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Short communication

Capture, transport, prophylaxis, acclimation, and continuous spawning of Mahi-mahi (*Coryphaena hippurus*) in captivity

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ABSTRACT

Successful culture of marine fish relies upon availability of high quality fertilized eggs obtained from broodstock. However, some of the most critical aspects of obtaining such eggs are often overlooked. These aspects include the capture, transport, acclimation, and spawning of sexually mature wild-caught fish. Mahi-mahi (*Coryphaena hippurus*), also known as dolphinfish, have been identified as one of the most promising candidate species for development of warm-water marine finfish aquaculture due to their high growth rate, market presence, and global distribution. In addition, mahi-mahi have proven to be a useful model species for physiology and environmental toxicology research, specifically in studies examining tropical and subtropical pelagic teleosts. One of the keys to aquaculture development of this species is the ability to obtain year-round production of fertilized embryos. This study documents the technical methods utilized to reach a point of consistent mahi-mahi egg production year-round, while also detailing the live transport tank and land-based spawning tank design, implementation, and operation. Following three different groups of wild-caught mahi-mahi broodstock from the point of capture throughout their lifespan, this study provides novel information on growth, survival, and spawning of this species in captivity. Results from this research have allowed for significant new insights into the effects of a variety of environmental stressors on the early life stages of this species. Furthermore, the ability to maintain consistent spawning populations of mahi-mahi in captivity has allowed for reliable and consistent production of fully-weaned fingerlings of this species, thereby resolving one of the key industry bottlenecks that has been limiting expansion of mahi-mahi commercial-scale aquaculture.

1. Introduction

The marine aquaculture sector continues to expand globally as advances in technology and efficiency open opportunities for sustained growth of this sector. Aside from the dominance of Atlantic salmon (*Salmo salar*) in the marine finfish aquaculture sector, a variety of other marine finfish species are cultured in significant quantities throughout the world (*FishStatJ - Fisheries and aquaculture software*, 2016). However, given the projected gap between seafood supply and demand forecasted for the future (Kobayashi et al., 2015), the search for novel species for the marine finfish aquaculture industry is ongoing. When selecting new species for commercial aquaculture production, factors such as market presence, price, availability, ease of culture, and growth rate represent some of the most important variables to consider. The mahi-mahi (*Coryphaena hippurus*) seemingly has all of the attributes necessary to make it a leading candidate for further aquaculture development. Beginning in the early 1980's researchers began developing technology for domestication of this species (Hagood et al., 1981; Kraul, 1989; Szyper et al., 1984), yet to date there has been no long-term commercial-scale success with mahi-mahi aquaculture. Reasons for this are numerous and extend beyond the scope of this study, but they likely center upon the rather consistent availability of wild mahi-mahi in the marketplace, the significant capital investment required to grow this species to comparable harvest size with the wild product (> 5 kg), and the technological challenges of raising this species on a commercial-scale in captivity. However, given the rising interest in developing sources of sustainable seafood and the growing popularity of plate-size whole-fish in the marketplace, there is a renewed interest in further aquaculture development of mahi-mahi as a means to meet these interests. Mahi-mahi can reach plate size (~400–500 g) in less than half the time required for other species commonly presented in this manner, such as snapper (*Lutjanus spp.*) and the Mediterranean sea bass (*Dicentrarchus labrax*), or branzino as it is more commonly known, and their food conversion ratio (FCR) during this growth cycle ranges

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from 1.5–2.0 (dry feed/live fish) (Benetti et al., 1995; Kraul, 1989). Aside from interest in this species from a food-fish perspective the mahi-mahi has been identified as a promising model species for research examining the effects of climate change (Bignami et al., 2014) and open ocean pollution events, such as the *Deepwater Horizon* oil spill in 2010 (Burggren et al., 2015; Edmunds et al., 2015; Esbaugh et al., 2016; Incardona et al., 2014; Mager et al., 2014; Stieglitz et al., 2016a). Unlike more commonly cultured marine finfish species such as salmon and sea bass, fertilized embryos of mahi-mahi are not commercially available. Therefore, development of a broodstock program requires the successful capture, acclimation, and spawning of this species on a regular basis in captivity. This same hurdle exists for the culture of other relatively novel high-value marine finfish species such as cobia (*Rachycentron canadum*), tuna (*Thunnus spp.*), grouper (*Epinephelus* spp. and *Mycteropera* spp.), and snapper (*Lutjanus* spp.), yet to date there is no documented methodology for development of a year-round spawning stock of mahi-mahi. For the first time, this study documents the successful capture, handling, acclimation, and spawning of three separate groups of mahi-mahi at the University of Miami Experimental Hatchery (UMEH) on Virginia Key, Florida, USA. Building upon early research and development efforts with this species, the following technical methods represent a reliable process that can be successfully applied throughout the world, given the circum-global distribution of mahi-mahi in tropical and subtropical seas.

2. Capture and transport

Mahi-mahi utilized in this study were caught in the Straits of Florida off the coast of Miami, Florida, USA using hook and line angling techniques. While some fish were captured on J-style hooks (Mustad® model 7766 sizes 5/0–7/0, Norway) using trolled feathers and hard plastic lures, the majority of fish were caught using bait, live or dead, on circle hooks (Mustad® model 39938-BLN sizes 3/0–6/0, Norway). By using small gap circle hooks craniofacial injuries were minimized during the angling process. Captured fish were carefully lifted from the water, hooks were extracted without physically contacting the fish using a commercial de-hooking device (R & R Tackle Co., Miami, Florida, USA), and then the fish were placed in a custom-modified 1.1 m^3 (1.65 m diameter × 0.76 m height) cylindrical polyurethane transport tank (Fig. 1) equipped with a center standpipe to limit the ability of fish from conducting direct wall strikes from one side of the tank to the other. Any fish showing signs of excessive bleeding and/or poor hook placement were not placed in the transport tank. Vertical lines were painted on the interior of the tank walls to help fish orient to captive conditions and to reduce the occurrence of contact with the tank walls. The tank was equipped with a transport lid that has holes spaced evenly around the surface area to allow for water to pass through while reducing sloshing that occurs in offshore sea conditions. While in use the water level of the transport tank was elevated above the transport tank lid, and this served to minimize the sloshing action of water inside the transport tank. Compressed oxygen was used to supersaturate the transport tank water at a level of 9–12 mg L^{-1}, while raw seawater (32–34 ppt salinity) was pumped through the tank at a rate of approximately 1000% daily exchange (~42% of tank volume per hour). Over the course of this study three different broodstock capture trips were completed resulting in the capture of three distinct groups of wild mahi-mahi that were brought into captivity. The average size of captured fish was 2.6 ± 0.3 kg (Table 1), and female fish were more commonly captured than male fish. Fish were maintained at a density of 30–40 kg m^{-3} in the transport tank for durations of up to 6–8 h. Upon arrival at the UMEH facility on Virginia Key, Florida, USA the raw seawater flow to the transport tank was discontinued and the water level was subsequently lowered to allow for the tank lid to be removed. Supplemental oxygen continued to be used to maintain fish under static conditions during the transfer process to a 15 m^3 (4.57 m diameter × 0.91 m depth) land-based quarantine tank. Using a water-filled custom fabricated sling, similar to that which is described in Farwell (2001), fish were individually transported from the transport tank on board the boat to the land-based quarantine tank. Survival from the point of capture to arrival at land-based tanks averaged 95%.

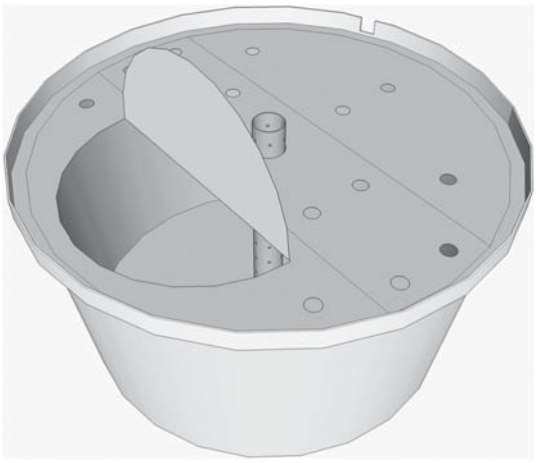

Fig. 1. Custom-modified 1.1 m^3 live fish transport tank.

Table 1
Growth metrics and FCRs of broodstock fish. Values sharing lower case letters within rows are not significantly different. Combined gender data not included in statistical analyses. *Age at capture estimated as described in Section 6. FL = fork length; TL = total length; DPH = days-post-hatch; GSI = gonadosomatic index; HSI = hepatosomatic index; VSI = visceral somatic index; SGR = specific growth rate; AGR = absolute growth rate; RGR = relative growth rate; FCR (w:w) = food conversion ratio of wet food weight: wet fish weight; FCR (d:w) = food conversion ratio of dry food weight: wet fish weight.

Gender	Male		Female		Combined	
	Mean	SE	Mean	SE	Mean	SE
n	3		10		13	
Initial FL (cm)	65.5	4.3	65.7	3.4	65.7	2.7
Initial TL (cm)	80.5	5.4	78.3	4.0	78.8	3.3
Initial Mass (kg)	2.8	0.5	2.6	0.3	2.6	0.3
Initial condition factor (*K*)	1.0	0.1	0.9	0.0	0.9	0.0
Age at capture (DPH)*	369	28.8	424	28.6	411	23.4
Days in captivity	149	14.8	95	22.2	108	18.4
Final FL (cm)	111.2[a]	1.6	92.3[b]	6.2	96.7	5.2
Final TL (cm)	130.2	7.4	109.4	7.3	114.2	6.3
Final mass (kg)	14.9[a]	0.2	8.1[b]	1.4	9.7	1.3
Final condition factor (*K*)	1.1	0.1	1.0	0.0	1.0	0.0
GSI (%)	0.6[a]	0.1	3.5[b]	0.4	2.8	0.5
HSI (%)	1.1[a]	0.1	2.1[b]	0.1	1.9	0.2
VSI (%)	4.6[a]	0.3	8.8[b]	0.6	7.8	0.7
SGR (cm) (%)	0.4	0.1	0.3	0.1	0.3	0.0
SGR (g) (%)	1.2	0.3	1.4	0.2	1.3	0.1
AGR (cm day^{-1})	0.3	0.1	0.2	0.0	0.3	0.0
AGR (g day^{-1})	83.2	12.8	58.4	4.7	64.1	5.3
RGR (cm) (%)	71.2	11.8	43.2	10.6	49.7	9.0
RGR (g) (%)	471.9	120.3	268.8	67.7	315.6	61.8
FCR (w:w)	6.2	1.4	7.6	0.8	7.3	0.7
FCR (d:w)	1.6	0.4	2.0	0.2	1.9	0.2

3. Prophylaxis, initial feeding, and transfer to maturation tanks

Prophylactic techniques were utilized to limit the introduction of pathogens to the captive environment. Mahi-mahi are susceptible to a number of different parasites (Palko et al., 1982; Williams Jr. and Bunkley-Williams, 2009) and diseases (Leamaster and Ostrowski, 1988), which have the potential to spread rapidly under captive conditions. Prevention of outbreaks begins with strict biosecurity measures and prophylactic treatment of incoming wild fish. Using

protocols similar to those described by Benetti and Feeley (1999) and Benetti et al. (2008), a Formalin (37% Formaldehyde solution) treatment was administered to the wild mahi-mahi in a 15 m^3 quarantine tank at a dose of 100 ppm for 1 h within 12 h of introduction to the tank. In rare cases when fish showed signs of significant craniofacial injury and/or external epidermal damage, oxytetracycline HCl treatment was administered as bath treatments on 5–7 consecutive days at a dose of 50 mg L^{-1}. Freshly thawed squid (*Loligo opalescens*) and sardines (*Sardinella aurita*) were provided to the fish beginning on the day after capture. Typically, only ~10% of fish ate in captivity on the first day yet by 3–5 days later all healthy fish would readily consume the provided food. Those fish which did not eat usually showed signs of significant ocular trauma due to poor hook placement. Survival from the time fish were introduced to land-based tanks to the time at which all fish were actively feeding and ready to be transferred to maturation tanks averaged 80%. Prior to transfer to the maturation tanks, the quarantine tank was lowered to a water depth of 30–40 cm and clove oil (Spices USA, Inc., Medley, Florida, USA) was added at a treatment dose of 5–8 ppm to lightly anesthetize the fish. To aid in the mixing of clove oil within the treatment tank the clove oil was initially emulsified by vigorous agitation in a small volume of seawater until the solution turned milky white prior to addition of the emulsified oil solution to the tank water. Following a period of 15–20 min the mahi-mahi began to exhibit reduced swim velocity and mild disorientation resulting from the anesthesia. The anesthetized fish were placed in the previously described transport sling, and then the fish and sling were submerged in a freshwater bath as buckets of freshwater were added to the sling to provide a freshwater bath treatment of ~5 min for each fish. Freshwater treatment is commonly used for treatment of ectoparasites of marine fish, and at this stage of the fish transfer a full external examination was performed to allow for manual removal of any remaining lice and/or large parasites. Following this process fish were weighed, measured, tagged (Pentair Aquatic Eco-Systems, Inc.® fish tags model FTN100, Apopka, Florida, USA), and subsequently released from the transport sling into the broodstock maturation tank. Sizes of broodstock maturation tanks ranged from 30 m^3 (4.57 m diameter × 1.83 m depth) to 80 m^3 (7.62 m diameter × 1.83 m depth).

4. Maturation tank recirculating aquaculture system (RAS)

The maturation tanks used for maintaining and spawning mahi-mahi are similar in design to those described previously for use with other species such as cobia (Benetti et al., 2008, 2007; Stieglitz et al., 2012) (Fig. 2). The tank systems range in size from 30 to 80 m^3, with RAS components sized appropriately for each respective system.

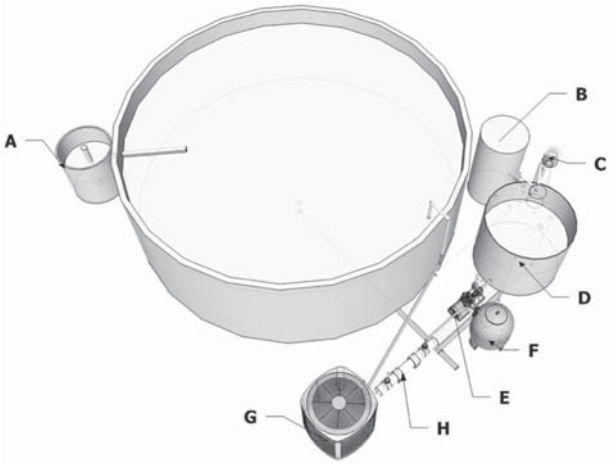

Fig. 2. Diagram of mahi-mahi maturation tank recirculating aquaculture system (RAS). System components: (A) egg collector; (B) biofilter; (C) foam fractionator; (D) sump; (E) pump; (F) sand filter; (G) heater/chiller; (H) UV sterilizer.

Biomass densities in each system are maintained proportionately to tank volume and are typically maintained at a level < 0.8 kg m^{-3}. As detailed in Fig. 2, components of the RAS maturation system include a centrifugal pump, mechanical filtration using broken glass media, UV sterilizer, heater/chiller unit, moving bed biofilter, foam fractionator, and egg collector. Using these systems allows for full control of the water chemistry and temperature parameters while reducing use of new seawater (~10–15% new seawater added per day). Fish are initially stocked at a density of 0.2 kg m^{-3} and biomass within the tanks never exceeds 0.8 kg m^{-3} over the course of maintaining broodstock fish in the RAS systems.

5. Spawning

Given the aggressive nature of sexually mature male, or "bull", mahi-mahi against other fish, primarily other males, the broodstock maturation systems are stocked at a sex ratio of 1 male to a group of females (3–10 individuals). While captured and stocked fish were all sexually mature, the characteristic blunt head shape associated with mature male mahi-mahi was not always obvious at the time of stocking. This resulted in occasionally and unknowingly stocking multiple males in a tank. Evidence of such occurrences came with the subsequent killing of any additional male fish by the dominant bull mahi-mahi within days of initial tank stocking. Whether males lacking prominent secondary sexual characteristics ("sneaker males") are capable of reproductive success in the wild even in presence of the larger bourgeois males is unknown. Such alternative reproductive strategies amongst male fishes is common in nature (Taborsky, 2001), yet this is the first time evidence suggesting this strategy amongst mahi-mahi has been described. In the wild, larger and older mahi-mahi are known to school in harems comprised of a single large male and multiple females yet schools of young adult mahi-mahi may be comprised of multiple sexually mature males and numerous mature females. This grouping pattern may favor the sneaker males in the young adult stages, whereby it is easier for them to blend into the school of fish, similar to the way in which sneaker males blend into the harem of females commonly found in nest building fish species.

Newly stocked mahi-mahi typically spawn the first evening post capture likely as a result of the stress from capture and handling. This can be explained by the fact that corticosteroids act on the hypothalamic-pituitary-gonadal axis and the cortisol surge associated with capture and transport likely triggers ovulation and spawning in the fish (Billard et al., 1981). The quality of this initial "stress-spawn" is generally poor, with low fertilization rates and high prevalence of sinking eggs. Initiation of regular spawning activity occurs on average 11 days post capture, provided that fish are eating well, water temperatures are maintained at an average of 26–27 °C, and the fish are in good health following handling and prophylaxis. Mahi are gonochoristic batch spawners, with spawning activity taking place in warm waters (≥ 24 °C) throughout their distribution range (Oxenford, 1999; Palko et al., 1982). Given that mahi-mahi are known to spawn in areas of warm offshore water temperatures (Palko et al., 1982) the water temperatures in the RAS maturation systems were maintained between 26 and 27 °C throughout the year in order to maintain spawning of this species in captivity on a year-round basis. Captive female mahi can spawn every other day, when provided adequate nutrition and environmental conditions, whereas male mahi have the ability to spawn on consecutive nights on a continuous basis. There appears to be (de)synchronization of female spawning by different individuals spawning on opposing days as spawning events took place in each maturation tank every day, if there were multiple females in the tank.

Over the course of this study, mahi spawned in water temperatures as low as 19 °C and as high as 31 °C, though the average spawning temperature was 26.7 °C. Spawning events typically occurred approximately 2–5 h before sunrise under average spawning water tempera-

tures, while cooler and warmer water temperatures appeared to result in earlier and later spawning times, respectively (personal observation). A similar connection between spawning time and water temperature has been reported for captive yellowfin tuna (*Thunnus albacares*) broodstock (Margulies et al., 2007) and may be indicative of a life history strategy employed by tropical and sub-tropical pelagic spawning teleosts. Such a strategy may exploit advantages associated with a narrow range of hatching times at dusk, especially considering the onset of negative buoyancy in the embryos of mahi-mahi (Stieglitz et al., 2016a) and yellowfin tuna (Margulies et al., 2007) during the hours leading up to hatch. Advantages of consistent timing of the onset of negative buoyancy and hatching may include reduction of yolk-sac larvae exposure to sea surface UV radiation, reduced levels of predation at depth, and improved first-feeding success. Given the observations of spawning time variation and water temperature, this topic warrants further research to determine the exact correlation between these events, as well as the mechanisms leading to their occurrence.

6. Feeding and growth

The ages of fish at time of capture were estimated using age at length data based on von Bertalanffy growth parameters (L_∞ and K) for the Florida Straits region (Beardsley, 1967; Chang and Maunder, 2012) and the t_0 estimate from Benetti et al. (1995). Following capture, the number of days fish lived in captivity was tracked and fish typically survived in captivity for an extended period of time (Table 1). In instances where euthanasia was necessary the fish were first anesthetized using a light dose of clove oil, as previously described for tank transfer procedures, and then upon removal from the tank a lethal overdose of Tricaine-S (tricaine methanesulfonate, Western Chemical, Inc., Ferndale, Washington, USA) was applied to the gills of the anesthetized fish. On average, males lived longer in captivity than females, which can largely be attributed to male aggression. In addition, males grew faster than females in captivity. Causes for this likely include the fact that female mahi can and will, provided sufficient energetic inputs, spawn every other day in captivity releasing ~5% of their bodyweight per spawning event (Kraul, 1989). Fish were fed to satiation every day a diet of whole and chopped sardines (*Sardinella aurita*) and squid (*Loligo opalescens*) (Table 2). Fish were also fed a dietary supplement primarily comprised of *MadMac-MS* (Aquafauna Bio-Marine, Inc., Hawthorne, CA, 90250, USA) once per week at a dose of 10% of food weight for the day and vitamin capsules were included in the diet once per week at a dose of 1% of food weight for the day (Table 3). Feed rates in captive fish in the first few weeks post capture averaged 12% tank biomass per day and decreased to 5% tank biomass per day by the end of time in captivity as fish grew larger. Feed intake was calculated based on the mass of food fed to the fish in the tank. In rare cases where all food was not consumed by the fish during a feeding event, the leftover food was immediately removed from the tank, weighed, and subtracted from the feeding data. Fish were observed during feeding events to make sure food intake was relatively equal between individuals. All fish appeared to consume equal amounts of food during feeding events regardless of gender. Specific growth rate (SGR), absolute growth rate (AGR), and relative growth rate (RGR) were calculated for individual genders as well as cumulatively using methodology described in Benetti et al. (1995) (Table 1). Additionally, food conversion ratios (FCRs) were calculated in two ways, the first using the moisture level of the feed and the weight gained by the fish (w:w) and the second using the assumed dry weight of the feed and weight gained by the fish (d:w) (Tables 1 and 2). Differences in mean growth metrics and FCRs between male and female broodstock fish (Table 1) were analyzed statistically using parametric *t*-tests and differences in growth rates (Fig. 3) were analyzed using analysis of covariance (ANCOVA) following log transformation of data (XLSTAT; Ver 18.06; Addinsoft). In all statistical analyses values were considered statistically different at $p < 0.05$. Over the course of this study, males grew significantly faster than females (ANCOVA: $p < 0.0001$)(Fig. 3). This trend also appears to hold true in nature, whereby "bull" mahi grow faster and are larger at age than their female counterparts (Palko et al., 1982). In order to gain insight on the condition of wild fish at the time of capture and at the end of the study period, condition factor (K) was calculated at the beginning and end of the trial using the equation $K = (W^*10^3)/L^3$ where W equals the weight of fish (kg) and L equals the fish fork length (cm) (Table 1). There was no significant change in condition factor between newly captured fish and those which had been in captivity for an extended period of time. Furthermore, gonadosomatic index (GSI), hepatosomatic index (HSI), and visceral somatic index (VSI) were calculated by dividing the weight of the described organ(s) (gonad, liver, or visceral mass) by the weight of the fish and multiplying by 100 (Table 1). Absolute and relative growth rates of captive mahi in this study were higher than those reported in Benetti et al. (1995), while specific growth rate was less. Such differences are likely due to the older age and larger size of the fish used in this study, and the fact that SGR decreases with age and size in fish.

Table 2
Proximate analysis of broodstock diet.

Food type	Water (%)	Ash (%)	Protein (%)	Lipid (%)	Calories gram^{-1}
Spanish sardines (*Sardinella aurita*)	68.8	3.58	17	9.83	1900
Pacific squid (*Loligo opalescens*)	79.4	2.01	17.5	0.37	1060

7. Conclusions

Mahi-mahi are known to have high energetic requirements that are necessary to maintain their "high-performance" lifestyle (Brill, 1996), and the data presented in this study supports previous bioenergetics research indicating mahi-mahi are efficient in their use of ingested energy (Benetti, 1992). This efficiency is particularly evident when this species is compared to other highly active large sub-tropical pelagic teleosts maintained in captivity, notably tuna. Efficiency can be measured in a number of ways, but in aquaculture a species' FCR is the most commonly used metric. Captive yellowfin tuna have a wet weight FCR ranging from 10.9:1 (Wexler et al., 2003) to 37.2:1 (Estess et al., 2017) and captive Pacific bluefin tuna (*Thunnus orientalis*) have wet weight FCRs ranging from 17.8:1 to 22.6:1 (Estess et al., 2014) when fed similar diets (squid, sardines, vitamin/mineral supplements) to those utilized for the captive mahi-mahi in this study. Such FCRs exceed those documented for mahi-mahi in this study (6.2:1 to 7.6:1), and it is important to note that the mahi FCR data was obtained under a period of continuous spawning which would theoretically increase the FCR due to the amount of ingested energy allocated to spawning (Kraul, 1989). The efficiency found in mahi-mahi is the result of species-specific physiological and anatomical traits (Benetti, 1992; Brill, 1996; Stieglitz et al., 2016b) and intuitively the greater energetic cost associated with maintaining endothermic metabolism in the aforementioned tuna species leads to higher FCRs compared to mahi-mahi. Therefore, while it is true that a number of sub-tropical marine pelagic species with active lifestyles exhibit "high performance" traits in terms of their growth, swimming speed, and digestion (Brill, 1996), it appears that the mahi-mahi may represent the most efficient combination of growth, food conversion, and spawning frequency of those species examined to date. The year-round spawning of mahi-mahi described in this study requires a high turnover rate of ingested energy to spawned biomass, and therefore maintaining adequate broodstock nutrition is one of the most critical aspects of developing a year-round spawning stock of this species in captivity. Further examination of egg quality

Table 3
Composition of broodstock diet supplements.

Food supplement	Water (%)	*MadMac-MS* product (%)	*Vitamin Pre-Mix* product (%)	Taurine (%)	Lecithin (%)	Astaxanthin (%)
Dietary supplement: *MadMac-MS* UMEH custom mix	50	44.6	2.3	2.7	0.25	0.15
Vitamins (1 g gelatin capsules)	–	–	85	–	10	5

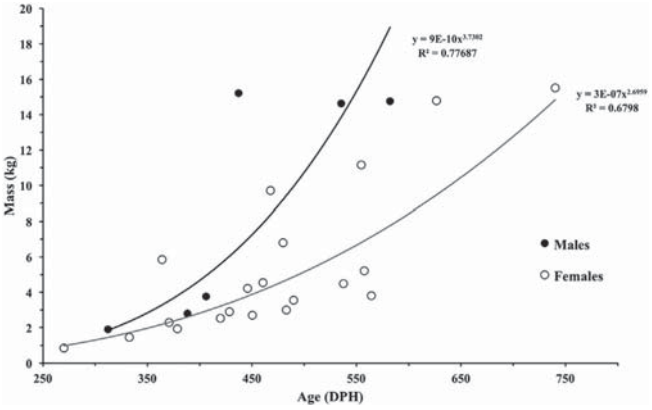

Fig. 3. Growth of broodstock over time in captivity. Male broodstock grew significantly faster than female broodstock (ANCOVA: $p < 0.0001$). DPH = days-post-hatch.

over time may reveal novel insights on this topic and would help inform broodstock management strategies for maintaining peak reproductive performance in this species in captivity.

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