Reduced swimming and metabolic fitness of aquaculture-reared California Yellowtail (*Seriola dorsalis*) in comparison to wild-caught conspecifics

Nicholas C. Wegner[1*], Mark A. Drawbridge[2], John R. Hyde[1]

[1]Fisheries Resources Division, Southwest Fisheries Science Center, NOAA Fisheries, 8901 La Jolla Shores Dr, La Jolla, CA 92037, USA

[2]Hubbs-SeaWorld Research Institute, 2595 Ingraham St, San Diego, CA 92109, USA

*Corresponding author. Tel.: +1 8585467080.

E-mail address: nick.wegner@noaa.gov (N.C. Wegner).

ABSTRACT

Aspects of swimming and metabolic physiology were measured in aquaculture-reared California Yellowtail (*Seriola dorsalis*) in comparison to wild-caught individuals in order to examine potential differences in health and fitness associated with captive rearing, and to help identify areas for targeted improvement in *Seriola* aquaculture. Incremental swimming velocity trials using a swim tunnel respirometer on small yellowtail (mean body length = 18.9 cm, mass = 80.1 g) showed that aquaculture-reared fish had a significantly slower mean maximum sustainable swimming speed (U_{crit}) (4.16 ± 0.62 BL s^{-1}) in comparison to that of wild-caught fish (4.80 ± 0.52 BL s^{-1}). In addition, oxygen consumption ($\dot{M}_{O_2}$) measurements at varying swimming speeds allowed for estimation of standard metabolic rate, which was significantly higher in aquaculture-reared yellowtail (7.31 ± 2.32 vs. 3.94 ± 1.60 mg O_2 kg^{-1} min^{-1} at 18°C). Aquaculture fish also had a lower aerobic scope (9.20 ± 3.44 mg O_2 kg^{-1} min^{-1}) in comparison to wild-caught yellowtail (15.80 ± 5.78 mg O_2 kg^{-1} min^{-1}), which likely contributed to their reduced capacity for fast sustainable swimming. Reduced physical fitness is commonplace in aquaculture-reared fishes, and the examination of wild-caught yellowtail in this study provides baseline metrics that can be used to gauge the health and fitness of future *S. dorsalis* production. In particular, the lower standard metabolic rate and higher aerobic scope of wild-caught fish represent desirable metabolic characteristics that if achievable in aquaculture through better-rearing practices could allow for increased feed conversion efficiencies and potentially faster growth. At a minimum, a 35-40% reduction in metabolic costs at low swimming speeds (to those observed for wild-caught yellowtail) should result in substantial cost savings for feed in aquaculture operations.

48

49

50   **1. Introduction**

51

52   Species of the carangid genus *Seriola*, or amberjacks, are becoming an increasingly popular

53   target for aquaculture development due to their fast growth rates and high flesh quality. While

54   species such as the Japanese Amberjack (*S. quinqueradiata*) and, to a lesser extent, the Greater

55   Amberjack (*S. dumerili*) have been produced in aquaculture for several decades, these operations

56   have been largely dependent on the regional harvest of wild-caught seed (from larvae to large

57   juveniles) that are then reared to market size (Nakada, 2002; Ottolenghi et al., 2004). In most

58   locations, however, the availability of wild seed is a major biological bottleneck that limits

59   *Seriola* aquaculture outgrowth capacity. With recent advances in hatchery-production

60   techniques, wild-captured or domestically-bred broodstock are now being used to produce eggs

61   and larvae for growout operations. This has greatly increased prospects for further *Seriola*

62   aquaculture development and expansion.

63

64   Much of this new work has focused on the yellowtail jack species complex (*S. lalandi*) (Abbink

65   et al., 2012; Moran et al., 2007; Stuart and Drawbridge, 2013), which is allowing for *Seriola*

66   expansion into more temperate waters in areas such as the United States, New Zealand,

67   Australia, and Chile. While *S. lalandi* was previously recognized as a single circumglobal

68   species, recent genetic research has revealed at least three closely-related but distinct species – *S.*

69 *dorsalis* from the Northeast Pacific, *S. aureovittata* from the Northwest Pacific, and *S. lalandi*

70 from the Southern Hemisphere (Martinez-Takeshita et al., 2015), the last of which should likely

71 be further split between the waters of South Africa and the South Pacific (Purcell et al., 2015).

72 The genetic distinction between these species is thought to represent local adaptation to regional

73 environmental conditions and highlights the need for comparative studies of culturing methods

74 as well as the need for caution when translocating seed between regions for aquaculture growout

75 (Purcell et al., 2015).

76

77 Despite advances in hatchery production for several species, most of the world's current *Seriola*

78 aquaculture production is still based on the capture of wild juveniles. This is largely because

79 wild-caught seed is generally considered cheaper than hatchery production, especially in places

80 such as Japan where the capture of wild seed has been the standard for more than 50 years

81 (Nakada, 2002; 2008). In addition, hatchery-reared individuals are often thought to be of lower

82 quality, showing higher incidences of deformity and having slower growth rates. Still, hatchery

83 production is a much more sustainable practice that could help prevent overfishing naturally-

84 occurring populations for aquaculture use and, in theory, circumvent the juvenile bottleneck on

85 aquaculture expansion by allowing *Seriola* aquaculture in regions of the world where juveniles

86 are not available for capture from the wild. These concepts, coupled with declines in the

87 availability of wild seed (Nakada, 2008), highlight the need for continued research to optimize

88 domestic production.

89

90 This study focuses on the health and fitness of the California Yellowtail, *S. dorsalis*, for which

91 hatchery-rearing and growout protocols are currently being tested and are in high demand for US

92   aquaculture development (Jirsa et al., 2011; Rotman et al., 2017; Stuart and Drawbridge, 2011;

93   Stuart and Drawbridge, 2013; Stuart et al., 2010). To better understand the often referenced

94   inferiority of aquaculture-produced seed, this study establishes baseline physiological metrics of

95   the health and fitness of aquaculture-reared *S. dorsalis* in comparison to wild-caught counterparts

96   and in comparison to metrics available for other *Seriola* species. Specifically, we examine

97   aspects of *S. dorsalis* swimming performance (e.g., critical swimming speed, cost of transport),

98   which have been used as indicators of fish "physiological well-being" (Brauner et al., 1994;

99   Claireaux et al., 2005; Farrell et al., 1997; Hammer, 1995; McKenzie et al., 2012; Plaut, 2001),

100   and are likely representative of regular "health checks" made by large-scale *Seriola* aquaculture

101   operations [fish health is regularly checked by observing the swimming speed and behavior of

102   individuals during feeding, and the swimming activity of the school as a whole (Nakada, 2008)].

103   In addition, we compare the metabolic physiology of culture-reared and wild-caught individuals

104   as differences in metabolic fitness affect fish growth, feed conversion efficiency, and likely

105   provide insight into how exercise training and other manipulations may positively affect fish

106   health and growth (Davison and Herbert, 2013; Palstra et al., 2015).

107

108   **2. Materials and methods**

109

110   *2.1 Fish collection and husbandry*

111

112   Aquaculture-reared *S. dorsalis* were derived from eggs produced by wild-captured broodstock

113   housed at the Hubbs-SeaWorld Research Institute and reared according to current protocols

114   (Stuart and Drawbridge, 2013). Young juveniles were transferred to the Southwest Fisheries

115   Science Center (SWFSC) at approximately 5-6 cm body length (= total length, BL) where they

116   were housed in 300 x 150 x 90 cm (*l* x *w* x *h*) oval tanks (approximately 3,200 l) and held at

117   ambient ocean temperature. Wild-caught yellowtail were captured at 12-15 cm BL by hook and

118   line from local waters (<20 km from shore) associated with drifting kelp. Upon transfer to the

119   SWFSC these fish were housed in identical tanks and temperatures as the aquaculture-reared

120   individuals. Both aquaculture-reared and wild-caught yellowtail were fed commercial pellet fish

121   feed (BioTrout, Bio-Oregon, Longview, WA) to satiation 1-2 times daily six days a week. Wild-

122   caught fish were held 2-4 months in captivity before swim tunnel experimentation. All

123   yellowtail husbandry and experimentation was conducted in accordance with protocol SW1401

124   of the SWFSC Animal Care and Use Committee.

125

126   *2.2 Swim tunnel experimentation*

127

128   Exercise endurance testing and respirometry measurements were made on 10 aquaculture-reared

129   (18.63 ± 1.12 cm BL, 90.19 ± 19.88 g; condition factor = 1.38 ± 0.14; means ± standard

130   deviation) and seven wild-caught (19.31 ± 1.35 cm BL, 65.80 ± 13.35 g, condition factor = 0.91

131   ± 0.07) *S. dorsalis* following methods established for active pelagic fishes [including the closely

132   related *S. lalandi* (Clark and Seymour, 2006; Brown et al., 2011)] using a Brett-style swim

133   tunnel respirometer. The acrylic, variable-speed 5.4 l swim tunnel respirometer (Loligo Systems,

134   Tjele Denmark) had a 30 x 7.5 x 7.5 cm working section and was contained within a surrounding

135   buffer tank for thermal insulation and to provide properly aerated seawater for flushing the

136   system between respirometry measurements. The buffer tank was fed by a continuous influx of

137   ambient filtered seawater that averaged 17.64 ± 1.61°C across experiments. Fish were starved

138   for approximately 24 hours before being placed in the swim tunnel, where they were allowed to

139   swim steadily at a preferred, low, sustainable speed (typically about 20-25 cm s^{-1}) with a

140   continuous inflow of aerated seawater for a 1 h acclimation period prior to experimentation.

141

142   The maximum sustainable swimming speed (critical swimming speed, U_{crit}) was determined by

143   increasing the velocity of the swim tunnel water by 5 or 10 cm s^{-1} steps every 30 minutes until

144   the fish could no longer maintain steady swimming (defined as no longer being able to stay off

145   the screen at the back of the working section) or erratic and non-directional burst activity

146   occurred. U_{crit} was determined by the equation:

147

148    $$U_{crit} = U_i + U_{ii} (T_i / T_{ii}) \tag{1}$$

149

150   where U_i is the fastest swimming speed maintained for the full 30 minutes, U_{ii} is the velocity step

151   (5 or 10 cm s^{-1}), T_i is the time swimming at the highest velocity (at which fatigue occurred), and

152   T_{ii} is the length of time for each step in swimming speed (30 min). Water velocity within the

153   swim tunnel was calibrated using a vane wheel flow probe connected to a handheld flowtherm

154   NT (Höntzsch GmbH, Waiblingen, Germany). Following experimentation, swim tunnel water

155   velocity was corrected for both the cross-sectional area of the vane probe and for the solid

156   blocking effect of the fish in the tunnel according to Bell and Terhune (1970) resulting in true

157   velocity step increases of 3.8 to 4.1 and 7.6 to 10.2 cm s^{-1} depending on fish size.

158

159   The oxygen consumption rate ($\dot{M}_{O_2}$) was determined for each fish at each swimming speed using

160   a fiber optic oxygen sensor within the swim tunnel respirometer connected to a Fibox 3 fiber

161   optic oxygen transmitter (PreSens Precision Sensing GmbH, Regensburg, Germany). Shortly (1-

162   2 min) after the step increase in swimming speed, the swim tunnel respirometer was temporarily

163   sealed from the inflow and outflow of fresh seawater from the surrounding buffer tank using

164   manual valves, and the oxygen concentration within the now closed system was recorded once

165   every 5 s. The oxygen level was allowed to drop until the swim tunnel water reached

166   approximately 80% saturation, at which point the system was flushed (to return the oxygen

167   saturation level to near 100%) and then resealed to continue $\dot{M}_{O_2}$ measurements if time allowed

168   within that velocity step.

169

170   *2.3 Calculation of oxygen consumption, standard metabolic rate, aerobic scope, and cost of*

171   *transport*

172

173   Typically, 2-3 sequential $\dot{M}_{O_2}$ traces (from ~100-80% oxygen saturation, $R^2 > 0.990$) were

174   recorded during each 30 min velocity step, and these were combined to determine a single mean

175   oxygen consumption rate for each individual at each speed. Following the completion of the

176   experiment, the fish was removed from the swim tunnel for mass and length measurements, and

177   the respirometer was resealed to measure background respiration, which was subtracted from

178   fish $\dot{M}_{O_2}$.

179

180   To compensate for differences in fish mass and water temperature between trials, $\dot{M}_{O_2}$

181   measurements were adjusted to a water / body temperature of 18°C (using $Q_{10} = 2$) and to a body

182   mass (M) of 80 g (using $M^{0.80}$) (Pirozzi and Booth, 2009; Schmidt-Nielsen, 1984). Oxygen

183   consumption data were then used to create an exponential regression relationship for $\dot{M}_{O_2}$ vs.

184   swimming speed for each individual. Each regression line was extrapolated to a swimming

185   speed of 0 cm s^{-1} to estimate the standard metabolic rate for that fish. [Note: In some cases, slow

186   swimming speeds (typically <30 cm s^{-1}) were accompanied with added pectoral fin movement

187   and unnatural swimming positions likely associated with swimming below the minimum speed

188   required to maintain hydrostatic equilibrium within the swim tunnel. As in similar studies on

189   pelagic fishes (e.g., Sepulveda et al., 2003), higher than expected $\dot{M}_{O_2}$ measurements at these

190   slow speeds (defined as low-speed $\dot{M}_{O_2}$ measurements that were higher than those of faster

191   speeds) were thus not included in regression analyses for estimating standard metabolic rate.

192   Likewise, as some component of metabolic demand at the final (fastest, non-sustainable)

193   swimming speed would have been derived anaerobically, $\dot{M}_{O_2}$ measurements at this speed were

194   not included in analyses other than determining aerobic scope.] Aerobic scope for each

195   individual was determined by subtracting the standard metabolic rate from the highest observed

196   oxygen consumption rate ($\dot{M}_{O_{2max}}$) during swimming (in all cases this was at the fastest

197   swimming speed).

198

199   Cost of transport (COT, mg O$_2$ kg^{-1} m^{-1}) was calculated using mass and temperature-adjusted

200    $\dot{M}_{O_2}$ data using the equation:

201

202    $$COT = \dot{M}_{O_2} / U \qquad\qquad (2)$$

203

204   where U is the swimming speed. Cost of transport data were plotted for each fish versus

205   swimming speed and the resulting second-order polynomial function was used to estimate the

206   optimal swimming speed, U_{opt} (defined by the lowest consumption of oxygen per distance swam

9

207 or vertex of the *COT* parabola), for each individual. [Note: slower swimming speeds with

208 unnatural swimming movements needed to generate lift were included in this analysis.]

209

210 *2.4 Statistics*

211 Means ± standard deviation of the various swimming and metabolic metrics were calculated

212 from individual fish data. Pairwise comparisons of metrics between aquaculture-reared and

213 wild-caught yellowtail were conducted using a two-tail t-test ($\alpha = 0.05$).

214

215 *2.5 Condition factor and deformities*

216 Following experimentation in the swim tunnel respirometer, all fish were measured and

217 condition factor (reported above) was determined as (mass/length) x 100. In addition, fish were

218 examined for obvious external deformities that could have affected swimming performance.

219 Due to differences in body shape (condition factor), aquaculture-reared fish were later

220 euthanized with an overdose of MS-222 and radiographic images were taken using a portable

221 MinXray HF 100H+ (MinXray, Northbrook, IL, USA) to examine potential skeletal deformities.

222

223 **3. Results**

224

225 Fish swimming and oxygen consumption data are shown in Table 1. The mean maximum

226 sustainable swimming speed for 10 aquaculture-reared yellowtail (77.08 ± 9.36 cm s^{-1}, $4.16 \pm$

227 0.62 BL s^{-1}) was significantly slower than that determined for seven wild caught individuals of

228 similar size (92.93 ± 13.32 cm s^{-1}, 4.80 ± 0.52 BL s^{-1}) ($P = 0.011$). Aggregate data showing the

229 relationship between $\dot{M}_{O_2}$ and swimming velocity for the 10 aquaculture-reared and seven wild-

230   caught yellowtail are shown in Figure 1A, and these data reveal that at low, basal swimming

231   speeds (20-30 cm s^{-1}) the oxygen consumption rates of aquaculture-reared yellowtail were 36-

232   42% higher than their wild-caught counterparts. Extrapolation of regression equations for

233   individual fish to a swimming speed of 0 cm s^{-1} shows that the estimated standard metabolic rate

234   of aquaculture-reared yellowtail (7.31 ± 2.32 mg O$_2$ kg^{-1} min^{-1}) was significantly greater than

235   that of wild-caught individuals (3.94 ± 1.60 mg O$_2$ kg^{-1} min^{-1}) (P = 0.003) (18°C, mass = 80 g).

236   Although not significant, the lower maximum oxygen consumption rate ($\dot{M}_{O_{2max}}$) for

237   aquaculture-reared yellowtail (16.52 ± 1.54 vs. 19.74 ± 5.74 mg O$_2$ kg^{-1} min^{-1}), coupled with

238   their significantly higher standard metabolic rate, resulted in a significantly lower aerobic scope

239   in comparison to wild-caught fish (9.20 ± 3.44 vs. 15.80 ± 5.78 mg O$_2$ kg^{-1} min^{-1}) (P = 0.024).

240   This higher standard metabolic rate also appeared to contribute to a higher cost of transport for

241   aquaculture-reared individuals (aggregate data for *COT vs.* swimming velocity shown in Fig.

242   1B). However, U_{opt} did not differ significantly between aquaculture and wild-caught animals

243   (67.45 ± 9.90 or 3.63 ± 0.53 BL s^{-1} vs. 70.24 ± 16.73 cm s^{-1} or 3.65 ± 0.92 BL s^{-1}).

244

245   None of the wild-caught or aquaculture-reared yellowtail showed obvious external deformities.

246   However, sagittal radiographic images revealed that four of the nine aquaculture fish examined

247   had varying degrees of shortening and or thickening of vertebrae in the caudal region.

248

249   **4. Discussion**

250

251   The results of this study show reduced fitness of aquaculture-reared yellowtail in comparison to

252   wild-caught individuals as manifested through several physiological metrics including critical

253   swimming speed, oxygen consumption rates, standard metabolic rate, aerobic scope, and cost of

254   transport. Most previous comparisons of the swimming and metabolic capacity of wild-caught

255   and culture-reared fishes have shown similar gaps in fitness (Basaran et al., 2007; Brauner et al.,

256   1994; Duthie, 1987; McDonald et al., 1998; Shustov and Shchurov, 1988; Young and Cech Jr,

257   1993), and this is often thought to be the result of domestication selection through multiple

258   generations of captive breeding (Araki et al., 2008; Zhang et al., 2016). However, in this study,

259   the culture-reared juveniles came from wild-captured broodstock (i.e., were F1 generation), and

260   thus domestication selection through multiple generations did not occur. Such reductions in

261   fitness are thus likely associated with rearing in a suboptimal aquaculture setting (e.g., lower

262   water or diet quality, decreased physical activity), or may reflect suboptimal phenotypes having a

263   higher chance for survival in captivity. Both scenarios are likely at work and highlight the need

264   for both genetic studies for the selection of broodstock that produce the highest quality offspring

265   as well as experimentation to determine best rearing practices (i.e., determination of feed, water,

266   and other environmental impacts on fish fitness and growth).

267

268   Although some of the observed fitness differences in this study may have resulted from the

269   survival of suboptimal phenotypes, none of the aquaculture-reared fish tested in the swim tunnel

270   experiments showed major external deformities. However, all of the culture-reared fish did have

271   a more compact (anterio-posteriorly compressed) and deeper (dorso-ventrally elongated) body

272   shape in comparison to the wild-caught fish resulting in a significantly greater body condition

273   factor, or greater mass per length. Radiographic examination of aquaculture-reared fish

274   following exercise showed that many had varying degrees of minor vertebral abnormalities

275   (typically irregular compressions and thickening of vertebrae in the caudal region), which are

276   common in aquaculture and often result in decreased swimming performance (Boglione et al.,

277   2013). Such vertebral deformities are typically thought to be related to deficient nutritional

278   regimes or other environmental stressors during early rearing (Boglione et al., 2014; Boglione et

279   al., 2013; Cahu et al., 2003; Lall and Lewis-McCrea, 2007). However, recent work has also

280   suggested that the lack of exercise commonplace in aquaculture operations decreases skeletal

281   mineralization and can lead to vertebral defects (Deschamps et al., 2009; Solstorm et al., 2016).

282

283   Despite the fitness gap typically observed between aquaculture-reared and wild-caught fish, there

284   are some cases in which cultured fish do not show obvious inferiority (Peake et al., 1997;

285   Thorstad et al., 1997). This suggests that optimal rearing conditions can produce fish of similar

286   or perhaps even better quality than that of wild stocks. Interestingly, the standard metabolic rates

287   determined for aquaculture-reared *S. lalandi* in previous studies (Brown et al., 2011; Clark and

288   Seymour, 2006) are similar to those of the wild-caught *S. dorsalis* examined in the present study

289   when adjusted for size and temperature (Table 2), and this likely reflects the better established

290   rearing protocols for *S. lalandi*. For *S. dorsalis*, rearing techniques from eggs and larvae to

291   market size are still largely in their infancy (Stuart and Drawbridge, 2013), and the metrics

292   determined herein for wild-caught animals can provide helpful achievable standards

293   (benchmarks) for enhancing the swimming and metabolic fitness of those reared in aquaculture.

294

295   In addition to customary efforts to enhance the nutritional and water quality aspects of

296   aquaculture, there has been renewed interest over the last several years to "farm a fitter fish"

297   through the use of exercise conditioning (Palstra and Planas, 2011, Palstra and Planas, 2013).

298   Such exercise training can be induced by forcing fish to swim against a current, and this is

299   thought to help provide active fish species with increased physical activity that is typically

300   lacking during aquaculture growout. In many cases, exercise has been shown to have substantial

301   health benefits as manifested through increased growth rates and better feed conversion

302   efficiencies (for review see Davison and Herbert, 2013). For some species, including most

303   salmonids, swimming against a current promotes schooling behavior and decreases

304   energetically-costly agonistic interactions (e.g., aggressive biting behavior) (Adams et al., 1995;

305   Christiansen and Jobling, 1990; East and Magnan, 1987), which in turn appear to reduce stress as

306   often indicated by lower circulating cortisol and catecholamine levels (Davison, 1997;

307   Woodward and Smith, 1985). A reduction in stress lowers metabolism and, in theory, allows

308   more energy to be partitioned toward growth (Barton, 1997; Barton and Iwama, 1991; Pankhurst

309   and Van Der Kraak, 1997; Pickering, 1992). While it is still somewhat unclear for salmonids the

310   extent to which increased growth rates result directly from changes in behavior, stress, feeding or

311   a suite of other interrelated factors, exercise-induced growth and feed conversion benefits of

312   similar magnitude are prevalent in many other active fishes that do not display such obvious

313   exercise-induced changes in behavior (Ibarz et al., 2011; Li et al., 2013; Nakagawa et al., 1991;

314   Palstra et al., 2015; Yogata and Oku, 2000). This suggests that exercise-induced enhancements

315   to health and growth may result largely from physiological changes, which could parallel the

316   swimming and metabolic differences observed between aquaculture-reared and wild-caught fish

317   in this study. While only preliminary exercise training studies have been conducted for *S.*

318   *dorsalis*, these have shown positive increases in growth (Peters, 2009), and work on other

319   *Seriola* species (*S. lalandi* and *S. quinqueradiata*) have shown up to a 46% increase in growth

320   rate and a up to a 32% decrease in the feed conversion ratio associated with exercise training

321   (Brown et al., 2011; Palstra et al., 2015; Yogata and Oku, 2000). For *S. lalandi*, Palstra et al.

322   (2015) achieved 46% faster growth rates in exercised fish while providing them with the same

323   amount of food as non-exercised controls.

324

325   Such large increases in growth without a change in food consumption require changes to

326   metabolic efficiency in the form of lower maintenance costs (e.g., a lower standard metabolic

327   rate) or lower costs of growth (more efficient nutrient assimilation and tissue generation). The

328   significantly higher standard metabolic rate of the aquaculture-reared fish in this study in

329   comparison to wild-caught fish and those of other *Seriola* metabolic studies (Table 2), suggests

330   maintenance metabolic costs in cultured *S. dorsalis* could be lowered by up to 50%, which would

331   potentially allow more energy to be allocated toward growth. Such decreases in standard or

332   resting metabolic rate have been shown in some cases for Rainbow Trout (*Oncorhynchus mykiss*)

333   (Skov et al., 2011; Woodward and Smith, 1985) and Zebrafish (*Danio rerio*) (Bagatto et al.,

334   2001) following exercise training at optimal swimming speeds. Although not statistically

335   significant, Brown et al. (2011) showed a 7-8% decrease in standard metabolic rate for exercised

336   *S. lalandi* in comparison to non-exercised controls (Table 2), which likely contributed to the 10%

337   increase in growth rate experienced by the exercised fish.

338

339   In addition to changes in standard metabolic rate, exercise training has also been shown in some

340   cases to increase $\dot{M}_{O_{2max}}$ (Gallaugher et al., 2001; Li et al., 2013), contributing to a higher aerobic

341   scope. Although not statistically significant, the $\dot{M}_{O_{2max}}$ of the wild-caught fish in this study was

342   approximately 20% greater than that of aquaculture-reared fish. This appears to contribute to the

343   15% higher U_{crit} in the wild-caught fish, and, in conjunction with a lower metabolic rate,

344   contributes to a 72% larger aerobic scope (Table 1). Gallaugher et al. (2001) suggested that

15

345   increases in $\dot{M}_{O_2max}$ associated with exercise training can facilitate the balance of multiple

346   energetically-demanding physiological processes. In the context of promoting fish growth, an

347   increase in maximum aerobic performance may allow for an increase in digestive metabolic

348   capacity (specific dynamic action), and thus growth could potentially be enhanced through the

349   simple digestion and assimilation of more feed. Indeed, Palstra et al. (2015) suggested that if

350   exercised-conditioned *S. lalandi* had been given additional feed in their experiments (i.e., fed to

351   satiation and not limited to what was given to control fish), growth would have likely increased

352   by more than the observed 46%. As such, Davison and Herbert (2013) and others have

353   hypothesized that a high aerobic scope may be a good predictor of the success of exercise

354   training, although this has not always proved to be the case (Khan et al., 2014).

355

356   **5. Conclusions**

357

358   By comparing aquaculture-reared and wild-captured *S. dorsalis*, this study suggests that aspects

359   of both the swimming and metabolic physiology of this species can be improved in culture

360   growout operations. Assuming similar growth rates, a 35-40% reduction in the metabolic costs

361   of aquaculture-reared yellowtail while swimming at basal speeds (to those observed in wild-

362   caught fish) (Figure 1A), should result in lower feed requirements and substantial cost savings to

363   aquaculture producers. In addition, the observed differences in standard metabolic rate and

364   aerobic scope in this study in conjunction with the success of exercised induced-growth in

365   closely related *Seriola* species, suggests exercise conditioning could have potentially large

366   impacts on *S. dorsalis* physiology and growth and highlights the need for such experimentation.

367   Finally, this study provides baseline physiological metrics that can be used to quantify *S. dorsalis*

368 fitness. Such metrics may be advantageous in providing time-sensitive quantifications and

369 screenings to fish health and fitness in aquaculture in comparison to more traditional and time

370 and resource-intensive growout trials of large numbers of fish over several months.

371

372 **Acknowledgements**

373

377

378

379

380

381

382

383

384

385

386

387

388

389

390

391

References

392 **References**

393

394 Abbink, W., Garcia, A.B., Roques, J.A.C., Partridge, G.J., Kloet, K., Schneider, O., 2012. The

395   effect of temperature and pH on the growth and physiological response of juvenile

396   yellowtail kingfish *Seriola lalandi* in recirculating aquaculture systems. Aquaculture.

397   330, 130-135.

398 Adams, C.E., Huntingford, F.A., Krpal, J., Jobling, M., Burnett, S.J., 1995. Exercise, agonistic

399   behaviour and food acquisition in Arctic charr, *Salvelinus alpinus*. Environmental

400   Biology of Fishes. 43, 213-218.

401 Araki, H., Berejikian, B.A., Ford, M.J., Blouin, M.S., 2008. Fitness of hatchery-reared salmonids

402   in the wild. Evolutionary Applications. 1, 342-355.

403 Bagatto, B., Pelster, B., Burggren, W.W., 2001. Growth and metabolism of larval zebrafish:

404   effects of swim training. Journal of Experimental Biology. 204, 4335-4343.

405 Barton, B., 1997. Stress in finfish: past, present and future - a historical perspective. in: Iwama,

406   G.K., Pickering, A.D., Sumpter, J.P., Schreck, C.B. (Eds.), Fish Stress and Health in

407   Aquaculture. Cambridge University Press, Cambridge, pp. 1-33.

408 Barton, B.A., Iwama, G.K., 1991. Physiological changes in fish from stress in aquaculture with

409   emphasis on the response and effects of corticosteroids. Annual Review of Fish Diseases.

410   1, 3-26.

411 Basaran, F., Ozbilgin, H., Ozbilgin, Y.D., 2007. Comparison of the swimming performance of

412   farmed and wild gilthead sea bream, *Sparus aurata*. Aquaculture Research. 38, 452-456.

413 Bell, W.H., Terhune, L.D.B., 1970. Water tunnel design for fisheries research, Fisheries

414   Research Board of Canada Technical Report, pp. 69.

415   Boglione, C., Pulcini, D., Scardi, M., Palamara, E., Russo, T., Cataudella, S., 2014. Skeletal

416   anomaly monitoring in rainbow trout (*Oncorhynchus mykiss*, Walbaum 1792) reared

417   under different conditions. PLOS ONE. 9, e96983.

418   Boglione, C., Gisbert, E., Gavaia, P., Witten, P.E., Moren, M., Fontagné, S., Koumoundouros,

419   G., 2013. Skeletal anomalies in reared European fish larvae and juveniles. Part 2: main

420   typologies, occurrences and causative factors. Reviews in Aquaculture. 5, S121-S167.

421   Brauner, C.J., Iwama, G.K., Randall, D.J., 1994. The effect of short-duration seawater exposure

422   on the swimming performance of wild and hatchery-reared juvenile coho salmon

423   (*Oncorhynchus kisutch*) during smoltification. Canadian Journal of Fisheries and Aquatic

424   Sciences. 51, 2188-2194.

425   Brown, E.J., Bruce, M., Pether, S., Herbert, N.A., 2011. Do swimming fish always grow fast?

426   Investigating the magnitude and physiological basis of exercise-induced growth in

427   juvenile New Zealand yellowtail kingfish, *Seriola lalandi*. Fish Physiology and

428   Biochemistry. 37, 327-336.

429   Cahu, C., Infante, J.Z., Takeuchi, T., 2003. Nutritional components affecting skeletal

430   development in fish larvae. Aquaculture. 227, 245-258.

431   Christiansen, J.S., Jobling, M., 1990. The behaviour and the relationship between food intake

432   and growth of juvenile Arctic charr, *Salvelinus alpinus* L., subjected to sustained

433   exercise. Canadian Journal of Zoology. 68, 2185-2191.

434   Claireaux, G., McKenzie, D.J., Genge, A.G., Chatelier, A., Aubin, J., Farrell, A.P., 2005.

435   Linking swimming performance, cardiac pumping ability and cardiac anatomy in

436   rainbow trout. Journal of Experimental Biology. 208, 1775-1784.

437   Clark, T.D., Seymour, R.S., 2006. Cardiorespiratory physiology and swimming energetics of a

438   high-energy-demand teleost, the yellowtail kingfish (*Seriola lalandi*). Journal of

439   Experimental Biology. 209, 3940-3951.

440   Davison, W., 1997. The effects of exercise training on teleost fish, a review of recent literature.

441   Comparative Biochemistry and Physiology. 117A, 67-75.

442   Davison, W., Herbert, N.A., 2013. Swimming-enhanced growth. in: Palstra, A.P., Planas, J.V.

443   (Eds.), Swimming Physiology of Fish: Towards Using Exercise to Farm a Fit Fish in

444   Sustainable Aquaculture. Springer, Heidelberg, pp. 177-202.

445   Deschamps, M.-H., Labbé, L., Baloche, S., Fouchereau-Péron, M., Dufour, S., Sire, J.-Y., 2009.

446   Sustained exercise improves vertebral histomorphometry and modulates hormonal levels

447   in rainbow trout. Aquaculture. 296, 337-346.

448   Duthie, G.G., 1987. Observations of poor swimming performance among hatchery-reared

449   rainbow trout, *Salmo gairdneri*. Environmental Biology of Fishes. 18, 309-311.

450   East, P., Magnan, P., 1987. The effect of locomotor activity on the growth of brook charr,

451   *Salvelinus fontinalis* Mitchill. Canadian Journal of Zoology. 65, 843-846.

452   Farrell, A.P., Bennett, W., Devlin, R.H., 1997. Growth-enhanced transgenic salmon can be

453   inferior swimmers. Canadian Journal of Zoology. 75, 335-337.

454   Gallaugher, P.E., Thorarensen, H., Kiessling, A., Farrell, A.P., 2001. Effects of high intensity

455   exercise training on cardiovascular function, oxygen uptake, internal oxygen transport

456   and osmotic balance in chinook salmon (*Oncorhynchus tshawytscha*) during critical

457   speed swimming. Journal of Experimental Biology. 204, 2861-2872.

458   Hammer, C., 1995. Fatigue and exercise tests with fish. Comparative Biochemistry and

459   Physiology. 112A: 1-20.

460   Ibarz, A., Felip, O., Fernández-Borràs, J., Martín-Pérez, M., Blasco, J., Torrella, J.R., 2011.

461   Sustained swimming improves muscle growth and cellularity in gilthead sea bream.

462   Journal of Comparative Physiology. 181B, 209-217.

463   Jirsa, D., Davis, A., Stuart, K., Drawbridge, M., 2011. Development of a practical soy-based diet

464   for California yellowtail, *Seriola lalandi*. Aquaculture Nutrition. 17, e869-e874.

465   Khan, J.R., Trembath, C., Pether, S., Bruce, M., Walker, S.P., Herbert, N.A., 2014.

466   Accommodating the cost of growth and swimming in fish—the applicability of exercise-

467   induced growth to juvenile hapuku (*Polyprion oxygeneios*). Frontiers in Physiology. 5,

468   448.

469   Lall, S.P., Lewis-McCrea, L.M., 2007. Role of nutrients in skeletal metabolism and pathology in

470   fish - An overview. Aquaculture. 267, 3-19.

471   Li, X.-M., Yu, L.-J., Wang, C., Zeng, L.-Q., Cao, Z.-D., Fu, S.-J., Zhang, Y.-G., 2013. The effect

472   of aerobic exercise training on growth performance, digestive enzyme activities and

473   postprandial metabolic response in juvenile qingbo (*Spinibarbus sinensis*). Comparative

474   Biochemistry and Physiology. 166A, 8-16.

475   Martinez-Takeshita, N., Purcell, C.M., Chabot, C.L., Craig, M.T., Paterson, C.N., Hyde, J.R.,

476   Allen, L.G., 2015. A tale of three tails: Cryptic speciation in a globally distributed marine

477   fish of the genus *Seriola*. Copeia. 103, 357-368.

478   McDonald, D.G., Milligan, C.L., McFarlane, W.J., Croke, S., Currie, S., Hooke, B., Angus, R.B.,

479   Tufts, B.L., Davidson, K., 1998. Condition and performance of juvenile Atlantic salmon

480   (*Salmo salar*): effects of rearing practices on hatchery fish and comparison with wild fish.

481   Canadian Journal of Fisheries and Aquatic Sciences. 55, 1208-1219.

482 McKenzie, D.J., Höglund, E., Dupont-Prinet, A., Larsen, B.K., Skov, P.V., Pedersen, P.B.,

483   Jokumsen, A., 2012. Effects of stocking density and sustained aerobic exercise on

484   growth, energetics and welfare of rainbow trout. Aquaculture. 338, 216-222.

485 Moran, D., Smith, C.K., Gara, B., Poortenaar, C.W., 2007. Reproductive behaviour and early

486   development in yellowtail kingfish (*Seriola lalandi* Valenciennes 1833). Aquaculture.

487   262, 95-104.

488 Nakada, M., 2002. Yellowtail culture development and solutions for the future. Reviews in

489   Fisheries Science. 10, 559-575.

490 Nakada, M., 2008. Capture-based aquaculture of yellowtail. in: Lovatelli, A., Holthus, P.F.

491   (Eds.), Capture-based aquaculture. Global overview. FAO Fisheries Technical Paper No.

492   508. FAO, Rome, pp. 199-215.

493 Nakagawa, H., Nishino, H., Nematipour, G.R., Ohya, S., Shimizu, T., Horikawa, Y., Yamamoto,

494   S.-i., 1991. Effects of water velocities on lipid reserves in Ayu. Nippon Suisan Gakk. 57,

495   1737-1741.

496 Ottolenghi, F., Silvestri, C., Giordano, P., Lovatelli, A., New, M.B., 2004. Capture-based

497   Aquaculture. The Fattening of Eels, Groupers, Tunas and Yellowtails. FAO, Rome, 308

498   pp.

499 Palstra, A.P., Planas, J.V., 2011. Fish under exercise. Fish Physiology and Biochemistry. 37,

500   259-272.

501 Palstra, A.P., Planas, J.V. (Eds.), 2013. Swimming Physiology of Fish: Towards Using Exercise

502   to Farm a Fit Fish in Sustainable Aquaculture. Springer, Heidelberg, 428 pp.

503 Palstra, A.P., Mes, D., Kusters, K., Roques, J.A.C., Flik, G., Kloet, K., Blonk, R.J.W., 2015.

504 Forced sustained swimming exercise at optimal speed enhances growth of juvenile

505 yellowtail kingfish (*Seriola lalandi*). Frontiers in Physiology. 5, 506.

506 Pankhurst, N.W., Van Der Kraak, G., 1997. Effects of stress on reproduction and growth of fish.

507 in: Iwama, G.K., Pickering, A.D., Sumpter, J.P., Schreck, C.B. (Eds.), Fish Stress and

508 Health in Aquaculture. Cambridge University Press, Cambridge, pp. 73-93.

509 Peake, S., McKinley, R.S., Scruton, D.A., Moccia, R., 1997. Influence of transmitter attachment

510 procedures on swimming performance of wild and hatchery-reared Atlantic salmon

511 smolts. Transactions of the American Fisheries Society. 126, 707-714.

512 Peters, C.J., 2009. Continuous exercise enhances swim performance and alters growth rate, IGF-

513 I, and cortisol in juvenile marine finfish in aquaculture. University of San Diego. Masters

514 Thesis, 176 pp.

515 Pickering, A.D., 1992. Rainbow trout husbandry: management of the stress response.

516 Aquaculture. 100, 125-139.

517 Pirozzi, I., Booth, M.A., 2009. The routine metabolic rate of mulloway (*Argyrosomus japonicus*:

518 Sciaenidae) and yellowtail kingfish (*Seriola lalandi*: Carangidae) acclimated to six

519 different temperatures. Comparative Biochemistry and Physiology. 152A, 586-592.

520 Plaut, I., 2001. Critical swimming speed: its ecological relevance. Comparative Biochemistry

521 and Physiology. 131A, 41-50.

522 Purcell, C.M., Chabot, C.L., Craig, M.T., Martinez-Takeshita, N., Allen, L.G., Hyde, J.R., 2015.

523 Developing a genetic baseline for the yellowtail amberjack species complex, *Seriola*

524 *lalandi* sensu lato, to assess and preserve variation in wild populations of these globally

525 important aquaculture species. Conservation Genetics. 16, 1475-1488.

526   Rotman, F., Stuart, K., Drawbridge, M., 2017. Effects of taurine supplementation in live feeds on

527   larval rearing performance of California yellowtail *Seriola lalandi* and white seabass

528   *Atractoscion nobilis*. Aquaculture Research. 48, 1232-1239.

529   Schmidt-Nielsen, K., 1984. Scaling: Why is Animal Size So Important? Cambridge University

530   Press, 241 pp.

531   Sepulveda, C.A., Dickson, K.A., Graham, J.B., 2003. Swimming performance studies on the

532   eastern Pacific bonito *Sarda chiliensis*, a close relative of the tunas (family Scombridae)

533   I. Energetics. Journal of Experimental Biology. 206, 2739-2748.

534   Shustov, Y.A., Shchurov, I.L., 1988. Quantitative estimation of stamina of wild and hatchery-

535   reared Atlantic salmon (*Salmo salar* L.). Aquaculture. 71, 81-87.

536   Skov, P.V., Larsen, B.K., Frisk, M., Jokumsen, A., 2011. Effects of rearing density and water

537   current on the respiratory physiology and haematology in rainbow trout, *Oncorhynchus*

538   *mykiss* at high temperature. Aquaculture. 319, 446-452.

539   Solstorm, F., Solstorm, D., Oppedal, F., Fjelldal, P.G., 2016. The vertebral column and exercise

540   in Atlantic salmon—Regional effects. Aquaculture. 461, 9-16.

541   Stuart, K.R., Drawbridge, M., 2011. The effect of light intensity and green water on survival and

542   growth of cultured larval California yellowtail (*Seriola lalandi*). Aquaculture. 321, 152-

543   156.

544   Stuart, K.R., Drawbridge, M.A., 2013. Captive spawning and larval rearing of California

545   yellowtail (*Seriola lalandi*). Aquaculture Research. 44, 728-737.

546   Stuart, K.R., Keller, M., Drawbridge, M., 2010. Efficacy of formalin and povidone-iodine

547   disinfection techniques on the eggs of three marine finfish species. Aquaculture

548   Research. 41, e838-e843.

549   Thorstad, E.B., Finstad, B., Økland, F., McKinley, R.S., Booth, R.K., 1997. Endurance of farmed

550   and sea-ranched Atlantic salmon *Salmo salar* L. at spawning. Aquaculture Research. 28,

551   635-640.

552   Woodward, J.J., Smith, L.S., 1985. Exercise training and the stress response in rainbow trout,

553   *Salmo gairdneri* Richardson. Journal of Fish Biology. 26, 435-447.

554   Yamamoto, K.-I., Itazawa, Y., Kobayashi, H., 1981. Gas exchange in the gills of yellowtail,

555   *Seriola quinqueradiata* under resting and normoxic condition. Bulletin of the Japanese

556   Society of Scientific Fisheries. 47, 447-451.

557   Yogata, H., Oku, H., 2000. The effects of swimming exercise on growth and whole-body protein

558   and fat contents of fed and unfed fingerling yellowtail. Fisheries Science. 66, 1100-1105.

559   Young, P.S., Cech Jr, J.J., 1993. Improved growth, swimming performance, and muscular

560   development in exercise-conditioned young-of-the-year striped bass (*Morone saxatilis*).

561   Canadian Journal of Fisheries and Aquatic Sciences. 50, 703-707.

562   Zhang, Y., Timmerhaus, G., Anttila, K., Mauduit, F., Jørgensen, S.M., Kristensen, T., Claireaux,

563   G., Takle, H., Farrell, A.P., 2016. Domestication compromises athleticism and respiratory

564   plasticity in response to aerobic exercise training in Atlantic salmon (*Salmo salar*).

565   Aquaculture. 463, 79-88.

566

567

568

569

570

571

572 **Table 1:** Comparison of swimming and metabolic metrics (means ± standard deviation) for

573 aquaculture-reared (n=10) and wild-caught (n=7) California Yellowtail, *S. dorsalis*

	BL (cm)	U_{crit} (BL s^{-1})	SMR (mg O$_2$ kg^{-1} min^{-1})	$\dot{M}_{O_{2max}}$ (mg O$_2$ kg^{-1} min^{-1})	Aerobic Scope (mg O$_2$ kg^{-1} min^{-1})	U_{opt} (BL s^{-1})
Aquaculture	18.63 ± 1.12	4.16 ± 0.62*	7.31 ± 2.32*	16.52 ± 1.54	9.20 ± 3.44*	3.63 ± 0.53
Wild	19.31 ± 1.35	4.80 ± 0.52*	3.94 ± 1.60*	19.74 ± 5.74	15.80 ± 5.78*	3.65 ± 0.92

574 For direct comparison, metabolic data for each individual were adjusted to a mass of 80 g using

575 $M^{0.80}$ and a water temperature of 18°C using $Q_{10} = 2.0$. Statistical significance between

576 aquaculture-reared and wild-caught fish is indicated with an asterisk (*). Abbreviations: BL,

577 body length; U_{crit}, critical swimming speed; SMR, standard metabolic rate; $\dot{M}_{O_{2max}}$, maximum

578 oxygen consumption rate; U_{opt}, optimal swimming speed.

579

580

581

582

583

584

585

586

587

588

589

590

591

592

593   **Table 2:** Comparison of *Seriola* spp. standard metabolic rates (SMR), showing the elevated

594   oxygen consumption rate of aquaculture-reared *S. dorsalis* in the current study

Species	Adjusted SMR* (mg O_2 kg^{-1} min^{-1})	Reported SMR (mg O_2 kg^{-1} min^{-1})	Mass (g)	Temp (°C)	Source
S. dorsalis (aquaculture)	5.07	7.31	80	18.0	current study
S. dorsalis (wild)	2.73	3.94	80	18.0	current study
S. lalandi (non-exercised)	2.47	2.87	699	21.1	Brown et al. (2011)
S. lalandi (exercised)	2.29	2.66	699	21.1	Brown et al. (2011)
S. lalandi	1.78	1.55	2000	20	Clark and Seymour (2006)
S. lalandi	2.66	3.31	1900	25	Clark and Seymour (2006)
S. quinqueradiata	2.43	2.30	989	19.2	Yamamoto et al. (1981)

595   *For direct comparison, reported metabolic data from each study were adjusted to a mass of 1 kg

596   using $M^{0.80}$ and to a water temperature of 20°C using $Q_{10} = 2.0$. All SMR estimates for *S. lalandi*

597   are from aquaculture-reared fish. *S. quinqueradiata* from Yamamoto et al. (1981) were reared to

598   experimental size in an aquaculture setting, but were likely captured from the wild as young

599   juveniles. Data from Yamamoto et al. (1981) are for canulated resting fish.

600

601

602

603

604

605

606

607

608

609   Figure 1: **(A)** Oxygen consumption ($\dot{M}_{O_2}$) and **(B)** Cost of transport (COT) of aquaculture-reared

610   (grey circles) and wild-caught (black circles) California Yellowtail, *S. dorsalis*, swimming at

611   variable speeds in a swim tunnel respirometer. For direct comparison all data were adjusted to a

612   mass of 80 g using $M^{0.80}$ and water temperature of 18°C using $Q_{10} = 2.0$. These regression lines

613   are for observational purposes only and show aggregate data from all fish; standard metabolic

614   rate and U_{opt} data presented in the Results were determined as means from individual fish data.