are different or harvesting time to make measurements varied greatly among species;  
285 hence, basic statistics for traits studied were not summarised.

286

### 287 3. Factors affecting genetic parameters

288 The General linear model (GLM procedure) to examine the significance of fixed effects [including  
289 species (salmonids, carps, tilapias, crustaceans, molluscs and other fishes), experimental design  
290 (single-pair mating vs. mass spawning), statistical analytic method (REML, realised heritability and  
291 intraclass correlation analysis) and age of the publication (or assemble data collected) relative to  
292 2017] showed that only experimental design and analytic method were statistically significant for  
293 body weight ( $P < 0.01$  and  $0.05$ , respectively) (Table 4).

294

### 295 4. Heritability

296

297 The number of studies, weighted mean heritabilities ( $\pm$  standard errors, S.E), between-study  
298 variances,  $Q$ -statistics and 95% confidence intervals (CI) of the estimate for different traits grouped

299 for all species are presented in Tables and 2. The results with specificities for some fish species are  
300 considered below.

301 a. Growth related traits

302 Regardless of whether analyses were conducted separately for each species or for all species  
303 together, the weighted heritabilities for growth-related traits (body weight) were moderate (0.22 –  
304 0.33), suggesting that selective breeding is likely to prove successful for growth characters. A  
305 number of studies calculated body shape based on body measurements (weight/ length or  
306 depth/length) (Trọng et al. 2013a) or from image analysis (Blonk et al. 2010). The average heritability  
307 estimate for body shape was low to moderate, suggesting that changing this trait in aquaculture  
308 species is possible as predicted from selection index theory (Nguyen et al. 2007). Prchal et al (2018)  
309 also informed that selection for a trait connected to a trait of interest may have additional effect on  
310 body shape. In addition to growth-related traits, the heritability for food utilisation efficiency (FUE)  
311 was moderate ( $0.23 \pm 0.10$ , 95% CI = 0.04 to 0.42). Direct selection for ratio traits (i.e., FUE) is,  
312 however, difficult. This trait can be sometimes improved indirectly through selection for increased  
313 growth or reduced body fat (Verdal et al. 2017).

314 b. Carcass and flesh/eating quality

315 A carcass trait of paramount importance in fish is fillet yield or edible tail meat for shrimp (Hung and  
316 Nguyen 2014). In both fish and shrimp, fillet or edible meat weight is moderately heritable ( $h^2 = 0.33$   
317  $\pm 0.10$ ), whereas the heritability estimate for fillet yield (or percentage of fillet over body weight)  
318 was of lower magnitude (mean  $h^2 = 0.20 \pm 0.13$ ,  $P > 0.05$ ). Flesh and eating quality are complex  
319 characteristics and they are strongly influenced by environmental factors before slaughter, such as  
320 fasting, handling and post-mortem processing techniques (Hultmann et al. 2016). This is indicated by  
321 the low and insignificant heritability for the important flesh and eating quality attributes (pH, protein  
322 content) included in this review (Table 2). Almost all studies engaged total fat content of fillet  
323 (Hamzah et al. 2014b); information on fat deposits in different body compartments/locations could

324 have genetically different patterns (Kause et al. 2002; Tobin et al. 2006). Across the measures of fat  
325 content reported in the literature, this trait had moderate heritability (mean  $h^2 = 0.17$ ,  $P < 0.05$ ).  
326 Flesh colour in some fishes is an attribute of biological importance because it is positively correlated  
327 with pH, water holding capacity and eating characteristics (mean  $h^2 = 0.18$ ,  $P < 0.05$ ) and also  
328 because it affects market value. For example, deeply red salmon fillets are more highly valued than  
329 whitish ones. In fish, flesh colour was subjectively measured based on a scoring scale or objectively  
330 measured using a colour wheel or instrument. Norris and Cunningham (2007) reported higher  
331 heritability for objective than subjective measurements of flesh colour in Atlantic salmon. Based on a  
332 binary scale (visual observation of red or light colour), Nguyen *et al.* (2014) suggested that there is a  
333 possibility for improving red body colour of both raw and cooked banana shrimp.

334 Other flesh and eating quality characteristics reported in the literature exhibited additive genetic  
335 variation in muscle fibre types or fibre density in rainbow trout, with the estimate of heritability  
336 ranging from 0.10 to 0.33 (Vieira et al. 2007). Two studies reported heritability for fatty acid  
337 composition in Nile tilapia (Nguyen et al. 2010b) and Atlantic salmon (Leaver et al. 2011) and  
338 another in Whiteleg shrimp (Nolasco-Alzaga et al. 2018). For these flesh/eating quality attributes,  
339 the number of studies are very limited (<3); hence, the weighted heritability was not calculated.

340

#### 341 c. Disease resistance

342 Heritability estimates for disease resistance were mainly reported from challenge test studies for  
343 three types of pathogens (parasites, bacteria and virus). In practice, the resistance was measured as  
344 survival rate of the challenged animals with  $LD_{50}$  to a particular time point, after a period of 45-50  
345 days. Only one study proposed an alternative approach to estimate disease resistance, using qPCR  
346 analysis to measure HPV viral load of individual banana shrimp (*Fenneropenaeus merguensis*) (Knibb  
347 et al. 2015). I calculated weighted mean heritability separately for each disease type (bacterial,  
348 parasitic and viral) and across all the three types of pathogens (Table 2). The results showed that a

349 significant heritable genetic component exists for a variety of diseases in fishes, shrimps and  
350 molluscs. The magnitude of the heritability estimates was not significantly different among the three  
351 disease types (Tables 2). Three studies (Camara et al. 2017; Degremont et al. 2015; Liang et al. 2017)  
352 estimated heritability for disease resistance in mollusc (2 in oysters and 1 in clam).  
353 Six studies reported the heritability for indicators of stress resistance (i.e. cortisol level) or hypoxia  
354 and oxidative stress resistance. The weighted heritability for these indicators of stress tolerance was  
355 moderate ( $0.20 \pm 0.11$ ) but not significant ( $P > 0.05$ ).

356 Across species, the moderate level of heritability for resistance against a range of diseases and  
357 environmental stressors suggests that these traits would respond effectively to selection. Improving  
358 disease resistance is necessary to reduce mass mortality and associated loss of weight and economic  
359 opportunities for the aquaculture sector worldwide. Novel approaches (e.g., markers-assisted or  
360 genome-based selection) should be considered as conventional method based on challenge tests is  
361 associated with ethic issues or due to some notifiable status of some diseases or other veterinarian  
362 measures (Trinh et al. 2019).

363

#### 364 d. Reproduction

365 Reproductive traits reviewed here included sexual maturity, female weight prior to spawning, egg  
366 size, fecundity (egg numbers or egg volume), larval survival and fry weight. In selective breeding  
367 programs for many aquatic species, status of sexual maturity during the grow-out period was  
368 recorded as a binary character and analysed using both linear and threshold mixed models. Across  
369 the studies and species examined here, sexual maturity exhibited a low to moderate heritability  
370 (weighted mean  $h^2$  of 0.21 and confidence interval ranging from 0.04 to 0.38). However, the  
371 heritability for age at sexual maturity was high (Crandell and Gall 1993; Gjerde 1984). The mean  
372 heritability for female weight was moderate ( $h^2 = 0.35$ ). By contrast, the heritabilities estimated for  
373 other reproductive traits were low and non-significant (Table 2). There were no differences in the

374 heritability estimates for reproductive characteristics between fishes (Gima et al. 2014; Thoa et al.  
375 2017; Trọng et al. 2013c) and shrimps (Caballero - Zamora et al. 2015; Macbeth et al. 2007). The  
376 consistently low heritability for reproductive and fitness- related traits across aquatic species  
377 suggests that response to selective breeding to improve these characters, albeit possible, may be  
378 slow and difficult to achieve. In addition to the five important reproductive traits reviewed here, low  
379 to moderate heritability was reported for gonad weight/gonad somatic index (Charo-Karisa et al.  
380 2007) or spawning interval in Nile tilapia (Trọng et al. 2013b). The heritability for egg diameter or  
381 hatching rate was low (essentially not different from zero). Generally, reproductive traits are difficult  
382 to be investigated for heritability, as these characters are greatly affected by environmental and other  
383 variables (e.g., health status of fish, level of management of artificial reproduction) that bias the  
384 genetic variation estimates. Thus this area of research deserves further studies across aquaculture  
385 species.

386

387 e. Fitness-related traits

388

389 Two fitness related traits studied here were survival and deformity. Survival during grow-out showed  
390 a low but significant additive genetic variation, with the heritability mean estimate of 0.14 (95%  
391 confidence interval, CI from 0.08 to 0.21,  $P < 0.001$ ) across species. Existence of the heritable  
392 (additive) genetic component for survival during the early phase of growth (i.e., before physical  
393 tagging or 1-2 months after hatching) has been reported for tilapia (Thoa et al. 2015) and rainbow  
394 trout (Vehviläinen et al. 2012).

395 There are various forms of deformity in fishes such as lower jaw protrusion, nasal erosion, opercula  
396 distortion, cataracts, spinal abnormalities (lordosis, kyphosis, scoliosis, and ankylosis) as well as  
397 mouth and fin malformations. Estimates of heritability were reported for a range of deformity  
398 measures or for a specific type of deformity, such as humpback anterior dorsal fin, humpback



399 posterior dorsal fin and shortened tail fin in Atlantic salmon (Glover et al. 2005) or lordosis, cyphosis,  
400 scoliosis and vertebral fusion in European seabass (Karahan et al. 2013). Synthesised results from the  
401 literature showed that different measures of deformity can be considered as separate traits,  
402 including studies in rainbow trout (Vehviläinen et al. 2012) and kingfish (Nguyen et al. 2016).  
403 However, a range of measures of deformity was pooled in this study, mainly due to the limited  
404 sample size (small number of studies). The weighted heritability estimate for this trait was low and  
405 not significant (weighted mean  $h^2 = 0.18 \pm 0.11$ ,  $P > 0.05$ ).

406

#### 407 f. New traits

408 Novel traits considered in this review included behaviour, socially indirect genetic effects and  
409 uniformity. A detailed description of measurement methods is given in Supplementary N.4. Recent  
410 studies have attempted to qualify the level of genetic variation for these new traits, with the  
411 heritability ranging from 2 to 10% for uniformity (Sae-Lim et al. 2015) and direct or indirect social  
412 genetic traits (Nielsen et al. 2014). There is also evidence of genetic variability in personality-related  
413 characters in rainbow trout (Millot et al. 2014). However, the heritability estimates for these  
414 behavioural traits ranged from low in brown trout (Kortet et al. 2014) to moderate in Atlantic cod  
415 (Drangsholt et al. 2014). A high heritability for boldness (risk-taking score) was, however, reported  
416 for European seabass (Ferrari et al. 2016). There is a need for further studies to support a reliable  
417 systematic meta-analysis for novel traits across farmed aquaculture species of economic  
418 importance.

419

#### 420 5. Common full-sib effects

421 In aquatic species, different experimental designs have been utilized to estimate heritability-related  
422 parameters for a range of traits of economic importance. Common full-sib effects ( $c^2$ ) were a result

423 of separate family rearing of about one to two months until fish/shrimps reach a suitable size for  
424 physical tagging (5-10 g in fish and 1-2 g in shrimps). The  $c^2$  includes both common environmental  
425 and maternal effects, accounting for approximately 5 – 14% of the total phenotypic variance across  
426 species (Table 3). The  $c^2$  effects show a tendency to diminish in later phase of growth. For carcass  
427 and flesh quality traits, these effects were generally not significant. The  $c^2$  effects were not  
428 significant for eating quality characteristics or fillet fatty acid composition. Only one study (Hamzah  
429 et al. 2014a) reported  $c^2$  effects for reproductive traits, but the estimates were essentially zero.  
430 Maternal genetic effects have not been reported for disease resistance or measures of deformity.

431

## 432 6. Heritabilities in contrasting environments

433 Because expression of quantitative traits depends in part upon environmental factors, heritabilities  
434 estimated in diverse environments may differ. Figure 2 presents standardized mean differences in  
435 heritabilities for body weight between contrasting environments. There was non-significant  
436 difference in the magnitude of heritability between the environments, suggesting that there is no (or  
437 little) reduction in the additive genetic variance of body weight in the production environment  
438 compared with the nucleus. Additionally, previous studies (Nguyen 2016; Sae-Lim et al. 2016)  
439 showed that the between-environment genetic correlations for homologous body traits was positive  
440 and high when the environments used in the nucleus and production were similar. However, when  
441 the two environments differed, the genetic correlation estimates was low or moderate, suggesting  
442 that the G×E interaction effects are potentially important for complex traits in aquaculture species.

443

## 444 7. Genetic correlations

### 445 a. Correlations between body and carcass/flesh quality

446 Certain traits of breeding interest are correlated with one another. Knowledge of such correlations is  
447 needed to design purposeful breeding programs. Genetic correlations ( $r_g$ ) between flesh quality and  
448 body weight (the sole selection criterion of many breeding programs) are shown in Table 5. The  
449 genetic correlations between fillet fat content and body weight were moderate to high and mostly  
450 positive (mean  $r_g = 0.51 \pm 0.06$ ), except for the negative estimate reported in rainbow trout by Kause  
451 et al. (2002). The estimated correlation between moisture and body weight was positive in  
452 salmonids and tilapias, but negative in rainbow trout. Flesh or body colour exhibited a moderate to  
453 high positive correlation with body weight in Atlantic salmon (Quinton et al. 2005) and banana  
454 shrimp (Nguyen et al. 2014).

455

456 b. Correlations between body weight and disease resistance

457 Genetic correlations between body weight and disease resistance were either positive or non-  
458 significant in the literature (Table 6). Some studies, however, also reported negative (i.e.  
459 antagonistic) genetic association between growth and disease resistance, for example ranging from -  
460 0.01 to -0.33 in rainbow trout (Henryon et al. 2002) or -0.54 to -0.66 in Pacific white leg shrimp  
461 (Gitterle et al. 2005). Recent studies showed weak or non-significant genetic relationship between  
462 the two traits in rainbow trout (Yáñez et al. 2014) or shrimp (Phuthaworn et al. 2016). The weighted  
463 mean genetic correlation between the two traits (weight and disease resistance) was not significant  
464 (Table 6). When the analysis was conducted separately for each type of pathogen, a significant  
465 genetic correlation was observed between body weight and resistance to parasites ( $r_g = 0.23$ ).

466

467 c. Correlations between body weight and deformity

468 The reported estimates of genetic correlations between deformity and growth traits varied from  
469 negative (Gjerde et al. 2005) to positive (Karahhan et al. 2013) or non-significant (Kolstad et al.  
470 2006)(Figure 3). Across the studies, the estimate was not significant ( $r_g = -0.14$ , CI = -0.56 to 0.29,  $P >$

471 0.05). However, the genetic relationship between body weight and deformity varied with growth  
472 phase and trait definitions, e.g. fast-growing rainbow trout fingerlings are prone to skeletal  
473 deformities, while body weight and cataracts in the adult stage were negatively correlated (-0.52 to -  
474 0.62)(Vehviläinen et al. 2012). Nguyen et al. (2016) report that the degree of co-inheritance of  
475 deformity varied with trait combinations (i.e. positive between weight and jaw malformations but  
476 negative between weight and operculum). There is still very limited information regarding the  
477 genetic correlation of deformity with traits of economic importance, suggesting that a detailed  
478 recording of deformity characteristics would be necessary to characterize the genetic architecture of  
479 malformation in aquaculture populations reared in different culture environments.

480

#### 481 d. Correlation between weight and reproduction

482 The genetic correlation of body weight during grow-out and fecundity-related traits in females was  
483 moderate and positive (Table 7). Selection for high growth is thus expected to bring about  
484 favourable changes in reproductive performance (fecundity and fry weight) of the aquatic animals,  
485 thereby, leading to greater production of fry and fingerlings for marketing. This is important only in  
486 species or culture systems where the egg is the final product (e.g., sturgeon or salmon caviar).  
487 However, interpretation of these results should be with caution because the relationship between  
488 body weight and relative fecundity was not available in the literature. Further, the genetic  
489 relationship between body weight and number of fry at hatching or fry mortality during the early  
490 phase of rearing was weak and not significant in Coho salmon (Gall and Neira 2004), Nile tilapia  
491 (Hamzah et al. 2014a) or giant freshwater prawn (Vu and Nguyen 2019). In summary, genetic  
492 relationships between reproductive traits and growth deserve further studies, due to the limited  
493 number of studies available in the literature as well many other factors involved, e.g., age of  
494 maturation.

495

496 e. Correlation between weight and new traits

497 Currently, genetic associations of growth (or body weight) with behavioural and functional traits are  
498 not well documented. This is an important area that merits future studies to support the possibility  
499 of multi-trait selection and to gain knowledge to control unexpected changes from selection  
500 programs for high productivity.

501

502 8. Sample size

503 A parameter-estimation experiment needs sufficient power in order to yield a reliable estimate for  
504 design of an effective breeding program. The sample sizes required to obtain sufficient statistical  
505 power to detect significant heritability are given in Table 8. The statistical power depends on the  
506 level of heritability (low, moderate or high) and the probability of detecting significant heritabilities  
507 (95 or 99%). Statistical power increases with the number of sires and dams in the pedigree. For a  
508 given sample size, statistical power is higher for greater heritabilities. Statistical power also differs  
509 with levels of probability associated with detecting significant heritability. Across the three scenarios  
510 studied, with the hierarchical nested design a minimum 30 sires and 60 dams are required to obtain  
511 sufficient (>80%) power to detect a significant heritability estimate. Fewer than 30 families are not  
512 recommended because under this mating (nested) scheme, the likelihood of detecting significant  
513 heritability was low, ranging from 3.6 to 34.6%.

514

#### 515 **IV. DISCUSSION**

516 This is the first systematic meta-analysis of genetic parameters for aquatic animal species. The  
517 heritabilities, common full-sib effects and correlations provide information advancing our  
518 understanding of genetic architecture of economically important traits in aquatic animal species. My  
519 results also help to fill a gap in our knowledge regarding inheritance and relationships among

520 quantitative traits, providing knowledge to address challenges regarding genetic improvement of  
521 aquaculture species. In addition, this systematic meta-analysis identified limitations and proposed  
522 suggestions for future studies as well as possibilities to utilise advanced statistical methods and  
523 genome sequence technologies to understand complex quantitative traits of aquatic species.  
524 Specifically, the results synthesised from this study provide answers to the following questions:

525 1. Does the quantitative genetic basis of complex traits differ?

526 The weighted mean of heritability estimated from the meta-analysis (Figure 1 and Table 2) showed  
527 that quantitative genetic architecture differed among the five groups of traits reviewed. Growth-  
528 and carcass-related characters had moderate to high heritabilities. On the other hand, traits related  
529 to quality (fat content, colour) or fitness (reproduction: fecundity, early survival) are lowly or  
530 moderately heritable. Disease resistance to different types of pathogens (bacterial, viral and  
531 parasitic) exhibited substantial heritable genetic variance in a range of aquaculture species (Ødegård  
532 et al. 2011). My findings are consistent with the expectation of quantitative genetic and evolutionary  
533 theory as well as with observations in terrestrial farmed animals and model species (Safari et al.  
534 2005).

535

536 2. Can the traits studied show response to selection?

537 With abundant genetic variation in traits related to growth, genetic improvement of these  
538 characters should prove successful, as demonstrated in several selection programs across aquatic  
539 species ranging from fishes (Hamzah et al. 2014c) to crustaceans (Hung et al. 2013b) and molluscs  
540 (Liu et al. 2015). Across aquaculture species, genetic gain has ranged from 8 – 22% per generation  
541 (Gjedrem and Rye 2016; Nguyen 2016). On the other hand, selective breeding for other traits, such  
542 as reproduction, fitness and deformity, may be more difficult; hence, systematic data recording of  
543 sibling information from multi-generational, in-depth pedigree populations is needed to obtain  
544 reliable estimated breeding values for selection candidates. Genetic improvement for traits that

545 require sacrifice of animals such as flesh/eating quality or disease resistance is still difficult. Further,  
546 only sibling information can be used, thereby reducing accuracy of estimated breeding values and  
547 selection response. In these cases, genomic selection can potentially speed up genetic progress in  
548 traits that are difficult or expensive to measure (Boison et al. 2019).

549

550 3. Are there heritable additive genetic components for new traits?

551 In addition to the existence of useful additive genetic variance for fitness characters studied here  
552 (maturity, survival, reproduction), the proportion of genetic relative to total phenotypic variance for  
553 behavioural, social and immunological traits ranges from 0.03 to 0.45 (Ferrari et al. 2016; Kortet et  
554 al. 2014). These traits were not included in the meta-analysis, as only a limited number of studies are  
555 available in the literature and, the data mostly were recorded from a limited number of animals in  
556 shallow pedigrees of only one or two generations. Large-scale measurements for  
557 behavioural/functional and adaptive traits (e.g. stress tolerance to environmental factors) are still  
558 challenging due to the costs involved and sophistication of data recording, using video or laboratory-  
559 based tests. I also attempted to calculate the weighted heritability for these traits, but the estimates  
560 had large standard errors and thus they were not significantly different from zero. To understand  
561 quantitative genetic basis of traits that are expensive and difficult to measure (e.g., flesh and eating  
562 quality or disease resistance) in aquaculture species, development of new measurement methods is  
563 required to enable routine large-scale data recording for species of commercial importance (see  
564 section 4.7).

565

566 4. Does the heritability of traits differ between environments?

567 Heritability reported in various culture environments is mainly for growth related traits (weight or  
568 daily gain). Although magnitude of the heritability estimate varied with environments, the weighted

569 effect size was small and not significant (Figure 2). However, there are exceptions in the literature  
570 where there is a reduction in the heritability estimates for growth traits in poorly managed culture  
571 systems in comparison to those estimated in the nucleus under well-controlled environment  
572 (Bentsen et al. 2012). Under these circumstances, the difference in the magnitude of the estimate  
573 was mainly due to scaling effects. Previous reviews (Nguyen 2016; Sae - Lim et al. 2016) also  
574 indicated that the genotype by environment (G×E) interaction was important when the production  
575 system differs markedly from the selection environment (e.g., fresh vs. brackish water), while the  
576 G×E was not significant when the two environments were similar. Even similar heritabilities in  
577 different environments do not necessary indicate no environment because they can result in  
578 different selection responses. A recent study in red tilapia reported significant impact of culture  
579 environments on genetic gain (Nguyen et al. 2017). Hence, the G×E effect should be examined on  
580 case by case basis to assist the design and conduct genetic improvement programs for aquaculture  
581 species.

582

583 5. Are the maternal and common environmental effects important?

584 The significant  $c^2$  effects for growth traits suggest that they should be included in statistical models  
585 to account for upward bias in genetic parameter estimates (Joshi et al. 2018). They also should be  
586 included in genetic evaluation systems to avoid any possible overestimation of breeding values as  
587 demonstrated in several studies (Hung et al. 2013a; Oliveira et al. 2016). To reduce the  $c^2$  effects in  
588 genetic improvement programs, early communal rearing of all families should be practised as soon  
589 as after birth. This approach can be implemented by using DNA markers (microsatellite or single  
590 nucleotide polymorphism, SNP) for genetic tagging and construction of pedigrees (Ninh et al. 2013;  
591 Whatmore et al. 2013).

592



593 6. Is the sample size sufficient to detect significant heritability?

594 Except for some studies where sample sizes were small (and the results were excluded from the  
595 present meta-analysis), the majority of reports included in this review had sufficient statistical power  
596 to detect significant heritability ( $h^2$ ) for traits with moderate to high heritability (i.e. growth traits)  
597 across aquaculture populations. The non-significant weighted  $h^2$  for other traits (flesh quality,  
598 fitness, reproduction) indicates that a much larger sample size and deeper pedigree are needed to  
599 obtain reliable genetic parameter estimates for low heritability traits; priority should be given to  
600 estimate genetic properties of these traits in future studies. Moreover, due to reproductive biology  
601 of many aquaculture species where synchronised mating is still difficult, *in-vitro* fertilisation in  
602 combination with advanced mating design such as factorial mating (Dupont-Nivet et al. 2006) should  
603 be applied to enable the estimation of different variance components; this would allow separation  
604 of additive genetics from non-additive genetic effects that are not widely understood in many fishes,  
605 crustaceans and molluscs. Across species, the conventional quantitative genetic (infinitesimal) model  
606 and family structure of aquaculture pedigrees did not allow a neat estimation of non-genetic  
607 components (maternal and common environmental effects), but they could be important for fitness-  
608 related traits and worth considering in future studies.

609

610 7. Were the heritabilities for important traits affected by publication bias?

611 The effect of publication bias on the heritability, for example, of body weight or morphological  
612 deformity was not significant in this study (see the Begger's funnel plot and Egger regression  
613 asymmetry test in Supplementary File No.3). In addition, results of the sensitivity analysis performed  
614 by excluding studies with z-value greater than 3 (one study at a time or all together) gave almost  
615 identical heritability estimates for economically important traits (results not shown). This is also  
616 indicated by the narrow confidence interval, especially for body weight where the sample size for  
617 this trait was large. On the other hand, the effect of publication bias was present for other traits

618 (flesh quality attributes and reproduction), partially due to the limited sample size reported for these  
619 characters.

620

621 8. Can selection for high performance also improve other traits?

622 With the current knowledge, there is a good understanding of the genetic associations among body  
623 traits (weight, length, width and depth) and those of growth traits with carcass yield, suggesting that  
624 either weight or length can be used as alternative selection criterion, and that selection for one of  
625 the two traits can simultaneously improve overall production performance of the animals (Hung and  
626 Nguyen 2014). Genetic correlations of body weight with carcass/flesh quality and reproductive traits  
627 are consistent with realised correlated changes in both fishes (Hamzah et al. 2014a; Hamzah et al.  
628 2014b) and shrimps (Hung et al. 2013b). These changes are desired from genetic improvement  
629 perspectives. However, selection for high growth did not improve fillet yield in tilapia (Nguyen et al.  
630 2010a) or caused insignificant changes in survival or fecundity per unit of female weight (Hamzah et  
631 al. 2015; Hamzah et al. 2014a). When growth is not of interest, fillet yield can still be improved  
632 through sib or indirection selection by using various yield predictors (Prchal et al. 2018; Vu et al.  
633 2019). Furthermore, there is evidence in at least five populations of freshwater species (carps,  
634 tilapias and prawns) that selection for high growth didn't cause adverse impact on survival (Vu et al.  
635 2017). Based on the weighted genetic correlation estimates, it can be predicted that selection for  
636 high growth may not improve disease resistance across aquatic species, although the positive  
637 genetic correlation estimates between the two traits were reported in some studies. Furthermore,  
638 possible changes in fitness, social interaction or behavioural traits consequent to selection for high  
639 productivity were not well understood, because majority of breeding programs for aquaculture  
640 species have started rather recently, except for the two long run programs in Atlantic salmon in  
641 Norway (Gjedrem 2010) and Nile tilapia in the Philippines and then Malaysia (Hamzah et al. 2014a;  
642 Ponzoni et al. 2011).

643 9. Can traits showing antagonistic genetic relationships be improved simultaneously?

644 A number of traits included in this review showed antagonistic relationships that are not desired. For  
645 instance, based on the weighted genetic correlation estimate between body weight and sexual  
646 maturity, it can be predicted that selection for increased harvest body weight may produce early-  
647 maturing fish. On the one hand, the concomitant changes in the early maturity are desired for newly  
648 domesticated species in captivity (e.g., marine fishes). On the other, precocious reproduction in  
649 tilapia leads to low growth performance of stocked fish as a consequence of over-crowding and feed  
650 competition in production ponds. Under these circumstances, a restricted (or desired) selection  
651 index can be applied to simultaneously improve both traits (Nguyen et al. 2016; Sae-Lim et al. 2012).  
652 Multi-trait selection (Janssen et al. 2017) is recommended to maximise productivity and revenue as  
653 well as sustain long-term genetic improvement in order to meet future demand for high quality  
654 seafood by consumers and to adapt to environmental challenges.

655

656 10. Limitations and gaps in the literature

657 Only a few reports on heritability were found for traits that are expensive or difficult to measure,  
658 such as flesh/eating quality, behaviour and adaptive traits, across aquaculture species. The genetic  
659 association of these new traits with growth performance is inconclusive as the correlation estimates  
660 are not sufficient to support a systematic meta-analysis. To gain reliable estimates and better  
661 understanding about genetic relationships among these traits, a larger sample size from  
662 multigenerational pedigreed populations is needed. Until the present, objective measurements of  
663 traits that require slaughter of the animals are still not common in selective breeding programs for  
664 aquaculture species. For example, the application of near or mid infra-red spectroscopy may reduce  
665 costs of analysing fillet fatty acids in fish (Nguyen et al. 2010b), or quantitative real time PCR could  
666 be used to quantify viral copy numbers as an alternative approach to study disease resistance in  
667 shrimps (Phuthaworn et al. 2016). Challenges still remain to make objective and effective

668 measurements of flesh/eating quality and behavioural/physiological traits in aquatic species. The  
669 availability of imaging technologies (X-ray, computed tomography CT) or machine vision systems also  
670 enables detailed examination of quality traits and deformities in fish at a reasonably low cost  
671 (Saberioon et al. 2016). In the near future, laboratory-generated data such as qPCR to quantify viral  
672 load/or titre level to select for disease resistance, and molecular genetic information or genome  
673 sequence, are expected to become available to study genetic architecture of new traits in aquatic  
674 species.

675

## 676 11. New prospects for understanding complex traits

677 In addition to the application of new measurements/data recording methods (section 4.8), the  
678 development of statistical approaches and algorithms such as restricted maximum likelihood  
679 method (Thompson 2008) applied to a multi-trait mixed model (Henderson 1975) helped to improve  
680 the accuracy of the genetic parameter estimates reported in the literature in comparison to the  
681 conventional analysis of variance (ANOVA) used 20-30 years ago. Recent expansions of the mixed  
682 model methodology have provided opportunities to study new traits, including social indirect  
683 genetic effects (Bijma 2014) or double hierarchical linear generalised model (Rönnegård and Lee  
684 2013) to reduce environmental variation and improve uniformity (Hill and Mulder 2010) for aquatic  
685 species. The application of random regression analysis or cure survival model may help to  
686 understand disease tolerance and resistance in a range of species (Kause and Ødegård 2012).  
687 Structural equation models (Valente et al. 2010) can be applied to dissect complex biological  
688 relationships among traits, such as milk or fillet fatty acids (Bouwman et al. 2014). Particularly, the  
689 advent of high through-put whole genome sequencing and 'omic' related technologies coupled with  
690 better computational methods provide opportunities to better understand genetic architecture of  
691 quantitative complex traits in aquatic species. Genomic or genome-based selection has  
692 revolutionized breeding of dairy cattle and other livestock and plant sectors world-wide (Van

693 Eenennaam et al. 2014). Recent studies in aquaculture species indicated that the accuracy of  
694 genomic prediction for quantitative traits was moderate to high (Nguyen et al. 2018b; Tsai et al.  
695 2017; Yoshida et al. 2018), thereby the potential opportunities of genomic selection can offer to  
696 enhance aquaculture breeding in the near future.

697

## 698 **V. CONCLUSIONS**

699 Meta-analysis of information concerning genetic parameters of complex quantitative traits in  
700 aquatic species revealed that:

- 701 1. The weighted means heritabilities ( $h^2$ ) for body and carcass traits in aquaculture species  
702 were moderate, whereas they were low and not significant for flesh quality attributes,  
703 except fillet fat content and fillet (or body) colour. Resistance against bacterial, viral and  
704 parasitic diseases was moderately heritable. The  $h^2$  estimates for fecundity and deformity  
705 were low and not significantly different from zero.
- 706 2. There were prospects to investigate new functional traits, namely behaviour, adaptation,  
707 uniformity, social interaction indirect genetic effects and immune response. There is very  
708 limited published information regarding genetic relationships between these novel  
709 characters and growth (or other traits) to enable multi-trait selection in future breeding  
710 programs.
- 711 3. The genetic correlations of body weight with colour and fillet fat content were moderate to  
712 high and positive. However, the estimates between growth and other flesh- quality  
713 attributes were weak and not significant. There was insignificant genetic association  
714 between growth and disease resistance. Genetic relationship of reproductive traits with  
715 body weight and growth-related characteristics merit further studies.
- 716 4. The maternal and common environmental effect ( $c^2$ ) accounted for 5 to 14% of the total  
717 phenotypic variance for growth-related traits, whereas it was not significant for flesh-quality

- 718 attributes or reproductive characteristics, due to low number of investigations or non-  
719 optimal experimental design.
- 720 5. The effect of publication bias was not important for growth traits and deformity. On the  
721 other hand, it was apparent for disease resistance, flesh-quality attributes and reproductive  
722 characteristics.
- 723 6. There was small to moderate heterogeneity in the heritability and  $c^2$  effects for the majority  
724 of the traits studied. By contrast, the  $Q$ -statistics were significant for the genetic correlation  
725 estimates.
- 726 7. While results from the present meta-analysis provide fundamental information regarding  
727 genetic architecture of quantitative complex traits, genetic parameters should be estimated  
728 for each population before genetic improvement programs are initiated for a new species  
729 because the additive variation is different among populations within an individual species  
730 and it varies with environments and generations. The effect of genotype by environment is  
731 potentially important for complex traits, especially when the environments used in the  
732 nucleus differ from those practised under field production systems.

733

734

## 735 VI. FUTURE DIRECTIONS

- 736 1. Future research should focus on novel characteristics that are emerging as potential  
737 selection criteria in genetic improvement programs, such as flesh/eating quality and new  
738 traits of commercial interest such as behaviour, adaptation, immune response and disease  
739 resistance.
- 740 2. Little is known about genetic relationships among these traits with body weight which  
741 justifies further studies.

- 742 3. Large sample size and multigenerational data from long term genetic improvement  
743 programs would increase the accuracy of genetic parameter estimates, especially for traits  
744 with low heritability (e.g., reproduction and deformity).
- 745 4. Laboratory based data, such as viral load quantified by qPCR and molecular genetic  
746 information or genome sequence should be increasingly incorporated into selective  
747 breeding programs for aquatic species
- 748 5. New methods of measurements should be applied to enable large-scale routine data  
749 collection for traits that are difficult or expensive to measure
- 750 6. Whole genome sequencing provides options to dissect the genetic architecture of  
751 quantitative complex traits across species.
- 752 7. Dissecting the quantitative genetic architecture of novel traits also requires development of  
753 new means of measurements to enable large-scale data recording as well as effective tools  
754 to manage pedigrees.

755

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759

### 760 **Supplementary files**

761 Supplementary file No.1: PRISMA diagram flow to assess eligibility of studies included in the meta-  
762 analysis

763 Supplementary file No.2: A full list of references included in the review and analysis

764 Supplementary file No.3: Funnel plot to assess publication bias and sensitivity analyses

765 Supplementary file No.4: Detailed description of measurement methods for novel traits

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1067 **Figures**

1068 Figure 1: Weighted mean heritability ( $h^2$ ) for body weight and the maternal and common  
1069 environmental full-sib effects ( $c^2$ ) in six groups of species studied.

1070 Figure 2: Forest plot of the heritability difference between contrasting environments (Q-statistic =  
1071 22.530, p-value = 0.605) and between-study variance = 0.03

1072 Figure 3: Weighted genetic correlations ( $r_g$ ) of body weight with measures of deformity in fish and  
1073 shrimp (between-study variance = 0.32 and  $P > 0.05$ )

1074

1075 **Glossary**

1076 **Quantitative complex traits** are influenced by both genetics and the environment, which can be  
1077 expressed on continuous numerical scale (e.g. body weight) or non-continuous (meristic and  
1078 threshold traits).

1079 **Closed breeding nucleus** is a traditional breeding scheme where replacement animals come from  
1080 the nucleus and no animals outside the nucleus are added to the population.

1081 **Functional traits** are morphological, biochemical, physiological, structural, phenological or  
1082 behavioural characteristics that influence organism performance or fitness.

1083 **Heritability** estimates the degree of variation in a phenotypic trait in a population that is due  
1084 to genetic variation between individuals in that population

1085 **Common full-sib effects** are due to non-additive genetic, maternal and environmental effects and  
1086 common family-tank/hapa effects, as a result of separate rearing of each family before physical  
1087 tagging

1088

1089 **Phenotypic correlation** is a measure of the association between phenotypic values of characters

1090 **Genetic correlation** is a measure of the association between breeding values of quantitative  
1091 characters

1092 **Random regression analysis** is a statistical method used to analyse repeated measurements over  
1093 time or age (also termed as longitudinal data) to account for the mean and covariance structure that  
1094 may change with time.

1095 **Cure survival models** are used for modelling time-until-death data that include a fraction of non-  
1096 affected individuals, i.e., those that are liable to die due to the infection.

1097 **Structural equation models**, also known as path models, are used to understand the correlation  
1098 structure of continuously variable data

1099 **Double hierarchical linear generalised model (DHGLM)** is an extension of generalized linear model  
1100 to include a structure for one or more variance components and/or the residual variance. The  
1101 method is used for estimation in models with genetically structured heterogeneity of residual  
1102 variance for large quantitative data sets

1103

1104 Table 1: Data characteristics for reports on genetic parameters for growth related traits

Species	No. of studies	Age of pub years relative to 2017	Average data records	Average no of sires	Average no of dams	Design	Analytic methods
Salmonids	40	11.9	27,933	104	69	S, M, C	REML
Tilapias	34	7.9	16,096	164	223	S	IC, REML, $h^2_R$
Carp	8	8.8	4,208	166	279	S, M, C	REML
Other fishes	31	5.9	3,296	122	95	S, M, C	REML
Crustacean	24	7.0	41,135	294	392	S	REML
Molluscs	12	8.7	6,189	112	172	S, M	IC, REML, $h^2_R$
Across species	150	8.7	19,357	199	264	S, M, C	IC, REML, $h^2_R$

- 1105 Salmonids = Atlantic salmon (*Salmo salar*), Coho salmon (*Oncorhynchus kisutch*), rainbow trout  
1106 (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*), Arctic char (*Salvelinus alpinus*) and European  
1107 whitefish (*Coregonus lavaretus* L.)
- 1108 Tilapias = Nile (*Oreochromis niloticus*), blue (*Oreochromis aureus*), red (*Oreochromis sp*) and African  
1109 indigenous (*Oreochromis shiranus*) tilapia
- 1110 Carps = common carp (*Cyprinus carpio*), rohu carp (*Labeo rohita*), silver carp (*Hypophthalmichthys*  
1111 *molitrix*)
- 1112 Other fishes include yellowtail kingfish (*Seriola lalandi*), seabream (*Sparus aurata*), Asian seabass  
1113 (*Lates calcarifer*), European seabass (*Dicentrarchus labrax*), Atlantic cod (*Gadus morhua*), common  
1114 sole (*Solea solea*), striped catfish (*Pangasianodon hypophthalmus*), Channel catfish (*Ictalurus*  
1115 *punctatus*), turbot (*Scophthalmus maximus*), Yellow perch (*Perca flavescens*)
- 1116 Crustaceans = Whiteleg shrimp (*Penaeus (Litopenaeus) vannamei*), tiger prawn (*Penaeus monodon*),  
1117 giant freshwater prawn (*Macrobrachium rosenbergii*), banana prawn (*Fenneropenaeus merguensis*)  
1118 and redclaw crayfish (*Cherax quadricarinatus*)  
1119
- 1120 Molluscs = Pacific oyster (*Crassostrea gigas*), Sydney rock oyster (*Saccostrea glomerata*), tropical  
1121 oyster (*Saccostrea cucullata*), Pearl oyster (*Pinctada fucata*), silver-lip Pearl oyster (*Pinctada*  
1122 *maxima*), Chinese Pearl oyster (*Pinctada martensii*), Chilean mussel (*Mytilus chilensis*),  
1123 Mediterranean mussel (*Mytilus galloprovincialis*), small abalone (*Haliotis diversicolor*), South African  
1124 abalone (*Haliotis midae*), red abalone (*Haliotis rufescens*), tropical abalone (*Haliotis asinina*), scallop  
1125 (*Placopecten magellanicus*), Japanese scallop (*Patinopecten yessoensis*), catarina scallop (*Argopecten*  
1126 *ventricosus*) and Manila clam (*Ruditapes philippinarum*)
- 1127 S = Single pair mating with known parental identities to maintain pedigree using conventional  
1128 physical tags (Passive Integrated Transponder, PIT tags for fish and visible implant elastomer, VIE for  
1129 crustaceans), M = Mass spawning using DNA markers for parentage assignment, and C = Combined  
1130 conventional and molecular genetic pedigree methods
- 1131 IC = Intraclass correlation, REML = Restricted Maximum Likelihood Method under the mixed model  
1132 framework, and  $h^2_R$  = realised heritability
- 1133
- 1134



1135 Table 2: Number of literature estimates ( $N$ ), weighted mean heritability ( $h^2$ ), between study variance  
 1136 ( $\sigma_B^2$ ),  $Q$  statistics and 95% confidence interval (CI) of the heritability estimate for economic traits  
 1137 across aquaculture species.

Traits	$N$	$h^2 \pm s.e.$	$\sigma_B^2$ variance	$Q$ -statistic	95% CI of $h^2$
<b>Growth traits</b>					
Body weight	193	0.30±0.02***	0.14×10 <sup>-5</sup>	82.0	0.27 – 0.33
Feed utilisation	14	0.23±0.10*	0.92×10 <sup>-1</sup>	5.5	0.04 – 0.42
<b>Carcass and flesh quality traits</b>					
Fillet weight	8	0.33±0.10***	0.10×10 <sup>-6</sup>	0.69	0.14 – 0.51
Fillet yield	3	0.20±0.13 <sup>ns</sup>	0.40×10 <sup>-1</sup>	1.31	-0.05 – 0.45
pH	1	0.15±0.14 <sup>ns</sup>	0.01×10 <sup>-6</sup>	0.00	-0.13 – 0.32
Colour	11	0.18±0.07*	0.51×10 <sup>-1</sup>	1.84	0.04 – 0.32
Protein content	5	0.05±0.14 <sup>ns</sup>	0.63×10 <sup>-3</sup>	0.01	-0.22 – 0.33
Fat content	18	0.17±0.07*	0.10×10 <sup>-6</sup>	3.98	0.03 – 0.31
<b>Reproductive traits</b>					
Sexual maturity	9	0.21±0.09*	0.10×10 <sup>-6</sup>	1.1	0.04 – 0.38
Female weight	7	0.35±0.13**	0.49×10 <sup>-2</sup>	1.66	0.11 – 0.60
Fecundity	9	0.14±0.12 <sup>ns</sup>	0.18×10 <sup>-6</sup>	0.03	-0.10 – 0.37
Fry weight	2	0.09±0.13 <sup>ns</sup>	0.19×10 <sup>-4</sup>	0.02	-0.16 – 0.35
Fry survival	6	0.08±0.14 <sup>ns</sup>	0.89×10 <sup>-4</sup>	0.16	-0.19 – 0.36
<b>Disease resistance</b>					
Virus	27	0.27±0.04***	0.58×10 <sup>-6</sup>	11.9	0.18 – 0.35
Bacteria	21	0.32±0.05***	0.18×10 <sup>-6</sup>	13.5	0.23 – 0.41
Parasites	15	0.20±0.06**	0.16×10 <sup>-6</sup>	4.5	0.09 – 0.31
Others	5	0.20±0.11 <sup>ns</sup>	0.68×10 <sup>-2</sup>	2.3	-0.01 – 0.42
All diseases	55	0.26±0.02**	0.20×10 <sup>-5</sup>	67.5	0.22 – 0.30
<b>Fitness related traits</b>					
Deformity	11	0.18±0.11 <sup>ns</sup>	0.43×10 <sup>-3</sup>	0.84	-0.04 – 0.39
Survival	31	0.14±0.03***	0.45×10 <sup>-5</sup>	21.0	0.08 – 0.21

1138 \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$  and ns = non-significance

1139

1140 Table 3: Number of literature estimates ( $N$ ), weighted mean maternal and common environmental  
 1141 effects ( $c^2$ ), between study variance ( $\sigma_B^2$ ),  $Q$  statistics and 95% confidence interval (CI) for economic  
 1142 traits across aquaculture species.

Traits	$N$	$c^2 \pm s.e.$	$\sigma_B^2$ variance	$Q$ -statistic	95% CI of $c^2$
<b>Growth traits</b>					
Body weight	45	0.10±0.02**	0.97×10 <sup>-5</sup>	12.7	0.05 – 0.14
Feed utilisation	2	0.14±0.17 <sup>ns</sup>	0.15×10 <sup>-6</sup>	0.01	-0.18 – 0.47
<b>Carcass and flesh quality traits</b>					
Fillet weight	2	0.07±0.09 <sup>ns</sup>	0.36×10 <sup>-2</sup>	0.15	-0.10 – 0.25
<b>Reproductive traits</b>					
Sexual maturity	1	0.090±0.04 <sup>ns</sup>	0.00×10 <sup>-5</sup>	0.01	-0.18 – 0.26
<b>Fitness related traits</b>					
Survival	6	0.04±0.05 <sup>ns</sup>	0.10×10 <sup>-6</sup>	0.32	-0.05 – 0.13

1143 \*\* $P < 0.01$  and ns = non-significant

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1146 Table 4: *F*-value of factors included in the analysis of heritability for growth related traits studied

Traits	<i>N</i>	<i>R</i> <sup>2</sup>	Species	Design	Analysis method	Assemble data collected
Body weight	193	0.65	1.4	3.6**	3.1*	0.3
Survival	31	0.93	2.4	0.2	0.5	0.1
Sexual maturity	9	0.87	3.9	n.a.	n.a.	6.6

1147 \**P*<0.05, \*\**P*<0.01.

1148 These effects on other traits (feed utilisation, flesh quality, reproduction, disease resistance and  
1149 deformity) were also not significant

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1153 Table 5: Number of literature estimates ( $N$ ), weighted mean genetic correlations of flesh quality  
1154 traits with body weight ( $r_g$ ), between study variance ( $\sigma_B^2$ ),  $Q$  statistics and 95% confidence interval  
1155 (CI) of the genetic correlation estimate

Traits	$N$	$r_g$	$\sigma_B^2$ variance	$Q$ -statistic	95% CI
Protein	2	0.02	0.02	13	-0.17 – 0.21
Fat	12	0.51***	0.16	2474	0.33 – 0.67
Moisture	4	-0.19	0.02	81	-0.32 – -0.06
pH	1	0.01	n.a.	n.a.	n.a.
Colour	6	0.31**	0.29	2605	-0.08 – 0.62

1156 \*\*P < 0.01 and \*\*\*P < 0.001

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1159 Table 6: Number of literature estimates (N), weighted mean genetic correlations of disease  
1160 resistance with body weight ( $r_g$ ), between study variance ( $\sigma_B^2$ ),  $p$ -value of  $Q$  statistics and 95%  
1161 confidence interval (CI)

Traits	$N$	$r_g$	$\sigma_B^2$ variance	$Q$ -statistic	95% CI
Bacteria	8	0.09	0.04	<0.001	-0.03 – 0.21
Virus	8	0.02	1.60	<0.001	-0.63 – 0.68
Parasites	10	0.24*	0.19	<0.001	-0.12 – 0.59
Across types of pathogens	26	0.13	0.72	<0.001	-0.07 – 0.33

1162 \*P < 0.05

1163 Table 7: Number of literature estimates ( $N$ ), weighted mean genetic correlations of reproductive  
1164 traits with body weight ( $r_g$ ), between study variance ( $\sigma_B^2$ ),  $Q$  statistics and 95% confidence interval  
1165 (CI)

Traits	$N$	$r_g$	$\sigma_B^2$ variance	$Q$ -statistic	95% CI
WBS	3	0.31***	0.00	0.44	0.29 – 0.33
ES	3	0.36**	0.05	213	0.12 – 0.56
TNE	5	0.20*	0.04	212	0.02 – 0.36
EV	2	0.50**	0.14	389	0.04 – 0.79
NFH	3	0.04 <sup>ns</sup>	0.01	27	-0.04 – 0.18

1166 WBS= weight before spawning, ES= egg size (measured as diameter or volume), TNE= total number of  
1167 eggs, EV= total volume of eggs, NFH= number of fry hatched

1168 \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$  and ns = non-significant

1169

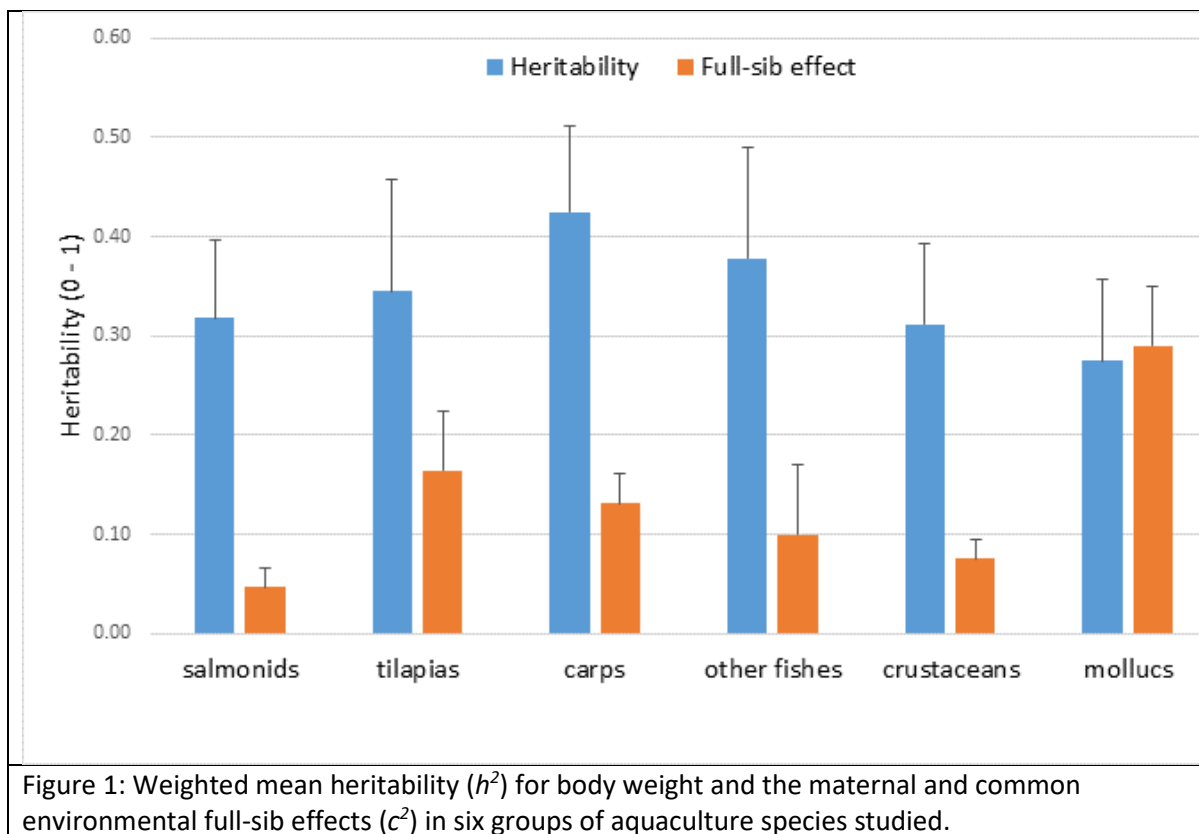
1170 Table 8: Number of sires and dams required in a nested design (one male is mated two females)

	Option 1		Option 2				Option 3					
	<i>P</i> = 0.05		<i>P</i> = 0.01		<i>P</i> = 0.05		<i>P</i> = 0.01		<i>P</i> = 0.05		<i>P</i> = 0.01	
Sires	15	15	15	15	30	30	30	30	45	45	45	45
Dams	30	30	30	30	60	60	60	60	90	90	90	90
$h^2$	0.07	0.20	0.07	0.20	0.07	0.20	0.07	0.20	0.07	0.20	0.07	0.20
<b>Power</b>	<b>35.7</b>	<b>82.8</b>	<b>16.5</b>	<b>67.1</b>	<b>87.6</b>	<b>99.8</b>	<b>73.4</b>	<b>99.8</b>	<b>99.6</b>	<b>100</b>	<b>98.4</b>	<b>99.9</b>

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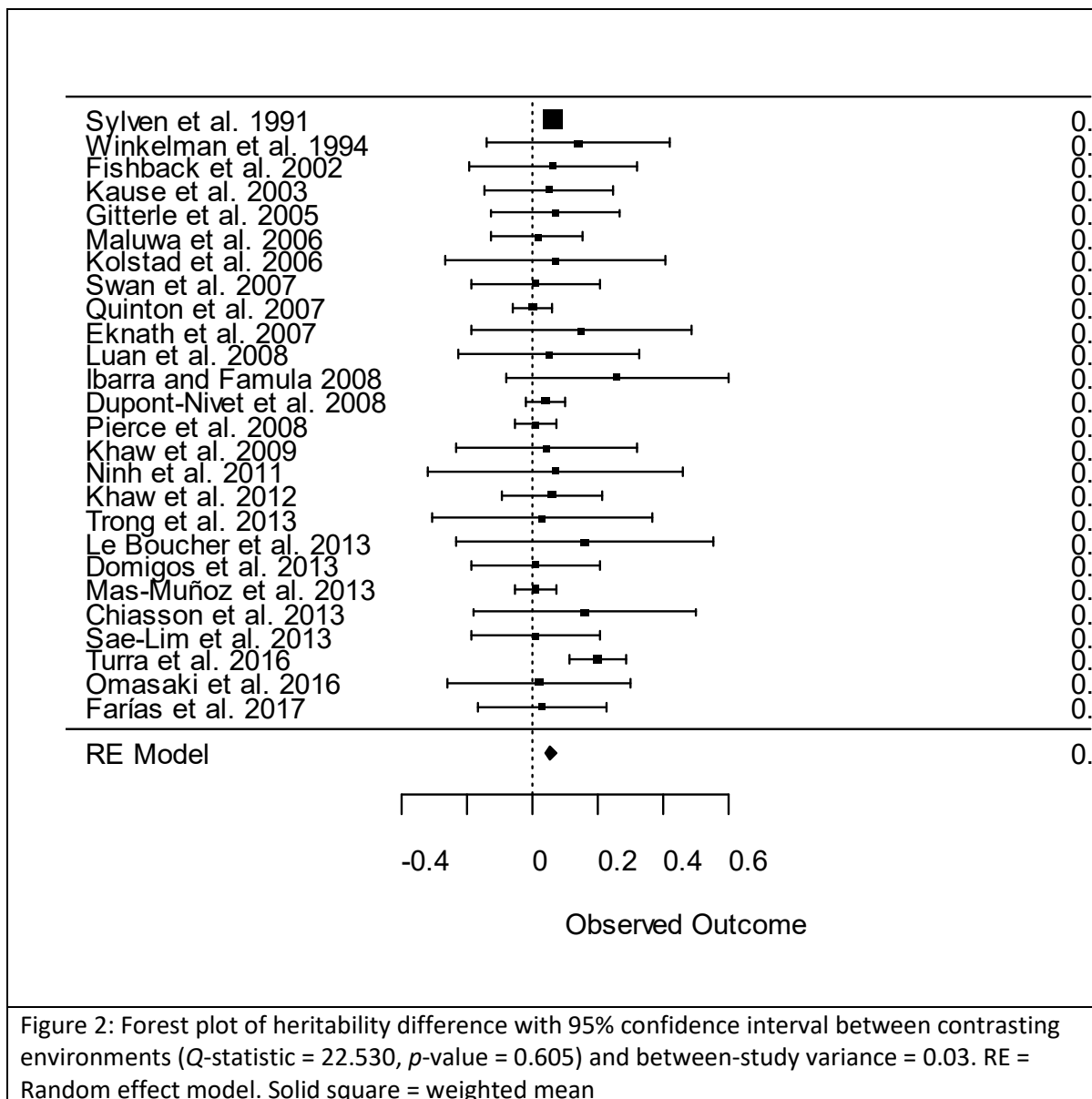
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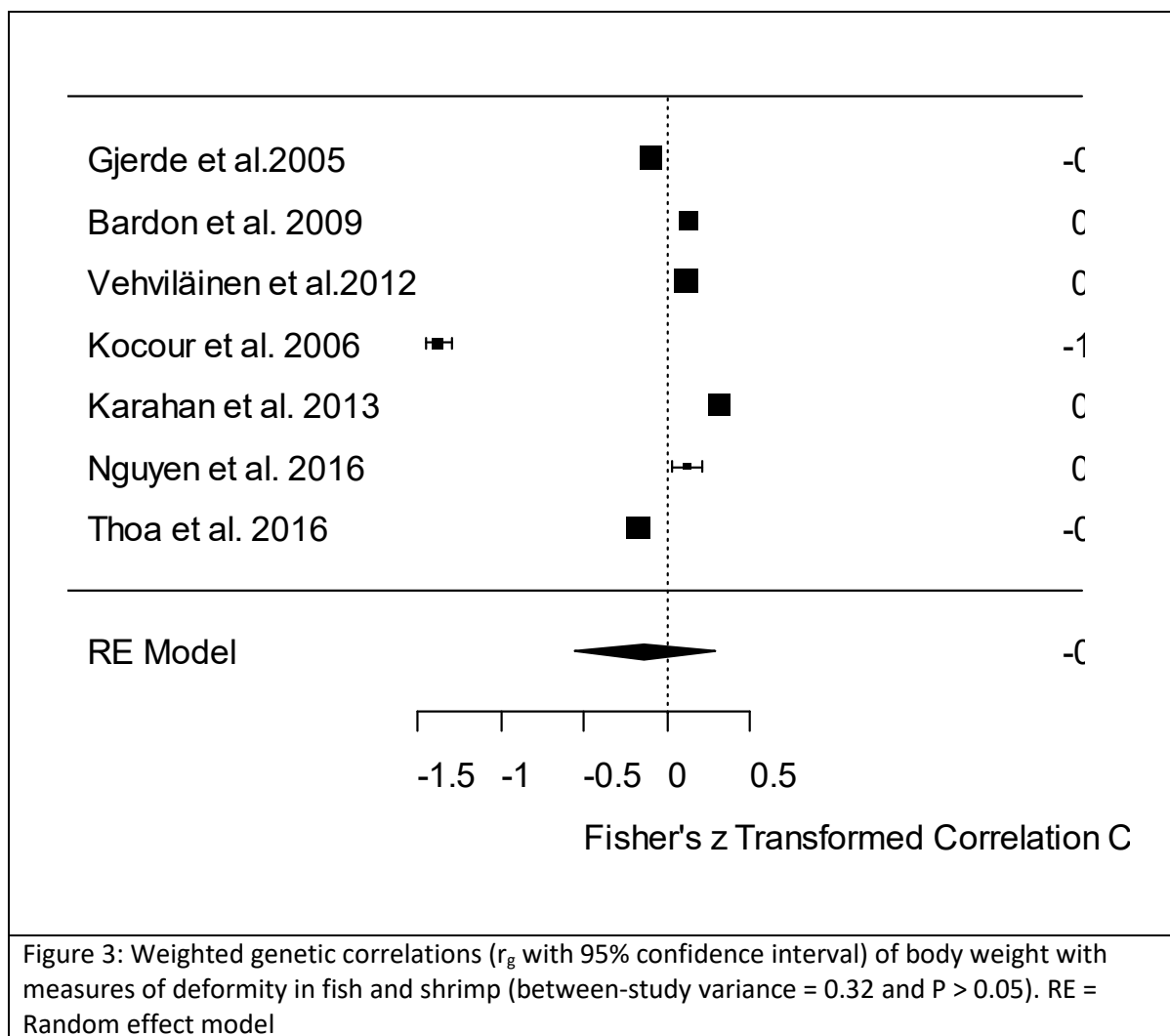
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