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Fatty acid biomarkers reveal maternal energy allocation strategies in spawning Snapper (*Chrysophrys auratus*)

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ABSTRACT

Investigating the dynamic interplay between energy storage and provisioning offers valuable insights into reproductive strategies. In this study we utilised fatty acids as proxy biomarkers to investigate the energetic provisioning strategy of spawning Snapper (*Chrysophrys auratus*). Fatty acid profiles of liver, ovaries, and skeletal muscle showed significant variations in composition and concentration. The liver was rich in saturated fatty acids (ΣSFA, 68.52%), the ovaries were predominantly composed of polyunsaturated fatty acids (ΣPUFA, 43.44%), and skeletal muscle exhibited near equal proportions of ΣSFA (42.52%) and ΣPUFA (40.46%). This pattern indicates a mixed reproductive strategy, where high accumulation of SFA in the liver supports capital breeding traits, while higher PUFA levels in the ovaries, and equal SFA and PUFA composition in muscle tissue indicate characteristics associated with income breeding. We also found no convincing evidence to support the lipid provisioning aspect of the Big Old Fat Fecund Female Fish (BOFFFF) hypothesis, as older snapper did not provision higher concentrations of fatty acids in their ovaries. These findings provide new insights into resource allocation strategies of snapper during reproduction, suggesting that protecting a range of age classes, rather than focusing solely on older individuals, may be more effective for managing and ensuring stock sustainability.

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Introduction

Life-history theory posits that animals maximize fitness by efficiently allocating energy to reproduction (Stearns 2000). Research on energy allocation has traditionally focused on a three-way trade-off between cellular maintenance, growth and reproduction, providing a nuanced understanding of provisioning strategy (Perrin and Sibly 1993; Reznick and Yang 1993; Huynh et al. 2007; Villamarín et al. 2016). The breeding strategy of fishes generally involves the partitioning of energy during reproduction, with the two main

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strategies being identified as capital and income breeding (McBride et al. 2015). At the extreme ends of this continuum, capital breeders store energy seasonally for gonad development, which is often a pre-programmed response to environmental variables such as day length and temperature (Mourente et al. 2001). In capital breeders, the majority of energy required for vitellogenesis and embryogenesis are acquired early and provisioned from stored reserves (Wiegand 1996). In contrast, income breeders rely on their daily diet to meet the caloric demands of reproduction, as they lack mechanisms for long-term energy storage (McBride et al. 2015). While most organisms are known to develop a combination of both strategies, they can also adjust their approach based on environmental cues, food availability, or endogenous factors (Houston et al. 2007; Alonso-Fernández and Saborido-Rey 2012).

Analysing how caloric reserves are distributed across various organs during reproduction can reveal key maternal energy allocation strategies that support offspring development (Huynh et al. 2007). Physiological biomarkers are widely distributed molecules that can be used as proxies to provide valuable insights into life history traits (Brosset et al. 2021). Lipids, as essential hydrocarbon-based molecules involved in complex cellular processes (Vilella et al. 2013), have become an increasing focus of compositional analysis in aquatic sciences (Couturier et al. 2020). As the main source of metabolic energy in fishes (Tocher 2003; Yanes-Roca et al. 2009), lipids play a crucial role in survival, reproduction, and life history strategies (Adams 1999; Copeman et al. 2002; Parrish et al. 2005; Hulbert et al. 2014; Dreier et al. 2020). In particular, reproduction is a complex physiological process which requires substantial amounts of energy and resource investment (Schneider 2004). For example, following synthesis and release via receptor-mediated endocytosis, vitellogenin is transported from the liver – the lipidation organ – to the ovaries, where it is incorporated into growing oocytes along with other lipid precursors essential for reproduction (Wallace and Selman 1981; Wiegand 1996; Dreier et al. 2020). Hence, lipids can be used as potential biomarkers to investigate various reproductive parameters (Salze et al. 2005; Johnson 2009; Yanes-Roca et al. 2009; Sinanoglou et al. 2011; Żarski et al. 2017).

The aim of this study was to utilise fatty acids as biomarkers to analyse the transfer of maternal endogenous energy during the spawning season of New Zealand Snapper *Chrysophrys auratus*. The specific objectives were two-fold. Firstly, to ascertain and compare the relative concentration of fatty acids in the liver, ovaries and skeletal muscle of snapper, where fatty acid oxidation is an important aspect of fuel homeostasis (Schneider 2004). Secondly, to assess whether maternal age influenced the concentration of fatty acids in the ovaries, providing insights into the BOFFFF (Big Old Fat Fecund Female Fish) hypothesis (Hixon et al. 2014). Snapper holds high commercial, recreational and ecological value in New Zealand (Shears and Babcock 2002; Parsons et al. 2014). However, stocks have been historically subjected to intensive fishing pressure (Willis et al. 2003; Paul 2014). Snapper are widely distributed throughout Australasia but are limited by colder southern waters. As a result, they are most common in northern New Zealand, with large stocks along the west coast and the east coast north of East Cape (Crossland 1981; Paulin 1990). While they can be found at a maximum depth of 200 meters, snapper more commonly reside in waters <70 meters, and are present over a wide range of substrates, inhabiting varying ecosystems throughout their life (Parsons et al. 2014). Archaeological evidence has shown that snapper can reach a

maximum total length of 100 cm, and live up to 60 years (Leach 2006). The reproductive development of snapper has been characterised as functional gonochorism, with approximately half of the population undergoing protogynous sex change from non-functional juvenile females to males (Francis and Pankhurst 1988). Snapper becomes sexually mature as early as 23 cm, with 100% maturity by 30 cm (Crossland 1981). As iteroparous serial broadcast spawners, snapper typically spawn from the beginning of spring to the end of summer, between October to March (Sim-Smith et al. 2012). By investigating the energetic axis of snapper between its liver, ovaries, and skeletal muscle during the spawning season, we hope to advance our understanding of resource provisioning and reproductive dynamics in this species (Sim-Smith et al. 2013; Allen et al. 2018; Sabetian et al. 2020).

Methods

Ethics statement

Animal ethics approval was not required as samples for this study were collected from post-processed frames of snapper donated by recreational fishers.

Specimen collection and sampling

Notices on community fishing Facebook groups were used to acquire donated snapper frames from recreational fishers in Doubtless Bay (34°53'58.5"S 173°26'42.0"E) on the east coast of the North Island of New Zealand between 17th August 2019 to 27th January 2020. Doubtless Bay sits within the SNA1 snapper management area and is an important spawning aggregation location (Crossland 1982; Hurst et al. 2000). Macroscopic analysis of gonads was used to initially identify female ovaries (Mackie et al. 2009), pending histological confirmation of sex. All possible males were discarded from sample collection. Standard fish length was measured (mm) before sagittal otoliths were removed, cleaned, and stored for age analysis. Ovarian, liver, and skeletal muscle tissue (from the pectoral region) were extracted for lipidomics analysis. A subsample of ovarian tissue was fixed in 10% buffered formalin for histological confirmation of sex and reproductive stage, while a second sub-sample of ovaries, along with liver and skeletal muscle tissues were initially frozen in a domestic freezer (−20°C) while in the field, and subsequently transferred to a −80°C freezer at Auckland University of Technology.

Reproductive and age analysis

Ovarian tissue were processed according to standard histolotogical protocols following Sabetian et al. (2015). Reproductive stage for each specimen was determined based on the most developed oocyte present, following the methods outlined by West (1990). In total, 100 ovaries were histologically confirmed as 'spawning' because they were either dominated by the yolk globule stage (YGS), or contained hydrated or ovulated oocytes (Mackie et al. 2009). Age determination was based on thin transverse sections of sagittal otoliths (Secor et al. 1995). Annual age representation was determined by counting

opaque growth rings, visible as dark bands under transmitted light, using a camera-mounted compound microscope. The annual periodicity of opaque and translucent zones in snapper otoliths was confirmed by Francis et al. (1992). Because this study was conducted in the spawning season of snapper (i.e. birth months) (Crossland 1981), ages deduced from the number of opaque zones on the otoliths were counted to whole numbers. In total 88 specimens were successfully aged (Figure 1) from the 100 females, ranging from 300–640 mm standard length.

Fatty acid analysis

Fatty acid composition was analyzed in the skeletal muscle of all 100 females. However, due to labeling issues caused by an ineffective cryomarker, analysis was only possible for 96 ovaries and 71 livers. Fatty acids, defined as low-molecular-weight lipids, were identified and quantified using gas chromatography-mass spectrometry (GC-MS) with electron ionisation, following established protocols (Quehenberger et al. 2011). Lipid extraction and derivatization were based on Zhou et al. (2014). Liver, ovaries, and skeletal muscle samples (2–5 g) were snap-frozen in liquid nitrogen, freeze-dried, and homogenised. Approximately 20 mg of homogenised tissue was extracted using toluene-based solutions containing surrogate and internal standards, followed by derivatization with acetyl chloride and incubation at 100°C. The organic phase was purified and prepared for GC-MS analysis. GC-MS was performed using an Agilent 7890A GC coupled with a 5975C mass spectrometer, equipped with a polar Rtx-2330 column (100 m x 0.25 mm, Shimadzu) and helium as the carrier gas. Samples were injected in splitless mode, and temperature programming followed established protocols (Mossoba and Kramer 2010). Detection occurred in electron-impact ionisation mode (70 eV) with scan mode

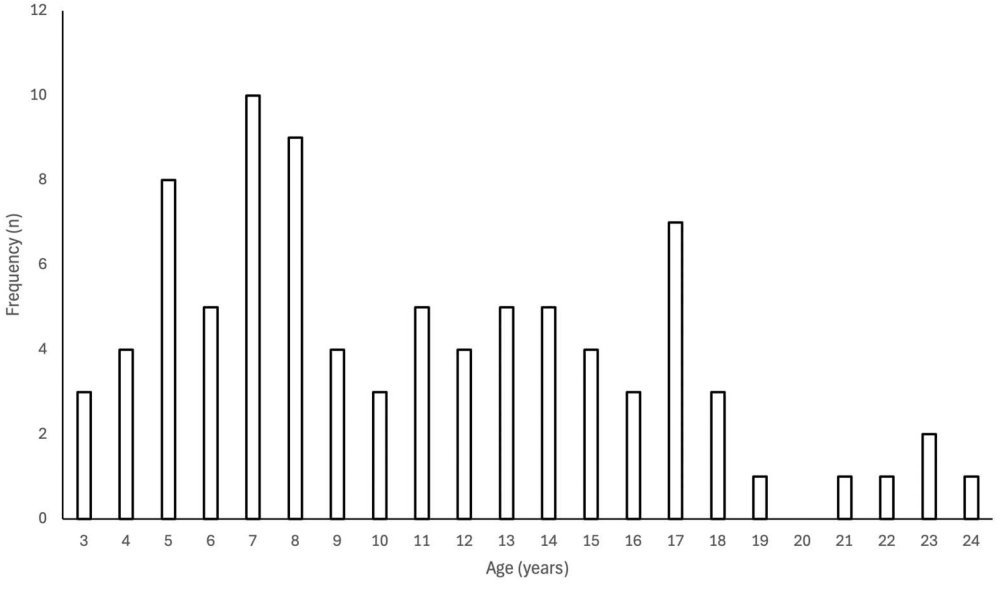

Figure 1. Age distribution of recreationally-caught snapper *Chrysophrys auratus* from Doubtless Bay.

Table 1. Mean (±SE) relative fatty acid content (%) in Liver, Ovary, and Skeletal Muscle of spawning Snapper (*Chrysophrys auratus*).

Fatty Acid	Liver	Ovary	Muscle	*p*
Σ SFA	68.52 ± 1.42^{A}	37.49 ± 0.47^{B}	42.52 ± 0.46^{C}	<0.0001*
C14:0	2.51 ± 0.13^{A}	2.14 ± 0.12^{AB}	1.84 ± 0.10^{B}	0.0007*
C15:0	1.38 ± 0.08^{A}	1.04 ± 0.06^{B}	–	0.0001*
C16:0 [PAL]	42.80 ± 0.88^{A}	25.71 ± 0.35^{B}	28.59 ± 0.33^{C}	<0.0001*
C17:0	2.16 ± 0.10^{A}	1.00 ± 0.03^{B}	–	<0.0001*
C18:0	18.67 ± 0.48^{A}	7.14 ± 0.16^{B}	9.79 ± 0.15^{C}	<0.0001*
Σ MUFA	18.60 ± 0.79^{A}	19.07 ± 0.63^{A}	17.02 ± 0.72^{A}	0.0843
C16:1(n-7)	3.50 ± 0.26^{A}	4.46 ± 0.27^{B}	3.21 ± 0.17^{A}	0.0003*
C18:1(n-9) [OLA]	12.92 ± 0.58^{A}	12.55 ± 0.45^{A}	11.87 ± 0.52^{A}	0.0352
C20:1	–	1.00 ± 0.04	–	–
Σ PUFA	12.89 ± 1.20^{A}	43.44 ± 0.96^{B}	40.46 ± 1.00^{B}	<0.0001*
C18:2(n-6)	–	1.44 ± 0.06^{A}	1.22 ± 0.03^{B}	<0.009*
C20:4(n-6) [ARA]	3.14 ± 0.28^{A}	9.47 ± 0.73^{B}	6.59 ± 0.36^{C}	<0.0001*
C20:5(n-3) [EPA]	2.35 ± 0.28^{A}	7.01 ± 0.28^{B}	5.77 ± 0.24^{C}	<0.0001*
C22:6(n-3) [DHA]	6.04 ± 0.71^{A}	24.05 ± 0.64^{B}	25.75 ± 0.90^{B}	<0.0001*
Σ (n-3) / Σ (n-6)	2.02 ± 0.15^{A}	3.91 ± 0.23^{B}	4.38 ± 0.18^{B}	<0.0001*
DHA/EPA	3.00 ± 0.15^{A}	3.85 ± 0.16^{B}	5.19 ± 0.28^{C}	<0.0001*
DHA/OLA	0.55 ± 0.08^{A}	2.20 ± 0.10^{B}	2.73 ± 0.16^{C}	<0.0001*
DHA/ARA	2.05 ± 0.15^{A}	4.54 ± 0.35^{B}	4.73 ± 0.24^{B}	<0.0001*

Notes: ANOVA *p values of < 0.05 indicate significant difference between tissues. Different superscript letters (A, B, C) in the same row indicated significant statistical difference between individual tissues ($p < 0.05$, Tukey-HSD post-hoc test). SFA, Saturated Fatty Acids; MUFA, Monounsaturated Fatty Acids; PUFA, Polyunsaturated Fatty Acids; EPA, Eicosapentaenoic Acid; DHA, Docosahexaenoic Acid; ARA, Arachidonic Acid; OLA, Oleic Acid; PAL, Palmitic Acid. All individual fatty acids that contributed to more than 1% towards total fatty acid content are depicted in this table. Fatty acid content less than 1% are denoted with a dash (–).

acquisition (41–420 amu). Fatty acid concentrations were calculated using calibration curves prepared from a 37-mix standard (Nu-Chek-Prep).

Statistical analysis

All statistical analyses were performed using R version 4.2.1 (R Development Core Team 2024). The assumptions of normality (Shapiro–Wilk test) and homogeneity of variance (Fligner-Killeen test) were met by all fatty acids. One-way Analysis of Variance (ANOVA) and Tukey-HSD post-hoc tests were performed to determine differences in fatty acid profiles between liver ($n = 71$), ovary ($n = 96$) and skeletal muscle ($n = 100$) tissues (Table 1). A p-value of < 0.05 was considered statistically significant. Subsequent to ANOVA, the fatty acid profile of ovarian tissues of samples that were successfully aged ($n = 88$) were subjected to more flexible generalised additive models (GAMs) to test our hypothesis of maternal age influence on lipid concentration. GAMs were fitted with a Gamma error distribution when the fatty acid as the response variable is right-skewed, and otherwise with a default Gaussian distribution (GAMs, R-package mgcv, Wood 2011), which enabled us to examine both linear and non-linear relationships between lipid concentration and maternal age. We conducted separate GAMs for all fatty acids and ratios that showed concentrations higher than 1% (see Table 1).

Results

The liver was heavily dominated by Saturated Fatty Acids (SFAs; 68.52%), followed by Monounsaturated Fatty Acids (MUFA; 18.60%), and Polyunsaturated Fatty Acids

(PUFAs; 12.89%) (See Table 1). The ovaries were dominated by PUFA (43.44%), followed by SFA (37.49%) and MUFA (19.07%). Skeletal muscle was equally dominated by SFA (42.52%) and PUFA (40.46%), followed by MUFA (17.02%). Although in different relative concentrations, the same fatty acid species, in the same order, contributed heavily to total SFA, MUFA and PUFA content across all tissues. Palmitic acid (PAL; C16:0) and Stearic acid (C18:0), contributed the most to SFA content in liver (42.8%, 18.67%), ovaries (25.71%, 7.14%), and skeletal muscle (28.59%, 9.79%), respectively. Oleic acid [OLA; C18:1(n-9)] and Palmitoleic acid [C16:1(n-7)] contributed the most to MUFA content in the liver (12.92%, 3.5%), ovaries (12.55%, 4.46%), and skeletal muscle (11.87%, 3.21%), respectively. Docosahexaenoic acid [DHA; C22:6(n-3)] and Arachidonic acid [ARA; C20:4(n-6)] contributed the most to PUFA content in the liver (6.04%, 3.14%), ovaries (24.05%, 9.47%), and skeletal muscle (25.75%, 6.59%), respectively.

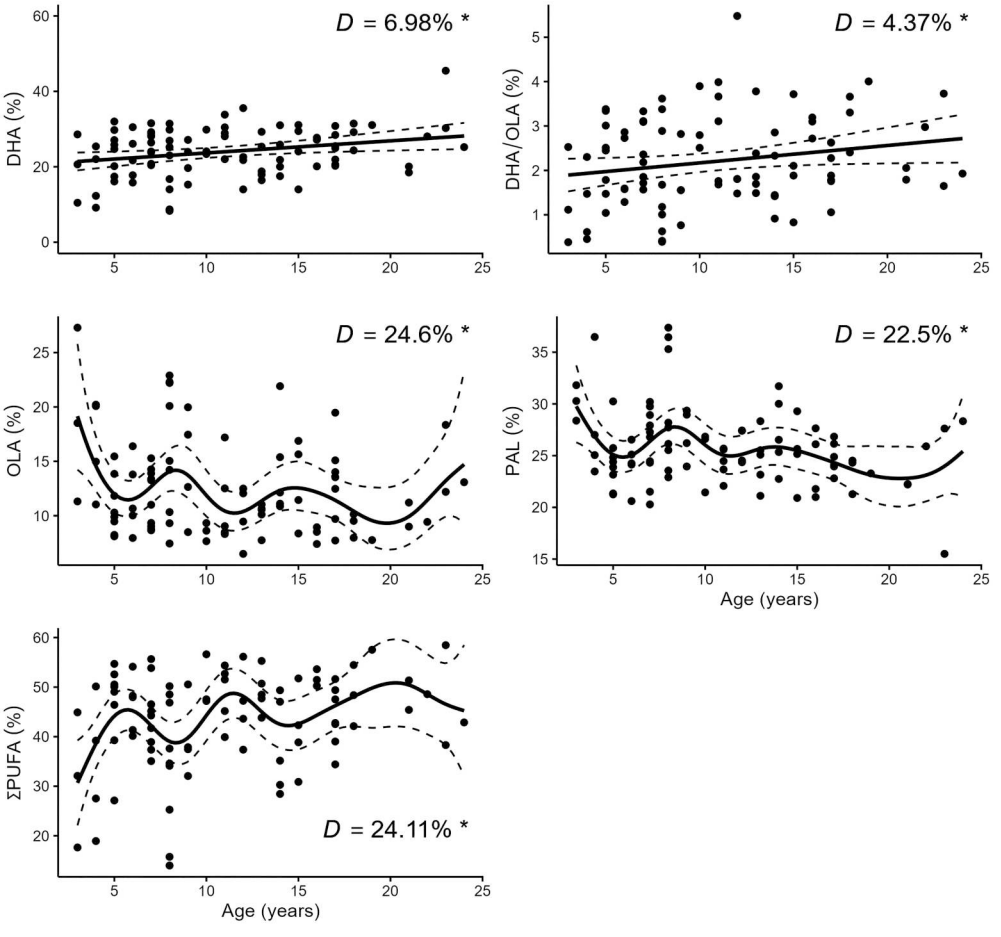

Figure 2. Concentrations of fatty acids depicting a significant non-linear relationship as a function of age in the ovarian tissue of spawning female snapper *Chrysophrys auratus*. Solid lines represent fits from Generalised Additive Models with Gaussian error distribution or with gamma error distribution when data are positively skewed, dashed lines indicate 95% confidence intervals. D = deviance explained, *$p < 0.05$.

ANOVA and post-hoc tests revealed significant differences across nearly all fatty acid profiles between liver, ovaries, and skeletal muscle (Table 1). Of note, was the significantly higher PAL content in the liver (42.8%), compared to the ovaries (25.71%) and skeletal muscle (28.59%). Stearic acid was similarly significantly higher in the liver (18.67%), compared to ovaries (7.14%), and skeletal muscle (9.79%). The other interesting trend in relative content was the significant multi-fold increase in ARA, Eicosapentaenoic [EPA; C20:5(n-3)], and DHA from the liver (3.14%, 2.35%, 6.04%), to ovaries (9.47%, 7.01%, 24.05%), and skeletal muscle (6.59%, 5.77%, 25.75%), respectively. In terms of ratios, Σ(n−3)/Σ(n−6) was significantly higher in the ovaries and skeletal muscle, when compared with the liver, while the multi-fold increase in DHA in the ovaries and skeletal muscle also led to significantly higher DHA/EPA, DHA/OLA, and DHA/ARA ratios when compared to the liver.

All ovarian fatty acids and ratios depicted in Table 1 were subjected to GAMs in order to determine the presence of non-linear relationships between age and fatty acid content (Figure 2). DHA, OLA, DHA/OLA ratio, PAL, and ΣPUFA where the only FAs which showed significant non-linear relationship. DHA ($p = 0.0123$) depicted a slightly increasing trend with age, which also influenced the DHA/OLA ratio ($p = 0.0493$) with a similar trend, while OLA ($p = 0.0253$), PAL ($p = 0.033$) and ΣPUFA ($p = 0.017$) depicted a humped response with age, where concentrations rose or declined between certain age groups. In line with the spread of our samples in the very young and old ranges, the level of uncertainty increased slightly in those age ranges, represented by wider 95% confidence intervals.

Discussion

This study used fatty acids as biomarkers to investigate the allocation of caloric reserves in spawning snapper, providing insights into their energetic provisioning strategy. The first objective set out to elucidate the fatty acid profiles and composition of the liver, ovaries, and skeletal muscle. Analysis revealed distinct fatty acid profiles across snapper tissues; the liver exhibited very high SFA concentration, the ovaries showed higher PUFA concentration, and skeletal muscle contained near equal distributions of SFA and PUFA. These findings suggest that snapper may employ a mixed income and capital breeding strategy. The high accumulation of SFA in the liver, a key site for energy storage (Guil-Guerrero et al. 2011), aligns with a capital breeding approach, where stored reserves are mobilised for cellular functions (Legrand and Rioux 2010). In contrast, the elevated PUFA levels in the ovaries and the balanced SFA and PUFA profiles in muscle tissue point to the potential use of dietary inputs (Tocher 2003), characteristic of income breeding to meet the demands of gamete production and energy metabolism throughout the spawning season.

A closer look at specific fatty acids revealed a more intriguing picture. Although in different relative concentrations, the same fatty acids contributed most to the total content of their respective family groups. Regardless of tissue type, Palmitic and Stearic acid contributed the most to ΣSFA, Oleic acid contributed the most to ΣMUFA, and DHA contributed the most to ΣPUFA content. Though present in varying relative concentrations, this trend was also observed in the liver, intestine, roe, milt, and flesh of spawning and non-spawning Pacific herring *Clupea harengus pallasi*

(Huynh et al. 2007). This is not entirely surprising, as Palmitic acid, for instance, is recognised as a predominant source of metabolic energy for growth and egg formation (Tocher 2003), while Essential Fatty Acids (EFAs) like DHA, ARA, and EPA play crucial roles in the production of intra- and extracellular signalling molecules involved in regulating somatic growth, reproduction, immune response, and messengers in the central nervous system (Rowley et al. 1995; Sargent et al. 1999; Mayes and Botham 2003; Jaya-Ram et al. 2008; Castro et al. 2009).

The second objective of this study was to determine whether maternal age correlated with higher ovarian fatty acid concentration during reproduction. We addressed this using generalised additive models to analyse lipid concentrations in the ovaries, focusing on fatty acids that comprised more than 1% of the total content. Results showed that significant non-linear patterns were observed only for DHA, OLA, PAL, DHA/OLA ratio, and ΣPUFA (Figure 2). However, there was no consistent increasing trend in fatty acid concentration with age. Specifically, DHA and the DHA/OLA ratio showed a tentative increase with age, whereas OLA, PAL, and ΣPUFA exhibited a humped response, with varying higher and lower concentrations observed across different age ranges.

The BOFFFF hypothesis popularised the notion that bigger and older mothers invest greater lipid reserves to their eggs, which is thought to produce robust larvae better equipped to survive periods of starvation, thereby increasing their chances of survival (Hixon et al. 2014). The BOFFFF hypothesis was inspired by the findings of Berkeley et al. (2004), who used oil globule volume in rockfish (*Sebastes melanops*) larvae as a qualitative proxy for lipid content and attributed the extended survival and faster growth of starved larvae to correlation with the older age of their mothers'. In this investigation, we did not find strong evidence that spawning snapper provisioned higher fatty acid content in their ovaries as a function of age. This finding aligns with Allen et al. (2018), who investigated the relationship between ovarian concentrations of triacylglycerol (TAGs) and maternal age in snapper, finding no consistent correlation. A study by Martin (2009) investigating reproductive parameters in small, medium and large-sized snapper found that maternal size did not influence the total concentrations of lipids, proteins or free amino acids of their eggs. Martin (2009) further demonstrated that, although medium-sized snapper consistently produced more eggs (standardized per kilogram of biomass) and the largest eggs, hatching success did not differ significantly between medium and large snapper. This trait, along with the fact that larger eggs did not always contain larger yolks or produce larger larvae, challenges the assumed correlation between egg, larval size, and hatching success (Kamler, 2005).

The BOFFFF hypothesis is a counter-intuitive notion that attributes observed larval fitness to a correlation with their mothers' 'big' size and 'old' age. However, this is contrary to everything that is known about ageing and cellular senescence (Monaghan et al. 2008; Nussey et al. 2013), which show that reproductive performance typically follows a parabolic or inverted U-shape trajectory that peaks in midlife, followed by a gradual decline with age (Stearns 2000; Reid et al. 2003; Marasco et al. 2018). Marshall et al. (2010) reviewed empirical studies on the relationship between maternal age and offspring fitness, finding no evidence or theoretical justification that older mothers 'produce offspring with higher per capita fitness'. Gaining deeper insights into progeny fitness requires a multi-dimensional approach to investigating the drivers of offspring viability and success. For example, Kamler (2005), argue for equal focus on

both the maternal and paternal drivers of progeny performance, while Cheung et al. (2019) advocate for the partitioning of genotypic and phenotypic factors, focusing on maternally-inherited egg transcriptomes to study the role of maternal-effect genes on reproductive success. Similarly, in batch spawning bonga shad *Ethmalosa fimbriata*, reproductive potential and energetic strategies were found to reflect adaptations to environmental conditions rather than a simple correlation with age or size, emphasising the dynamic nature of reproductive investment under varying ecological pressures (Döring 2018). Examining offspring fitness from an evolutionary perspective can also provide valuable insights and deepen our understanding. For example, Marasco et al. (2019) examined the 'lansing effect' in zebra finches—the idea that offspring of older parents have reduced lifespans—finding a significant decline in offspring telomere length with increasing maternal age. They also found intriguing differences in the survival of male and female offspring, which underscore the complexity and crucial role of genetic dynamics as intergenerational mediators of optimal reproductive strategies.

This study delineates fatty acid composition within key organs of snapper during its spawning period, thereby shedding light on the species' reproductive energetics strategy. Although the predominant fatty acids identified in this study (e.g. PAL, OLA, ARA, EPA, DHA) have previously been highlighted as playing vital roles in fish health and reproductive success (Sargent et al. 1999; Tocher 2003; Arts and Kohler 2009; Librán-Pérez et al. 2019), the intriguing variations in their concentrations between organs serving as source (liver) and sink (ovary, muscle) shed light on resource partitioning strategy of snapper during spawning. Such findings challenge existing paradigms by highlighting the dynamic interplay between different physiological demands and organ-specific metabolic activities during the reproductive phase. This nuanced understanding not only enriches our knowledge of snapper reproductive biology but also contributes to broader insights into the evolutionary strategies employed by teleosts in optimising reproductive fitness. Moreover, the differential accumulation of specific fatty acids across organs suggests a sophisticated regulatory mechanism underlying lipid metabolism and allocation, which needs to be investigated further with a broader focus that includes non-spawning snapper. These insights could potentially inform conservation and management strategies, particularly in the context of identifying and protecting age cohorts that contribute most to reproductive success.

A key limitation of this study is the lack of a temporal profile that would encompass long-term fatty acid analysis before, during, and after the spawning season. Such data are essential for determining whether energy transfer strategies change according to different life-history priorities throughout snapper's annual life cycle. By elucidating where essential nutrients are distributed and utilised before, during, and after reproduction, we can begin to lay the foundation for future research aimed at understanding the ecological resilience and adaptability of snapper in the face of changing environmental conditions. Future research should also consider exploring the same questions under controlled laboratory conditions. This would allow for the regulation of physical (e.g. captivity), environmental (e.g. temperature), and ecological (e.g. diet) parameters, enabling a more detailed exploration of the complex relationship between nutrition, metabolism, and reproductive success in this species.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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