



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

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## ARTICLE INFO

### Keywords:

Specific dynamic action  
Pelagic  
Respirometry  
Nutrition  
Swim performance  
Aquaculture

## 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 ( $706 \pm 25$  g;  $38 \pm 0.7$  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 ( $473 \pm 45$  kJ), nor did the duration of SDA ( $36 \pm 2.1$  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 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 ( <i>Loligo opalescens</i> )	Sardines ( <i>Sardinella aurita</i> )	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 <sup>-1</sup> 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<sup>3</sup> 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<sub>2</sub>) 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<sup>-1</sup> 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<sup>-1</sup>) 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<sup>-1</sup> 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

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