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Nutritional physiology of mahi-mahi (*Coryphaena hippurus*): Postprandial metabolic response to different diets and metabolic impacts on swim performance

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ABSTRACT

Migratory pelagic fish species, such as the mahi-mahi (*Coryphaena hippurus*), must balance numerous metabolic demands simultaneously in order to survive in a challenging oceanic environment. Energetic support for such demands comes from a variety of natural prey items in the wild and can come from manufactured pelletized feed in captivity. This study quantified postprandial metabolism, commonly referred to as specific dynamic action (SDA), over time in adult mahi-mahi (706 ± 25 g; 38 ± 0.7 cm FL) in response to satiation feeding using three different natural and manufactured diets. Results indicate that during satiation feeding the amount of food ingested is dictated by energy content rather than prey mass, regardless of moisture content of the diet. Ingested meal energy did not differ significantly across groups (473 ± 45 kJ), nor did the duration of SDA (36 ± 2.1 h). Satiation feeding levels ranged from 2.9–16.2% bodyweight depending on the diet. Peak SDA and SDA magnitude were both significantly decreased in response to dry pelletized diet compared to the natural forage diets, despite equivalent energy consumption. Swim performance and maximum metabolic rate were not impacted significantly in satiation fed fish compared to unfed fish, supporting the evidence that mahi-mahi are able to maintain multiple metabolic demands at one time without compromising performance.

1. Introduction

One of the keys to understanding the bioenergetics of different organisms is examining the metabolic costs of different routine activities. For fish, such activities include swimming, digestion, reproduction, and the costs associated with maintaining homeostasis in variable environmental conditions. Species specific differences in the metabolic costs of these different activities can confound interspecies comparisons complicating identification of commonalities between species. For this reason, it is important to quantify metabolism under controlled conditions, limiting factors that could contribute to variation in metabolic findings. In particular, the postprandial metabolic cost, commonly referred to as specific dynamic action (SDA), is a metric of interest that has historically garnered significant attention (Chabot et al., 2016; Jobling, 1981; Secor, 2009). The SDA response has been documented in a diverse number of vertebrate and invertebrate species primarily because this aspect of metabolism is important to understanding the overall bioenergetics of species. SDA is dependent on a number of known factors including primarily animal size, environmental conditions, meal composition, and meal quantity (Chabot et al., 2016; Jobling, 1981; Secor, 2009). In fish species, in addition to understanding the basic physiology of the organism, quantifying SDA is a useful metric of overall animal function for studies related to resource management, aquaculture, environmental toxicology, and nutrition. In these disciplines SDA is used to note the impacts of different diets and environmental conditions on overall bioenergetics of a species. While understanding basic metabolic responses, such as SDA, for each species when attempting to construct bioenergetics models is important; for many fish species bioenergetics models use generalized values for SDA which can lead to imprecise predictions. Similarly, lack of knowledge regarding the species- and diet-specific postprandial metabolic costs invariably lead to inadequate design of life support systems, feeding regimes, and waste water treatment in aquaculture and should be considered during the design, construction, and operation of aquaculture systems.

Additionally, there are key differences in how fish metabolize different diets, though traditionally most reports of postprandial metabolism in any given species utilize only one type of diet for each experiment. Differences in protein:energy ratios, moisture content, and other aspects of diet composition are known to differentially affect the

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postprandial response in some species (Jobling, 1981; Secor, 2009). However, for many species the effects of such variation in diet on whole-animal physiology and metabolism have not been quantified. This is particularly true for species that are difficult to maintain in captive environments, such as adult specimens of the carnivorous pelagic species the mahi-mahi (*Coryphaena hippurus*). As a globally distributed species of high economic and ecological value, this fish has also been used as a model organism for documenting the effects of adverse environmental impact events such as oil spills (Esbaugh et al., 2016; Mager et al., 2014; Pasparakis et al., 2016; Stieglitz et al., 2016b, 2016a) and climate change (Bignami et al., 2014) in the subtropical and tropical pelagic oceans. Identifying and quantifying the different factors that impact metabolic function in this species can reveal new information on whole-animal physiological impacts of environmental perturbations. While metabolic rates and the SDA response have been quantified on a limited basis in juveniles (9.8–17.1 g) of this species (Benetti, 1992) the SDA response of adult of mahi-mahi is unknown. Mahi-mahi is known to have one of the fastest growth rates of any of the teleosts, is extremely fecund, and is highly migratory (Benetti et al., 1995; Merten et al., 2014a, 2014b; Palko et al., 1982). Balancing these multiple metabolic demands surely requires rapid and efficient cycling of metabolic substrates likely requiring significant energy inputs (Brill, 1996). Being ram ventilators, mahi-mahi are in constant motion which potentially results in overlap between the metabolic costs of digestion and swimming. Swim performance and the scope for activity have been shown to be compromised in some fish species as a result of postprandial metabolism (Alsop and Wood, 1997; Jobling, 1981; Muir and Niimi, 1972), yet such interactions have yet to be examined in adult mahi-mahi. In order to test these different aspects of metabolic states and nutritional physiology in mahi-mahi adults were fed different diets, both natural and manufactured, and the SDA response was quantified. To investigate possible metabolic compromise caused by multiple metabolic stimuli fed and unfed fish were subjected to swim performance testing to identify compromise in metabolic endpoints resulting from the costs associated with postprandial metabolism.

2. Materials and methods

2.1. Experimental animals

The mahi-mahi used in this study were obtained from the University of Miami Experimental Hatchery (UMEH), and were the offspring of captive wild broodstock fish caught off the Atlantic coast of Miami, Florida, USA (Stieglitz et al., 2017). All fish used in the following studies were from the same cohort and all experienced the same rearing conditions. Prior to use fish were regularly fed rations of both squid, sardines, and a formulated dry pelletized diet (Table 1). All animals and experimental procedures described in this study were in accordance with the University of Miami Institutional Animal Care and Use Committee (IACUC) protocol numbers 15–019 and 15–067.

Table 1
Proximate analysis of diets. *Assumed digestible protein (DP) of 85% and digestible energy (DE) of 90%.

Diet type (*as fed*)	Squid (*Loligo opalescens*)	Sardines (*Sardinella aurita*)	Skretting Europa (*9.0 mm pellet*)
Protein (%)	17.5	17.0	45.4
Lipid (%)	0.4	9.8	20.8
Ash (%)	2.0	3.6	9.6
Moisture (%)	79.4	68.8	9.1
Energy (MJ kg^{-1} diet)	4.4	8.0	21.8
DP:DE Ratio*	37.2	20.2	19.7

2.2. Feeding

Mahi-mahi were individually placed in isolated tanks (1 m^3 volume) approximately one – two weeks prior to use to allow for accurate quantification of natural feeding behavior without competition or aggression from other fish. Fish were fed to satiation on a daily basis. Prior to use in respirometry trials, fish were fasted for a minimum of 48 h. For SDA studies, fish were fed to satiation using either chopped squid (*Loligo opalescens*), chopped sardines (*Sardinella aurita*), or a pelletized diet (Europa 9.0 mm, Skretting, Tooele, Utah, USA) (Table 1). Feeding stopped when the animal reached satiation, defined as the point at which fish stopped showing interest in the provided feed. Fish were maintained undisturbed for a period of 25 min after reaching satiation to reduce incidence of regurgitation during the transfer process. After the 25-minute period, fish were carefully removed from the tank, placed in a sterilized seawater filled oxygenated transport bucket, and transported in ~5 min to the swim chamber respirometer. From completion of feeding to the point at which oxygen consumption measurements were commenced was ~30 min. Any uneaten or regurgitated feed in the feeding tank or transport bucket was collected, weighed, and subtracted from the total amount of feed initially provided to the fish during feeding. In the case of the pelletized diet, the number of uneaten or regurgitated pellets was quantified and weight was calculated by multiplying the known mean mass of each pellet by the number of pellets collected to eliminate bias introduced by using the hydrated weight of the uneaten or regurgitated pellets.

2.3. Swim chamber respirometry

Two 90-L Brett-type swim chamber respirometers (Loligo Systems ApS) were used in this study, supplied with UV-sterilized temperature-controlled seawater. Control of the intermittent respirometry trials (20-minute measurement loops) was provided AutoResp™ 2.1.0 Software (Loligo Systems ApS). Oxygen consumption (MO_2) was measured using Pt100 fiber-optic probes and Fibox 3 minisensor oxygen meters (PreSens Precision Sensing). Details on methods of calibration and operation of the swim chamber respirometers are presented in Stieglitz et al. (2016b). Since mahi-mahi are ram ventilators, a constant swim speed of ~1 BL s^{-1} was maintained in the swim chamber over the course of the respirometry trials. Initial attempts to feed mahi-mahi within the swim chamber respirometer were unsuccessful, requiring the aforementioned feeding and measurement methodology. To determine the point at which the animal was acclimated to the swim chamber (no longer showed oxygen consumption resulting from handling stress at ~1 BL s^{-1}) a subsample of unfed fish were tested using the same isolation and transfer methodology described in 'Feeding' section. This time point, determined to be ~4 h for this size class of fish, was used to initiate the data analyses and any SDA derived oxygen consumption leading up to this point was assumed to increase linearly from time '0 h.', as described in other studies of teleost fish SDA (Chabot et al., 2016).

To investigate the interaction between feeding and swimming metabolism, individual fish from the same cohort were fed to satiation on a dry pelletized diet in the same manner as described in the 'Feeding' section and subsequently transferred to one of the swim chamber respirometers for swim performance testing. For comparison purposes, swim performance testing of unfed fish was also completed. In both fed and unfed treatment groups, fish were randomly placed into one of the two swim chamber respirometers used in this study. Following the acclimation period, previously determined to be ~4 h, a U_{crit} swim performance test was used to assess swim performance of the fed or unfed fish following methodology that has previously been described in detail in Stieglitz et al. (2016b). In summary, 20-minute measurement loops were used with 0.5 BL s^{-1} speed increments until fatigue was reached. The point of fatigue was defined as the time at which fish were either unable to move off of the rear grate of the working section of the swim

chamber due to the water velocity or where gait transitioned from steady high speed swimming to erratic burst and glide swimming with frequent touching of the back grate. The time spent swimming at the final speed T (seconds), along with the time interval for each loop t (seconds), the increment in swim speed dU (cm per second), and the highest swim velocity maintained for a full interval U_f (cm per second) were all used to calculate U_{crit}, reported in BL s^{-1}, using the following equation described by Brett (1964):

$$U_{crit} = [U_f + (T/t)dU]/\text{cm fork length}.$$

2.4. Data analysis

Prior to calculation of SDA variables, criteria for determining completion of digestion were established. Digestion was determined to be complete when two criteria were met: (a) when MO_2 measurements plotted over time plateaued at a reduced level within one standard deviation of the mean of the lowest 2 h period, considered the RMR of the fish at 1 BL s^{-1} as described above, and (b) when the slope of the line plotting MO_2 over time in the aforementioned 20 min measurement loops beginning at this 2 h period was not negative. Calculation of SDA variables: peak SDA (SDA_{peak}), time to SDA_{peak}, magnitude of SDA (SDA_{mag}), and the duration of SDA (SDA_{dur}) were determined by fitting a nonparametric quantile regression function to the data using the R script provided by Chabot et al. (2016). This included the R-package *quantreg* (Koenker, 2017) that provides the *rqss* function, where values of tau (τ), the penalty parameter (λ), and the tolerance value were set at 0.2, 30, and 2%, respectively, using R (*R Core Team,* 2017). Given the elevated oxygen consumption associated with recovery from handling and fish acclimation to the swim chambers, the first 4 h of MO_2 data following introduction to the chambers were eliminated from the portion of data to which the curve was fit. As described by Chabot et al. (2016), during this period postprandial metabolism, and hence the fit of the curve, is assumed to increase linearly. Unless otherwise specified, statistical differences between variables reported in this portion of the study were completed using analysis of variance (ANOVA) (XLSTAT; Ver 19.03; Addinsoft), with specific differences between means of individual groups tested using Tukey's HSD. In all statistical analyses, values were considered significantly different at $p < 0.05$. In the comparison of swim performance and oxygen consumption endpoints in fed versus unfed fish the statistical analyses used to compare mean values were either student's *t*-tests, when parametric statistical methods were appropriate, or Mann Whitney *U* tests when differences in sample sizes required the use of nonparametric statistics (XLSTAT; Ver 19.03; Addinsoft). Standard metabolic rate (SMR), routine metabolic rate (RMR), maximum metabolic rate (MMR), aerobic scope (AS), and cost of transport (COT) were calculated for fish used in the swim performance portion of this study following methodology detailed in Stieglitz et al. (2016b), whereby MO_2 data from U_{crit} tests were log transformed and plotted versus swim speed and a linear regression was fitted to the data to allow for determination of SMR (y-intercept) and MMR (extrapolated MO_2 value at U_{crit}), as well as the difference between these two variables which is AS. Only regressions with an r^2 value ≥ 0.7 were used for calculation of metabolic rate data. These data (SMR, MMR, and AS) were then scaled to a standard mass of 750 g using allometric scaling coefficients developed from the unfed fish used in the swim performance (U_{crit}) testing of this study ('*Supplementary Data*'), and statistical differences between treatment groups were analyzed using student's *t*-test. Mean values of fish mass and water temperature were compared statistically between treatment groups in order to note any potential differences between such parameters in the portion of the study that did not involve swim performance (U_{crit}) testing. COT data analysis consisted of dividing U_{crit} test MO_2 values by swimming velocity at each increment and fitting a second order ($k = 2$) polynomial regression model to the data. This model also allowed for calculation of optimal swim speed (U_{opt}) by fitting the first derivative of the polynomial regression model to zero (Palstra et al., 2008), and only individuals with model regression r^2 values ≥ 0.5 were used for COT analysis. Unless otherwise specified, all values reported in this study are represented as mean ± SEM. Proximate analyses (Midwest Laboratories, Inc., Omaha, Nebraska, USA) of diets used in this study were completed to determine the protein, lipid, ash, moisture, and energy content of each diet. SDA coefficients were calculated by dividing SDA by meal energy.

Table 2
Overview of postprandial metabolism responses for different diet treatment groups. [1]Factorial scope was calculated using the standard metabolic rate (SMR) obtained from unfed fish in the swim performance portion of the study. Values with different letter notations within the same row are significantly different from each other.

	Squid (*Loligo opalescens*)		Sardines (*Sardinella aurita*)		Skretting Europa (*9.0 mm pellet*)	
	Mean	SE	Mean	SE	Mean	SE
n	8		8		10	
Consumption (% bw)	16.2[a]	1.2	10.9[b]	1.2	2.9[c]	0.4
Total meal energy (kJ)	467.9[a]	44.9	514.5[a]	54.9	445.1[a]	73.8
Peak SDA ($mg\ O_2\ kg^{-1}\ h^{-1}$)	407[a]	47.8	339[a]	65.0	138[b]	20.1
Factorial scope[1]	2.0[a]	0.2	1.7[a]	0.3	0.7[b]	0.1
SDA duration (hrs)	37.0[a]	2.7	35.2[a]	4.0	35.6[a]	2.4
SDA magnitude ($mg\ O_2\ kg^{-1}$)	5799[a]	1249.3	5697[a]	1249.3	2265[b]	319.8
SDA coefficient (%)	11.5[a]	1.2	9.0[a]	1.5	7.3[a]	2.1

3. Results

3.1. Postprandial metabolism over time

The proximate analyses of the diets used in this portion of the study revealed notable differences in composition between each diet (Table 1). Across the three different diet treatments there was no significant difference in the size of the fish (658 ± 26 g; 36.5 ± 0.9 cm FL) or the water temperatures during the testing (26.3 ± 0.04°C) ($p > 0.05$). However, there were significant differences (ANOVA: $F(2,23) = 51.536$, $p < 0.0001$) in the amount of food consumed by each group indicating differences in the amount of diet required for reaching satiation (Table 2). Also, the factorial scope was significantly less in the pellet diet treatment group compared to the other diets (ANOVA: $F(2,23) = 10.316$, $p = 0.001$; Tukey's HSD post hoc test: $p < 0.01$), as was the SDA_{mag} (ANOVA: $F(2,23) = 6.707$, $p = 0.005$; Tukey's HSD post hoc test: $p < 0.05$), and the SDA_{peak} (ANOVA: $F(2,23) = 10.316$, $p = 0.001$; Tukey's HSD post hoc test: $p < 0.01$) (Table 2). Ingested meal energy did not differ significantly across groups (473 ± 45 kJ), nor did the duration of SDA (36 ± 2.1 h), or the SDA coefficient of the diets (9 ± 1.3%) ($p > 0.05$) (Table 2). In all cases, the *rqss* analytical method described previously appeared to model the postprandial metabolic response well, with representative data sets for each diet treatment group presented in Fig. 1. The typical pattern of postprandial metabolism for each diet treatment group revealed an SDA_{peak} occurring at the 4 h mark, and this likely represents a conservative estimate of SDA_{peak} in this species since the peak may in fact occur earlier in the postprandial period during which time the fish is acclimating to the swim chamber (See 'Materials and Methods section – Data Analysis; Fig. 1). While there were no significant differences in SDA coefficients between diet types it appears that both of these variables, SDA coefficient and diet type, provide significant information to explain the variability in the SDA_{mag} response, with SDA coefficient being the most influential of the two ($p < 0.05$, ANCOVA)(Fig. 2).

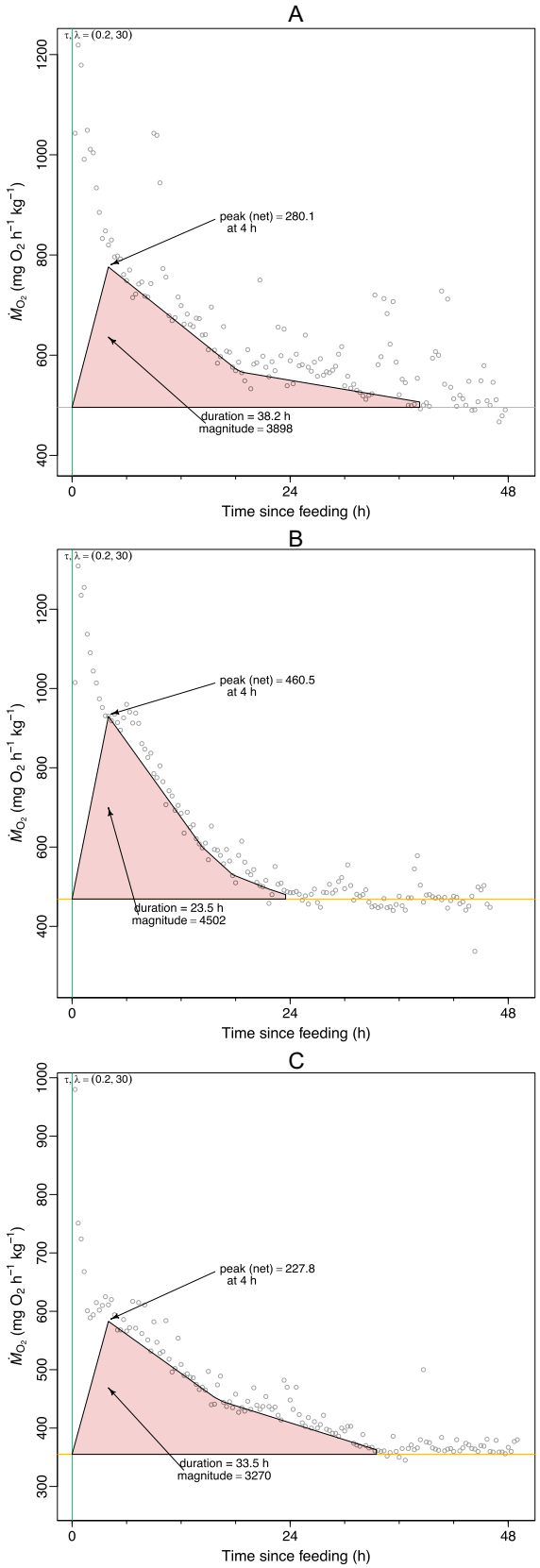

Fig. 1. Representative plots of postprandial metabolism over time in each respective treatment: (A) sardine diet: 330 kJ meal energy; (B) squid diet: 278 kJ meal energy; (C) Skretting pellet diet: 259 kJ meal energy.

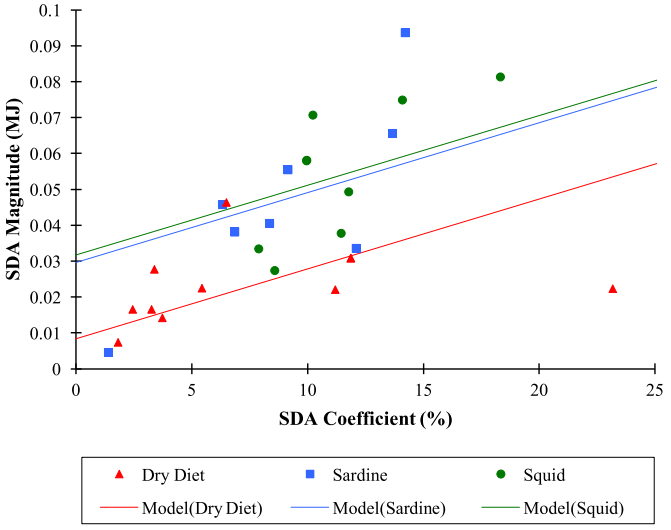

Fig. 2. Regression of SDA magnitude (SDA_{mag}) by SDA coefficient ($r^2 = 0.534$). The analysis of covariance (ANCOVA) model illustrates the impact of diet treatment and SDA coefficient on SDA magnitude (SDA_{mag}), with SDA coefficient being the most influential variable explaining SDA_{mag}.

3.2. *Effects of postprandial metabolism on swim performance and metabolic endpoints*

There was no significant difference in the size of fish (786 ± 45 g; 40.3 ± 0.7 cm FL), the water temperatures during swim performance testing (26.4 ± 0.04°C), the aerobic swim performance (U_{crit}) and optimal swim speed (U_{opt}) of the fish, the maximum metabolic rate (MMR) of the fish, or the COT_{Ucrit} between the fed and unfed groups of fish ($p > 0.05$). However, the COT_{min} of the fed group of fish was significantly higher than that of the unfed group ($p < 0.05$) (Table 3). Both fed and unfed fish were acclimated to the swim chamber at a swimming speed of 1 BL s^{-1} and once acclimated the metabolic rate was used to represent RMR (Table 3; Fig. 3). Given that mahi-mahi are ram ventilators, the RMR at low water velocity (~1 BL s^{-1} swim speed) is analogous to the SMR of fish species which are more sedentary and rest relatively motionless on the bottom of swim chamber respirometers at low velocity. Comparison of the factorial aerobic scope, defined in this case as the MMR divided by RMR, between fed and unfed fish in the swim performance study revealed a significant decrease in this parameter in the fed fish (2.01 ± 0.16) compared to the unfed fish (3.45 ± 0.30) ($p < 0.05$) (Table 3). With MMR between treatments being effectively equal, this difference in factorial aerobic

Table 3
Comparison of swim performance, metabolic endpoints, and cost of transport between fed and unfed fish in the swim testing portion of the study. Values with different letter notations within the same row are significantly different from each other.

	Unfed Fish		Fed Fish	
	Mean	SE	Mean	SE
n	8		8	
Consumption (% bw)	–	–	3.2	0.4
Total meal energy (kJ)	–	–	492.7	79.2
SMR (mg O_2 kg^{-1} h^{-1})	204.5	12.2	–	–
RMR (mg O_2 kg^{-1} h^{-1})	398.1[a]	23.5	640.8 [b]	34.5
MMR (mg O_2 kg^{-1} h^{-1})	1324.4[a]	49.3	1265.5[a]	75.4
Aerobic scope (mg O_2 kg^{-1} h^{-1})	1119.3	53.4	–	–
COT_{min} (mg O_2 kg^{-1} m^{-1})	0.24[a]	0.02	0.31[b]	0.02
COT_{Ucrit} (mg O_2 kg^{-1} m^{-1})	0.38[a]	0.03	0.38[a]	0.02
U_{crit} (BL s^{-1})	2.76[a]	0.13	2.67[a]	0.17
U_{opt} (BL s^{-1})	1.72[a]	0.08	2.06[a]	0.12
Factorial scope (MMR/RMR)	3.45[a]	0.30	2.01[b]	0.16

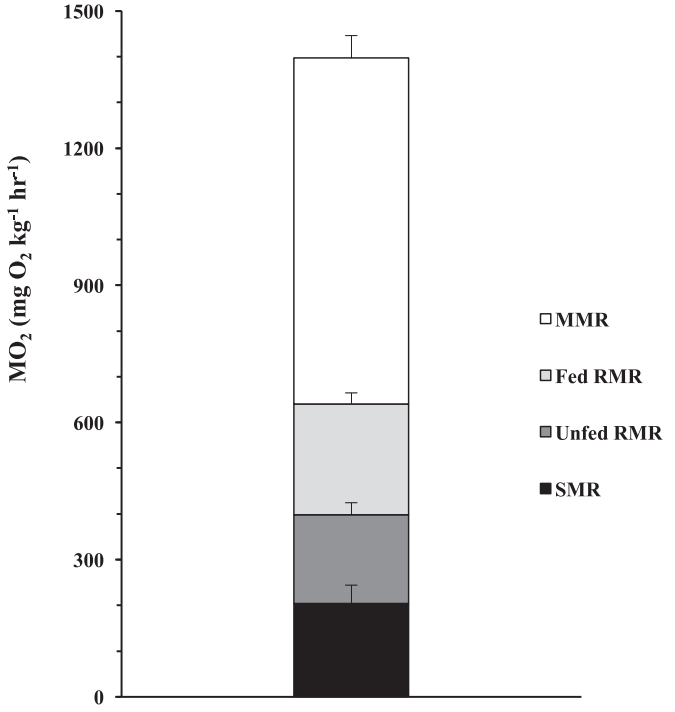

Fig. 3. Impact of specific dynamic action on routine metabolic rate (RMR) of acclimated steady swimming at 1 BL s^{-1}. When plotted together with the standard metabolic rate (SMR) and maximum metabolic rate (MMR) of unfed fish, the impacts of postprandial metabolism on the overall aerobic scope (MMR-SMR) available for other metabolic demands can be seen yet swim performance (U_{crit}) and MMR are not significantly reduced in fed fish compared to unfed fish ($p > 0.05$).

scope is due to the significantly increased RMR in the fed fish (640.8 ± 34.5 mg O_2 kg^{-1} h^{-1}) compared to the unfed fish (398.1 ± 23.5 mg O_2 kg^{-1} h^{-1}) (Fig. 3).

4. Discussion

The results from this study indicate that mahi-mahi have a robust digestive capacity, with an ability to consume and metabolize large quantities of food over a relatively short timeframe. While there were significant differences in the amount of food consumed to reach satiation depending on the diet type, the amount of energy consumed was nearly equivalent across diets. These results reveal an interesting pattern whereby satiation appears to be dictated by the energy consumed and not by the mass of the diet. This pattern is supported by the general idea that feed intake in fish is primarily influenced by dietary energy content of the feed (Houlihan et al., 2008). For instance, when comparing natural forage types mahi-mahi must consume almost 50% more squid to match the amount of energy derived from a satiation feeding of sardines. This is likely due to the low lipid levels found in the squid, and therefore lower overall energy on a per unit basis, compared to the sardines (Table 1). It appears that the fish fed up until a point of energetic satiation, and due to the higher energy content of the sardines this results in a reduced mass of sardines consumed compared to squid. This same concept of energy satiation directly relates to the results obtained with the pelletized dry diet. Due to the energy density of this diet very little was consumed to reach satiation, compared to the natural diets at energetic satiation equivalents. Satiation in fish is typically reached when stretch receptors in the lining of the stomach signal that fullness has been reached, though in cases of nutrient-rich low-moisture diets (i.e. manufactured pelletized diets), water imbibed for hydration of the meal can add to the bloating of the stomach and may result in reduced meal mass being consumed (Anderson, 2006). Typically these factors occur prior to the rise of nutrient levels in blood resulting from initial digestion, which would support the idea that stomach fullness and orogastric factors associated with feeding lead to satiation as opposed to circulating nutrient levels in the bloodstream (Anderson, 2006; Holmgren et al., 1983). However, a stretch mediated mechanism of satiation did not appear to be present in mahi-mahi, with results from this study indicating that caloric intake is the limiting factor in this species. Given the ability of this species to rapidly cycle metabolic substrates (Brill, 1996) the circulating nutrient levels in the bloodstream likely occur earlier in this species following initial feeding, supporting the notion that caloric ingestion is the satiation-inducing mechanism in mahi-mahi.

It was theorized that perhaps the consumption of the dry pelletized diet would lead to higher SDA_{mag} and SDA_{peak} due to the costs involved in hydrating this energy dense diet once ingested compared to diets with higher moisture contents that are more similar to natural prey items. However, from an energetic cost (i.e. SDA) standpoint this does not appear to be the case in mahi-mahi based on the results of this study. Contrary to dogma surrounding fish nutrition and physiology that suggest higher moisture content is associated with a reduced metabolic cost of digestion, the dry pelletized diet used in this study resulted in a significantly decreased SDA_{mag} and SDA_{peak} compared to the higher moisture containing natural diets. Anecdotally this difference persisted in a subset of fish that after being fed the pelletized diet exhibited notable distension of the abdomen following hydration of the diet (*personal observation*), which may have been exacerbated by bloating and subsequent constriction of the pyloric sphincter (Anderson, 2006). Some evidence of decreased digestibility of formulated diets compared to natural prey items has previously been reported (Jobling, 1986), thus the decreased SDA response could be indicative of a decreased digestibility and assimilation of this diet. However, the reduced response could result from very efficient processing of the diet if well formulated to be easily assimilated. Given that squid and sardines are regularly consumed by mahi-mahi in the wild, the results of this study reveal interesting information regarding the energetic costs associated with digesting these diet types. Additionally, differences in lipid composition between the two natural forage items used in this study likely impact the overall nutritional benefit obtained by the predator species, similar to results documented with yellowfin tuna (*Thunnus albacares*)(Klinger et al., 2016), Pacific bluefin tuna (*T. orientalis*)(Clark et al., 2010), and southern bluefin tuna (*T. maccoyii*) (Fitzgibbon and Seymour, 2009). Since compositional differences in diet types can lead to differences in SDA response, SDA coefficients are sometimes used for comparison purposes (Secor, 2009). In this study, statistical analysis (ANCOVA) revealed that the SDA coefficient of the diet provided significant information to explain the variability noted in SDA_{mag} response between diets (Fig. 2). Comparative analysis of SDA coefficients between diets for different fish species may allow for optimization of the nutritional physiology of such species thereby aiding in the development of economically and ecologically efficient diets for marine fish species.

SDA duration is an important variable to consider when optimizing feeding regimes in captivity and to understand feeding patterns of fish in the wild. Results from this study indicate that regardless of the diet, the duration of SDA following satiation feeding was similar (~36 h) (Table 2). In contrast to these results, SDA response studies of southern bluefin tuna report notable differences in the duration of SDA depending on the amount of lipids in the diet (Fitzgibbon and Seymour, 2009), yet the high lipid diets in this study also were inherently higher in total energy compared to the low-lipid diets which may explain the differences in results compared to the mahi-mahi in this study. Such differences between species reveal the importance of quantifying the SDA response on a species-specific basis, as opposed to using generalized values to model metabolic endpoints across different species.

Different fish species possess different physiological attributes that have evolved in a manner to allow species to effectively exploit their range of distribution. While some of the unique physiological attributes

of mahi have been previously documented (Benetti, 1992; Brill, 1996), this study represents the first published account of postprandial metabolism in adult specimens of this species. These findings reveal physiological attributes which allow mahi-mahi to thrive in the pelagic environment of subtropical and tropical oceans, whereby feeding opportunities may be limited, but when available may be abundant. In order to thrive in such a habitat, this species is adapted to be able to capitalize on feeding opportunities by having an ability to consume large quantities of prey, up to 22% bw documented in this study, in a single satiation feeding event, larger than has been documented for species of tuna such as skipjack tuna (*Katsuwonus pelamis*): 8.6% bw (Magnuson, 1969); southern bluefin tuna (*T. maccoyii*): 11.9% bw (Fitzgibbon and Seymour, 2009); and Pacific bluefin tuna (*T. orientalis*): 13% bw (Clark et al., 2010). Duration of the SDA response in pelagic predatory fish such as mahi and tuna is relatively rapid compared to other fish species, as reviewed by Secor (2009), which allows these species to be able to digest large meals relatively rapidly to be able to exploit the next feeding opportunity. Despite the endothermic physiology of tuna, which would theoretically allow for reduced SDA durations in these species, postprandial metabolism studies of tuna reveal SDA durations in the range of those reported in this study for the mahi-mahi, despite differences in animal masses, meal sizes, environmental conditions, and experimental methodology (Clark et al., 2010; Fitzgibbon et al., 2007; Fitzgibbon and Seymour, 2009; Klinger et al., 2016). Given that mahi-mahi differs from other apex pelagic predatory fish in the fact that they do not expend additional energy supporting endothermic processes as found in many of the tuna and billfish species (Block, 2011; Dickson and Graham, 2004), these differences may partially explain the rapid growth rates of mahi-mahi as well as their high fecundity. Furthermore, the expeditious digestion of prey items supports recent evidence of relatively rapid transfer of energetic inputs to reproductive organs in this species (Kloeblen et al., 2017).

These concepts are supported by the swim performance portion of this study, in that there were no significant differences in aerobic swim performance (U_{crit}) or MMR of fed versus unfed fish. It has been hypothesized that given the relatively high swim speeds of mahi-mahi and the high metabolic costs associated with such swimming ability, that postprandial metabolism would reduce the overall swim performance and MMR of this species. Such compromises have been noted in other teleosts (Alsop and Wood, 1997), though no study has examined whether such a tradeoff in metabolic performance occurs in pelagic apex predatory fish species. The fact that there is no change in swim performance or MMR of mahi-mahi following satiation feeding reveals an impressive ability of this species to carry out multiple energetically demanding processes at the same time, and the data also provides insight as to the amount of available aerobic scope consumed by postprandial metabolism (Fig. 3) during routine swimming speeds.

While some species of fish exhibit increased swimming speeds during the SDA period, such alterations in preferred swim speeds are typically not possible to measure accurately in swim chamber respirometers. However, cost of transport and U_{opt} data can be utilized as a proxy for this type of data. This study did not show any significant difference in U_{opt} between fed and unfed fish, suggesting that a higher swim speed following feeding would not necessarily be optimal compared to the U_{opt} of unfed fish.

As expected, the RMR of fed fish was significantly higher than that of unfed fish, due to the metabolic costs associated with SDA (Table 3). For the purposes of this study, RMR was the relevant metabolic endpoint for describing stable low-level metabolism due to the necessity for ram ventilation in this species and the fact that calculating SMR from fed fish would result in erroneous measures. The increased metabolic costs associated with SDA also resulted in a significantly reduced factorial scope compared to that of unfed fish (Table 3). Clearly, satiation feeding imposes a significant metabolic demand on this species yet this demand does not compromise the overall swim performance of individuals indicating that U_{crit} is not solely limited by aerobic scope in this species.

5. Conclusions

Pelagic predatory fish, such as mahi-mahi, have a need to fuel and balance numerous metabolic demands throughout their lifecycles. Postprandial metabolism is one of the key aspects of metabolism which can provide insight into habits of prey consumption, migration, reproduction, growth, and overall bioenergetics of a species. This study documents the SDA response to three different diet types, both natural forage items and manufactured pellets, providing new insight into the nutritional physiology of this species. Satiation feeding appears to be dictated by meal energy as opposed to prey mass, and a formulated dry pelletized diet results in significantly lower SDA_{peak} and SDA_{mag} compared to natural forage diets of squid and sardines. Additionally, swim performance studies of fed and unfed fish indicate that aerobic swim performance is not compromised in this species following feeding despite reduced factorial aerobic scope. Results from this study will aid in the understanding of the bioenergetics of this species under both wild and captive conditions. Also, this information highlights potential areas for advancements in culture methods and provides critical baseline information on this species revealing often overlooked aspects of whole-animal physiology which may be affected by adverse environmental impact events.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cbpa.2017.10.016.

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