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Swim bladder inflation failure affects energy allocation, growth, and feed conversion of California Yellowtail (*Seriola dorsalis*) in aquaculture

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ABSTRACT

This study examines the effects of swim bladder inflation failure, a common developmental abnormality in finfish aquaculture, on the energy allocation, growth, and development of California Yellowtail (*Seriola dorsalis*). Health and fitness metrics including oxygen consumption, aerobic scope, critical swimming speed, feed conversion ratio, and growth rate, were monitored over a 32-week growout period in three groups of *S. dorsalis*: aquaculture-reared fish that failed to inflate their swim bladders (uninflated), aquaculture-reared fish with properly inflated swim bladders (inflated), and wild-caught individuals (wild). After the growout period, the uninflated fish had significantly lower body mass (636.1 ± 80.4 g vs. 758.6 ± 92.7 g inflated), shorter body length (36.5 ± 1.9 cm vs. 39.6 ± 2.0 cm inflated), and smaller girth (21.5 ± 1.2 cm vs. 23.2 ± 1.1 cm inflated) than the inflated fish. In addition, the uninflated fish had the least efficient feed conversion ratio (2.08 uninflated vs. 1.49 inflated, 1.41 wild), needing 39.8% more feed than the inflated fish, and 47.8% more feed than the wild fish to gain equivalent mass. These differences in growth and feed conversion appear to be primarily attributed to differences in energy allocation. Measures of oxygen consumption using a swim tunnel respirometer at two time points during the growout period showed that uninflated fish had significantly higher metabolic costs than both the inflated and wild groups over a large range of the swimming speeds tested. In addition, the uninflated fish were often observed swimming faster in their growout tank, likely to generate enough lift to compensate for the lack of a buoyant swim bladder. The wild-caught fish had the lowest feed conversion ratios and had significantly lower metabolic costs than both the inflated and uninflated aquaculture-reared fish at the beginning of the growout period (shortly after capture from the wild). The results of this study show that rearing *S. dorsalis* without a functional swim bladder is not economically feasible based on their poor growth and feed conversion ratios, and suggest that there is room for improvement in the metabolic efficiency of cultured *S. dorsalis* with properly inflated swim bladders.

1. Introduction

In aquaculture, successful mass production of high-quality juvenile marine finfish is dependent on successful larval rearing (Kjørsvik et al., 2003; Planas and Cunha, 1999; Tucker Jr., 1998; Woolley and Qin, 2010). For many cultured marine finfish, a sensitive time during larval development is the period of swim bladder inflation. Many important aquaculture species are physoclists as adults, but transient physostomes as larvae, and must gulp air at the surface to inflate their swim bladders before the pneumatic duct connecting the swim bladder to the esophagus closes. While the etiology of inflation failure is not entirely understood, it is typically attributed to variables that inhibit or discourage fish from gulping air at the surface, including water quality issues that can affect surface tension in larval-rearing tanks, stocking density, lighting, and tank flow dynamics. Failing to inflate the swim bladder can affect large portions (> 50%) of a given cohort (see Woolley and Qin, 2010 for review) and has been a significant problem with many important cultured species including Atlantic Salmon (*Salmo salar* (Poppe et al., 1997)), Southern Bluefin Tuna (*Thunnus maccoyii* (Woolley et al., 2013)), Gilthead Seabream (*Sparus auratus* (Prestinicola et al., 2014)), European Seabass (*Dicentrarchus labrax* (Chatain, 1989)), Walleye (*Stizostedion vitreum* (Marty et al., 1995)), Striped Trumpeter

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(Latris lineata (Trotter et al., 2001)), and Yellowtail Kingfish (*Seriola lalandi* (Woolley et al., 2014)). Although improvements in larval rearing protocols, including reduced turbulence, the addition of blowers, and the use of skimmers to remove surface oils, have been shown to help increase swim bladder inflation rates for several species (Chatain and Ounais-Guschemann, 1990; Kitajima et al., 1994), swim bladder inflation failure for a given cohort can still be 5–10%, even for species with well-established rearing protocols.

The swim bladder is used by most fish species to regulate buoyancy. Failure to inflate the swim bladder typically causes a fish to expend more energy to maintain hydrostatic equilibrium, which can impact energy allocation toward growth (Bone and Moore, 2008; Brix, 2002; Steen, 1970). Indeed, several studies have reported reduced growth in larval fishes with uninflated swim bladders (Battaglene and Talbot, 1992; Chatain, 1989; Czesny et al., 2005; Hashimoto et al., 2012; Jacquemond, 2004b; Kindschi and Barrows, 1993); however, the magnitude of the response is variable. Additionally, several physical deformities, including spinal malformations such as lordosis, often result from swim bladder inflation failure (Boglione et al., 1995; Chatain, 1989; Chatain, 1994; Daoulas et al., 1991; Kitajima et al., 1994; Kitajima et al., 1981). Due to such developmental consequences, uninflated fish are usually assumed to be inferior, and are typically sacrificed at a young age, resulting in large losses of potential product (Woolley and Qin, 2010). The failure of swim bladder inflation can thus pose a significant issue in commercial production for many species.

Although most species show slower growth rates and deformities associated with failure to inflate the swim bladder, some species, such as the Eurasian Perch (*Perca fluviatilis*) and Pacific Bluefin Tuna (*Thunnus orientalis*), appear able to inflate their swim bladder after the typically narrow window during early larval development, or otherwise progressively overcome their reduced larval growth due to initial inflation failure (Jacquemond, 2004a; Kurata et al., 2015). The effect of swim bladder inflation failure on growth and development of fish species is thus complex and varied, and despite the prevalence of this phenomenon, research on long-term growth and development is still needed for most species to inform hatcheries of the value of rearing these fish.

This study examines the effects of swim bladder inflation failure in the carangid genus *Seriola,* which is cultured in several countries, and accounts for over 150,000 t of finfish production annually (FAO, 2018). Because of the importance of this group to global aquaculture, there has been increased demand over the past several years to optimize *Seriola* hatchery techniques in order to reduce aquaculture reliance upon wild seed and to promote the development and expansion of *Seriola* aquaculture into new regions (Moran et al., 2007; Stuart and Drawbridge, 2013; Yang et al., 2016). The timing during which swim bladder inflation occurs in *Seriola* is relatively narrow and appears to take place from 2 to 10 days post hatch (Stuart and Drawbridge, 2013; Woolley and Qin, 2013), giving these fish a limited window to complete this important inflation process. Although current hatchery research is continuing to improve swim bladder inflation rates and reduce other common hatchery deformities for *Seriola* (Moran et al., 2007; Stuart and Drawbridge, 2013; Yang et al., 2016), there are many variables that effect the ability to gulp air at the surface. These variables, in addition to the restrictive timing, still result in cohorts with inflation failure rates from 0 to 95% (unpublished data). This study seeks to examine the effects of swim bladder inflation failure on *S. dorsalis* health, fitness, and development over several months of growout to determine if this species can overcome initial swim bladder inflation failure.

2. Methods

We used a number of recently established swimming and metabolic fitness metrics for *S. dorsalis* (critical swimming speed, standard metabolic rate, cost of transport, and aerobic scope) (Wegner et al., 2018) to compare aquaculture-reared fish that failed to inflate their swim bladders (uninflated) to aquaculture-reared fish with properly inflated swim bladders (inflated), as well as wild-caught controls (wild). In addition, somatic growth and feed conversion were monitored and compared between these three groups over a 32-week growout period.

2.1. Fish collection and sorting

Cultured *S. dorsalis* were produced by Hubbs-SeaWorld Research Institute (HSWRI, San Diego, CA) from wild-captured broodstock and transferred to the experimental aquarium facility at the Southwest Fisheries Science Center (SWFSC, La Jolla, CA) at approximately 75 days post hatch. Prior to transfer, fish were sorted into two groups, one group with fully functional and inflated swim bladders (inflated, $n = 40$), and a second group with non-functional, uninflated swim bladders (uninflated, n = 40). Sorting was done by mildly anaesthetizing the fish using MS-222 (tricane methanesulphonate, 75 mg L^{-1}) and placing them in a hypersaline solution (50 ppt). Positively buoyant fish were determined to have properly inflated swim bladders, while negatively buoyant fish were determined to have uninflated swim bladders (Woolley and Qin, 2010). Fish were allowed to recover from transfer stress for approximately one week before experimentation began, at which point they had resumed normal eating and swimming behavior for several days. Wild juvenile *S. dorsalis* (wild, $n = 39$) associated with drifting kelp off the coast of San Diego, CA were captured by hook and line. These fish were held in captivity at the SWFSC for up to seven weeks before experimentation began to allow sufficient time for recovery from capture and transition to a commercial pellet feed. All transport, husbandry, and experimentation were done according to the SWFSC Institutional Animal Care and Use Committee Protocol #SW1401. Wild fish were collected with California Department of Fish and Wildlife Scientific Collecting Permit SC-12372.

2.2. Growth and feed conversion

All fish were grown out for a 32-week period to examine potential differences in somatic growth between experimental groups. Each group was housed in separate oval tanks (one tank per group; 304 × 154 × 80 cm, volume = 3.34 m^3) supplied with ~23 L min^{-1} of flow-through filtered seawater drawn from the end of the Scripps Institution of Oceanography pier. Water temperature (18.00–18.13 °C) and dissolved oxygen levels (~100%) were kept consistent between tanks, and the lack of directional flow (e.g., spray/flow bars were not used) allowed for more spontaneous swimming activity in each tank. Somatic measurements [total length or body length (BL), fork length (FL), body mass (M), and girth] were taken for all fish from each group at the start of the growout period (inflated $n = 40$, uninflated n = 40, wild $n = 39$), and again after 32 weeks (inflated $n = 37$, uninflated $n = 35$, wild $n = 32$) by lightly anaesthetizing yellowtail with MS-222 (80 mg L^{-1}). Any visible spinal deformities (e.g., lordosis) were also noted when the fish were measured. Condition factor (CF) for each fish was calculated using:

$$CF = (M/BL^3) \times 100 \quad (1)$$

During growout all fish were fed commercial pellets (EWOS, Surrey, BC, Canada) two to four times daily, six days a week. For the first eight weeks, each group was fed 5% body mass day^{-1} in pellets; however, as the fish easily consumed this amount, the feeding regime was amended for the remaining 24 weeks to hand feed to satiation as to not limit growth. Fish were observed during feedings to evaluate swimming and feeding behaviors, as well as general health and well-being. Feed conversion ratio (FCR) was calculated for this 24-week period using:

$$FCR = \frac{\text{total dry feed consumed (g)}}{\text{total weight gained (g)}} \quad (2)$$

2.3. Swim tunnel trials

In order to examine potential differences in swimming and metabolic fitness between groups, several fitness metrics were measured through incremental velocity tests using variable-speed Brett-style swim tunnel respirometers (Loligo Systems, Viborg, Denmark). This was done at two points during the growout period using randomly selected fish from each group that were fasted for 20 to 24 h prior to being placed in the respirometer. Fish were tested at 64.3 ± 18.1 g and 18.2 ± 1.6 cm BL (Size A, mean ± standard deviation: wild $n = 8$, inflated $n = 6$, uninflated $n = 7$) using a 5.4 L respirometer with a 30 × 7.5 × 7.5 cm working section, and again approximately 16 weeks later when fish were 415.3 ± 58.0 g and 32.3 ± 1.5 cm BL (Size B: wild $n = 8$, inflated n = 7, uninflated n = 8) using a 29.6 L respirometer with a 55 × 14 × 14 cm working section. Testing was restricted to sizes at which fish could comfortably fit in the working section and successfully complete the swimming regime (corresponding to a median time in captivity for the wild fish of 71 days at Size A and 185 days at Size B). The swim tunnel respirometer was submerged in an exterior buffer tank to help maintain a stable temperature during experimentation (~18 °C, consistent with the growout temperature) and to flush the system with fully oxygenated water between respirometry measurements (see below). Water flow into and out of the swim tunnel from the surrounding buffer tank was controlled by manual valves.

Consistent with methods used by Wegner et al. (2018), fish were acclimated in the swim tunnel at a low flow speed (typically under 30 cm s^{-1} at Size A, and under 40 cm s^{-1} at Size B) for at least one hour before incremental velocity testing began. This one-hour acclimation period started once the fish was swimming steadily with a regular gait. Following the acclimation period, fish were forced to swim against a calibrated flow speed for 30 min, after which the flow speed was raised by 5 or 10 cm s^{-1} in a stepwise fashion at 30-min intervals. Incremental velocity increases were repeated until the fish fatigued, which was indicated by resting against the back fence of the working section and the inability to swim forward when encouraged through visual cues.

Following each trial, swimming speed was adjusted for the solid blocking effect of both the cylindrical vane wheel flow meter probe (Höntzsch Gmbh, Waiblingen, Germany) used to calibrate the swim tunnel (using the continuity equation $A_1V_1 = A_2V_2$), and for the size-specific blocking effect of each fish (according to Bell and Terhune, 1970). Following all flow speed adjustments, critical swimming speed (U_{crit}, cm s^{-1}) was determined for each fish according to Brett's (1964) equation:

$$U_{crit} = U_i + \left(\frac{t_f}{t_i} \times U_{ii} \right) \quad (3)$$

where U_i is the highest speed sustained for a full 30-min increment (cm s^{-1}), t_f is the time swam at the fatigue velocity in minutes, t_i is the prescribed time interval for each velocity increment (30 min), and U_{ii} is the last incremental velocity step increase (cm s^{-1}).

2.4. Respirometry and Metabolic Performance

Oxygen consumption data were recorded for each fish in the swim tunnel respirometer while swimming at each 30-min velocity step using a Fibox 3 fiber optic oxygen transmitter (PreSens Precision Sensing GmbH, Regensburg, Germany). Approximately two minutes after each step-wise increase in speed, the respirometer was sealed from the surrounding buffer tank using manual valves and the oxygen level (as % air saturation) was recorded every five seconds using PreSense software version PST3v602. Oxygen saturation within the respirometer was not allowed to drop below 80% before the system was manually flushed with water from the surrounding buffer tank and brought back to full saturation, at which point the swim tunnel respirometer was resealed and oxygen measurements were repeated if time allowed. The recorded decrease in oxygen saturation was used to calculate oxygen consumption ($\dot{M}_{O2}$) at each swimming speed. If multiple oxygen traces were completed during a given speed, they were averaged to find the mean oxygen consumption at that speed.

At the conclusion of each swim tunnel trial, the fish was removed from the working section, and the chamber was resealed for a measurement of background respiration, which was then subtracted from the fish's calculated $\dot{M}_{O2}$. Each fish was then lightly anaesthetized using MS-222 (80 mg L^{-1}) to measure size (BL, FL, mass, and girth), and then temporarily placed in a holding tank, separate from the growout tanks, to ensure it was not repeatedly tested in the swim tunnel at that given size point (Size A or Size B). Once all respirometry measurements were completed at a given size for all three groups, fish were placed back in their original tanks for continued growout.

The mean water temperature for all swim tunnel trials was 18.17 ± 0.30 °C; however, temperature ranged from 16.94–19.38 °C, so for direct comparison between groups, metabolic data were adjusted to a temperature of 18.0 °C (using $Q_{10} = 2$, Pirozzi and Booth, 2009), and metabolic data for each fish were scaled to a common body mass (65 g at Size A and 410 g at Size B) using $mass^{0.80}$ (Brett and Groves, 1979).

For each fish, $\dot{M}_{O2}$ was plotted against swimming speed (in cm s^{-1}), which typically resulted in a checkmark-shaped curve (common for pelagic fishes), with increased oxygen consumption at low swimming speeds representing the added energetic cost needed to maintain hydrostatic equilibrium at these inefficient velocities (Webb, 1998). In order to estimate standard metabolic rate (SMR), $\dot{M}_{O2}$ values at low speeds that were higher than the vertex of the curve were excluded (Sepulveda et al., 2003; Wegner et al., 2018) before the aggregate data were used to generate regressions for $\dot{M}_{O2}$ in relation to swimming speed for each group (uninflated, inflated, wild) at each size measured (Size A, B). Regression relationships between log oxygen consumption and swimming speed were determined using a bootstrap analysis in which 10,000 linear regression replicates were created from aggregate data for each group at each size using RStudio (v1.0.143). Each regression replicate drew an even number of data points from each fish, with replacement, so that each fish was equally represented in the analysis and individual variation was accounted for. Bootstrap regressions were then extrapolated to a swimming speed of 0 cm s^{-1} and averaged to estimate standard metabolic rates (SMR) for each group at each size. Bootstrap regressions were used since it could not be confirmed that these metabolic data met all of the assumptions for traditional parametric analysis due to the non-independence of the data for each fish, the small sample size, and the distribution of the data. Aerobic scope for each group and size was determined using individual fish data to estimate standard metabolic rate and then subtracting it from the highest metabolic rate recorded for that fish.

To understand metabolic costs associated with level of swimming activity, bootstrapped $\dot{M}_{O2}$ regressions were used to calculate the cost of transport (COT, mgO_2 kg^{-1} m^{-1}) over the range of swimming speeds examined, using the relationship:

$$COT = \dot{M}_{O2}/U \quad (4)$$

where U is the swimming speed (m min^{-1}). COT data was then graphed against swimming speed and polynomial regression coefficients were determined. The lowest point (vertex) of the polynomial regression of each graph represents the optimal swimming speed (U_{opt}) and lowest COT, or min COT. These values were calculated for each regression and then averaged for each group.

2.5. Statistical analysis

Metrics of growth, critical swimming speed, and aerobic scope were determined as means ± standard deviation from individual fish data and potential differences between uninflated, inflated, and wild yellowtail were compared statistically using a single factor ANOVA,

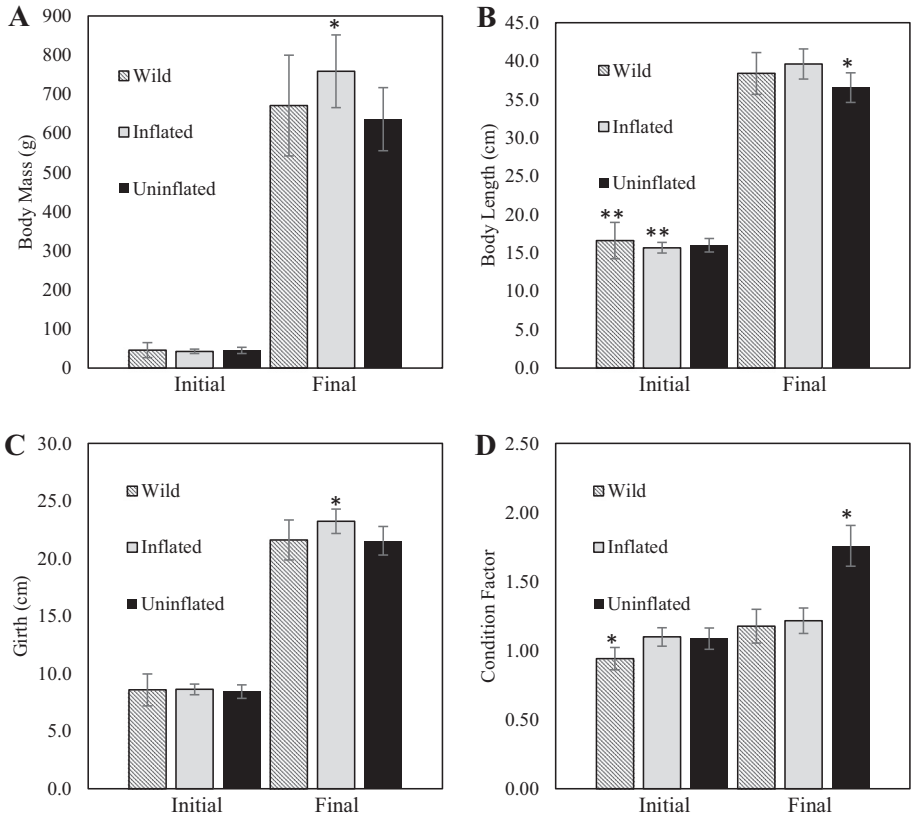

Fig. 1. Comparison of (A) body mass, (B) body length, (C) girth and (D) condition factor of all groups at the start (initial) and end (final) of a 32-week growout period. Statistical significance is only shown between groups within each time point. *Indicates significant difference of one group from the other two. **Used to indicate significant difference between the two groups indicated.

Table 1
Metrics of metabolic performance for aquaculture-reared *S. dorsalis* with properly inflated and uninflated swim bladders compared to wild-caught controls.

Group	SMR Size A (mgO_2 kg^{-1} min^{-1})	SMR Size B (mgO_2 kg^{-1} min^{-1})	Aerobic scope size A (mgO_2 kg^{-1} min^{-1})	Aerobic scope size B (mgO_2 kg^{-1} min^{-1})
Uninflated	5.55 ± 0.56*	3.52 ± 0.45	18.69 ± 5.04	17.42 ± 4.29
Inflated	4.17 ± 0.21*	3.16 ± 0.38	18.91 ± 3.51	16.49 ± 2.60
Wild	3.18 ± 0.19*	2.93 ± 0.24	20.62 ± 3.77	13.39 ± 3.41

Mean standard metabolic rates (SMR) were adjusted to a temperature of 18 °C using a $Q_{10} = 2$, and standardized to 65 g at Size A, and to 410 g at Size B using $mass^{0.80}$. Values are group means ± standard deviation. *Indicates significant difference of one group from the other two.

followed by a Tukey post-hoc test if $P \leq .05$. Bootstrapped regression equations for $\dot{M}_{O2}$ and COT in relation to swimming speed were used to test for significant differences in the metabolism of different groups at different swimming speeds. Significant difference in the oxygen consumption, U_{opt}, and min COT between groups was confirmed if < 5% of the replicate regressions intersected at the points being compared.

3. Results

3.1. Growth and feed conversion

Somatic measurements at the beginning and end of the growout period for each group are shown in Fig. 1. At the start of the study, fish body mass (44.3 ± 12.4 g), FL (14.9 ± 1.4 cm), and girth (8.5 ± 0.9 cm) did not differ significantly between groups; however, the wild fish had significantly longer BL than the inflated fish (16.6 ± 2.4 cm vs. 15.7 ± 0.7 cm respectively), and a significantly lower condition factor than both other groups (0.94 ± 0.08 wild vs. 1.10 ± 0.07 inflated, 1.09 ± 0.08 uninflated). After a 32-week growout, inflated fish had significantly greater mass (758.6 ± 92.7 g inflated vs. 671.1 ± 128.9 g wild, 636.1 ± 80.4 g uninflated) and girth (23.2 ± 1.1 cm inflated vs. 21.6 ± 1.7 cm wild, 21.5 ± 1.2 cm uninflated) than the other two groups, while uninflated fish had significantly shorter BL (36.5 ± 1.9 cm uninflated vs. 39.6 ± 2.0 cm inflated, 38.4 ± 2.7 cm wild), and significantly higher condition factor (1.76 ± 0.15 uninflated vs. 1.22 ± 0.09 inflated, 1.18 ± 0.12 wild). At the end of the growout period, 40% (14/35) of the uninflated fish had mild to severe lordosis, with a majority of cases manifesting as a mild curvature of the anterior third of the vertebral column. These fish were not significantly different in mass, BL, FL, girth, or condition factor than uninflated fish without spinal deformities. Such spinal deformities were not observed in the inflated or wild groups.

Uninflated fish had the least efficient feed conversion ratio (2.08 uninflated, vs. 1.49 inflated, 1.41 wild) and needed 39.8% more feed than the inflated group, and 47.8% more feed than the wild group to gain equivalent mass.

3.2. Swimming and metabolic performance

Metabolic performance data are shown in Table 1 and Fig. 2. At Size A, uninflated fish had significantly greater oxygen consumption rates than the inflated fish for swimming speeds from 0 to 76 cm s^{-1} (0 to 4.2 BL s^{-1}), and the wild fish from 0 to 109 cm s^{-1} (0 to 6.0 BL s^{-1}; Fig. 2A). SMR was also significantly higher for the uninflated fish (5.55 ± 0.56 mgO_2 kg^{-1} min^{-1}) compared to both other groups (4.17 ± 0.21 mgO_2 kg^{-1} min^{-1} inflated, 3.18 ± 0.19 mgO_2 kg^{-1} min^{-1} wild). Additionally, at Size A, inflated fish had significantly greater oxygen consumption than wild fish for all speeds tested, including a higher SMR. At Size B, after approximately 16 weeks of growout, there was no longer a significant difference in SMR between any of the groups (Table 2); however, the uninflated fish did have significantly higher oxygen consumption than the inflated fish for

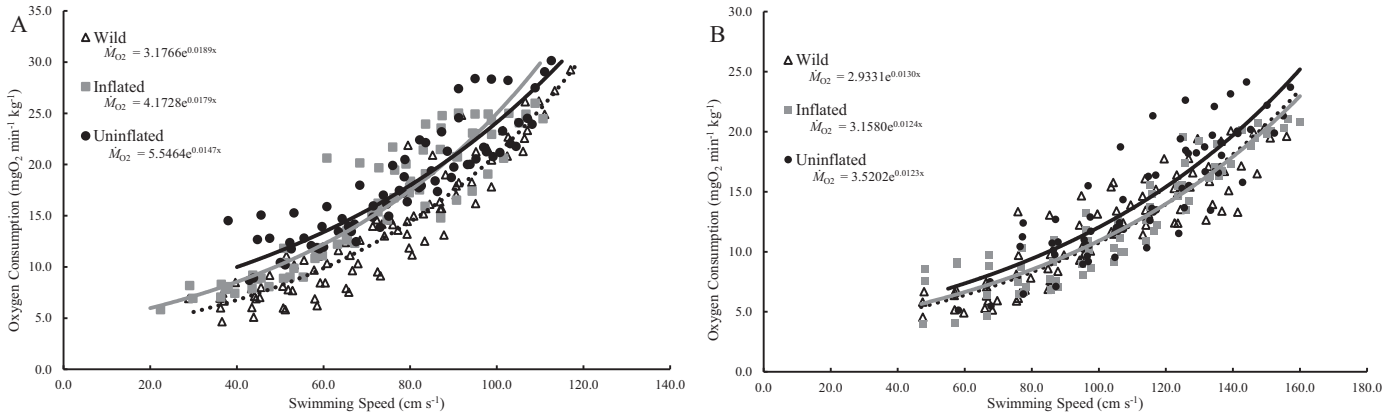

Fig. 2. Oxygen consumption rate ($\dot{M}_{O2}$) at various swimming speeds for wild fish (dotted line), aquaculture-reared fish with inflated swim bladders (grey line), and aquaculture-reared fish with uninflated swim bladders (black line) at (A) Size A (65 g) and approximately 16 weeks later at (B) Size B (410 g). For A, wild n = 8, inflated n = 6, uninflated n = 7. For B, wild n = 8, inflated n = 7, uninflated n = 8. Regressions shown were generated from bootstrap analysis.

speeds from 78 to 152 cm s^{-1} (2.4 to 4.7 BL s^{-1}), and the wild fish from 52 to 144 cm s^{-1} (1.6 to 4.5 BL s^{-1}; Fig. 2B). There was no significant difference in the aerobic scope between groups at either Size A or Size B (Table 2).

Metrics of swimming performance are shown in Table 2 and Fig. 3. Critical swimming speed (U_{crit}) was not significantly different between any of the groups at either Size A or Size B (Table 1). At Size A, U_{crit} was 5.25 ± 0.55 BL s^{-1} (95.81 ± 14.52 cm s^{-1}) for uninflated fish, 5.38 ± 0.80 BL s^{-1} (95.09 ± 13.29 cm s^{-1}) for inflated fish, and 5.34 ± 0.59 BL s^{-1} (99.76 ± 11.69 cm s^{-1}) for wild fish. At Size B, U_{crit} was 4.35 ± 0.58 BL s^{-1} (139.99 ± 11.99 cm s^{-1}) for uninflated fish, 4.42 ± 0.32 BL s^{-1} (142.95 ± 11.10 cm s^{-1}) for inflated fish, and 4.37 ± 0.31 BL s^{-1} (142.56 ± 10.32 cm s^{-1}) for wild fish.

At Size A, the uninflated group had a significantly higher U_{opt} (77.66 ± 4.38 uninflated vs. 65.92 ± 2.68 inflated, and 62.11 ± 2.80 cm s^{-1} wild; or 4.38 ± 0.25 uninflated vs. 3.62 ± 0.15 inflated, and 3.36 ± 0.15 BL s^{-1} wild) and min COT (0.352 ± 0.006 uninflated vs. 0.339 ± 0.005 inflated, 0.275 ± 0.005 mgO$_2$ kg^{-1} m^{-1} wild) compared to the other two groups. Although the U_{opt} of the inflated group was not significantly different from the wild group, the min COT was significantly higher. At Size B, there was no longer any significant difference in U_{opt} between groups (2.78 ± 0.27 uninflated, 2.76 ± 0.26 inflated, and 2.61 ± 0.18 BL s^{-1} wild, or 89.86 ± 8.72 uninflated, 89.20 ± 8.44 inflated, and 84.11 ± 5.83 cm s^{-1} wild); however, the uninflated group had a significantly higher min COT than both other groups (0.195 ± 0.007 uninflated vs. 0.176 ± 0.006 inflated, 0.174 ± 0.004 mgO$_2$ kg^{-1} m^{-1} wild; Table 1).

Note: At Size B, three of the eight (37.5%) uninflated yellowtail randomly selected for swim tunnel trials had lordosis. Measures of metabolic and swimming metrics for lordotic individuals fell within the range of the other uninflated yellowtail.

4. Discussion

This study demonstrates that cultured *S. dorsalis* without properly inflated swim bladders have reduced fitness compared to cultured fish with properly inflated swim bladders and wild-caught controls, as indicated through a number of physiological metrics (e.g., higher oxygen consumption rates for a range of swimming speeds, higher minimum costs of transport, slower growth, and higher feed conversion ratios). In addition, while *S. dorsalis* with inflated swim bladders showed superior fitness in comparison to fish with uninflated bladders, our results indicate that there is still room for targeted improvement in the fitness of these aquaculture-reared fish, such as lowering feed conversion ratio and standard metabolic rate to levels observed for wild-caught controls. Although the wild fish demonstrated more favorable fitness in these key areas, their fitness advantage was lost over time in captivity, indicating that the tank-based aquaculture setting used in this study is likely suboptimal for the fitness of this species.

S. dorsalis with uninflated swim bladders had a higher feed conversion ratio and grew slower than fish with properly inflated swim bladders, having a significantly lower body mass, girth, and length at the end of the growout period (Fig. 1). This is consistent with previous studies on other fish species in which short duration growouts of larval fish without properly inflated swim bladders showed slower growth (Battaglene and Talbot, 1992; Chatain, 1989; Czesny et al., 2005; Hashimoto et al., 2012; Jacquemond, 2004b; Kindschi and Barrows, 1993). However, our 32-week growout of juvenile *S. dorsalis* indicates a continued growth and feed conversion disadvantage and demonstrates that unlike *P. fluviatilis* L. (Jacquemond, 2004a) and *T. orientalis* (Kurata et al., 2015), *S. dorsalis* does not appear able to overcome initial swim bladder inflation failure and catch up to the size of conspecifics with inflated bladders. This inability to overcome initial swim bladder failure was further manifested in the development of lordosis in 40% of the uninflated group by the end of the 32-week growout. While lordosis, did not appear to have immediate significant effects on growth or fitness in comparison to non-lordotic uninflated fish, it seems likely that the lordosis would have led to additional health and fitness issues if growout had continued.

The reduced growth and feed conversion efficiency of the uninflated fish appears to be a direct result of their reduced buoyancy. The

Table 2
Metrics of swimming performance for aquaculture-reared *S. dorsalis* with properly inflated and uninflated swim bladders compared to wild-caught controls.

Group	U_{crit} Size A (BL s^{-1})	U_{crit} Size B (BL s^{-1})	U_{opt} Size A (BL s^{-1})	U_{opt} Size B (BL s^{-1})	Min COT Size A (mgO$_2$ kg^{-1} m^{-1})	Min COT Size B (mgO$_2$ kg^{-1} m^{-1})
Uninflated	5.25 ± 0.55	4.35 ± 0.58	4.38 ± 0.25*	2.78 ± 0.27	0.352 ± 0.006*	0.195 ± 0.007*
Inflated	5.38 ± 0.80	4.42 ± 0.32	3.62 ± 0.15	2.76 ± 0.26	0.339 ± 0.005*	0.176 ± 0.006
Wild	5.34 ± 0.59	4.37 ± 0.31	3.36 ± 0.15	2.61 ± 0.18	0.275 ± 0.005*	0.174 ± 0.004

Values are group means ± standard deviation. * Indicates significant difference of one group from the other two. Abbreviations: U_{crit}, critical swimming speed; U_{opt}, optimal swimming speed; min COT, minimum cost of transport.

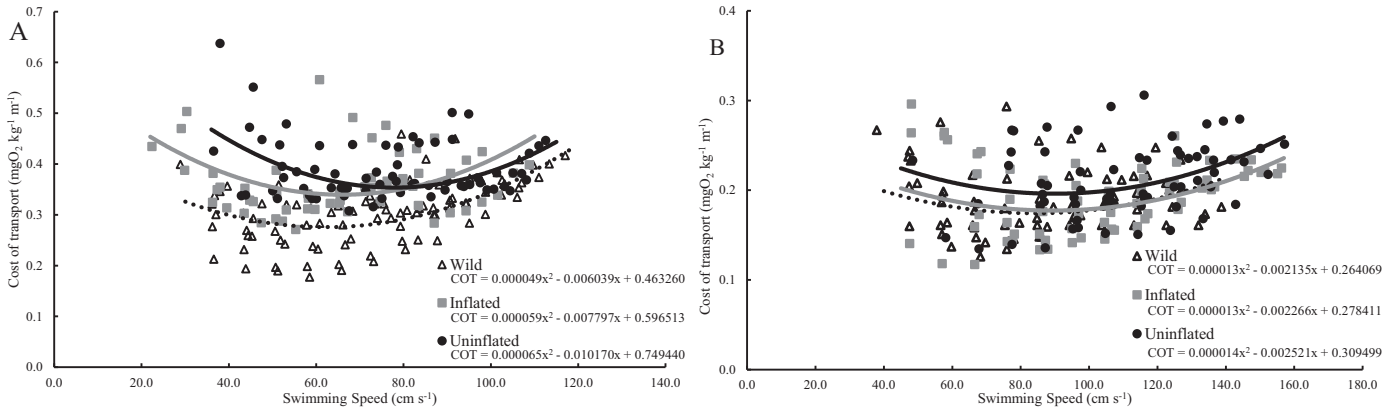

Fig. 3. Cost of transport (COT) at (A) Size A (65 g) and approximately 16 weeks later at (B) Size B (410 g) for wild fish (dotted line), aquaculture-reared fish with inflated swim bladders (grey line), and aquaculture-reared fish with uninflated swim bladders (black line). For A, wild n = 8, inflated n = 6, uninflated n = 7. For B, wild n = 8, inflated n = 7, uninflated n = 8. Regressions shown were derived from bootstrap analysis.

uninflated fish used in this study were negatively buoyant and denser than the other groups (1.06 g cm^{-3} vs. 1.02 g cm^{-3}), which required them to swim at faster speeds to generate lift and maintain hydrostatic equilibrium. This was especially apparent during the swim tunnel trials in which the uninflated fish had a much harder time swimming at low speeds, resulting in a lack of metabolic data for this group under ~2 BL s^{-1}. These observations are consistent with previous descriptions of negatively buoyant fish requiring minimum speeds of 1–3 BL s^{-1} to avoid sinking (Brix, 2002; Pelster, 1997). Additionally, the shallow depth of the swim tunnel respirometer in this study often necessitated uninflated fish to swim at even faster speeds to prevent them from brushing or dragging along the bottom due to their steep swimming angle used to generate lift. The reduced buoyancy of the uninflated fish thus resulted in a significantly higher optimal swimming speed than the other two groups at Size A, which is consistent with observations of the uninflated fish swimming continuously faster than the other groups in the growout tanks. Although maintaining these faster swimming speeds is energetically costly, the added exercise may have helped the uninflated fish retain some aspects of swimming fitness, including the ability to reach critical swimming speeds and aerobic scopes comparable to those achieved by inflated and wild fish.

In addition to increased energetic demands associated with constantly swimming at a faster speed, uninflated fish were generally less efficient swimmers at a given speed and had higher oxygen consumption rates for many of the swimming speeds tested during growout (Fig. 2). In particular, uninflated fish had a significantly higher minimum cost of transport than the other groups at both sizes tested, even though the optimal swimming speed did not significantly differ between groups at Size B. This reduced swimming efficiency would have further increased energetic demands and food consumption without a concomitant increase in growth. Taken together, the upshifted, less efficient metabolic curves for the uninflated fish (Fig. 2) and the faster basal swimming speed required to maintain hydrostatic equilibrium appear to explain both the slower growth rates and higher feed conversion ratios for uninflated fish. For example, based on the mean lowest maintainable swimming speeds of fish in the respirometer at Size A, the uninflated fish needed to swim about 76% faster than the inflated fish (40.3 cm s^{-1} vs. 22.8 cm s^{-1} respectively) to generate sufficient lift. At these speeds, using the less efficient metabolic curves shown in Fig. 2A, uninflated fish had a 59.7% higher oxygen consumption rate than *S. dorsalis* with inflated swim bladders. This 59.7% higher energetic requirement matches closely with the 39.8% increase in feed intake combined with the 19.3% smaller final body mass of the uninflated fish as compared to the inflated fish.

In addition to documenting the inferior fitness of the uninflated fish, this study also revealed some fitness differences between the wild and inflated fish as evidenced by the lower oxygen consumption rates of the wild-caught fish at Size A, including a lower standard metabolic rate. The wild-caught fish also had a more efficient feed conversion ratio than both aquaculture-reared groups. Similar disparities in fitness between wild-caught and healthy aquaculture-reared conspecifics have been recently reported for *S. dorsalis* (Wegner et al., 2018) and are a common challenge in aquaculture for a range of species (Basaran et al., 2007; Duthie, 1987; Hammenstig et al., 2014; McDonald et al., 1998; Pedersen et al., 2008; Shustov and Shchurov, 1988). Wegner et al. (2018) found that cultured *S. dorsalis* had a significantly lower critical swimming speed, higher standard metabolic rate, and reduced aerobic scope in comparison to wild-caught fish; however, no significant difference in critical swimming speed or aerobic scope was found between groups in the current study. These different results between studies can likely be attributed to improvements in larval *S. dorsalis* husbandry practices (e.g., bacterial mitigation, live feed management) that contributed to better survival, hardiness, and enhanced fitness of the 2015 cohort used in this study compared to the 2012 cohort used in Wegner et al. (2018).

While this study thus suggests that changes to larval production protocols for *S. dorsalis* have had positive effects on the fitness of hatchery fish; it also highlights areas in which further improvement can be made. Although the inflated fish had a significantly larger final body mass and girth than the wild fish, they also had a poorer feed conversion ratio (1.49 vs. 1.41) equating to more food necessary to gain equivalent mass. The better growth performance of the inflated fish can be thus attributed to their greater food consumption, eating 28.2% more food than the wild fish; however, they only gained 21.2% more mass. The more efficient feed conversion of the wild fish was likely associated with their significantly lower standard metabolic rate and minimum cost of transport when they were initially brought into captivity (Size A). This suggests that continued improvement of metabolic fitness in aquaculture-reared fish may prove beneficial for feed conversion efficiency, and since aquaculture feed can be the largest operational expense for intensive aquaculture facilities (Hasan and De Silva, 2007), improvement in metabolic fitness could have major financial implications that make it an important area for further research and optimization.

The apparent degradation of some fitness metrics of the wild fish over time in captivity (e.g., wild fish had a significantly lower standard metabolic rate in comparison to other groups at Size A, but not at Size B after approximately four months in captivity) likely indicates the wild fish were transitioned to a suboptimal environment. In the wild, fish actively search for prey, avoid predators, and may encounter strong current regimes, conditions that likely help to improve and maintain fitness through sustained aerobic activity that fish do not experience in

captivity. Research involving sustained exercise has shown positive effects on the growth (Davison and Goldspink, 1977; Ibarz et al., 2011; Palstra et al., 2015; Totland et al., 1987; Walker and Emerson, 1978) and behavior (Adams et al., 1995; Christiansen and Jobling, 1990; East and Magnan, 1987) of several species, although a majority of work in this area has focused on salmonids, and more research is needed on other active species such as *S. dorsalis*. Work to date on *Seriola* exercise training has shown improved growth and feed conversion after sustained exercise (Brown et al., 2011; Palstra et al., 2015; Peters, 2009; Yogata and Oku, 2000); however, it remains largely unknown how much exercise is needed to optimize such positive responses or for how long such benefits may persist post exercise training. Such information is likely critical for determining how much exercise is necessary to elicit a lasting response and at what point exercise should be introduced in the rearing process. Further research on protocols to improve and prolong periods of metabolic fitness could greatly benefit commercial producers of *Seriola* and similar species.

5. Conclusions

While *S. dorsalis* with uninflated swim bladders seem comparable to the other groups in some metrics of fitness, such as critical swimming speed, their less efficient cost of transport and need to swim at higher speeds to maintain hydrostatic equilibrium appear to result in less favorable feed conversion ratios and slower growth. This reduced growth and feed efficiency, in addition to lordosis which would reduce market price, indicate that *S. dorsalis* without properly inflated swim bladders are not economical to rear for commercial production when healthy fish with properly inflated swim bladders are available. However, this study also suggests that metabolic fitness of aquaculture-reared *S. dorsalis* with properly inflated swim bladders can potentially be further optimized to enhance feed conversion ratios similar to those observed in wild individuals. Improved fitness could potentially be achieved through exercise, as limited prior research on *S. dorsalis* and other *Seriola* species has shown promising links between sustained exercise and improved feed conversion and growth (Brown et al., 2011; Palstra et al., 2015; Peters, 2009; Yogata and Oku, 2000). Although wild fish proved to be more fit in key areas as demonstrated by their lower feed conversion ratios and standard metabolic rates, their fitness advantage was not retained with time in captivity, further illuminating the need for more effective rearing protocols that can enhance fitness and growth in captivity.

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References

Adams, C.E., Huntingford, F.A., Krpal, J., Jobling, M., Burnett, S.J., 1995. Exercise, agonistic behaviour and food acquisition in Arctic charr, *Salvelinus alpinus*. Environ. Biol. Fish 43, 213–218.

Basaran, F., Ozbilgin, H., Ozbilgin, Y.D., 2007. Comparison of the swimming performance of farmed and wild gilthead sea bream, *Sparus aurata*. Aquac. Res. 38, 452–456.

Battaglene, S., Talbot, R., 1992. Induced spawning and larval rearing of snapper, *Pagrus auratus* (Pisces: Sparidae), from Australian waters. New Zeal. J. Mar. Fresh. 26, 179–185.

Bell, W.H., Terhune, L.D.B., 1970. Water tunnel design for fisheries research. Fisheries Research Board of Canada Technical Report No, pp. 195 (69 pp).

Boglione, C., Marino, G., Fusari, A., Ferreri, F., Finoia, M., Cataudella, S., 1995. Skeletal anomalies in *Dicentrarchus labrax* juveniles selected for functional swimbladder. ICES Mar. Sci. Symp. 201, 163–169.

Bone, Q., Moore, R.H., 2008. Biology of Fishes, Third Edition. Taylor & Francis, New York (332 pp).

Brett, J.R., 1964. The respiratory metabolism and swimming performance of young sockeye salmon. J. Fish. Res. Bd. Can. 21, 1183–1226.

Brett, J.R., Groves, T.D.D., 1979. Physiological energetics. In: Hoar, W.S., Randall, D.J., Brett, J.R. (Eds.), Fish Physiology. Bioenergetics and Growth Vol. 8. Academic Press, New York, pp. 279–352.

Brix, O., 2002. The physiology of living in water. In: Hart, P.J.B., Reynolds, J.D. (Eds.), Handbook of Fish Biology and Fisheries. Fish Biology Vol. 1. Blackwell, Malden, MA, pp. 71–96.

Brown, E.J., Bruce, M., Pether, S., Herbert, N.A., 2011. Do swimming fish always grow fast? Investigating the magnitude and physiological basis of exercise-induced growth in juvenile New Zealand yellowtail kingfish, *Seriola lalandi*. Fish Physiol. Biochem. 37, 327–336.

Chatain, B., 1989. Problems related to the lack of functional swimbladder in intensive rearing of *Dicentrarchus labrax* and *Sparus auratus*. Adv. Trop. Aquac. 9, 699–709.

Chatain, B., 1994. Abnormal swimbladder development and lordosis in sea bass (*Dicentrarchus labrax*) and sea bream (*Sparus auratus*). Aquaculture 119, 371–379.

Chatain, B., Ounais-Guschemann, N., 1990. Improved rate of initial swim bladder inflation in intensively reared *Sparus auratus*. Aquaculture 84, 345–353.

Christiansen, J.S., Jobling, M., 1990. The behaviour and the relationship between food intake and growth of juvenile Arctic charr, *Salvelinus alpinus* L., subjected to sustained exercise. Can. J. Zool. 68, 2185–2191.

Czesny, S.J., Graeb, B.D.S., Dettmers, J.M., 2005. Ecological consequences of swim bladder noninflation for larval yellow perch. Trans. Amer. Fish. Soc. 134, 1011–1020.

Daoulas, C., Economou, A.N., Bantavas, I., 1991. Osteological abnormalities in laboratory reared sea-bass (*Dicentrarchus labrax*) fingerlings. Aquaculture 97, 169–180.

Davison, W., Goldspink, G., 1977. The effect of prolonged exercise on the lateral musculature of the brown trout (*Salmo trutta*). J. Exp. Biol. 70, 1–12.

Duthie, G.G., 1987. Observations of poor swimming performance among hatchery-reared rainbow trout, *Salmo gairdneri*. Envir. Biol. Fish. 18, 309–311.

East, P., Magnan, P., 1987. The effect of locomotor activity on the growth of brook charr, *Salvelinus fontinalis* Mitchill. Can. J. Zool. 65, 843–846.

FAO, 2018. Fishery Statistical Collections. Global Aquaculture Production 1950–2015. Data query January, 2018.

Hammenstig, D., Sandblom, E., Axelsson, M., Johnsson, J.I., 2014. Effects of rearing density and dietary fat content on burst-swim performance and oxygen transport capacity in juvenile Atlantic salmon *Salmo salar*. J. Fish Biol. 85, 1177–1191.

Hasan, M.R., De Silva, S.S., 2007. Feeds and fertilizers: the key to long term sustainability of Asian aquaculture. In: Hasan, M.R., De Silva, S.S., Hecht, T., Tacon, A.G. (Eds.), Study and analysis of feeds and fertilizers for sustainable aquaculture development. pp. 19-47. Food and Agriculture Organization of the United Nations Fisheries Technical Paper No. 497, (Rome).

Hashimoto, H., Imai, A., Iwasaki, T., Hamasaki, K., Teruya, K., Hamada, K., Mushiake, K., 2012. Feeding and growth of larval greater amberjack *Seriola dumerili* with non-inflated, normal inflated and over-inflated swim bladders. Aquac. Sci. 60, 99–106.

Ibarz, A., Felip, O., Fernández-Borràs, J., Martín-Pérez, M., Blasco, J., Torrella, J.R., 2011. Sustained swimming improves muscle growth and cellularity in gilthead sea bream. J. Comp. Physiol. 181B, 209–217.

Jacquemond, F., 2004a. Separated breeding of perch fingerlings (*Perca fluviatilis* L.) with and without initial inflated swim bladder: comparison of swim bladder development, skeleton conformation and growth performances. Aquaculture 239, 261–273.

Jacquemond, F., 2004b. Sorting Eurasian perch fingerlings (*Perca fluviatilis* L.) with and without functional swim bladder using tricaine methane sulfonate. Aquaculture 231, 249–262.

Kindschi, G.A., Barrows, F.T., 1993. Survey of swim bladder inflation in walleyes reared in hatchery production ponds. Prog. Fish Cult. 55, 219–223.

Kitajima, C., Tsukashima, Y., Fujita, S., Watanabe, T., Yone, Y., 1981. Relationship between uninflated swim bladders and lordotic deformity in hatchery-reared red sea bream *Pagrus major*. Bull. Jap. Soc. Sci. Fish. 47, 1289–1294.

Kitajima, C., Watanabe, T., Tsukashima, Y., Fujita, S., 1994. Lordotic deformation and abnormal development of swim bladders in some hatchery-bred marine physoclistous fish in Japan. J. World Aquacult. Soc. 25, 64–77.

Kjørsvik, E., Hoehne-Reitan, K., Reitan, K., 2003. Egg and larval quality criteria as predictive measures for juvenile production in turbot (*Scophthalmus maximus* L.). Aquaculture 227, 9–20.

Kurata, M., Ishibashi, Y., Seoka, M., Honryo, T., Katayama, S., Fukuda, H., Takii, K., Kumai, H., Miyashita, S., Sawada, Y., 2015. Influence of swimbladder inflation failure on mortality, growth and lordotic deformity in Pacific bluefin tuna, *Thunnus orientalis*, (Temminck & Schlegel) postflexion larvae and juveniles. Aquac. Res. 46, 1469–1479.

Marty, G.D., Hinton, D.E., Summerfelt, R.C., 1995. Histopathology of swimbladder non-inflation in walleye (*Stizostedion vitreum*) larvae: role of development and inflammation. Aquaculture 138, 35–48.

McDonald, D.G., Milligan, C.L., McFarlane, W.J., Croke, S., Currie, S., Hooke, B., Angus, R.B., Tufts, B.L., Davidson, K., 1998. Condition and performance of juvenile Atlantic salmon (*Salmo salar*): effects of rearing practices on hatchery fish and comparison with wild fish. Can. J. Fish. Aqua. Sci. 55, 1208–1219.

Moran, D., Smith, C.K., Gara, B., Poortenaar, C.W., 2007. Reproductive behaviour and early development in yellowtail kingfish *(Seriola lalandi* Valenciennes 1833). Aquaculture 262, 95–104.

Palstra, A.P., Mes, D., Kusters, K., Roques, J.A., Flik, G., Kloet, K., Blonk, R.J.W., 2015. Forced sustained swimming exercise at optimal speed enhances growth of juvenile yellowtail kingfish (*Seriola lalandi*). Front. Physiol. 5, 506.

Pedersen, L.F., Koed, A., Malte, H., 2008. Swimming performance of wild and F1-hatchery-reared Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) smolts. Ecol. Fresh. Fish 17, 425–431.

Pelster, B., 1997. Buoyancy at depth. In: Randall, D.J., Farrell, A.P. (Eds.), Fish

Physiology. Deep Sea Fishes Vol. 16. Academic Press, San Diego, pp. 195–237.
Peters, C.J., 2009. Continuous exercise enhances swim performance and alters growth rate, IGF-I, and cortisol in juvenile marine finfish in aquaculture. University of San Diego (Masters Thesis, 176 pp).
Pirozzi, I., Booth, M.A., 2009. The routine metabolic rate of mulloway (*Argyrosomus japonicus*: Sciaenidae) and yellowtail kingfish (*Seriola lalandi*: Carangidae) acclimated to six different temperatures. Comp. Biochem. Physiol. 152A, 586–592.
Planas, M., Cunha, I., 1999. Larviculture of marine fish: problems and perspectives. Aquaculture 177, 171–190.
Poppe, T.T., Hellberg, H., Griffiths, D., Meldal, H., 1997. Swimbladder abnormality in farmed Atlantic salmon *Salmo salar*. Dis. Aquat. Org. 30, 73–76.
Prestinicola, L., Boglione, C., Cataudella, S., 2014. Relationship between uninflated swim bladder and skeletal anomalies in reared gilthead seabream (*Sparus aurata*). Aquaculture 432, 462–469.
Sepulveda, C.A., Dickson, K.A., Graham, J.B., 2003. Swimming performance studies on the eastern Pacific bonito *Sarda chiliensis*, a close relative of the tunas (family Scombridae) I. Energetics. J. Exp. Biol. 206, 2739–2748.
Shustov, Y.A., Shchurov, I.L., 1988. Quantitative estimation of stamina of wild and hatchery-reared Atlantic salmon (*Salmo salar* L.). Aquaculture 71, 81–87.
Steen, J.B., 1970. The swim bladder as a hydrostatic organ. In: Hoar, W.S., Randall, D.J. (Eds.), Fish Physiology. Reproduction and Growth, Bioluminescence, Pigments, and Poisons Vol. 3. Academic Press, New York, pp. 413–443.
Stuart, K.R., Drawbridge, M.A., 2013. Captive spawning and larval rearing of California yellowtail (*Seriola lalandi*). Aquac. Res. 44, 728–737.
Totland, G.K., Kryvi, H., Jødestøl, K.A., Christiansen, E.N., Tangerås, A., Slinde, E., 1987. Growth and composition of the swimming muscle of adult Atlantic salmon (*Salmo salar* L.) during long-term sustained swimming. Aquaculture 66, 299–313.
Trotter, A.J., Pankhurst, P.M., Hart, P.R., 2001. Swim bladder malformation in hatchery-reared striped trumpeter *Latris lineata* (Latridae). Aquaculture 198, 41–54.
Tucker Jr., J.W., 1998. Marine Fish Culture. Kluwer Academic Press, Norwell, MA (750 pp).
Walker, M.G., Emerson, L., 1978. Sustained swimming speeds and myotomal muscle function in the trout *Salmo gairdneri*. J. Fish Biol. 13, 475–481.
Webb, P.W., 1998. Swimming. In: Evans, D.H. (Ed.), The Physiology of Fishes, Second Edition. CRC Press, Boca Raton, pp. 3–24.
Wegner, N.C., Drawbridge, M.A., Hyde, J.R., 2018. Reduced swimming and metabolic fitness of aquaculture-reared California Yellowtail (*Seriola dorsalis*) in comparison to wild-caught conspecifics. Aquaculture 486, 51–56.
Woolley, L.D., Qin, J.G., 2010. Swimbladder inflation and its implication to the culture of marine finfish larvae. Rev. Aquac. 2, 181–190.
Woolley, L.D., Qin, J.G., 2013. Ontogeny of body density and the swimbladder in yellowtail kingfish *Seriola lalandi* larvae. J. Fish Biol. 82, 658–670.
Woolley, L.D., Fielder, S.D., Qin, J.G., 2013. Swimbladder inflation associated with body density change and larval survival in southern bluefin tuna *Thunnus maccoyii*. Aquac. Int. 21, 1233–1242.
Woolley, L.D., Fielder, D.S., Qin, J.G., 2014. Swimbladder inflation, growth and survival of yellowtail kingfish *Seriola lalandi* (Valenciennes, 1833) larvae under different temperature, light and oxygen conditions. Aquac. Res. 45, 1489–1498.
Yang, S.G., Hur, S.W., Ji, S.C., Lim, S.G., Kim, B.S., Jeong, M., Lee, C.H., Lee, Y.-D., 2016. Morphological development of embryo, larvae and juvenile in yellowtail kingfish, *Seriola lalandi*. Dev. Reprod. 20, 131–140.
Yogata, H., Oku, H., 2000. The effects of swimming exercise on growth and whole-body protein and fat contents of fed and unfed fingerling yellowtail. Fish. Sci. 66, 1100–1105.