Vol. 659: 199–217, 2021
https://doi.org/10.3354/meps13583

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published February 4

Growth and energy storage responses vary seasonally in the Australasian snapper *Chrysophrys auratus* with only modest changes in aerobic scope

Denham Cook[1,3,4,*], Neill Herbert[2], Alistair Jerrett[1]

[1]Seafood Production Group, The New Zealand Institute for Plant and Food Research Limited, 293-297 Akersten Street, Port Nelson, Nelson 7010, New Zealand

[2]Leigh Marine Laboratory, Institute of Marine Science, University of Auckland, Leigh 0941, New Zealand

[3]*Present address:* Faber R&D Ltd, PO Box 8330, Cherrywood, Tauranga 3110, New Zealand

[4]*Present address:* University of Waikato Coastal Marine Field Station, 58 Cross Road, Sulphur Point, Tauranga 3114, New Zealand

ABSTRACT: Many temperate marine species cope with profound seasonal changes in temperature. One way in which these species have adapted to these conditions is by adopting life-history traits that employ seasonally dependent growth, maximising growth in the warmer summer period before experiencing a period of negligible growth and maintenance in the cooler winter period. This strategy is considered to ensure that temperate species survive the unproductive winter period. However, in the field of eco-physiology, the inability to grow in low temperature environments is considered to result from physiological limitations on growth and digestion imposed by low aerobic scope (AS). In this study, we investigate the seasonal growth, bioenergetic changes and metabolic oxygen requirements (including AS) of the Australasian snapper (Sparidae: *Chrysophrys auratus*) over natural seasonal cycles. We demonstrate that snapper undergo marked growth over a 7 mo period spanning spring, summer and autumn, then negligible (or even negative) growth in the winter. These growth responses coincide with marked changes in physiological character, including changes in energy storage, body composition, gonadal development and haematological variation. The biological changes observed occur in combination with a broad AS curve that was relatively insensitive to the seasonal temperatures experienced in their natural range. Within this broad AS curve, variations in growth rate could not be explained by changes in AS, and vastly different rates of biological activity were observed despite only modest change in AS availability. The relevance of the oxygen capacity-limited thermal tolerance framework to the seasonal responses of snapper is discussed.

KEY WORDS: Sparid · Bioenergetics · Metabolism · Life history · Respiration

1. INTRODUCTION

Temperature has a profound effect on the physiochemical and biological processes of ectotherms including fish (Hochachka & Somero 2002, Schulte 2015). The ability of fish to match these temperature constraints with their biological requirements is widely considered to be a determinant of the geographic range each species adopts (Hochachka & Somero 2002). While some species generally located in both high (polar) and low latitude (tropical) environments are exposed to relatively small variations in annual temperature, species in mid-latitude (temperate) environments are exposed to substantial annual temperature variation. When seasonal extremes are large and fish remain resident in a geographical

*Corresponding author: denham@faberscience.com

location (rather than migrating to different locations/thermal environments), they will be exposed to these seasonal temperature fluctuations (Healy & Schulte 2012). As opposed to species from stable thermal environments (stenotherms), fish permanently occupying these thermally variable thermal environments possess notable eurythermal tolerance and the capability to modulate biological and physiological processes, ensuring biological fitness (Davison 1984, Schulte 2007, Payne et al. 2016).

In response to variable and marked seasonal temperature differences, many fish show an oscillating growth pattern (Fulton 1904, Pauly 1990). This life-history trait suggests that fish have adapted to predictable seasonal variations by matching environmental temperatures to their biological requirements, maximising growth when seasonal conditions are optimal before switching to an energy-storage and low-growth phase in sub-optimal conditions (Pitcher & Macdonald 1973, Conover 1992, Varpe 2017). In the field of eco-physiology, the inability to grow in sub-optimal temperatures has been considered to relate to the temperature dependence of oxygen uptake that is theorized to limit an animal's capacity to grow, digest and perform behavioural activities—perhaps due to constraints on mitochondrial function (Fry 1947, Metcalfe et al. 2002, Claireaux & Lefrancois 2007, Iftikar & Hickey 2013). This physiological mechanism is widely incorporated within the aerobic scope (AS) framework, and the framework of oxygen- and capacity-limited thermal tolerance (OCLTT; Claireaux & Lefrancois 2007, Pörtner & Knust 2007, Pörtner & Farrell 2008). These frameworks identify that temperature presents a directive forcing on the metabolic oxygen consumption rates of an organism (including maximum and standard or routine metabolic rates) such that optimum temperatures for a species associate with peak values of AS (the difference between standard or routine metabolic rate and maximum metabolic rate), whereas higher and lower temperatures either side of this peak feature reductions in AS, constraining oxygen utilisation by metabolically active tissues and therefore depressing the performance capabilities and biological activity requirements of the fish.

The concepts of AS and OCLTT have been widely adopted as a basis to investigate the thermal performance of fish (in the context of invasion ecology and climate variability) but the applicability of the concept has received increasing recent attention and scrutiny (Clark et al. 2013, Farrell 2016, Pörtner et al. 2017). Numerous researchers have shown that the AS of several species do not conform to the typical bell-shaped curve first described by Fry (1971), instead responding with a steadily increasing, flat or broadened AS response with increasing temperatures (Farrell 2016, Lefevre 2016, Norin & Clark 2016, Poletto et al. 2017). This variety of AS response does not neatly tie into OCLTT theory, as it fails to identify single points of thermal optima and associated pejus temperatures, which brings into question whether AS provides an overarching representation of combined physiological performance in the face of thermal variability (Clark et al. 2013, Norin & Clark 2016). More importantly, the range of elevated AS does not always associate with peaks in organismal performance, such as growth, thus challenging the functional relevance of elevated AS (Gräns et al. 2014). On the basis of such discrepancies, alternative hypotheses have recently been proposed. For example, Clark et al. (2013) proposed the multiple performance–multiple optima theory, whereby multiple physiological processes are performed simultaneously by fish, each having an independent thermal optimum range. The 'plastic floors and concrete ceilings' theory of Sandblom et al. (2016) is another slightly modified theory on this theme. As contemporary research efforts have largely focused on the applicability of the AS concept and OCLTT hypothesis to predicted climate variability, we consider a re-evaluation of how the AS framework applies to the thermal variability associated with present-day seasonal cycles. By focusing on temperate fish, we consider that there is opportunity to investigate how the AS concept is interpreted alongside functionally relevant and seasonally dependent biological processes associated with the fitness, performance and life-history strategy of these eurythermal species.

Amongst the many temperate fishes, the Australasian snapper *Chrysophrys auratus* (Sparidae) is a ubiquitous coastal teleost that possesses a distribution that extends across much of the coastline of New Zealand and Australia (19 degrees of latitude from 23° to 42°S) (Parsons et al. 2014, Wakefield et al. 2015). Like many of the other sparids, which occupy subtropical and temperate habitats throughout the Pacific, Indian and Atlantic Oceans, Australasian snapper encounter a broad range of temperatures across their natural habitat range (approximately 11–25°C), with marked differences in the seasonal temperature extremes experienced in the different locations (Parsons et al. 2014, Wakefield et al. 2015). In association with this relatively broad thermal range, snapper across their New Zealand distribution show the aforementioned high summertime, low wintertime growth pattern (Francis 1994, Sim-Smith

et al. 2013, Wellenreuther et al. 2019, Flikac et al. 2020b). These marked, seasonally dependent growth responses of snapper are considered to be associated with the notably cool seasonal (winter) temperatures experienced at the southern (austral) limits of the species distribution. To understand whether the growth and life-history strategies of temperate species coincide with the ecophysiological AS framework, we sought to investigate the respiratory physiology and bioenergetics strategies of Australasian snapper. This was achieved by a combination of seasonal observations and experimental characterisations (including measuring the growth, physiological condition and metabolic oxygen consumption rates) of a laboratory-reared population of sexually mature (adult) *C. auratus*. These individuals were subject to the natural seasonal temperature regime within the southern range of their geographic distribution, which happened to be the location of the present study (Nelson, New Zealand). Links between these various biological processes were then investigated and interpreted alongside the seasonal performance of the individuals, allowing us to investigate: (1) growth and temperature responses in this species, (2) how other biological processes (i.e. resource allocation) interact with temperature and season, and (3) how these biological activities can be interpreted within the AS framework, and whether AS is a good predictor of life-history performance strategies.

2. MATERIALS AND METHODS

2.1. Fish husbandry and handling

Adult snapper used in this study originated from a tank-based brood population of 27 wild-caught snapper captured from the immediate Tasman Bay region and held at the Plant & Food Research facility in Nelson, New Zealand, in 2006. Fertilised eggs were collected following a natural spawning event (ambient temperature and light conditions) on 10 December 2010, and incubated in a 5000 l tank held at ambient seasonal temperatures. Once hatched, larvae were provided with live feed comprised of enriched rotifers and *Artemia*. This population of fish was then weaned onto an inert feed and grown for the next 3–5 yr as a single tank population within standardised 5000 l tanks (i.e. with regular tank rotations) at densities typically not exceeding 10 kg m^{-3}. Prior to the onset of experimentation, excess, deformed or poor condition individuals were hand graded and then removed from the population on a regular basis (e.g. biannually, ~7 occasions in total) to maintain acceptable stocking densities and population welfare. During rearing, fish were fed to satiation with a diet that included wet fish (squid, mussels, pilchards and jack mackerel), an in-house formulated gel diet (of 21.3% protein, 2.7% lipid, 5.6% carbohydrate, 7.7% ash and 62.7% moisture) and commercial marine fish pellets (Skretting Nova). Fish were held at natural seasonal temperatures and light conditions throughout their life, including the period of growth observation and housing prior to respirometry. Water temperatures in tanks mimicked water temperatures in the Nelson Haven — a semi enclosed tidal inlet in Tasman Bay — from where seawater in the facility was extracted (Fig. 1). Respirometry investigations were performed in the 12 mo preceding the start of growth observations. This ensured that repeated handling of fish for growth assessments did not influence respirometry determinations. The same population/cohort of fish was used for both investigations to limit potentially confounding influences associated with culture history and parental origin, at the expense of maintaining comparable size and age characteristics between both the respirometry and growth assessments.

During respirometry investigations, a single population initially consisting of 395 individuals was retained in tanks of the same 5000 l design and seawater supply characteristics as described above. At

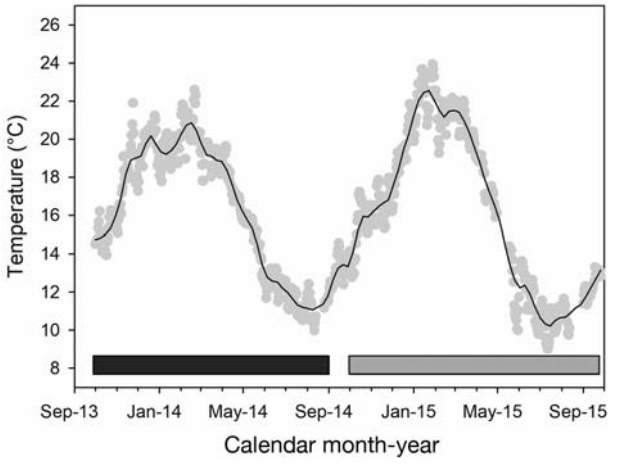

Fig. 1. Seasonal water temperature in the Nelson Haven facility over the 2 yr period overlapping with the present study (September 2013 to September 2015). Raw temperature recordings are depicted with light grey circles, smoothed (Loess transformed) with a black line. Experimental stages and events are presented above the horizontal axis, with dark grey identifying the respirometry phase of investigations, and light grey identifying the growth observation stage of the investigation

target ambient seasonal water temperatures of 12, 15, 18 and 21°C, during both the seasonal warming (winter–spring–summer) and cooling (summer–autumn–winter) phases occurring between September 2013 and July 2014, 6 individual fish were selected for respirometry experiments over a 2 to 3 wk period (required to complete all assessments). Fish exposed to respirometry were selected at random, with the provision that fish were between 300 and 500 g, to ensure a suitable fish size:respirometer volume ratio (and strong respiration signal) and to constrain any potential body size effects. In each instance, respirometry was performed at the ambient seasonal temperature experienced upon removal from their culture tank; thus the temperature at which respirometry was conducted varied by up to 0.5°C at any given reference temperature.

Upon the completion of respirometry investigations, 180 fish from the same population were placed in a new 5000 l tank. Fifty fish were individually PIT tagged (passive integrated transponders, inserted into the intraperitoneal cavity) in September 2014 to enable repeated growth determinations (including specific growth rate, length growth rate and Fulton's condition factor). The remaining 130 fish remained anonymous and were utilised for periodic sampling. Growth observations commenced in October 2014 and continued for a 10 mo period.

For all stages of live animal handling (including tagging, growth determinations and transfer to respirometers), the source tank of fish was anaesthetised with 20 ppm AQUI-S™ (AQUI-S NZ). Anaesthetic induction took between 20 and 30 min before the fish were in stage II–III anaesthesia and able to be gently handled with no observed escape behaviours. This ensured that fish were in as near as possible to a 'resting' state without any metabolic perturbations or reductions in metabolic energy stores that would occur during unsedated handling (Small & Chatakondi 2005).

2.2. Respirometry

All measures of oxygen consumption were obtained using automated, intermittent flow respirometry (Steffensen 1989). Respirometers consisted of cylindrical, 7.5 l volume PVC chambers sealed with detachable clear acrylic end pieces. Each respirometer contained a 1.5 l blanking spacer to limit behavioural activity in the chamber (working respirometer volume = 6 l). A small submersible pump (Mi-mouse) located in an external loop provided continual circulation of water through the respirometers, and passed water directly over a galvanic oxygen sensor (Mini Probe, Oxyguard) and a mixing baffle. Two independent respirometers could be run in parallel while immersed and secured in a larger 200 l freshwater reservoir.

An aerated water supply to the respirometer consisted of 600 l header tank and pressure pump (Eheim 3400 Universal Pump) that supplied UV-sterilised and 10-µm-filtered ambient seawater in a 'single pass' fashion (i.e. not recirculated) to eliminate the potential for metabolic waste build-up. This pressurised supply served to fill and flush seawater through the respirometer units. Precise water temperature control was achieved by passing incoming water through 2 SMO 254 stainless steel plate heat exchangers (WCR). The first heat exchanger was supplied with water cooled by an LTD 6/20 water bath (Grant Instruments), while the second heat exchanger was circulated from the 200 l water reservoir. Further temperature control in the 200 l water reservoir was achieved using a custom refrigeration unit and a GR 150 bath heater (Grant Instruments).

For respirometer measurements, a programme of flush, wait and measurement phases (300, 60 and 300–540 s, respectively) was initiated by a data acquisition unit (DAQ, Powerlab 18/30 ADInstruments) and a custom-built relay and solenoid control system that controlled intermittent water flow through the respirometer via the TTL output and event control functions of the DAQ. Water entering the respirometer passed through a manifold and a set of diaphragm valves (model 514, Georg Fischer) and flow meters (Flowstat ES, AW Lake Company) to ensure that the 2 respirometers were equally and appropriately purged of water (equal to 3 times the respirometer volume) from the preceding measurement phase (Steffensen 1989). Oxygen recording, water supply rates, water temperatures and trigger events were all recorded by the DAQ for later analysis.

The decline in pO_2 during measurement phases was used to calculate the mass-specific rate of oxygen consumption (MO_2) using standard methods described elsewhere (Steffensen 1989, Cook et al. 2013). MO_2 values were used to calculate maximum metabolic rate (MMR), standard metabolic rate (SMR), routine metabolic rate (RMR) and AS. Measures of MMR were calculated upon introduction of the fish into the respirometer and their subsequent recovery from anaesthesia, transfer and the repayment of associated oxygen debt. The duration of recordings were shortened over this period to

between 180 and 170 s to capture the initially high rates of respiration observed over this initial period that fish were introduced to the respirometer. This technique was selected as peak MO_2 rates were comparable to preliminary values from fish actively chased prior to introduction to the respirometer (D. Cook pers. obs.), and values for snapper observed previously (Cook et al. 2011). After measuring MO_2 for 60 h across at least 240 cycles of respirometry, RMR was estimated according to the average of all MO_2 values across that period when chamber O_2 was >85% saturation. SMR was subsequently defined according to the quantile method (Chabot & Claireaux 2008, Cook et al. 2011). A 15% quantile value was selected, as this value typically coincided with the modal value of MO_2 when all data points were plotted in a frequency distribution. RMR was determined as the mean value of respiration recorded throughout the entire duration of respirometry. AS was calculated from the difference between the SMR and MMR of each individual fish, both as a factorial (FAS, MMR:SMR) and in absolute (AAS, MMR − SMR) units. Following each respirometric determination, fish were removed from the chamber, and euthanised using the iki jime technique. Measurements of background respiration were then recorded in the respirometers with the fish removed, to determine bacterial loadings in the respirometer. Bacterial/background respiration in the chamber was negligible at most experimental temperatures, but was up to 2.6% of routine metabolic oxygen consumption rate of individual fish at 21°C. This was accounted for in calculations. Morphometric measurements (length, mass, gonad mass, liver mass, maturation stage) and general condition of fish were then recorded.

2.3. Growth profiling and characterisation

Upon completion of respirometry investigations in June 2014, growth observations commenced in October 2014 (also see Section 2.1). Periodic sampling of fish length (to the nearest mm) and mass (to the nearest gram) was performed with every 3°C change in temperature since the previous sampling event (beginning at 15°C). At each periodic measurement period, 8 anonymous (i.e. untagged) fish were selected at random, terminally sampled using the iki jime brain ablation technique, and then processed for physiological measures (metabolic reserve status, ionoregulatory status and proximate body composition; see Section 2.4).

2.4. Sample collection and biochemical analysis techniques

Physiological and biochemical determinations were performed on all individuals terminally sampled during growth observations (beginning in October 2014). Following euthanisation, a 2 to 3 ml sample of mixed whole blood was collected from the caudal vein of fish using 21 gauge hypodermic needles and EDTA-treated vacutainers (BD), then placed on ice. Whole blood was centrifuged (3900 rcf, Hettich Universal 320R with a 1324 rotor) at 4°C, for 5 min and replicate samples of 200 µl blood plasma was aliquoted into 1.5 ml cryovials (Nunc Cryotube, Thermo Fisher Scientific) and then stored at −80°C for later analysis of plasma metabolites. Six successive white muscle tissue samples were then immediately taken from the D-muscle block immediately anterior to the dorsal fin, freeze clamped between aluminium plates pre-cooled in liquid nitrogen, then wrapped in aluminium foil and stored at −80°C until analysis.

Plasma osmolarity was determined from freeze-thawed plasma samples using a Wescor vapour pressure osmometer (Vapro 5520, Wesco). Ketones were measured on a portable blood analyser (Freestyle Optimum Neo, Abbot Group) that has not yet been validated for fish. Plasma glucose and ammonia were measured using commercially available enzymatic assays kits (Megazyme K-Amair and K-Gluc, Food Tech Solutions), with the assays performed and analysed in a 96-well microplate format (Clariostar, BMG Labtech).

Analysis of glucose, glycogen and lactate from white muscle and liver involved homogenisation of tissue samples in a bead mill (BBX24B, Next-Advance). Approximately 0.1 g of homogenised tissue was diluted in 0.5 ml ice-cold 0.6 M perchloric acid (containing 30% methanol). Following centrifugation, removal of the pellet and neutralisation with potassium hydroxide, the supernatant was stored at −80°C prior to analysis. Tissue glucose analysis was performed using the assays and tissue preparation steps described above for blood plasma. Plasma protein was measured using the BCA protein assay (Peirce, Thermo Fisher Scientific) in 96-well plate format. Tissue protein was quantified by first preparing 60 µg of finely diced white muscle tissue in 1500 µl of extraction solution (T-PER Thermo Fisher Scientific) and mechanically disrupted in a bead mill before centrifugation and collection of supernatant. Tissue lactate was analysed using commercially available enzymatic assays kits (Megazyme K-Late,

Food Tech Solutions). Glycogen (as glycosyl units) was determined on thawed tissue samples as per the methods of Keppler & Decker (1974), which involves the enzymatic breakdown of glycogen using the enzyme amino-glucosidase in a bicarbonate buffer. White muscle moisture content was measured by freeze-drying samples and calculating moisture content according to the relative mass of tissue remaining ([dry tissue mass/wet tissue mass] × 100). Tissue lipid concentrations were analysed in pooled samples of white muscle from 4 individuals at each sampling point (n = 2 per sampling interval). Lipids were extracted from white muscle using a modified Bligh and Dyer extraction protocol (Bettjeman et al. 2018).

2.5. Growth determinations, condition indices and maturation characterisation

Measurements of fish growth were performed between September 2014 and September 2015, and performed as described in Section 2.1. Growth was calculated as absolute growth rate (GR, g d^{-1}), specific growth rate (SGR, % body mass d^{-1}) and length-growth rate (LGR, mm d^{-1}) according to Eqs (1–3):

$$\mathrm{GR} = 100\frac{M(t_1) - M(t_0)}{\Delta t} \quad (1)$$

$$\mathrm{SGR} = 100\frac{\ln M(t_1) - \ln M(t_0)}{\Delta t} \quad (2)$$

$$\mathrm{LGR} = 100 \times \frac{L(t_1) - L(t_0)}{\Delta t} \quad (3)$$

Morphometric indices (including hepatosomatic index, gonadosomatic index, viscerosomatic index, spleen somatic index and visceral fat accumulation) were determined from 8 terminally sampled individuals collected at each sampling interval, as described in Section 2.1. Condition indices including Fulton's condition factor (CF), and organosomatic indices including gonadosomatic index (GSI), hepatosomatic index (HSI), splenosomatic index (SSI), viscerosomatic index (VSI) and cardiosomatic index (CSI) were calculated according to Eqs (4 and 5):

$$\mathrm{CF} = 100 \times \frac{M}{L^3} \quad (4)$$

$$\text{Organosomatic index (\% body mass)} = 100\frac{\mathrm{OM}}{M} \quad (5)$$

where M is mass (in g), L is length (in cm), t is time (of measurement, either t_0, t_1 or Δt), and OM is organ (liver, spleen, viscera, heart) mass.

The maturation stages of snapper were ascribed macroscopically according to the criteria of Jackson (2010). For females, a 6-stage classification system (immature, resting, developing, developed, spawning and spent) was used, whereas for males a 5-stage classification system (immature, resting, developed, spawning and spent) was adopted.

2.6. Data presentation and analytical methods

Seasonal temperature data were collected, then presented in raw form, and also smoothed with a Loess transformation for presentation purposes. Respirometric data were analysed with a 2-way ANOVA, with time point (date) and fish mass treated as the first and second order treatment variables, respectively. Response variables passed homoscedasticity and normality requirements on all but 3 occasions, in which cases data were log transformed.

Respirometric outcomes were log transformed to account for the expected curvilinear relationship with temperature, and then plotted. Seasonal temperatures were presented both as the temperature at the point of measurement and as the mean temperature experienced in the 28 d prior to analysis (Giomi et al. 2016). Seasonal temperature (°C) is therefore denoted as either measurement temperature or mean proximate temperature (°C), accordingly. Determinations of Q_{10} values were calculated using the standard equation $Q_{10} = (K_2/K_1)^{10(t_2-t_1)}$ where K_1 and K_2 are the mean of oxygen consumption rate data at the temperatures t_1 and t_2, respectively.

Fish growth responses (length and mass) from the repeated sampling of fish identifiable by PIT tag were investigated with a linear mixed model (LMM). The model treated time point and temperature as treatment variables, and fish ID (i.e. PIT tag identifier) as a random effect. Both treatment variables were centred. Fish growth responses were also plotted against seasonal temperature and analysed with a linear regression for presentation purposes.

Fish growth responses were compared to respirometric outcomes at comparable nominal measurement temperatures, upon the assumption that the respiratory character of snapper is representative of adult (mature) snapper and therefore applicable to snapper up to 1 yr older in age (during which growth observations were collected). Data were then analysed with linear regressions.

Fish morphometric indices and biochemical/metabolic properties were also analysed with 2-way

ANOVA, with time point and sampling order (i.e. order of dissection and sampled collection) treated as the first and second order treatment variables, respectively. Sampling order, which was considered relevant as time can have a known effect on post-mortem changes in anaerobic metabolite concentrations, was uniformly identified to have no statistically significant effects on outcomes. Response variables that did not meet homoscedasticity and normality requirements were log transformed.

Most statistical analyses and figure generation were performed in SigmaPlot (V12.5. Systat Software). Analysis using LMMs was performed in Genstat (V20.1, VSN International). Statistical significance was accepted at $p < 0.05$.

3. RESULTS

3.1. Seasonal temperatures

Seasonal temperatures over the duration of the experiments ranged between extreme values of 8.9 and 24.0°C. Mean water temperature in the period September 2013 to September 2014 (where respirometry investigations were performed) was 16.3°C, whereas mean temperature between September 2014 and September 2015 (when growth characterisations and morphometric sampling was performed) was 16.0°C. Annual variations in the seasonal temperature range were slight yet apparent between these 2 time frames. Daily temperature data are portrayed in Fig. 1, and summary values are reported for particular sampling events in relevant tables.

3.2. Oxygen consumption

Measurements of MO_2 recorded over a period of 3–4 d showed a typical response, with elevated rates of MO_2 recorded upon introduction to the respirometer, followed by more settled respiration patterns in the >60 h period of observation and measurement. Steadying values of MO_2 identified that more than 2 d was required for determinations of SMR, RMR, MMR and derived AS metrics. Time point and the associated seasonal temperature significantly influenced numerous measures of oxygen consumption in snapper, including SMR, RMR and MMR. AS showed a relatively broad and flat non-linear response to season, with AAS showing a very slight peak in the warmer summer (February to March) period. A more pronounced inverted non-linear response was seen for FAS, with a more obvious peak across the cooler months of July to October (Fig. 2). Differences in the FAS and AAS response identify a relative increase in maintenance metabolic processes (or SMR) relative to MMR.

Plots of seasonal temperature against log-transformed values of SMR, RMR and MMR identified significant temperature effects when expressed as both measurement temperatures and proximate temperatures (Fig. 3, Table 1). Differences in metabolic rates (SMR, RMR and MMR) between the warming and cooling seasonal phases were considered to be negligible.

Size metrics of fish utilised during respirometry (including mass and length) were comparable between sampling events ($F = 1.85$, $p = 0.13$; and $F = 0.06$, $p = 0.676$, respectively; Table 1). Variations in organosomatic indices (including CF, HSI and GSI) varied on a seasonal basis ($F = 4.00$, 7.07 and 2.87, all $p > 0.05$; Table 2) and were considered acceptable given the nature and intention of the study design. Sex ratios varied between temperature-specific sample sets; however, this random outcome was not of sufficient statistical power to allow further analysis.

3.3. Q_{10} responses with seasonal temperature changes

As described above, metabolic oxygen consumption rates (including SMR, RMR, MMR and AS) all varied with temperature. Rates of change (or Q_{10} values) ranged from 1.7 to 6.6, 0.7 to 17.7, 1.2 to 3.4, and 1.2 to 3.4 for SMR, RMR, MMR and AS, respectively,

Table 1. Statistical parameters describing the relationship (of the form $f = y_0 + a \cdot x$) between temperature and $\log_{10}$-transformed metabolic rate calculations in snapper as determined throughout the annual seasonal cycle (approximately 10–21°C) and depicted in Fig. 3. SMR: standard metabolic rate; RMR: routine metabolic rate; MMR: maximum metabolic rate

Reference temperature	Metabolic rate	y_0	a	r^2	F	p
Measurement	SMR	−22.87	19.92	0.82	24.07	<0.01
Measurement	RMR	−35.68	24.49	0.93	69.81	<0.01
Measurement	MMR	−81.47	39.82	0.81	22.10	<0.01
Proximate	SMR	−23.86	20.13	0.86	3.50	<0.01
Proximate	RMR	−33.79	23.27	0.84	27.12	<0.01
Proximate	MMR	−79.31	38.65	0.77	17.56	<0.01

at each incremental temperature change throughout the season (Table 2). The largest Q_{10} values were observed in summer and autumn.

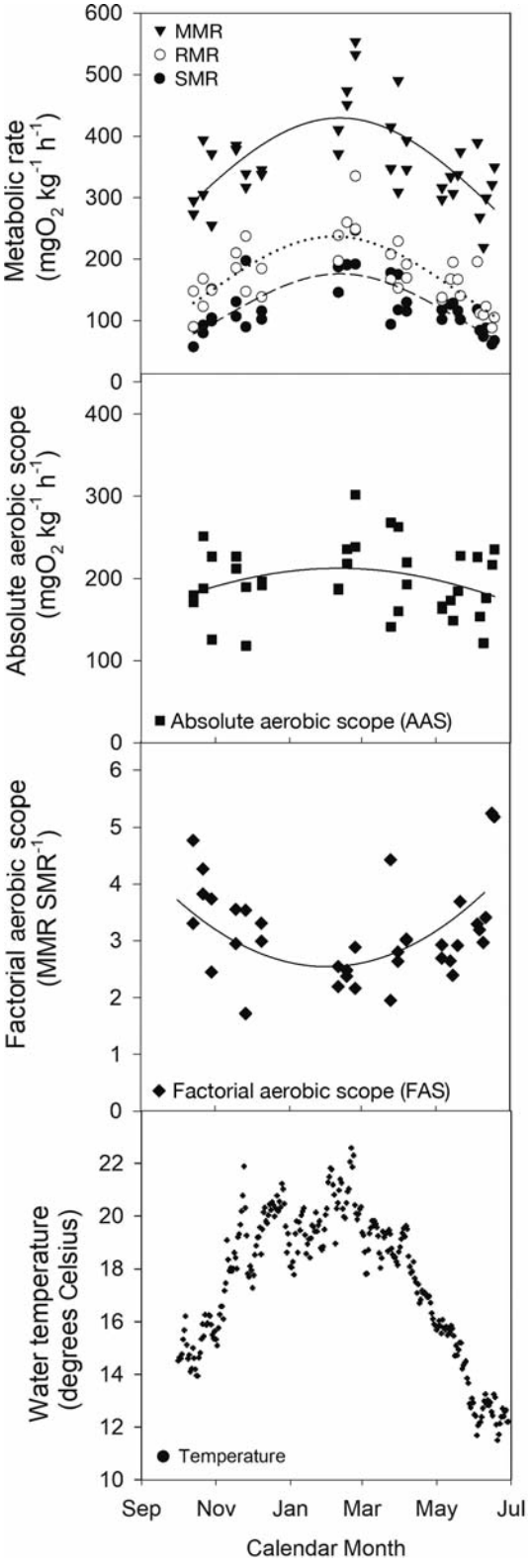

Fig. 2. Metabolic oxygen consumption rates of snapper at different seasonal time periods (where December–February represents the austral summer). SMR: standard metabolic rate; RMR: routine metabolic rate; MMR: maximum metabolic rate. Mathematical relationships between seasonal time point and temperature are presented for visualisation purposes and are described with non-linear regressions according to the formula: $f = a \cdot \exp(-0.5((x-x_0)/b)^2)$, where: SMR (broken line), a = 146.8, b = 94.4, x_0 = 41679, r^2 =0.62; RMR (dotted line), a = 197.4, b = 104.4, x_0 = 41674.4, r^2 = 0.59; MMR (solid line), a = 358.0, b = 137.9, x_0 = 41679.1, r^2 = 0.43; AAS, a = 209.9, b = 245.1, x_0 = 41662.0, r^2 = 0.06. FAS was described in the form $f = y_0 + ax + bx^2 + cx^3$, where y_0 = 99371.8, a = –3.89, b = 1.5E^{-1}, c = 5.03E^{-10}

3.4. Growth profiling

Throughout the 12 mo period of observation, 4-yr-old snapper grew from an average of 286 to 339 mm fork length, and 507 to 860 g (Table 3). Both sampling time point and temperature were found to have significant effects on length- and mass-based growth, with significant interactions between the 2 terms detected (Table 4). Peak mean mass over the investigated period was observed to be 886 g, indicating that fish lost mass in the later stages of observation. This mass loss was identified during sampling in June and July, so negligible growth (expressed in g d^{-1}, % body mass d^{-1} and mm d^{-1}) occurred between May and September. Growth in mature snapper therefore occured predominantly over a 7 mo period when temperatures were greater than 12–15°C.

When growth rate was compared with seasonal temperature (warming and cooling phases separated) in terms of both temperature at measurement (Fig. 4A,C) and mean proximate temperature (Fig. 4B,D), a set of linear relationships was identified. When partitioned according to seasonal phase, notable hysteresis between growth rates in the seasonal warming and cooling phase was identifiable when interpreted alongside the measurement temperatures of the sampling event, but was not present when interpreted alongside the proximate temperature (Fig. 4A–D).

Organosomatic indices (including liver, gonad, visceral mass, spleen and visceral fat) all varied in statistically significant fashion throughout the season (Table 5). GSI, VSI and SSI were all elevated in the warmer summer period compared with the winter, while HSI and visceral fat contents were higher in the winter. CSI was observed to vary by a small (but statistically significant) amount, peaking in the autumn. CF measurements were variable and not significant.

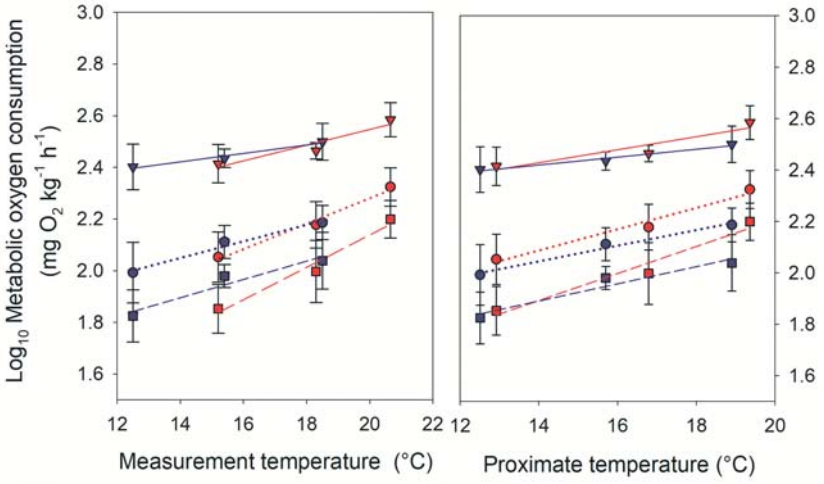

Fig. 3. Relationships between metabolic oxygen consumption (SMR, RMR and MMR) and temperature (expressed as both measurement and proximate temperatures). Squares, circles and triangles represent SMR, RMR and MMR, respectively. Error bars represent 95% confidence intervals. Blue data points and regressions indicate measures determined during the seasonal cooling phases (e.g. summer–autumn–winter), while red data points and regressions indicate measures recorded during the seasonal warming phase (winter–spring–summer). Linear regressions are presented for visualisation purposes only with SMR depicted with a broken line, RMR depicted with a dotted line and MMR depicted with a solid line

3.5. Interaction between aerobic scope and growth

To examine whether the aerobic metabolic potential of snapper was linked to (and therefore a potential driver of) growth rate differences in snapper, the SGR of snapper at each of the nominal measurement temperatures was compared against AAS (Fig. 5A) and MMR (Fig. 5B) at comparable temperatures. SGR increased linearly with AAS, but the correlations were far from statistically significant during both the seasonal warming ($r^2 = 0.40$, $F = 0.666$, $p = 0.56$), and cooling phases ($r^2 = 0.66$, $F = 1.94$, $p = 0.40$) (Fig. 5A). SGR also appeared to increase in a linear fashion with MMR during the seasonal warming, but not significantly ($r^2 = 0.85$, $F = 12.67$, $p = 0.17$). In contrast, SGR appeared to decrease in a linear fashion

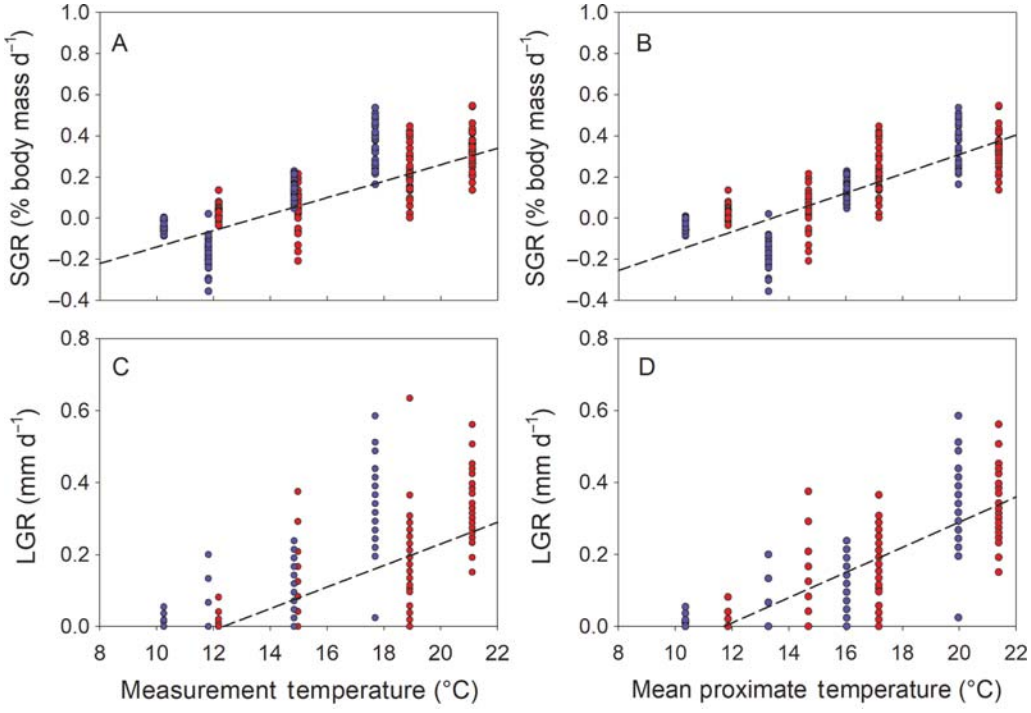

Fig. 4. Temperature–growth relationship of adult snapper expressed as both (A,B) specific growth rate (SGR) and (C,D) length-growth rate (LGR). Temperature was expressed as both the temperature at the time of measurement (measurement temperature) and mean temperature experienced since the preceding sampling event (proximate temperature). Blue data points indicate measures recorded during the seasonal cooling phases (e.g. summer–autumn–winter), while red data points indicate measures recorded during the seasonal warming phase (winter–spring–summer). Linear regressions are presented for both the seasonal warming and cooling phases to assist with visualisation. Some data points overlap

Table 2. Summary values of oxygen consumption characteristics and morphometric descriptors of snapper at different seasonal time periods and temperatures. Mean values are reported with 95% confidence values contained in brackets. All values for respirometry are expressed in units of mg O_2 kg^{-1} h^{-1}. Q_{10} values were calculated with reference to the measurement temperature of the preceding measurement event. Reproductive state refers to a general description of the reproductive conditions observed amongst those individuals that underwent respirometry. Sex ratio refers to the sex of fish according to the convention female:male:immature. SMR: standard metabolic rate; RMR: routine metabolic rate; MMR: maximum metabolic rate; AAS: absolute aerobic scope; CF: condition factor; HSI: hepatosomatic index; GSI: gonadosomatic index; N: no. of individuals sampled.

Sampling period	Measurement temperature (°C)	Season	Mean proximate temperature (°C)	Fish mass (g)	Length (mm)	SMR	RMR	MMR	AAS	Q_{10} (SMR)	Q_{10} (RMR)	Q_{10} (MMR)	Q_{10} (AAS)	CF	HSI	GSI	Reproductive state	Sex ratio	N
October	15.2 (0.29)	Spring	13.2	329.6 (86.4)	257.7 (22.4)	72.5 (11.2)	115.1 (18.5)	263.0 (36.85)	263.0 (36.9)					1.88 (0.11)	1.03 (0.12)	1.50 (0.90)	Immature, developing	5:0:1	6
November–December	18.30 (0.19)	Spring–summer	16.4	274.1 (25.7)	240.8 (7.3)	102.9 (27.6)	153.2 (24.8)	292.1 (17.4)	190.0 (32.9)	3.1	2.5	1.4	0.35	1.95 (0.11)	0.94 (0.17)	2.05 (0.81)	Developing, in spawn	5:1:0	6
February–March	20.65 (0.11)	Summer–autumn	19.4	345.0 (33.3)	258.2 (9.4)	160.1 (21.4)	213.6 (30.0)	388.1 (46.7)	228.0 (33.4)	6.6	4.1	3.4	2.17	2.00 (0.11)	0.61 (0.11)	1.26 (1.03)	Immature, developing, in spawn	3:2:1	6
March–April	18.50 (0.14)	Autumn	19.5	351.1 (46.1)	256.0 (14.1)	112.3 (22.9)	115.1 (19.1)	319.6 (42.9)	207.3 (50.7)	5.2	17.7	2.5	1.65	2.09 (0.11)	0.99 (0.51)	1.23 (0.58)	Developed, in spawn, spent	4:2:0	6
May	15.35 (0.43)	Autumn	16.8°C	368.1 (33.3)	257.7 (8.8)	95.9 (7.7)	130.6 (15.9)	273.1 (18.4)	217.2 (24.9)	1.7	0.7	1.6	0.86	2.15 (0.08)	1.46 (0.22)	0.38 (0.16)	Developed	5:0:1	6
June	12.50 (0.15)	Winter	13.4°C	380.2 (42.2)	260.0 (10.5)	68.4 (13.5)	101.6 (25.2)	256.6 (40.1)	188.2 (36.3)	3.3	2.4	1.2	1.65	2.16 (0.10)	1.64 (0.30)	0.47 (0.19)	Developed	3:3:0	6

with MMR during the cooling phase but, again, the relationship was far from significant ($r^2 = 0.87$, $F = 6.79$, $p = 0.23$; Fig. 5B). No link between SGR and aerobic metabolic capacity was therefore evident.

3.6. Maturation indices

During the growth trial, snapper were observed to be approaching spawning condition in September, whereupon evidence of female gonad development was observed (Table 5). Females were in either a developing or a developed state between October and February, after which they entered a resting gonad maturation phase. No females were observed in a spawning state, while 2 females in a spent spawning state were observed in April. Males were observed to be in a developed state from October and were in either developed or in-spawn states of maturation between December and April, after which they returned to a resting state.

3.7. Haematological characteristics and metabolic energy stores

Biochemical changes were pronounced throughout the seasons. Plasma osmolarity, plasma ketones and plasma glucose protein were all statistically elevated in the warmer summer months, whereas plasma protein was statistically and subtly higher in the winter period. Plasma ammonia was highest in the spring. Similar statistically significant changes in tissue metabolite concentrations were also observed, whereby white muscle protein, glycogen and lipid, as well as liver glycogen, were all highest over the winter period. Only plasma glucose and white muscle lactate were statistically unchanged across sampling periods (Table 6). Tissue moisture content varied over a narrow (but statistically significant) band, with no particular seasonal trends.

Table 3. Seasonal growth responses of adult snapper. Mean values are reported with 95% confidence values contained in brackets. Values of growth rate (GR) are expressed as g d^{-1}, specific growth rate (SGR) is expressed as % body mass gain d^{-1}, while length-growth rate (LGR) is expressed as mm d^{-1}. N: no. of individuals sampled

Sampling period	Nominal temperature range (°C)	Mean proximate temperature (°C)	Temperature at measurement (°C)	Sampling day	Mass (g)	Length (mm)	GR	SGR	LGR	N
September	12.81		12.81	0	507.1 (58.3)	285.7 (6.2)				50
October	12–15	14.46	14.97	24	542.0 (63.6)	289.7 (10.6)	1.16 (1.27)	0.13 (0.07)	0.18 (0.28)	41
December	15–18	17.17	18.91	76	654.3 (93.9)	306.9 (13.0)	1.70 (0.50)	0.27 (0.06)	0.26 (0.06)	37
February	18–21	21.39	21.11	149	784.2 (101.8)	326.0 (12.2)	2.16 (0.34)	0.31 (0.04)	0.30 (0.04)	37
April	21–18	20.37	17.69	190	874.8 (108.4)	336.6 (11.9)	2.32 (0.63)	0.29 (0.07)	0.27 (0.08)	33
May	18–15	16.04	12.84	232	885.8 (103.5)	338.4 (12.2)	0.05 (0.78)	0.02 (0.31)	0.08 (0.03)	33
June	15–12	13.28	11.82	247	880.4 (104.3)	338.9 (13.1)	−1.64 (2.72)	−0.06 (0.13)	0.01 (0.02)	33
July	12–9	10.36	10.25	302	864.4 3 (109.3)	40.2 (10.9)	−0.48 (0.21)	−0.06 (0.03)	0.01 (0.01)	32
September	9–12	11.86	12.18	351	860.7 (77.3)	338.9 (13.1)	0.09 (0.12)	0.02 (0.11)	0.01 (0.01)	29

Table 4. Results from the linear mixed model used to investigate the effects of time and temperature on the seasonal growth responses of adult snapper. N: number of variables; $Sigma^2$: residual variance model; SE: standard error; Num. df: numerator degrees of freedom; Den. df: denominator degrees of freedom; *F*: *F*-statistic (or Wald statistic)

Response variable	N	Variable	Random effects		Fixed effects				
			$Sigma^2$	SE	Variable	Num. df	Den. df	*F*	p
Mass	331	Fish ID	9826.0	833.0	Time point	1	293.0	707.8	<0.001
					Temperature	1	284.8	15.6	<0.001
					Time point × Temperature	1	281.6	50.7	<0.001
Length	331	Fish ID	84.0	7.1	Time point	1	285.0	1821.9	<0.001
					Temperature	1	280.8	39.5	<0.001
					Time point × Temperature	1	279.1	77.6	<0.001

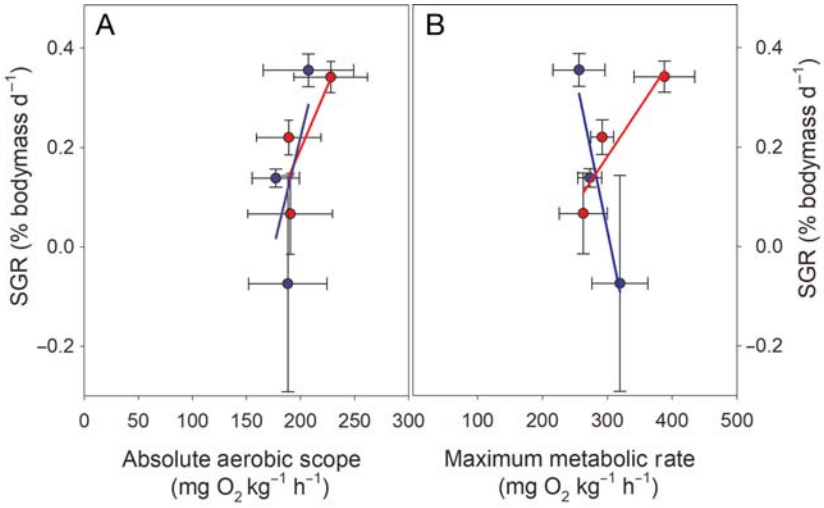

Fig. 5. Correlation between specific growth rate (SGR) and (A) absolute aerobic scope and (B) maximum metabolic rate of snapper at nominal seasonal measurement temperatures investigated. Blue symbols indicate measures recorded during the seasonal cooling phases (e.g. summer–autumn–winter), while red symbols indicate measures recorded during the seasonal warming phase (winter–spring–summer). Error bars represent 95% confidence intervals. Linear regressions are presented for both the seasonal warming and cooling phases in the same colour scheme described

Table 5. Seasonal morphometric indices and reproductive characterisations of adult snapper. Mean values are reported with 95% confidence values contained in brackets. 'Trend' identifies biochemical indices with trends that are: high in summer and low in winter (SH–WL), low in summer and high in winter (SL–WH) or variable (Var.). Values denoted with an * indicate a statistically significant difference from reference (October) values. Statistical significance is accepted at $p < 0.05$. CF: condition factor; HSI: hepatosomatic index; GSI: gonadosomatic index; CSI: cardiosomatic index; VSI: viscerosomatic index; SSI: splenosomatic index; N: no. of individuals sampled

Sampling point	Nominal temperature range (°C)	Mean proximate temperature (°C)	Temperature at measurement (°C)	CF	HSI	GSI	CSI	VSI	SSI	Visceral fat	Reproductive stages observed	Sex ratio	N
October	12–15	14.46	14.97	2.17 (0.05)	1.90 (0.39)	2.64 (0.47)	0.074 (0.007)	1.35 (0.07)	0.060 (0.007)	2.18 (1.71)	Females: developing, developed Males: developed	5:3:0	8
December	15–18	17.17	18.91	2.20 (0.06)	1.18 (0.20)*	5.55 (1.63)*	0.070 (0.006)	1.59 (0.17)*	0.085 (0.019)	0.79 (0.83)	Females: developing, developed Males: developed, in spawn	3:5:0	8
February	18–21	21.39	21.11	2.21 (0.04)	1.25 (0.31)	4.33 (0.47)*	0.067 (0.006)	2.96 (0.35)*	0.089 (0.016)*	1.96 (0.84)	Females: developing, developed Males: developed	3:5:0	8
April	21–18	20.37	17.69	2.24 (0.05)	1.01 (0.17)*	2.50 (0.84)	0.060 (0.008)	3.80 (0.69)*	0.082 (0.008)*	15.91 (7.85)*	Females: spent, resting Males: resting	6:2:0	8
May	18–15	16.04	12.84	2.28 (0.11)	1.36 (0.21)	1.15 (0.34)*	0.080 (0.012)	3.41 (0.24)	0.080 (0.016)*	20.34 (8.07)*	Female: resting Male: resting	5:3:0	8
June	15–12	13.28	11.82	2.20 (0.04)	1.30 (0.22)	0.81 (0.27)*	0.056 (0.007)	1.47 (0.26)	0.056 (0.005)	20.50 (5.12)*	Females: resting Males: resting	6:2:0	8
July	12–9	10.36	10.25	2.20 (0.0)	1.53 (0.49)	1.13 (0.36)*	0.067 (0.015)	1.23 (0.12)	0.063 (0.012)	20.14 (6.22)*	Females: resting Males: resting	3:5:0	8
September	9–12	11.86	12.18	2.20 (0.2)	2.12 (0.51)	1.15 (0.27)*	0.070 (0.006)	1.11 (0.30)	0.060 (0.007)	18.95 (7.52)*	Females: resting, developing	8:0:0	8
Trend					SL–WH	SH–WL	Var.	SH–WL	SH–WL	SL–WH			
F				1.085	4.50	22.29	2.51	43.76	5.49	10.15			
p				0.387	<0.001	<0.001	0.027	<0.001	<0.001	<0.001			

4. DISCUSSION

4.1. The biological activities of snapper associate with distinct phases of temperature change

The current research clearly showed that snapper undergo a marked and rapid reorganisation of their whole biology/physiology across the 4 seasons of the year that occurs with significant progressive shifts in water temperature at the temperate latitude of the South Island, New Zealand. Whole-animal growth processes varied (as expected) on a seasonally dependent basis, with maximal growth observed in the summer period and low growth in the winter, matching the same seasonally dependent patterns observed during ecological observations of wild juvenile (0+ age class snapper) and subadult snapper (<3+ year classes) (Francis 1994, Sim-Smith et al. 2013), as well as many other temperate species (Metcalfe et al. 2002, Olsen et al. 2006, Gillanders et al. 2012). The seasonal variations observed in the present study dictate that snapper are exposed to 2 periods of relatively stable temperatures at the extremes of their seasonal temperature window (summer: 20–23°C; winter: 9–12°C) and 2 intermediate periods of unstable temperature in autumn and spring, which are characterised by changes of 9–10°C over a 10 wk period (of both the warming and cooling seasonal phases). This natural regime thus does not compare with classical experimental thermal exposure protocols, which include either acute (e.g. 1°C h^{-1} for up to several hours) or chronic stable conditions (e.g. 6 wk at a fixed temperature; see also Morash et al. 2018). Exposing snapper to this natural seasonal cycle under laboratory conditions was thus deemed ecologically relevant and highly insightful, despite presenting a reduced degree of control over experimental variables.

Table 6. Ionoregulatory, metabolite and compositional changes in adult snapper. Mean values are reported with 95% confidence values contained in brackets. †Reduced samples sizes of n = 2 apply to white muscle (WM) lipid analyses. 'Trend' identifies biochemical indices with trends that are: high in summer and low in winter (SH–WL), low in summer and high in winter (SL–WH), high in spring only (SprH), variable (Var.), or no trend present (NT). Values significantly different from October reference values are denoted with an *. Statistical significance is accepted at $p < 0.05$. N: no. of individuals sampled

Sampling period	Nominal temperature range (°C)	Mean proximate temperature (°C)	Temperature at measurement (°C)	Plasma osmolarity (mOsmol l^{-1})	Plasma ketones (mmol l^{-1})	Plasma protein (mmol l^{-1})	Plasma ammonia (mmol l^{-1})	Plasma glucose (mmol l^{-1})	WM protein (g 100 g^{-1} ww)	WM glycogen (mmol g^{-1})	WM lactate (mmol g^{-1})	Moisture (%)	WM lipid (%)†	Liver glycogen (mmol g^{-1})	N
October	12–15	14.46	14.97	426.2 (19.4)	0.0 (0.0)	0.7 (0.1)	1.0 (0.3)	7.5 (1.5)	10.6 (1.6)	12.29 (6.9)	5.8 (1.1)	75.0 (0.7)	1.5 (0.3)	392.3 (56.1)	8
December	15–18	17.17	18.91	439.9 (9.3)	0.0 (–)	0.4 (0.1)*	0.5 (0.1)*	4.2 (0.6)*	11.8 (2.4)	3.52 (2.7)*	5.8 (1.1)	77.4 (1.2)*	1.6 (0.6)	69.4 (28.8)*	8
February	18–21	21.39	21.11	409.2 (18.1)	0.3 (0.2)	0.5 (0.1)*	0.6 (0.3)	5.7 (1.8)	13.0 (1.9)	4.7 (4.0)	6.5 (1.0)	76.4 (0.4)*	1.12 (0.0)	119.1 (48.8)*	8
April	21–18	20.37	17.69	427.1 (18.8)	0.8 (0.4)*	0.6 (0.1)	0.6 (0.4)	5.1 (1.8)	14.7 (1.8)	5.0 (2.6)	6.1 (0.8)	75.7 (0.9)	1.9 (0.1)	64.7 (28.6)	8
May	18–15	16.04	12.84	423.6 (13.2)	0.3 (0.1)	0.6 (0.1)	0.5 (0.2)	3.9 (1.4)*	14.0 (3.2)	9.5 (5.5)	6.0 (1.1)	74.9 (0.6)	2.19 (0.1)	222.5 (64.0)*	8
June	15–12	13.28	11.82	398.7 (7.0)*	0.1 (0.0)	0.8 (0.1)	0.5 (0.1)	2.8 (0.6)*	11.4 (2.2)	8.5 (3.8)	6.3 (1.4)	74.9 (0.4)	2.3 (0.4)	269.55 (42.7)*	8
July	12–9	10.36	10.25	408.4 (7.7)	0.0 (0.0)	0.8 (0.1)	0.6 (0.1)	5.0 (2.1)	13.9 (2.2)	13.6 (3.8)	6.2 (1.0)	74.1 (0.5)	2.5 (0.6)	314.1 (55.8)*	8
September	9–12	11.86	12.18	421.6 (15.0)	0.0 (–)	0.9 (0.1)	0.9 (0.2)	3.7 (0.8)*	15.0 (1.8)	13.8 (1.3)	5.8 (1.4)	76.3 (0.4)*	2.0 (0.4)	385.1 (50.5)	8
Trend				SH–WL	SH–WL	SL–WH	SprH	SH–WL	SL–WH	SL–WH	NT	Var.	SL–WH	SL–WH	
F				4.35	13.13	12.93	2.25	3.98	2.05	3.56	0.362	2.25	12.13	31.15	
p				<0.001	<0.001	<0.001	0.045	0.002	0.043	0.004	0.92	<0.01	0.096	<0.001	

4.2. Relationships between growth and temperature interact with seasonality and resource allocation

During warmer seasonal temperatures, snapper showed a marked elevation in growth rate that was most noticeable as temperatures increased above 15°C. Towards the end of this high growth phase, a simultaneous increase in bodily energy reserves (including glycogen and lipid stores) was observed during the autumn period once temperatures were falling from their summer maximum. Therefore, growth appears limited to a discrete part of the year that is approximately 6 to 7 mo long, after which snapper transition to a period of energy storage and biological maintenance/mass loss during the winter period. This energy partitioning strategy of adult snapper has also been observed in young-of-the-year (0+) snapper, which also transition from a period of fast growth over the summer period to a period of energy storage in preparation for winter (Sim-Smith et al. 2013). This observed season of maintenance/mass loss is also associated with marked reductions in feed consumption—as observed in juvenile snapper—despite the continual provision of food items (Flikac et al. 2020b). Further investigations into both the digestive process of snapper in winter, and the regulatory processes of growth and food consumption, are warranted.

An interesting observation from this study is that although the relationship between growth and temperature was positive, there appeared to be seasonal differences, whereby mass-based growth at equivalent temperatures in autumn (the cooling seasonal phase) was greater than in spring (the warming phase). This was apparent when mass-based growth was interpreted alongside measurement temperature and proximate temperature. The relationship between temperature and length-based growth was less clear, suggesting that skeletal growth

showed a more linear response to temperature (particularly with respect to proximate temperature). The hysteresis apparent in the somatic growth of snapper at the 2 comparable but seasonally distinct temperatures suggests that somatic growth is modulated by season.

In the present study, adult snapper were observed to retain lipid and glycolytic energy stores at stable concentrations throughout the winter period, despite a concurrent loss of somatic mass and white muscle dry mass. At the onset of spring visceral lipid and liver glycogen stores decreased abruptly, coinciding with an equally abrupt increase in GSI. This mobilisation of endogenous lipid and carbohydrate presumably occurred in preparation for the spawning season and in response to reproductive hormones triggering gonadal maturation, as has been suggested in other fish species and in line with the capital breeding strategies of fish (for reviews, see Johnson 2009, McBride et al. 2015). As spawning of snapper occurs between 16 and 21°C in Northern New Zealand (Scott & Pankhurst 1992), 18 and 24°C in Southern Australia (Saunders et al. 2012) and 16 and 22°C in the captive population studied herein (D. Cook pers. obs.), snapper exposed to the temperature regimes of the upper South Island of New Zealand can potentially possess a 5- to 6-mo-long spawning season. We argue that the preparatory demands of spawning are key to the relatively lower mass-based growth increments of snapper in spring. The abrupt reallocation of fuel reserves to gonadal tissues, the apparent prioritisation of energy store maintenance above the maintenance of somatic mass, and quantitatively lower rates of somatic growth in spring than in autumn (at comparable temperatures) provide collective evidence that spawning is a profound bioenergetic burden on fish, and that this activity must be carefully balanced against competing fitness demands.

4.3. Seasonally dependent changes in aerobic respiration

In the present study, the various determinations of snapper respiration rate (including SMR, RMR and MMR) increased with temperature. In the context of the local thermal regime, the lowest rates were detected at temperatures representative of the thermal minima (12°C) and the highest at the temperatures representative of the seasonal maxima (21°C). AS was elevated during the summer period when expressed in absolute terms (e.g. AAS), coinciding with the seasonal increase in citrate synthase activity observed in snapper elsewhere (Majed et al. 2002). However, when FAS was calculated, the opposite response was observed, with winter showing the greatest scope. When these changes in the respiration of snapper were analysed with reference to the measured and proximate temperatures, slightly higher correlation values were observed when most metabolic rate metrics were interpreted alongside measurement temperature, rather than the proximate temperature. Perhaps more importantly, no obvious differences were observed between the aerobic metabolic rates of snapper at seasonally distinct but thermally comparable time points, suggesting that seasonality does not influence the respiration rates of fish (as discussed in Norin & Clark 2016).

While both AAS and MMR correlated positively with temperature, the absolute difference between these metrics at their seasonal extremes was relatively small, varying by <25% over the course of the year (and an approximately 10°C temperature span). These small relative changes identify that snapper possess a broad AS curve, which, interestingly, does not associate with particularly high values of FAS (or AAS) compared with those of other species. Snapper possess an FAS of 3 to 4, but, by comparison, other species possess factorial values up to 25 or as low as 2 depending on their ecotype (i.e. pelagic to sedentary lifestyles; Killen et al. 2016, Halsey et al. 2018, Flikac et al. 2020a). The broad and flat AS curve possessed by snapper has also been seen in other highly eurythermic species including mumichogs, Atlantic cod and pink salmon (Clark et al. 2011, Healy & Schulte 2012, Tirsgaard et al. 2015). This broad and flat AS has been suggested to enable these species to perform various biological activities over a larger range of temperatures than species with more pronounced bell-shaped AS curves, at the expense of athleticism (Farrell 2016).

While a positive trend between AAS and MMR with temperature was identified, the opposite trend between FAS and temperature was apparent. This observation that factorial differences in AS are greater in the colder temperatures indicates that standard metabolic costs are much higher in the warmer summer conditions, as also identified by the elevated Q_{10} values observed for SMR (i.e. $Q_{10} > 5.0$). The costs of routine metabolism are equally, if not more so, pronounced in summer (with Q_{10} [RMR] = 2.5–17.7). Changes in the order of $Q_{10} = 2–3$ are considered normal for biological systems, and indicate that an ectotherm is partially compensating for changes in temperatures, whereas values greater

than 3 indicate additive biological effects influencing the temperature-dependent biological rate (Precht 1958). It is clear that the changes in the biological character of snapper during summer temperatures are more profound than the thermal effects on metabolism alone, and these changes in character reflect that additional temperature- and season-related phenomena are occurring.

Two of the additive processes observed to occur in the warmer seasonal period were reproduction and energy deposition. It is important to note that the respirometer-based measures of oxygen uptake in individuals in a reproductive state do not meet commonly held conditions necessary to quantify SMR, which is often required to be determined in ectotherms in a resting (inactive) post-absorptive state and in non-reproductive animals (Chabot et al. 2016). The metabolic costs of reproduction occurring over the summertime period in the present study would have therefore produced elevated measures of SMR (and the associated Q_{10} values). As we did not attempt to disentangle the metabolic costs of gonad maturation and the other metabolic changes associated with reproduction from seasonal temperatures (indeed, in the current observational context it would not be biologically meaningful to do so), the relevance of our summertime SMR measures in mature snapper should ordinarily be treated with caution. Moreover, with values of RMR showing even higher values of Q_{10} than SMR, the metabolic costs of reproduction in snapper are likely to be considerable. When summertime values of respiration (including SMR, RMR and MMR) are excluded because of the likely influence of reproduction, it is apparent that seasonal changes in temperature produced Q_{10} values ranging between 0.7 and 3.4, indicating that the respiratory character of snapper showed complete to partial compensation for temperature throughout seasonal changes. Overall, this highlights that snapper show a considerable ability to respond to and compensate for rapid changes in seasonal temperature experienced in natural conditions, and emphasises their eurythermal tolerance.

An alternative interpretation for the marked changes in summertime Q_{10} values for SMR, RMR and some measures of metabolic state (e.g. tissue glycogen stores) is that the metabolic responses of snapper to temperature are neither linear nor curvilinear (as is assumed when calculating Q_{10} values). In the study of Jerrett et al. (2002), excised white muscle tissue stored at a range of temperatures showed striking changes in various measures of glycolytic metabolism between 16 and 18°C that resembled step functions rather than (curvi-)linear transitions. These step functions suggest that abrupt changes in the anaerobic metabolic processes of snapper occur during transitions between winter (low temperature) and summer (high temperature) thermal conditions, and vice versa. Interestingly, these abrupt shifts in glycolytic activity coincide with noticeable changes in food intake and feeding behaviour (as reported in juveniles of the species) and biological condition (e.g. reproductive development), and occur at temperatures slightly above the onset of maintenance and/or negative growth (present study, Flikac et al. 2020a). Hypothetically, factors such as metabolic suppression that are more often associated with low-oxygen conditions, aestivation and diapause in fish may associate with these transitions (Richards 2010). Although it must be noted here that a study of the marine species *Tautogolabrus adspersus* (cunner), which exhibits winter dormancy and marked reductions in activity during cold exposure, has failed to identify aerobic signatures of such processes (Speers-Roesch et al. 2018). Whether such abrupt metabolic responses to temperature are typical of snapper at the coolest extent of their distribution or their entire distribution, or are common in other temperate marine species, presents an interesting basis for further investigation.

4.4. Interpreting metabolic measures and growth in light of AS theory and the OCLTT hypothesis

Within the OCLTT theory, a core assumption is that shifts in temperature to more optimum temperatures enable fish to overcome physiological limitations in oxygen uptake and increase their biological activity, while shifts away from optimal temperatures impose physiological limitations in oxygen uptake, limiting aerobic performance and biologically important activities (Pörtner & Knust 2007, Pörtner & Farrell 2008). It would therefore be assumed that the seasonal life-history strategy of snapper, which incorporates high rates of biological activity at seasonally elevated temperatures, would agree with the OCLTT theory. While the biological activities of snapper at their seasonal extremes are clearly different — and can be summarised by observations of marked growth, reproduction and energy deposition in the warm seasons, whereas winter is limited merely to maintenance — differences in AS are much less apparent, with only the aforementioned modest (<25%) increase in either AAS or MMR.

Changes in growth are considered one of the foremost biological activities that respond positively to increases in AS, and represent one of the core assumptions of the OCLTT hypothesis. Within this study, changes in growth rate did not match changes in AS, whereby notable increases in growth (from −0.1 to 0.3% d^{-1}) occurred without any meaningful increase in AS (or MMR). This observation resembles that observed in Atlantic halibut, which also show a mismatch between changes in AS and growth (Gräns et al. 2014). While this mismatch may indicate that snapper need to balance competing energetic demands and seasonally dependent activities (e.g. reproduction and energy deposition), which then affect the growth potential and/or AS utilisation of fish, this also highlights that biological consequences of an increase in AS should be interpreted carefully and may not conceptually influence fish in a singular and direct manner. This is in agreement with Fry's notions that performance and associated activities should be viewed broadly, to include numerous forms of physiological work, and that specific biological activities are not optimised to specific temperatures (Fry 1971, Farrell 2016).

A further assumption of the OCLTT hypothesis is that shifts away from optimal temperatures that promote improved aerobic performance and biological activity will be associated with an increased reliance on anaerobic metabolism. While marked decreases in aerobic performance (interpreted according to AS) were not observed during the transition to the low rates of biological activity of snapper observed in winter, there were also no observed seasonal changes in tissue lactate concentrations or a wintertime depletion of carbohydrate energy stores in snapper. Although these findings only provide a preliminary indication of the anaerobic functioning of snapper between seasons, they further demonstrate the relevance of the OCLTT theory to the seasonal thermal regimes and responses of snapper.

Their broad AS curve affords snapper with a relatively high aerobic capacity at cold seasonal temperatures, presenting an obvious energetic advantage by enabling fish to undertake high rates of aerobically fuelled activity (i.e. digestion, locomotion) throughout all seasons. However, this raises the question as to why snapper do not execute energetically demanding activities (e.g. growth) when temperatures are low and AS remains high. Reduced food availability in natural settings could arguably be one driver of reduced growth in snapper at cooler seasonal temperatures; however (as previously mentioned), when provided with unlimited food rations in this and other experimental settings, snapper retained the same low temperature–low growth (and even negative growth) response (Flikac et al. 2020b).

4.5. Ecological implications for snapper

This study showed that the responses of snapper to seasonal thermal cycles are not well described by the OCLTT framework. The interactions between seasonal activity cycles, respiratory physiology and the requirement to perform energetically demanding physiological and fitness processes (e.g. growth and reproduction) are interwoven and not easily disentangled at an organismal level. Laboratory-based investigations (including the present study) often fail to accommodate the numerous responses of fish that can be observed at the ecosystem level. For instance, this experimental investigation fails to account for many behaviours and responses that snapper may be able to perform under natural conditions. This includes, but is not limited to, migratory behaviours that could plausibly enable snapper to locate deeper and subsequently warmer locations that are unaffected by the diurnal cooling/warming cycles and seasonal severity of the shallow coastal environments experienced in this study. While the migratory behaviours of snapper can be described as varied (and therefore question the validity of this assumption), the inability to investigate such phenomena and real-world responses are an obvious limitation of this investigation (Mace & Drummond 1992, Francis 1995, Parsons et al. 2011, Parsons et al. 2014, Fowler et al. 2017).

As an alternative to the OCLTT hypothesis, traits-based ecophysiological models of fish responses to climatic warming (and hypothetically even seasonal thermal cycles) may provide an additive or alternative approach to understanding how physiological process and inter-related concepts including bioenergetics, ecology, thermal biology and/or oxygen limitations can be mechanistically described (Neubauer & Andersen 2019). In this light, some of the observations from the present study can be investigated, including the observation of wintertime negative growth at temperatures representative of those observed in the natural habitat of snapper, the observed mismatch between growth rate and AS, and the marked reductions in biological activity despite the presence of satisfactory AS values. This, in combination with further studies that investigate the seasonal responses of eurytherms (with an increased focus on the low temperature physiology),

may demonstrate how temperate species can occupy and thrive with thermally fluctuating environments that span both sub-optimal and optimal conditions on a predictable annual cycle.

4.6. Summary

Snapper adopt a strategy that balances a variety of biological processes, activities and fitness requirements within a broad and factorially small AS curve that supports reproduction, growth and energy storage in the spring–summer–autumn period, which is then followed by a period of winter maintenance and negative growth. Growth was not the same at equivalent temperatures across the different seasons, and temperature-dependent growth rates were not accompanied by an increase in AS. We argue that these seasonal differences in growth and a mismatch between growth rates and AS relate to different requirements for biological activity that must be balanced at the different times of the year. These observations strongly suggest that the life-history strategy and AS-based OCLTT concept are not mutually applicable to the seasonal responses of temperate species such as the snapper, and alternative conceptual frameworks need to be considered in this context.

Acknowledgements. We thank the following staff of Plant & Food Research (Nelson): Murray Birch for assistance with fabricating the respirometry apparatus; Nicholas Tuckey and Suzy Black for discussion on the topics contained; Therese Well, Sharon Ford, and Warren Fantham for the culture and husbandry of the study animals prior to, and during, the experiments described; Dan Killen and Asli Card for their support during lipid analyses; and Rodelyn Jaksons for her statistical expertise and advice. Experimental manipulations described in this study were performed in accordance with approvals provided by the Nelson–Marlborough Institute of Technology Animal Ethics Committee (AEC2010-PFR-01). The New Zealand Ministry of Business, Innovation and Employment funded the research (MBIE programme: C11X1203).

LITERATURE CITED

Bettjeman BI, Hofman KA, Burgess EJ, Perry NB, Killeen DP (2018) Seafood phospholipids: extraction efficiency and phosphorous nuclear magnetic resonance spectroscopy (^{31}P NMR) profiles. J Am Oil Chem Soc 95:779–786

Chabot D, Claireaux G (2008) Quantification of SMR and SDA in aquatic animals using quantiles and non-linear quantile regression. Comp Biochem Physiol A Mol Integr Physiol 150:S99

Chabot D, Steffensen JF, Farrell AP (2016) The determination of standard metabolic rate in fishes. J Fish Biol 88: 81–121

Claireaux G, Lefrancois C (2007) Linking environmental variability and fish performance: integration through the concept of scope for activity. Philos Trans R Soc B 362: 2031–2041

Clark TD, Jeffries KM, Hinch SG, Farrell AP (2011) Exceptional aerobic scope and cardiovascular performance of pink salmon (*Oncorhynchus gorbuscha*) may underlie resilience in a warming climate. J Exp Biol 214: 3074–3081

Clark TD, Sandblom E, Jutfelt F (2013) Aerobic scope measurements of fishes in an era of climate change: respirometry, relevance and recommendations. J Exp Biol 216: 2771–2782

Conover DO (1992) Seasonality and the scheduling of life history at different latitudes. J Fish Biol 41:161–178

Cook DG, Wells RMG, Herbert NA (2011) Anaemia adjusts the aerobic physiology of snapper (*Pagrus auratus*) and modulates hypoxia avoidance behaviour during oxygen choice presentations. J Exp Biol 214:2927–2934

Cook DG, Iftikar FI, Baker DW, Hickey AJR, Herbert NA (2013) Low-O_2 acclimation shifts the hypoxia avoidance behaviour of snapper (*Pagrus auratus*) with only subtle changes in aerobic and anaerobic function. J Exp Biol 216:369–378

Davison W (1984) Temperature acclimation in the rockfish *Acanthoclinus quadridactylus*. N Z J Zool 11:329–335

Farrell AP (2016) Pragmatic perspective on aerobic scope: peaking, plummeting, pejus and apportioning. J Fish Biol 88:322–343

Flikac T, Cook DG, Davison W (2020a) The effect of temperature and meal size on the aerobic scope and specific dynamic action of two temperate New Zealand finfish *Chrysophrys auratus* and *Aldrichetta forsteri*. J Comp Physiol B 190:169–183

Flikac T, Cook DG, Davison W, Jerrett A (2020b) Seasonal growth dynamics and maximum potential growth rates of Australasian snapper (*Chrysophrys auratus*) and yellow-eyed mullet (*Aldrichetta forsteri*). Aquacult Rep 17: 100306

Fowler AJ, Huveneers C, Lloyd MT (2017) Insights into movement behaviour of snapper (*Chrysophrys auratus*, Sparidae) from a large acoustic array. Mar Freshw Res 68:1438–1453

Francis MP (1994) Growth of juvenile snapper, *Pagrus auratus*. N Z J Mar Freshw Res 28:201–218

Francis MP (1995) Spatial and seasonal variation in the abundance of juvenile snapper (*Pagrus auratus*) in the north-western Hauraki Gulf. N Z J Mar Freshw Res 29: 565–579

Fry FEJ (1947) Effects of the environment on animal activity. Univ Tor Stud Biol Ser 55:1–62

Fry FEJ (1971) The effect of environmental factors on the physiology of fish. Fish Physiol 6:1–98

Fulton TW (1904) The rate of growth of fishes. 22nd Ann Rep Fish Board Scotland, Part III, p 141–240

Gillanders BM, Black BA, Meekan MG, Morrison MA (2012) Climatic effects on the growth of a temperate reef fish from the Southern Hemisphere: a biochronological approach. Mar Biol 159:1327–1333

Giomi F, Mandaglio C, Ganmanee M, Han GD, Dong YW, Williams GA, Sarà G (2016) The importance of thermal history: costs and benefits of heat exposure in a tropical, rocky shore oyster. J Exp Biol 219:686–694

Gräns A, Jutfelt F, Sandblom E, Jönsson E and others (2014) Aerobic scope fails to explain the detrimental effects on

growth resulting from warming and elevated CO_2 in Atlantic halibut. J Exp Biol 217:711–717

Halsey LG, Killen SS, Clark TD, Norin T (2018) Exploring key issues of aerobic scope interpretation in ectotherms: absolute versus factorial. Rev Fish Biol Fish 28:405–415

Healy TM, Schulte PM (2012) Thermal acclimation is not necessary to maintain a wide thermal breadth of aerobic scope in the common killifish (*Fundulus heteroclitus*). Physiol Biochem Zool 85:107–119

Hochachka PW, Somero GN (2002) Biochemical adaptation: mechanism and process in physiological evolution. Oxford University Press, New York, NY

Iftikar FI, Hickey AJR (2013) Do mitochondria limit hot fish hearts? Understanding the role of mitochondrial function with heat stress in *Notolabrus celidotus*. PLOS ONE 8: e64120

Jackson G, Norriss JV, Mackie MC, Hall NG (2010) Spatial variation in life history characteristics of snapper (*Pagrus auratus*) within Shark Bay, Western Australia. N Z J Mar Freshw Res 44:1–15

Jerrett A, Law R, Holland A, Black S (2002) Profiles of New Zealand snapper (*Pagrus auratus*) postmortem metabolism as affected by acclimated temperature and postmortem storage temperature. J Food Sci 67:2843–2850

Johnson RB (2009) Lipid deposition in oocytes of teleost fish during secondary oocyte growth. Rev Fish Sci 17:78–89

Keppler D, Decker K (1974) Glycogen. Determination with amyloglucosidase. In: Bergmeyer HU (ed) Methods of enzymatic analysis, Book 3. Academic Press, New York, NY, p 1127–1131

Killen SS, Glazier DS, Rezende EL, Clark TD, Atkinson D, Willener AS, Halsey LG (2016) Ecological influences and morphological correlates of resting and maximal metabolic rates across teleost fish species. Am Nat 187: 592–606

Lefevre S (2016) Are global warming and ocean acidification conspiring against marine ectotherms? A meta-analysis of the respiratory effects of elevated temperature, high CO_2 and their interaction. Conserv Physiol 4: cow009

Mace JT, Drummond KL (1992) Tasman Bay snapper studied. Catch 9:23–26

Majed SA, Wells RMG, McArdle BH (2002) Seasonal effect on lactate dehydrogenase and citrate synthase in snapper (*Pagrus auratus*). N Z J Mar Freshw Res 36:233–239

McBride RS, Somarakis S, Fitzhugh GR, Albert A and others (2015) Energy acquisition and allocation to egg production in relation to fish reproductive strategies. Fish Fish 16:23–57

Metcalfe NB, Bull CD, Mangel M (2002) Seasonal variation in catch-up growth reveals state-dependent somatic allocations in salmon. Evol Ecol Res 4:871–881

Morash AJ, Neufeld C, MacCormack TJ, Currie S (2018) The importance of incorporating natural thermal variation when evaluating physiological performance in wild species. J Exp Biol 221:jeb164673

Neubauer P, Andersen KH (2019) Thermal performance of fish is explained by an interplay between physiology, behaviour and ecology. Conserv Physiol 7:1coz025

Norin T, Clark TD (2016) Measurement and relevance of maximum metabolic rate in fishes. J Fish Biol 88:122–151

Olsen EM, Knutsen H, Simonsen JH, Jonsson B, Knutsen JA (2006) Seasonal variation in marine growth of sea trout, *Salmo trutta*, in coastal Skagerrak. Ecol Freshwat Fish 15:446–452

Parsons DM, Morrison MA, McKenzie JR, Hartill BW, Bian R, Francis RICC (2011) A fisheries perspective of behavioural variability: differences in movement behaviour and extraction rate of an exploited sparid, snapper (*Pagrus auratus*). Can J Fish Aquat Sci 68:632–642

Parsons DM, Sim-Smith CJ, Cryer M, Francis MP and others (2014) Snapper (*Chrysophrys auratus*): a review of life history and key vulnerabilities in New Zealand. N Z J Mar Freshw Res 48:256–283

Pauly D (1990) Length-converted catch curves and the seasonal growth of fishes. Fishbyte 8:33–38

Payne NL, Smith JA, van der Meulen DE, Taylor MD and others (2016) Temperature dependence of fish performance in the wild: links with species biogeography and physiological thermal tolerance. Funct Ecol 30:903–912

Pitcher TJ, Macdonald PDM (1973) Two models for seasonal growth in fishes. J Appl Ecol 10:599–606

Poletto JB, Cocherell DE, Baird SE, Nguyen TX, Cabrera-Stagno V, Farrell AP, Fangue NA (2017) Unusual aerobic performance at high temperatures in juvenile Chinook salmon, *Oncorhynchus tshawytscha*. Conserv Physiol 5: cow067

Pörtner HO, Farrell AP (2008) Physiology and climate change. Science 322:690–692

Pörtner HO, Knust R (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. Science 315:95–97

Pörtner HO, Bock C, Mark FC (2017) Oxygen- and capacity-limited thermal tolerance: bridging ecology and physiology. J Exp Biol 220:2685–2696

Precht H (1958) Concepts of the temperature adaptation of unchanging reaction systems of coldblooded animals. In: Prosser CL (ed) Physiological adaptation. American Physiological Society, Washington, DC, p 51–78

Richards JG (2010) Metabolic rate suppression as a mechanism for surviving environmental challenge in fish. In: Arturo Navas C, Carvalho JE (eds) Aestivation: molecular and physiological aspects. Springer, Berlin, p 443–485

Sandblom E, Clark TD, Gräns A, Ekström A and others (2016) Physiological constraints to climate warming in fish follow principles of plastic floors and concrete ceilings. Nat Commun 7:11447

Saunders RJ, Fowler AJ, Gillanders BM (2012) The spawning dynamics of snapper (*Chrysophrys auratus*) in northern Spencer Gulf, South Australia. N Z J Mar Freshw Res 46:491–510

Schulte PM (2007) Responses to environmental stressors in an estuarine fish: interacting stressors and the impacts of local adaptation. J Therm Biol 32:152–161

Schulte PM (2015) The effects of temperature on aerobic metabolism: towards a mechanistic understanding of the responses of ectotherms to a changing environment. J Exp Biol 218:1856–1866

Scott SG, Pankhurst NW (1992) Interannual variation in the reproductive cycle of the New Zealand snapper *Pagrus auratus* (Bloch & Schneider) (Sparidae). J Fish Biol 41: 685–696

Sim-Smith CJ, Jeffs AG, Radford CA (2013) Balancing the odds: the relationship between growth and energy storage in juvenile snapper (*Chrysophrys auratus*: Sparidae). Mar Freshw Res 64:1003–1010

Small BC, Chatakondi N (2005) Routine measures of stress are reduced in mature channel catfish during and after AQUI-S anesthesia and recovery. N Am J Aquaculture 67:72–78

Speers-Roesch B, Norin T, Driedzic WR (2018) The benefit of being still: energy savings during winter dormancy in fish come from inactivity and the cold, not from metabolic rate depression. Proc R Soc B 285: 20181593

Steffensen JF (1989) Some errors in respirometry of aquatic breathers: how to avoid and correct for them. Fish Physiol Biochem 6:49–59

Tirsgaard B, Behrens JW, Steffensen JF (2015) The effect of temperature and body size on metabolic scope of activity in juvenile Atlantic cod *Gadus morhua* L. Comp Biochem Physiol A Mol Integr Physiol 179:89–94

Varpe Ø (2017) Life history adaptations to seasonality. Integr Comp Biol 57:943–960

Wakefield CB, Potter IC, Hall NG, Lenanton RCJ, Hesp SA (2015) Marked variations in reproductive characteristics of snapper (*Chrysophrys auratus*, Sparidae) and their relationship with temperature over a wide latitudinal range. ICES J Mar Sci 72:2341–2349

Wellenreuther M, Le Luyer J, Cook D, Ritchie PA, Bernatchez L (2019) Domestication and temperature modulate gene expression signatures and growth in the Australasian snapper *Chrysophrys auratus*. G3: Genes Genomes Genetics 9:105–116

Editorial responsibility: Jana Davis, Annapolis, Maryland, USA
Reviewed by A. Morash and 2 anonymous referees

Submitted: June 16, 2020;
Accepted: November 12, 2020
Proofs received from author(s): January 22, 2021