



RESEARCH ARTICLE

The utility of non-lethal morphometrics to evaluate fish condition

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Abstract

The condition of fish relates to their energy reserves, and a suite of proxies exist to approximate condition, including biochemical and morphometric indices. Biochemical indices directly measure energy stores but are expensive and sometimes lethal. Morphometrics offer several advantages, but their utility as condition proxies is debated and largely untested experimentally. Here, we manipulated the condition of yellowfin bream (*Acanthopagrus australis*, Günther, 1859) via food reduction to simulate the effect of poor habitat quality and calculated a variety of condition indices through time. We measured four non-lethal morphometrics (Fulton's K, Le Cren's relative condition, width-to-length ratio and girth), the hepatosomatic index and a biochemical benchmark (liver lipid content). Girth and width-to-length ratio were reasonably well correlated with lipid content ($R^2=0.74$ and 0.56 , respectively). The hepatosomatic index was only weakly or uncorrelated to other indices, including lipid content ($R^2=0.35$). Where precise estimates of body condition are not needed or repeat measures on the same individual are useful, non-lethal morphometrics provide a fast, cheap and non-lethal alternative to biochemical and lethal morphometric methods for this species. We finish by outlining how artificial intelligence-based automation can be combined with morphometrics to further enhance ethical monitoring by eliminating the need to capture and handle fish entirely.

KEYWORDS

condition index, fish health, fisheries, fitness, health assessment, Moreton Bay

INTRODUCTION

Measuring the condition of animals is helpful in answering a suite of important ecological questions, including those related to habitat quality, environmental impact assessments and management outcomes (Stevenson & Woods Jr., 2006). The use of body condition as a proxy for health and energy availability in fish, as measured using various indices, is widespread in fisheries science (Schulte-Hostedde et al., 2005). An individual with a higher body condition is generally considered to have larger quantities of energy reserves and a higher evolutionary fitness (Labocha et al., 2014; Pangle & Sutton, 2005). Since fish body condition partly reflects the biological and physical conditions which an individual encounters, it can be used to assess how environmental variables such as habitat quality and climate change influence health, potentially providing insight into environmental pressures even before they manifest as changes in population abundances (Mathuriau et al., 2012).

A suite of biochemical and morphological indices are available to evaluate condition. Direct biochemical indices measure an individual's body

condition via the quantification of energetic reserves, usually expressed as lipid or protein content, and may also include the evaluation of RNA:DNA ratios, which reflects the capacity of cells to synthesize proteins (Siddiqua & Khan, 2022). Some morphometrics assess the relative size or mass of vital organs such as the liver (e.g., hepatosomatic index; HSI). Whilst these types of indices are generally the most informative with respect to individual condition, measuring them can be labour-intensive, expensive or lethal to the fish. Non-lethal morphometric indices, such as Fulton's K (K; Fulton, 1904), serve to estimate condition using body morphology; primarily relationships between body weight and size/shape (Osborne et al., 2021). Morphometrics can act as surrogates for condition under the assumption that heavier individuals (at a given length) have more fat stores and energy reserves, and thus better condition (McPherson et al., 2011). Deviation from an expected weight based on known length–weight relationships, such as those used to calculate Le Cren relative condition factor (Kn; Le Cren, 1951), can also provide a relative measure of fitness or condition (Lloret et al., 2013). These morphometrics are simple, quick and inexpensive to measure and are usually non-lethal. Despite these advantages, a recurring problem regarding the use of morphometrics is the lack of validation when interpreting findings, whereby morphometric indices are used as a measure of condition with no evidence they are related to energy stores or individual fitness (Green, 2001; Stevenson & Woods Jr., 2006).

Evaluating relationships between measures of condition may reveal morphometrics as a defensible and valuable approach to explore the same ecological questions that have typically relied on lethal approaches. Previous work investigating such relationships have largely focused on pelagic species with highly specialized morphology and physiology, or on only a narrow range of indices using inshore, benthic species. Whilst some of these studies have observed relationships between morphometric indices and lipid content (e.g., 35% Schloesser & Fabrizio, 2017, 45% Wuenschel et al., 2019 and 46% Albo-Puigerver et al. 2020), others report non-existent or weak relationships. For example, Davidson and Marshall (2010) and McPherson et al. (2011) found only weak correlations between Fulton's K and energy storage in North Sea herring (*Clupea harengus*, L.), suggesting morphometrics were not useful for estimating condition in this species (see Table S1). Similar outcomes were found for other temperate species such as Atlantic salmon (*Salmo salar*, L.; Kadri et al., 1995) and muskellunge (*Esox masquinongy*, Mitchell; Jonas et al., 1996). It therefore remains unclear whether morphometrics are reliable proxies for energy content for untested species.

The relationship between morphometric condition indices and energy reserves is typically investigated using wild fish populations from specific areas (e.g., Brosset et al., 2015; Gatti et al., 2018; Wuenschel et al., 2019). Whilst some variables can be controlled (e.g., sex), the relative condition of all fish could be very similar, potentially masking (or reducing) correlations that would be evident if condition varied more substantially. Through manipulating condition using, for example, food availability or contaminant exposure as proxies for poor habitat quality, we may be able to identify stronger correlations and reveal the true utility of morphometrics for evaluating fish health. Here, we manipulated the condition of a common fisheries species, yellowfin bream (*Acanthopagrus australis*, Günther, 1859), via reductions in feed as a proxy for poor habitat quality, and measured a suite of morphometric and biochemical indices through time to interrogate correlations amongst indices. The species is found in coastal habitats such as seagrass (Gaines et al., 2020) and saltmarsh (Jones et al., 2021), and around coastal urban infrastructure (Yabsley et al., 2020). Despite having a generalized diet of benthic invertebrates (Hadwen et al., 2007), its reliance on food webs based on vegetated coastal habitats such as seagrass,

saltmarsh and mangroves (Melville & Connolly, 2003) indicates a vulnerability to coastal habitat loss. Fishing pressure is evident in the much higher populations inside marine reserves than in adjacent fished areas (Gaines et al., 2020), and the fishery faces ongoing threats such as loss of the key breeding habitat of surf bars (Pollock, 1984).

MATERIALS AND METHODS

Fish sampling and laboratory preparation

We collected 48 juvenile bream (<13 cm fork length; 8.09 ± 2.65 ; mean \pm SD) from southern Moreton Bay in Queensland, Australia ($-27.891770S$, $153.379482E$) using squid-baited opera house traps in November and December 2021. Juveniles were selected for ease of capture and husbandry requirements in the lab. Upon collection, we vetted fish for abnormalities such as evidence of disease, parasites or pre-existing health issues (e.g., morphological deformities). We transported retained fish to the Marine Controlled Temperature Laboratory, Griffith University, where fish were acclimated for 7 days in seawater with 5 mL API Melafix antibacterial solution. Temperature and salinity were held constant at 24°C and 35ppt, respectively. We performed a 20% water change twice a week. The research was approved by the Griffith University Animal Ethics Committee (ENV/14/21AEC).

Experimental design

We randomly assigned fish to plastic aquaria (L: $38.5 \times$ W: $24.5 \times$ H: 24 cm) and assigned one of two treatments: a control group fed maximal food intake (hereafter control), and a restricted group fed at a 25% of control group (hereafter starved). To determine maximal food intake as a percentage of body mass, we conducted a pilot study, identifying that juvenile bream consume on average 4.7% of their body mass per day under our lab conditions. Diet was thawed brine shrimp, fed once per day.

At the beginning of the experiment (day 0), all fish (live) were placed on an ichthyometer and photographed from above and from the side (lateral and dorsal profile, respectively). Wet weight (W_T) was recorded using an Ohaus analytical balance (to the nearest 0.01 g). On days 7, 11 and 14, a subset of fish from control and treatment groups (7:7, 5:5, 5:2; control:treatment) were euthanized via a sea-ice slurry. Replication was reduced from the planned 8:8 for each sampling period due to mortality. Mortality was uniform between control and treatment groups at first, but by the final sample period was higher for the treatment group. In addition to photographs and wet weights being taken (as per day 0), we dissected out and quickly weighed livers. Fish were not fed within 24 h of sacrifice. Livers were cryogenically frozen and stored (-80°C) for subsequent lipid analysis. Photographs were processed using *ImageJ* (Schneider et al., 2012) to measure the biometric parameters: standard length (SL), fork length (FL), lateral height and pectoral width (PW; Table 1). The HSI was measured using the wet weights of the liver and whole body (Table 1).

NMR spectroscopy

To extract lipids from the liver samples, we used a modified version of the Bligh-Dyer methanol:chloroform extraction (Bligh & Dyer, 1959). Each

TABLE 1 Summary of biometric parameters used to calculate morphometric parameters, and the suite of condition indices categorized as morphometric and biochemical.

Measure	Abbreviation	Explanation/equation
Biometric parameters		
Standard length (cm)	SL	Distance between snout and start of caudal fin
Fork length (cm)	FL	Distance between snout and centre of caudal fork
Lateral height (cm)	LH	Distance between pelvic fin and dorsal fin
Pectoral width (cm)	PW	Distance between pelvic fins
Total weight (g)	TW	Weight of the whole fish
Liver weight (g)	LW	Weight of the liver
Proportion of mass gain (%) ^b	%MassGain	Per cent increase in mass
Morphometric indices		
Fulton K ^b	K	$100 \times TW/SL^3$
Le Cren's relative condition inde ^b	Kn	$TW \text{ (observed)}/TW \text{ (predicted)}^a$
Girth ^b	G	$\pi \cdot (\text{Height}/2) \cdot (\text{Width}/2)$
Width length ratio ^b	W:LRatio	Final PW/Final FL
Hepatosomatic index ^b	HSI	$100 \times (LW/TW)$
Biochemical indices		
Total lipids ^b	Lipid content	All lipids measured by H ¹ NMR spectroscopy
Total cholesterol ^b	TC	C18H3 in total cholesterol
Omega 3 fatty acid ^b	n-3 FA	CH3 in fatty acyl chain
Free cholesterol ^b	FC	C21H3 in free cholesterol
Esterified cholesterol ^b	EC	C19H3 in esterified cholesterol
β-carbon ^b	FA	COCH2 in fatty acyl (beta) chain
Unsaturated fatty acid ^b	UFA	=CHCH2CH=in unsaturated FA 20:4, 22:6
Triglyceride ^b	TG	Glycerol moiety in TAG CH-2, CHα-1/CHα-3, CHβ-1/CHβ-3
Phosphatidylcholine ^b	PC	PO-CH2 of phosphatidylcholine
Plasmalogen ^b	PlsE	Plasmenyl PC and/or PE
Glycerophospholipid ^b	GPL	CH2 of glycerophospholipid backbone

^aPredicted weight is determined by length–weight regression with alpha (0.01288) and beta (3.03) (Froese et al., 2014).

^bIndicates the 17 response variables analysed.

of the 32 samples was homogenized in 400 μL ice-cold methanol using an Ultra-Turrax T10 tissue homogenizer followed by ultra-sonication with a Q55 probe sonicator. After incubating the samples at –20°C for 1 hour, we used a solvent mixture consisting of methanol (MeOH), chloroform (CHCl₃) and deionized water (H₂O) in a 4:8:3 (2400 μL:4800 μL:1800 μL) ratio to facilitate separation and partitioning. The samples were then vortexed and centrifuged at (10 min, 16 000× g, at 4°C). The lower phase, which contained the non-polar lipids, were transferred to glass amber vials (1600 μL) and stored at –80°C and later transferred to a freeze-dryer allow the extracted lipids to lyophilize. Samples were resuspended in 200 μL deuterated chloroform (CDCl₃) containing 0.05% (w/v) sodium 3-(trimethylsilyl)propionate-2,2,3,3-d₄ (TSP) as an internal standard, vortexed and transferred to 3 mm

NMR tubes. NMR spectra were collected for each sample with an 800 MHz Bruker® Avance III HDX spectrometer housing a Triple (TCI) Resonance 5 mm Cryoprobe with Z-gradient and automatic tuning and matching, using CDCl_3 for field locking and TSP ($^1\text{H} \delta$ 0.00) as a chemical shift reference. Proton (^1H) spectra were acquired for all samples using zg30 pulse program with 128 scans, 0.8 s relaxation delay, 8.25 μs pulse width and a spectral width of 16 kHz ($^1\text{H} \delta$ -3.11–16.02). Spectra were normalized to TSP, and we integrated peaks corresponding to 10 distinct lipid classes, as outlined in [Table S2](#). Additionally, to facilitate our statistical comparison of indices, we calculated the total sum of the relative abundance across all lipid classes, representing the overall quantity of lipids in the whole liver.

Statistical analysis

All statistical analyses were performed using R version 1.4 (R Core Team 2015). To understand the effect of starvation on condition indices, we conducted analysis of variance (ANOVA) tests for each response variable ($N=17$; [Table 1](#)). We used a model with treatment and sample period (and their interaction) fitted as fixed effects, and fish length (at sampling) as a covariate. We confirmed normality with Q-Q plots and homogeneity of variance from residual plots (and log-transformed variables where needed). To interrogate correlations amongst the condition indices, we used the *corrplot* function in the *corrplot* package (Wei et al., 2021) to calculate and visualize correlation coefficients based on raw data and focusing on static metrics that can be quantified in standard surveys (i.e., not those that require repeated sampling of the same individual such as proportion mass gain).

RESULTS

Treatment effects

We first interrogate the effect of starvation on the biometric parameters, morphological indices and biochemical indices as a way of understanding how these metrics differ between treatments and how they change through time (i.e., with treatment intensity), primarily to aid interpretation of correlation strength and direction. Starvation had discernible effects on some, but not all, of the response variables. Fish size was an important covariate in 16 out of 17 response variables analysed (the exception was HSI). The consequence of manipulating food differentially affected morphometric and biochemical indices ([Figure 1a–d](#)). Whilst all fish lost mass over the experiment, starvation led to greater loss, particularly during the later sample periods ([Figure 1a](#)). Despite this, the width-to-length ratio was unaffected by starvation ([Figure 1b](#)). Whilst hepatosomatic index was consistently lower in starved fish ([Figure 1c](#)), we did not observe any treatment effects across lipid classes ([Figure 1d](#); see [Figure S1](#) for plots of the 10 separate lipid classes).

Correlations between condition indices

Most indices were positively correlated with one another ([Figure 2](#)). All 10 lipid classes were very highly correlated ($R^2 > 0.95$), so we pooled these into a single measure of the total lipid content to aid visualisation and interpretation (as described above). The width-to-length ratio and girth were

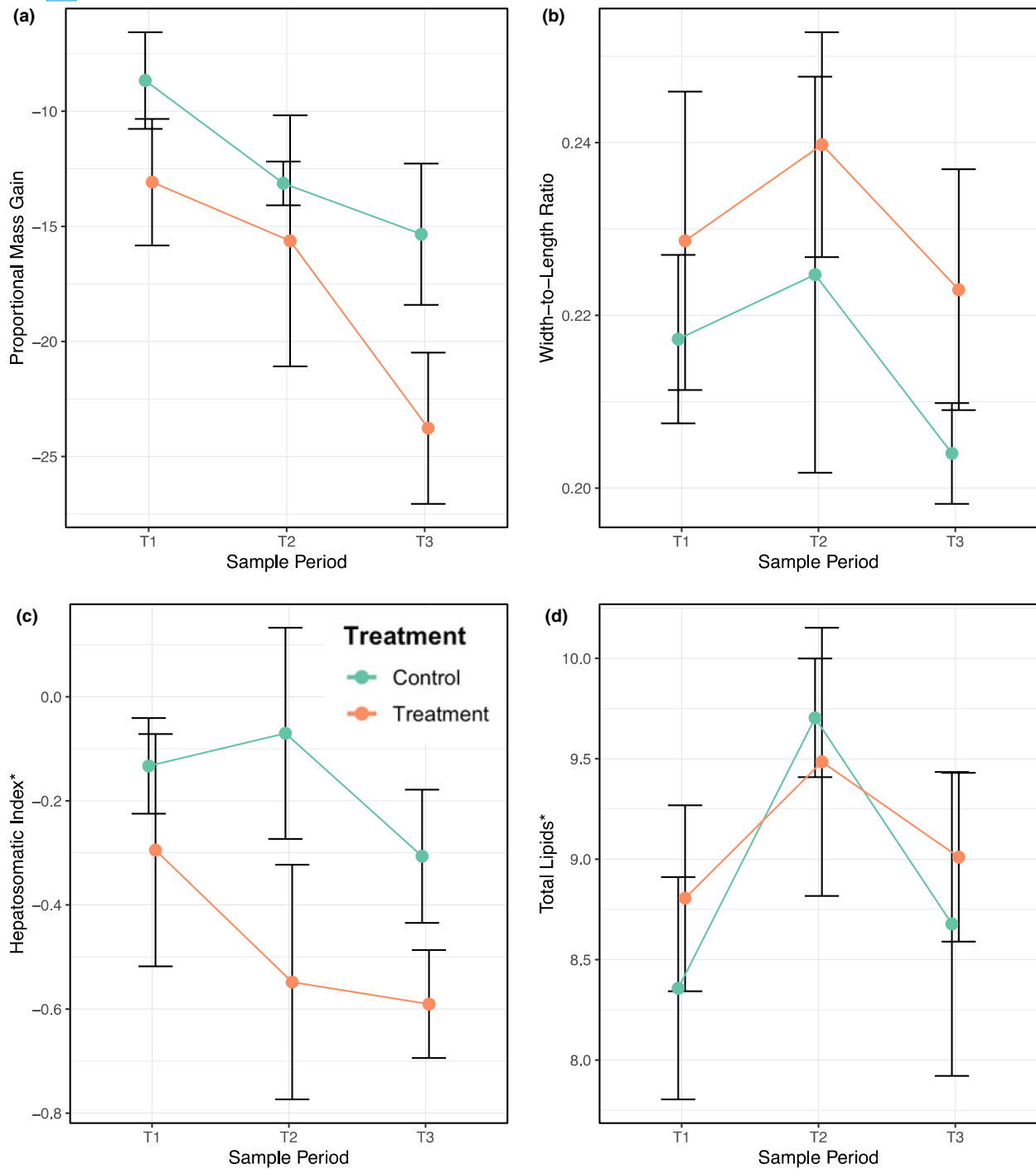


FIGURE 1 Mean (SE) parameter values through time based on model estimates that account for initial fish size. (a) biometric parameter – proportion mass gain (grams); (b) morphometric – width: length ratio; (c) hepatosomatic index; (d) biochemical – total lipids (relative abundance, unitless). Asterisks represent log-transformed variables. T1–T3 represents sample periods at 7, 11 and 14 days, respectively. For ANOVA outputs of all 17 indices, see [Table S2](#). For remaining morphometric plots, see [Figure S2](#).

strongly correlated with most other indices; more so than Fulton's K and Le Cren's relative condition (Kn; [Figure 2a](#)). Fish that had a higher width-to-length ratio (i.e., were fatter relative to length) had a higher-than-expected mass (Kn; $R^2=0.37$) and had higher lipid levels ([Figure 2a](#); $R^2=0.56$). On the contrary, the hepatosomatic index (HSI) was only weakly or uncorrelated with other indices ([Figure 2a](#)). Splitting the data into control ([Figure 2b](#)) and starved ([Figure 2c](#)) groups showed mostly stronger positive correlations between most indices for starved fish.

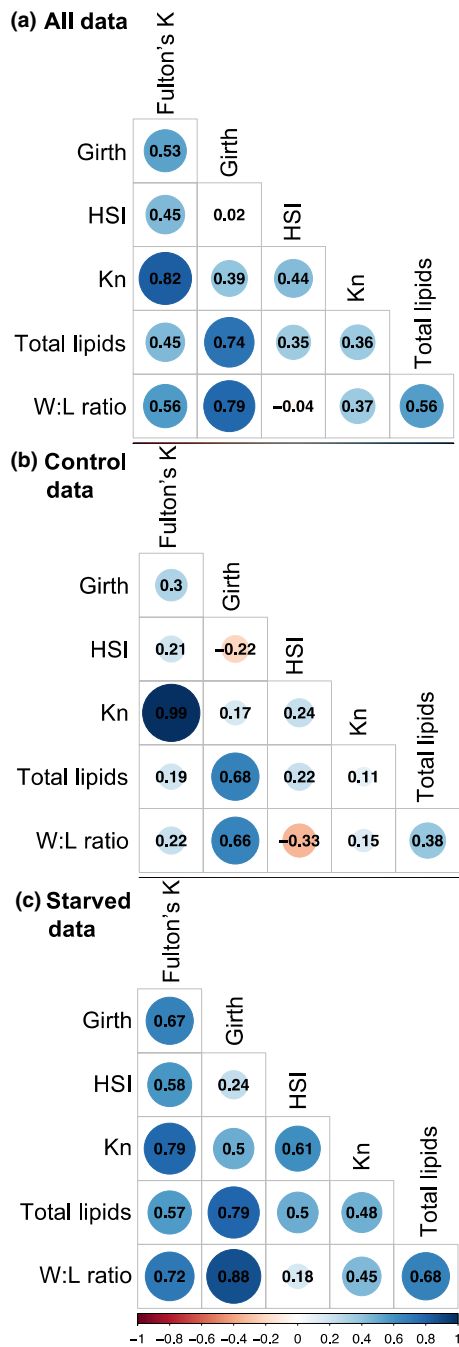


FIGURE 2 Correlations matrices of morphometric and biochemical variables of all data (a), control (b) and starved (c) for yellowfin bream. Total lipids, HSI and girth were log-transformed. The colour of circles indicates the strength of correlation and values within squares represent Pearson's correlation coefficient. Correlation strengths are highly similar for analyses on untransformed data (Figure S3).

DISCUSSION

Reducing feed levels had a rapid effect on some morphometric indices of fish condition, whilst the abundance of hepatic lipids remained unaffected. We identified a suite of important correlations that suggest the use of fast, cheap and non-lethal morphometrics could be used to approximate lipid levels and condition in bream. This is particularly true when approximate rather than precise estimates of condition will suffice and where resources

are limited. Additionally, as non-lethal sampling enables the assessment of individual rates through repeated sampling of uniquely identifiable individuals, using these metrics can increase statistical power in studies where high variation between individuals can mask subtle cause–effect relationships.

Correlations in condition indices

The non-lethal indices that most strongly correlated with lipid levels for juvenile bream were the width-to-length ratio and girth. These indices are related to one another, insofar that they represent some degree of ‘plumpness’. Despite not being widely utilized in the literature, the predictive power of these indices was high and consistent across control and starved groups. Hallier and Gaertner (2008) used thorax girth as a condition index to investigate the effect of fish aggregation devices (FADs) on tropical tuna species (skipjack tuna; *Katsuwonus pelamis* L. and yellowfin tuna; *Thunnus albacares* Bonnaterre 1788). They discovered a positive correlation between girth and growth rate, suggesting that girth was a reliable proxy of condition. Sardenne et al. (2016) employed a similar girth metric, the girth-length index, on the same species (as well as on bigeye tuna; *Thunnus obesus* Lowe 1839), but found no correlation with biochemical indices. Despite few studies validating the utility of girth or width-to-length ratio, our study shows these non-lethal morphometrics may have promise in evaluating fish condition, at least for yellowfin bream.

Relative to width-to-length ratio and girth, the two more ‘traditional’ morphometrics, K and Kn, had weaker correlations with lipids. Further, unlike the width-to-length ratio and girth which require only measuring distance (i.e., length, width, circumference), K and Kn require measuring fish weight, which has additional welfare and logistical implications. The relatively weak correlation between Kn and lipid content in our study is coherent with Brosset et al. (2015), who examined multiple fish species (European anchovy; *Engraulis encrasicolus* L., European pilchard; *Sardina pilchardus* Walbaum, European sprat; *Sprattus spattus* L.) under contrasting reproductive periods. They observed weak correlations between relative condition and lipid content even in a ‘non-reproductive period’, when energy storage strategies were not influenced by reproduction (Brosset et al., 2015). However, others have observed a positive correlation between Fulton’s K and whole-body crude lipid content in an over-wintering experiment with juvenile lake herring (*Coregonus artedii* Lesueur) that manipulated water temperature (Pangle et al., 2005). This may suggest that correlations amongst condition metrics naturally vary across species with different morphologies and physiologies, and highlights the need to test correlations on the study species before adopting specific metrics.

We also quantified the widely used hepatosomatic index, a measure of the weight of the liver relative to that of the fish. Since both the HSI and lipid extraction were from the same organ, we expected to observe strong correlations between these indices, regardless of treatment. Correlations were instead weak. Our findings match those of Schloesser and Fabrizio (2017) who assessed the relationship between indirect (K, Kn and HSI) and direct condition indices (lipid content) in juvenile fishes (summer flounder; *Paralichthys denatus* L., striped bass; *Morone saxatilis* L. and Atlantic croakers; *Micropogonias undulatus* L.). They also found a very weak correlation between HSI and lipid content, to such a degree that morphometric indices were a better predictor of lipid content. These findings could be because the liver may not be the primary storage organ for lipids in juveniles (Litvin et al., 2011). Juvenile fish allocate proportionately more energy for growth than storage relative to adults (Hurst & Conover, 2003), so indices

like HSI may be less suitable for juveniles. Further, given our treatment caused a rapid and considerable reduction in body mass, any effect on the HSI of a simultaneous reduction in liver mass may have been masked (Fitzhugh et al., 2010). For example, a fish that lost 30% of its body mass and 15% of its liver mass would have experienced an increase in its HSI over the experiment, despite absolute reductions suggesting a decrease in condition. In the wild where effects of habitat quality may occur more gradually, HSI may be a more accurate and suitable condition index.

Importance and limitations of manipulating condition

Whilst reducing feed levels did affect some indices of fish condition, other indices were unaffected. We postulated that directly manipulating fish condition might reveal stronger relationships between condition indices than other studies, and we found some evidence of this, whereby correlations were stronger between most indices for starved fish. We can postulate this is due to energy allocation changes or a potential condition threshold, below which all metrics respond to morphological changes more strongly. Whilst most research on relationships between condition indices has involved investigating a single population that has likely been exposed to similar environments and may thus share similar physiological health, one study that did investigate fish condition in populations from habitats of different quality found a significant correlation between the physiological condition of kingfish (*Seriola lalandi* Valenciennes) and the quality of recently occupied habitats (Champion et al., 2020). Ultimately, manipulating condition can provide an opportunity to expose a potential masking effect that occurs when evaluating metrics across individuals of markedly different conditions.

Whilst we advocate the manipulation of condition to better understand and quantify relationships between condition indices, our approach has some caveats. First, we observed a rather high mortality rate (33%) across treatments, and second, whilst starvation did affect some response variables, it did not affect all. This may have resulted from a treatment that was not intense enough, the fact laboratory fish are in a heightened state of stress, an experimental duration that was not long enough, or that certain indices were not indicators of condition in bream, despite being utilized in the literature for other species. Whilst lipid concentrations can respond rapidly to changes in food availability and body condition (McCue, 2010), we did not observe clear differences in lipid concentrations between starved and control fish. This suggests that lipid responses may vary in their sensitivity to short-term dietary changes. For instance, starvation significantly impacts fish, affecting various tissues, including muscle (Johansen & Overturf, 2006), and during periods of starvation, the main sources of energy are the depletion of lipid stores and the breakdown of muscle proteins (Furne & Sanz, 2018). The lack of clear differences in lipid concentrations between starved and control fish in our study could be related to the shorter-term nature of muscle glycogen as an energy reserve, or that starvation was not long enough to elicit a shift to ketosis. A longer starvation period might have had a more pronounced impact on hepatic lipids. Alternatively, investigating correlations at different temperatures, or testing a lower quality food (as opposed to less of the same food source) may reveal additional insights. Building on this, future studies might explore the use of blood or another tissue as indicators of condition, as they could provide insights into longer-term energy reserves in bream under varying conditions. In addition, higher food loads and thus waste could have reduced water quality in the control, masking any effect of food reductions;

however, frequent water changes should have mitigated this. Despite these limitations, our approach provides a robust test of correlations between condition indices that identified several non-lethal, simple and inexpensive morphometrics that can provide useful monitoring information for bream. Further work could manipulate condition in alternative ways such as by adding contaminants (e.g., heavy metals, pollutants, pharmaceuticals and environmental toxins) and evaluating how these manipulations affect the suite of condition indices and their relationships with one another. Finally, there is a clear need to improve how fish condition is assessed overall, including by linking metrics to evolutionary fitness and population dynamics.

Future directions – Using artificial intelligence to supercharge morphometric analysis

There are developing technologies and techniques that can enhance the ethics, logistics and benefits of using morphometrics to monitor fish condition. First, by integrating landmark-based geometric morphometrics and prediction models, we can accurately estimate individual weight or volume without having to physically handle fish. Holmes and Jeffres (2021) digitized anatomical landmarks in images of juvenile Chinook salmon (*Oncorhynchus tshawytscha* Walbaum) and applied predictive models to estimate the wet weight of each fish with a mean error of only 2.9%. Second, the use of artificial intelligence and deep learning to automatically detect and identify fish species from camera footage is rapidly accelerating (Ditria et al., 2020), and similar approaches are being investigated to automate sizing (Shi et al., 2020) and biomass estimation (Zhang et al., 2023). These techniques could be developed to provide width-to-length ratios and estimates of girth without needing to catch fish and impact their welfare (Murphy & Jenkins, 2010). Following confirmation that morphometrics provide reasonable proxies for species-specific condition, such autonomous monitoring could provide a substantial amount of data on the health of populations without capturing and stressing animals.

CONCLUSION

Measuring fish condition is essential for many facets of ecology, and fisheries and aquaculture science, but ethical and logistical considerations mean that many current methods are not ideal. Shifting towards simple-to-measure and non-lethal morphometrics offers a solution, but first requires evaluation and validation. By manipulating the condition of juvenile bream and measuring a range of condition indices encompassing morphology and biochemical condition, we found several important correlations between key indices. Width-to-length ratio and girth were the most reliable proxies of juvenile bream condition (based on lipid analyses). We advocate the manipulation of fish condition when examining relationships between morphometrics and lipid levels to avoid implications such as masked correlations and misinterpretations. Ultimately, several non-lethal morphometric parameters are capable of reflecting lipid levels and providing a useful means for estimating bream condition when precise estimates are not needed.

AUTHOR CONTRIBUTIONS

Beaudee Newbery: Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); visualization (equal); writing – original draft (equal); writing – review and

editing (equal). **Rod M. Connolly:** Conceptualization (equal); funding acquisition (equal); investigation (equal); methodology (equal); supervision (equal); writing – review and editing (equal). **Steve D. Melvin:** Data curation (equal); formal analysis (equal); methodology (equal); writing – review and editing (equal). **Michael Sievers:** Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); resources (equal); supervision (equal); visualization (equal); writing – review and editing (equal).

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DATA AVAILABILITY STATEMENT

Data available on request from the authors.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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