

Metabolic measurements and parameter estimations for bioenergetics modelling of Pacific Chub Mackerel *Scomber japonicus*

Chenyang Guo¹  | Shin-ichi Ito¹  | Nicholas C. Wegner² | Laura N. Frank³ | Emmanis Dorval³ | Kathryn A. Dickson⁴  | Dane H. Klinger⁵

¹Atmosphere and Ocean Research Institute, the University of Tokyo, Kashiwa, Japan

²Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, CA, USA

³Southwest Fisheries Science Center, Ocean Associates Inc., NOAA, La Jolla, CA, USA

⁴Department of Biological Science, California State University Fullerton, Fullerton, CA, USA

⁵Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, USA

Correspondence

Shin-Ichi Ito, Atmosphere and Ocean Research Institute, the University of Tokyo, 5-1-5 Kashiwanoha, Kashiwa, Chiba 277-8564, Japan.
Email: goito@aori.u-tokyo.ac.jp

Funding information

Nippon Foundation; KAKENHI, Grant/Award Number: JP15H05823 and JP18H03956; U.S. National Science Foundation

Abstract

As a crucial step in developing a bioenergetics model for Pacific Chub Mackerel *Scomber japonicus* (hereafter chub mackerel), parameters related to metabolism, the largest dissipation term in bioenergetics modelling, were estimated. Swimming energetics and metabolic data for nine chub mackerel were collected at 14°C, a low temperature within the typical thermal range of this species, using variable-speed swim-tunnel respirometry. These new data were combined with previous speed-dependent metabolic data at 18 and 24°C and single-speed (1 fork length per second: FL/s) metabolic data at 15 and 20°C to estimate respiration parameters for model development. Based on the combined data, the optimal swimming speed (the swimming speed with the minimum cost of transport, U_{opt}) was 42.5 cm/s (1.5–3.0 FL/s or 2.1 ± 0.4 FL/s) and showed no significant dependence on temperature or fish size. The daily mass-specific oxygen consumption rate (R , g O₂ g fish⁻¹ day⁻¹) was expressed as a function of fish mass (W), temperature (T) and swimming speed (U): $R = 0.0103W^{-0.490} e^{(0.0457T)} e^{(0.0235U)}$. Compared to other small pelagic fishes such as Pacific Herring *Clupea harengus pallasii*, Pacific Sardine *Sardinops sagax* and various anchovy species, chub mackerel respiration showed a lower dependence on fish mass, temperature and swimming speed, suggesting a greater swimming ability and lower sensitivity to environmental temperature variation.

KEYWORDS

bioenergetics modelling, metabolism, oxygen consumption rate, Pacific Chub Mackerel, *Scomber japonicus*, swimming speed, temperature

1 | INTRODUCTION

Pacific Chub Mackerel (*Scomber japonicus*) is a small pelagic fish species widely distributed throughout the coastal areas of subtropical

and temperate transition waters in the Indo-Pacific Ocean (Collette et al., 2011; FAO, 2018). In addition to being a common recreational target off the California coast in the northeast Pacific, chub mackerel also supports significant commercial fisheries, especially in the

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2019 The Authors. *Fisheries Oceanography* published by John Wiley & Sons Ltd

northwest Pacific. In previous decades, stock biomass and landings of chub mackerel have shown large variations, indicating a potential influence of environmental variables on recruitment and stock structure (Yatsu, Watanabe, Ishida, Sugisaki, & Jacobson, 2005). The total estimated chub mackerel biomass was high in the 1970s, but sharply decreased in the 1980s in both the western and eastern Pacific (Crone, Hill, Zwolinski, & Kinney, 2019; Patterson, Pitcher, & Stokes, 1993; Yukami et al., 2019). This fluctuation seemed to correspond with the Pacific decadal oscillation (PDO), which transitioned from a negative to a positive phase sometime in 1976–1977. Following declines in the 1980s, chub mackerel stocks remained at relatively low levels until the early 2000s on both sides of the Pacific. This is thought to be primarily due to oceanographic conditions in the northeast Pacific (Weber & McClatchie, 2012) and recruitment overfishing of some strong year-classes (heavy fishing pressure before the age of maturity) in the northwest Pacific during the 1990s (Kawai et al., 2002). However, chub mackerel biomass has increased in recent years in the northwest Pacific due largely to strong year-class recruitment (e.g., 2004 and 2013 year-class) likely associated with favourable environmental conditions as well as advances in fisheries management and exploitation in Japan (total allowable catch (TAC) system since 1997). Conversely, the biomass of the north-eastern stock still remains relatively low, and current landings are well below the acceptable biological catch (ABC) (Crone et al., 2019; Pacific Fishery Management Council, 2017).

To develop a more effective fisheries management strategy, the dynamics of recruitment and abundance fluctuations of chub mackerel over time need to be quantified throughout the species' geographic distribution. However, the mechanisms driving recruitment success remain largely unknown. Previous studies that focused on environmental influences, growth and recruitment have found that sea surface temperature, prey availability and transport by sea surface currents are important factors during the early life stages (Kaneko et al., 2019; Robert, Castonguay, & Fortier, 2009; Sassa & Tsukamoto, 2010; Watanabe & Yatsu, 2004; Weber & McClatchie, 2012; Yoneda, 2017). The growth rate of chub mackerel larvae has been positively correlated with higher habitat temperature and food availability, and larval distribution in the southern East China Sea has been shown to be affected by the intrusion level of the warm Kuroshio Branch Current (Sassa & Tsukamoto, 2010). For the closely related Atlantic Chub Mackerel (*Scomber scombrus*) in the southern Gulf of St. Lawrence, the high abundance of preferred prey and relatively warm temperature during the larval growth season were shown to influence the emergence of a strong year-class (Robert et al., 2009). Although larval growth appears to benefit from higher temperatures, eggs of higher quality are produced when adult chub mackerel experience relatively low temperatures before reproduction (Kaneko et al., 2019; Yoneda, 2017). As the environment changes with the shift of climatic phase, the interactive effects of these environmental factors may magnify or counteract each other, making it difficult to quantify the importance of each factor on growth and, subsequently, on recruitment.

Because it is usually difficult to obtain in situ observation data that include a comprehensive set of environmental variables, prey conditions and fish growth, all of which are measured and reported on temporal and spatial scales (Ito et al., 2015), individual-based models (IBMs) can be used to better understand stock-recruitment dynamics and to test for mechanisms that produce strong year-classes (DeAngelis & Grimm, 2014; Grimm & Railsback, 2004). As a widely used tool in fisheries science, IBMs have been applied to many fishes, from small freshwater to large pelagic species (e.g., Gibson et al., 2018; Letcher, Rice, Crowder, & Rose, 1996; Rose, Rutherford, Mcdermot, Forney, & Mills, 1999). An integral part of many IBMs is the bioenergetics modelling used to define growth parameters, fish movement and activity (Ito et al., 2004; Rose et al., 2015). Fish growth rates can be based on an energy budget equation that accounts for changes in biotic (e.g., body size and life stage) and abiotic (e.g., temperature) factors (Beauchamp, Stewart, & Thomas, 1989; Kitchell, Stewart, & Weininger, 1977; Railsback & Rose, 1999). Similarly, movement and activity level (including migration) are affected by such factors (Huse & Giske, 1998; Meliá et al., 2013). Although physical oceanic processes are generally well understood and can be successfully modelled, the biological processes of target organisms are less well studied and can be the primary source of uncertainty in developing IBMs (Buckley, 2000). Here, we seek to determine the bioenergetics parameters needed to construct a future individual-based model for chub mackerel.

For small pelagic fishes like chub mackerel, metabolism is usually the largest dissipation term in bioenergetics modelling. Oxygen consumption rate (the aerobic component of metabolic rates) has been measured in chub mackerel over a range of activity levels (swimming speeds) at temperatures of 18 and 24°C (Dickson, Donley, Sepulveda, & Bhoopat, 2002; Sepulveda & Dickson, 2000). As expected, these studies showed that chub mackerel oxygen consumption rate was positively correlated with fork length (*FL*) and swimming speed; for a chub mackerel of a given size, oxygen consumption rate was significantly higher at 24°C than at 18°C. Maximum sustained swimming speed also increased with fish *FL* and with temperature (Dickson et al., 2002). In addition, Klinger et al. (2015) measured routine oxygen consumption rates of chub mackerel at 20°C while investigating the effects of oil on fish respiration. Although Schaefer (1986) indicated that the typical temperature range of chub mackerel is 10–27°C based on chub mackerel distributions, no published study has examined the oxygen consumption rate and swimming performance of chub mackerel at relatively low temperatures (i.e., below 18°C). Low temperature affects muscle performance (Guderley, 2004), reduces sustained swimming speed (Schaefer, 1986; Van Der Lingen, 1995) and reduces oxygen consumption rates in fishes (Beamish, 1964; Clarke & Johnston, 1999; Oligny-Hébert, Senay, Enders, & Boisclair, 2015). Therefore, a bioenergetics model for chub mackerel based only on the existing data at 18°C and 24°C could result in considerable error, especially if used to assess swimming and metabolic performance at temperatures outside that range. Thus, to develop a bioenergetics model with higher accuracy and reliability, it was necessary to conduct additional experiments at lower temperatures to obtain

swimming and oxygen consumption data across a broader range of habitat temperatures typically experienced by chub mackerel.

This study thus measured oxygen consumption rates in chub mackerel swimming at a range of speeds at 14°C using methods similar to those used in previous studies at higher temperatures. These data were then combined with existing data to develop a more complete set of bioenergetic parameters for this species. Specifically, we compiled a large data set of metabolic information for chub mackerel and used it to estimate the parameters of the respiration term used in bioenergetics modelling. We also discuss the metabolism-related parameters of chub mackerel in comparison with those of other small pelagic fishes, including Pacific Herring *Clupea harengus pallasii*, Pacific Sardine *Sardinops sagax*, various anchovy species, Green Jack *Caranx caballus*, Kawakawa *Euthynnus affinis* and California Yellowtail *Seriola dorsalis*, in which oxygen consumption rates have been measured in a similar size range of individuals and at similar temperatures.

2 | MATERIALS AND METHODS

2.1 | Fish collection and husbandry

Chub mackerel (approximately 15–30 cm FL) were collected from the San Diego Ellen Browning Scripps Memorial Pier, Scripps Institution of Oceanography, La Jolla, CA, by hook and line and transferred to a 3200-L holding tank at the NOAA Southwest Fisheries Science Center (SWFSC) experimental aquarium in February 2017 and March 2019. Fish were held at 14–15°C with an 8:16-hr light:dark cycle and were fed with squid and Mazuri gel cubes (krill, astaxanthin and vitamin C) to satiation six days a week. Fish were held in captivity for at least 6 days to resume normal eating and swimming before any experimentation. To exclude the effect of post-prandial metabolism, fish were fasted at least 24 hr prior to the beginning of each respirometry trial.

2.2 | Respirometry

Two Brett-style variable-speed swim-tunnel respirometers (5-L for the fish under 80 g and 30-L for the fish over 80 g; Loligo Systems, Tjele, Denmark) were used to measure the maximum sustainable swimming speed (U_{\max}) and oxygen consumption rate of the chub mackerel at several swimming speeds up to U_{\max} . Temperature within the respirometer was kept constant ($14 \pm 0.2^\circ\text{C}$) through the use of a surrounding buffer tank receiving a constant supply of temperature-controlled seawater. Before beginning the measurement process, each fish was placed in the working section of the swim-tunnel respirometer and allowed to adjust to the respirometer for 2–3 hr to recover from handling and to allow oxygen consumption rate to stabilize (Peck & Moyano, 2016). Because the fish were stressed and swam quickly when first placed in the chamber, the flow speed was set at approximately 50 cm/s during the adjustment period to avoid injury caused by colliding with the chamber wall. The

chamber was partially covered with black plastic to prevent the fish from being startled by the activity of the laboratory staff, while providing enough light for the fish to recognize and adjust to the swim tunnel. Even with this plastic shield, some fish appeared to respond to outside stimuli, occasionally causing them to hit the chamber wall and stop swimming. If this occurred more than three times following the adjustment period, the data from that fish were excluded from further analysis.

After the adjustment period, measurements started when fish could swim in the middle of the chamber without showing any significant signs of stress (such as irregular tailbeat frequency or cessation of swimming) for at least 15 min. Each fish swam for sequential 30-min periods at each speed, starting at 50 cm/s with an interval increase of 8 or 10 cm/s. As flow speed increased, fish eventually changed their swimming style from cruising to “burst-and-glide” swimming, which is characterized by bursts of acceleration that last for a few seconds, followed by brief rests between accelerations. If the swimming style shifted more than 3 times during the 30-min measurement, it was concluded that the fish could not maintain that speed without recruiting the fast-glycolytic muscle to accelerate using anaerobic pathways of ATP production, and the experiment was stopped. U_{\max} for each species was defined as the preceding speed at which the fish maintained normal cruise swimming for the full 30 min (Dickson et al., 2002); U_{\max} is thus lower than critical swimming speed (U_{crit}) values determined by the Brett (1964) formula. At each swimming speed, 5–10 min after the speed was changed, the swimming tunnel was temporarily sealed from the seawater supply from the buffer tank, and the dissolved oxygen concentration (DO) of the water was recorded every 5 s using a Fibox 3 fibre optic oxygen transmitter (PreSens Precision Sensing GmbH). When DO decreased and approached 80% saturation, the DO measurements were temporarily paused, and fresh seawater was flushed into the respirometer from the surrounding buffer tank to achieve nearly 100% oxygen saturation before measurements resumed.

Following respirometry measurements, each fish was removed from the swim tunnel and anesthetized in seawater containing MS-222, and its fork length, total length, girth and mass (wet weight) were measured. The chamber was resealed to measure the background oxygen consumption rate, which was subtracted from the fish oxygen consumption rate. All handling, care and experimentation were approved by the SWFSC Animal Care and Use Committee (protocol #SW1401).

2.3 | Swimming speed correction, oxygen consumption rate and parameter estimation for bioenergetics modelling

The speed of the swim-tunnel respirometer was calibrated prior to measurements on each individual using a vane wheel flow probe connected to a hand-held flow metre (Höntzsch GmbH). Test velocities and fish swimming speeds were corrected for the solid-blocking effect of the vane probe and the fish following Bell and Terhune

(1970). Thus, the actual speeds and the interval increase differed slightly from the originally calibrated speeds.

The relationship between U_{\max} and fish size (mass, fork length) was assessed by linear regression. Oxygen consumption rate ($\dot{M}O_2$, mg O_2 /min) was calculated during each 30-min interval at a given swimming speed by linear regression of water DO versus time. The gross cost of transport (COT, mg O_2 kg⁻¹ m⁻¹) at each speed was calculated by dividing the $\dot{M}O_2$ by the corrected swimming speed and by fish mass in kg.

The daily mass-specific $\dot{M}O_2$ (R , g O_2 g fish⁻¹ day⁻¹) was expressed as:

$$R = \text{SMR} \times \text{activity} \quad (1)$$

where SMR is the standard metabolic rate of each fish at a speed of zero (e.g., Dewar & Graham, 1994), which is a function of body mass (W , g) and water temperature (T , °C):

$$\text{SMR} = a_R W^{b_R} e^{(c_R T)} \quad (2)$$

where a_R is the intercept of the allometric mass function for R and represents the $\dot{M}O_2$ of a 1-g fish at rest at 0°C, b_R is the slope of the allometric mass function for R , and c_R is a coefficient relating water temperature to R . Activity is a function of swimming speed (U , cm/s):

$$\text{activity} = e^{(d_R U)} \quad (3)$$

where d_R is a coefficient for swimming speed versus R .

For each swim-tunnel respirometry experiment, one fish of known weight was studied, and water temperature was maintained constant during the measurement period. Thus, variation in oxygen consumption rate depended only on swimming speed. The swimming speed dependence parameter d_R was estimated for each individual by exponential regression analysis of the relationship between R and U . The distribution of the d_R values was tested for normality or skewness by Lilliefors test. Based on the type of distribution, the value of d_R used in Equation (3) was the average of the normal distribution or the median of the skewed distribution.

Mass-related parameters (a_R , b_R) and the temperature dependence parameter (c_R) were estimated by multivariate non-linear regression after dividing the oxygen consumption rate by the activity effect. Since the number of data points differed greatly among the different temperatures (Table 1), data points were weighted by the reciprocal of the number of measurements at each temperature, to ensure the same contribution to parameter estimation. The weighting ratio at each temperature was 1/93:1/75:1/9:1/6:1/66 for 18, 24, 15, 20 and 14°C, respectively.

To assess the accuracy of the resulting modelled equation for R , we estimated oxygen consumption rate from temperature, fish mass and swimming speed and compared those values to actual oxygen consumption rate values measured in the experiments. The estimation error, E_{err} , was calculated as

$$E_{\text{err}} = \frac{R_M - R_E}{R_E} \times 100\% \quad (4)$$

where R_M was the measured oxygen consumption rate, and R_E was the estimated value.

The optimal swimming speed (U_{opt} , FL/s), which was typically applied in an IBM as the default cruising swimming speed because of its highest efficiency, was defined as the swimming speed with the minimum COT. Since COT can also be estimated with Equation (1) divided by U , U_{opt} was estimated as U where the first derivative of R/U by U becomes zero with the minimum COT.

Unless indicated, all of the linear or non-linear regression analyses used a significance level of $p < .05$ and were applied in MATLAB (version 2017a) using the trust-region algorithm, which is based on the non-linear least-square method.

3 | RESULTS

3.1 | Swimming speed and oxygen consumption rate at 14°C

In total, nine chub mackerel caught in 2017 and eleven caught in 2019 were monitored in the swim-tunnel respirometer, and nine individuals [17.1–30.5 cm fork length (FL), 21.4 ± 4.2 cm (mean \pm SD) and 43.4–252 g] adjusted successfully and provided useful data (Table 2: No. 1–5 from 2017 and No. 6–9 from 2019). The U_{\max} values for these nine chub mackerel at 14°C were 61–106 cm/s or 2.9–6.1 FL/s (Table 2). There was no significant relationship between U_{\max} , expressed either in cm/s or in FL/s, with fish mass or fork length (linear regression). For all nine fish, mass-specific $\dot{M}O_2$ increased exponentially with U , following Equations (1) and (3), and the mean SMR at 14°C was 1.43 ± 0.55 mg O_2 min⁻¹ kg⁻¹ (Figure 1a, Table 2). The gross COT ranged from 0.08 to 0.32 mg O_2 kg⁻¹ m⁻¹, and the minimum COT for each individual occurred at swimming speeds of 38–53 cm/s or 1.6–3.0 FL/s (Figure 1b).

3.2 | Parameter estimation using all available data

Data from this and previous studies (Table 1) were combined to estimate various model parameters. Each individual except one at 24°C showed a significant exponential relationship between swimming speed and oxygen consumption rate (Table 2, Table S1), which was used to estimate the swimming dependence parameter d_R . The value of d_R , ranged from 0.007 to 0.039, was normally distributed (Lilliefors test) and did not differ significantly between temperatures, but showed a negative relationship with fish mass (W) (ANCOVA, $p < .005$). This relationship was as follows:

$$d_R = -0.0000673W + 0.030 \quad (5)$$

with $r^2 = .276$, $p = .002$ (Figure 2). However, this mass dependency relationship was not suitable for extrapolation to larger individuals (greater than 446 g or 30 cm FL) because the value of d_R would be extremely small or even negative with a larger size, which is unrealistic.

TABLE 1 Data set information and references used for bioenergetic parameter estimation for the Pacific Chub Mackerel

Reference	Dickson et al. (2002)	Sepulveda and Dickson (2000)	D. H. Klinger (unpublished)	Klinger et al. (2015)	This study
Location	Coast of southern California, USA				
Individuals	12	12	9	6	9
Fork length (cm)	15.6–26.3 (20.9 ± 4.0)	14.0–24.7 (20.3 ± 3.4)	30.0–33.0 (31.1 ± 0.6)	31.0–32.5 (31.4 ± 0.4)	17.1–30.5 (21.4 ± 4.2)
Mass (g)	34–179	26–156	285–750	430–690	43–252
Temperature (°C)	18	24	15	20	14
Tested speed range (cm/s)	15–98	30–120	30–33	31–33	34–106
Tested speed range (FL/s)	0.8–4.3	1.4–5.9	1.0	1.0	1.3–6.1
Available data points	93	75	9	6	66

TABLE 2 Fork length (FL), mass (W), maximum sustainable speed (U_{max}) and exponential regression Equation (1) of mass-specific $\dot{M}O_2$ (R , $mg\ O_2\ min^{-1}\ kg^{-1}$) versus U (cm/s) derived during chub mackerel experimental trials conducted in this study at 14°C

No.	FL (cm)	W (g)	U_{max} (cm/s)	U_{max} (FL/s)	Exponential fit of R ($mg\ O_2\ min^{-1}\ kg^{-1}$) versus U (cm/s)	r^2	p
1	17.1	43.4	61	3.5	$R = 1.643e^{0.029U}$.977	<.002
2	17.4	45.6	106	6.1	$R = 1.881e^{0.022U}$.992	<.001
3	18.9	56.3	74	3.9	$R = 1.641e^{0.028U}$.942	<.002
4	17.7	54.1	61	3.5	$R = 1.543e^{0.028U}$.954	<.001
5	25.3	149.7	87	3.4	$R = 2.418e^{0.021U}$.936	<.005
6	22.1	114.0	82	3.7	$R = 1.191e^{0.025U}$.982	<.001
7	30.5	252.0	89	2.9	$R = 1.051e^{0.021U}$.979	<.001
8	23.0	123.8	81	3.5	$R = 0.991e^{0.025U}$.987	<.001
9	20.9	94.0	97	4.6	$R = 0.563e^{0.031U}$.995	<.001
Total					$R = 1.694e^{0.022U}$.555	<.001

Therefore, considering the relatively larger variation and the possibility of underestimation for large individuals, the parameter d_R was defined from the expected value of the normal distribution as 0.0235 s/cm.

The new data at 14°C were combined with the previous speed-dependent metabolic data at 18 and 24°C and single-speed metabolic data at 15 and 20°C, to evaluate SMR as a function of fish mass and water temperature (Figure 3). In the best-fitting model, the respiration-related parameters a_R , b_R and c_R were defined as 0.0103 $g\ O_2\ g\ fish^{-1}\ day^{-1}$, -0.490 and 0.0456/°C, respectively ($r^2 = .60$, $p < .001$, RMSE = 0.0009 $g\ O_2\ g\ fish^{-1}\ day^{-1}$). Thus, Equation (1) became $R = 0.0103W^{-0.490} e^{(0.0456T)} e^{(0.0235U)}$ after substituting in all determined parameters. Oxygen consumption rates were estimated using this equation at specific values of temperature, fish mass and swimming speed and then compared to actual R values measured in the experiments. Most of the data points estimated from the equation fell within the 95% confidence intervals of the actual data (Figure 4), and the RMSE of E_{err} was 32% (Figure 5). According to the Equation (1), $R/U = 0.0103W^{-0.490} e^{(0.0456T)} e^{(0.0235U)}/U$, where U_{opt} (U at the minimum COT) was 42.5 cm/s (1.5–3.0 FL/s, or 2.1 ± 0.4 FL/s) regardless of temperature and fish mass.

4 | DISCUSSION

This study obtained new swimming and oxygen consumption measurements for chub mackerel at 14°C that were combined with previous data at warmer temperatures to develop a suite of temperature- and mass-specific parameters that can be used for bioenergetics modelling. In addition, that temperature- and mass-specific respiration equation was used to estimate the optimal swimming speed, which is generally assumed to be the preferred migration speed of a species because of its highest energetic efficiency. This value can thus be incorporated into future IBMs for chub mackerel. In this section, we will discuss potential application of the experimental results to IBMs and the related issues. In addition, the estimated parameters of oxygen consumption will be compared with those available for other small pelagic fish species.

4.1 | Maximum sustainable swimming speed and swimming energetics at 14°C

As a common criterion for assessing the sustainable swimming capacity of a species, U_{max} can be used in an IBM to simulate chub mackerel

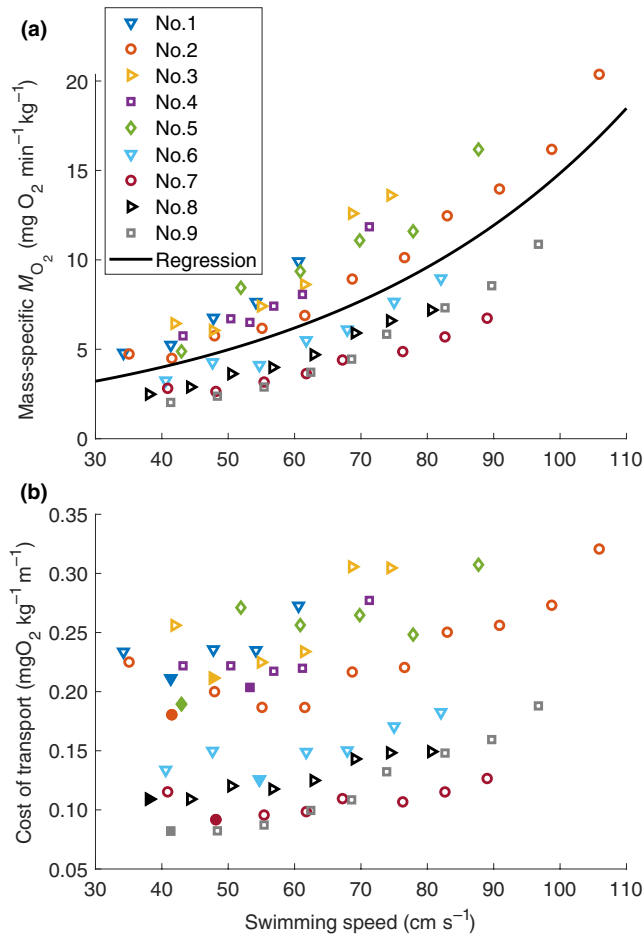


FIGURE 1 Relationship between swimming speed and (a) mass-specific \dot{M}_{O_2} and (b) cost of transport for the nine Pacific Chub Mackerel tested in this study at 14°C. The solid line in (a) represents the exponential regression of mass-specific \dot{M}_{O_2} (R , $\text{mg O}_2 \text{ min}^{-1} \text{ kg}^{-1}$) as a function of U for all data: $R = 1.694 e^{0.022U}$ ($r^2 = .555$, $p < .001$). Solid symbols in (b) are the minimum COT of each trial [Colour figure can be viewed at wileyonlinelibrary.com]

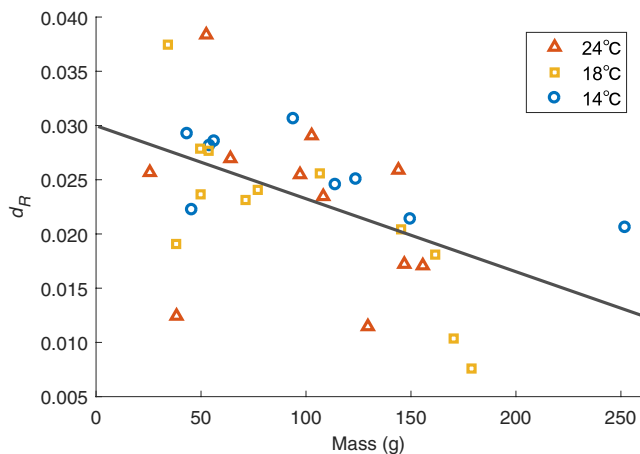


FIGURE 2 Relationship between fish mass and d_R at 14, 18, and 24°C. The solid line represents the linear regression of d_R as a function of fish mass: $d_R = -0.0000673W + 0.030$ ($r^2 = .276$, $p = .002$) [Colour figure can be viewed at wileyonlinelibrary.com]

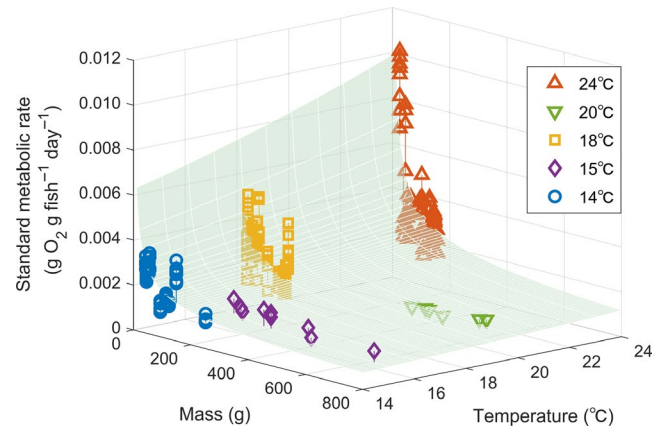


FIGURE 3 Standard metabolic rate (SMR, $\text{g O}_2 \text{ g fish}^{-1} \text{ day}^{-1}$) as a function of fish mass and temperature. The mesh surface shows the fitted relationship between the SMR and temperature and fish mass [Colour figure can be viewed at wileyonlinelibrary.com]

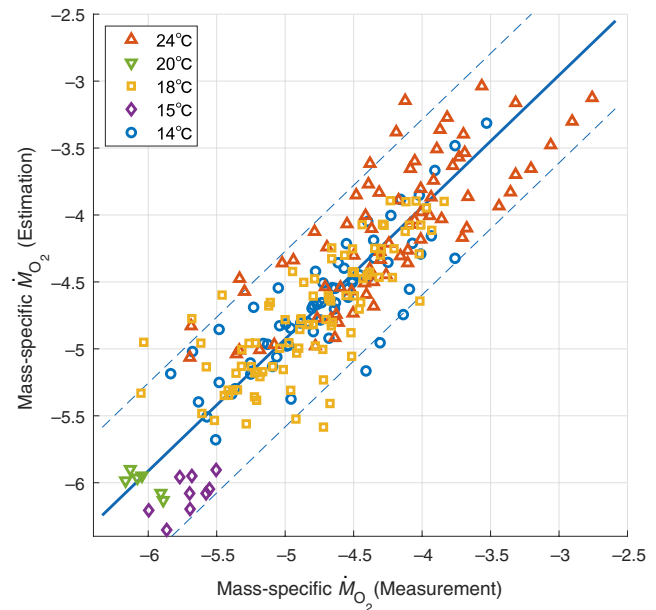


FIGURE 4 Comparison between the logarithmic daily mass-specific respiration rates (R , $\text{g O}_2 \text{ g fish}^{-1} \text{ day}^{-1}$) derived from the experimental measurements and calculated using Equation (1). The solid line is the linear regression using the estimated R (R_E) versus the measured R (R_M): $y = 0.985x$, $r^2 = .741$. The dashed lines represent the 95% confidence intervals [Colour figure can be viewed at wileyonlinelibrary.com]

migration routes and estimate possible distribution areas. U_{\max} at 14°C was 61–106 cm/s for 17.1–30.5 cm FL chub mackerel in the present study, which fell close to the U_{\max} value for 15.6–26.3 cm FL chub mackerel at higher temperatures (52.5–97.5 cm/s at 18°C and 70–120 cm/s at 24°C). Although Dickson et al. (2002) reported a significant increase of U_{\max} with temperature and fish size, at a given fish size, U_{\max} at 14°C did not differ significantly from those at other temperatures (ANCOVA), possibly because of relatively large individual differences, and this should be evaluated carefully before being applied in IBMs.

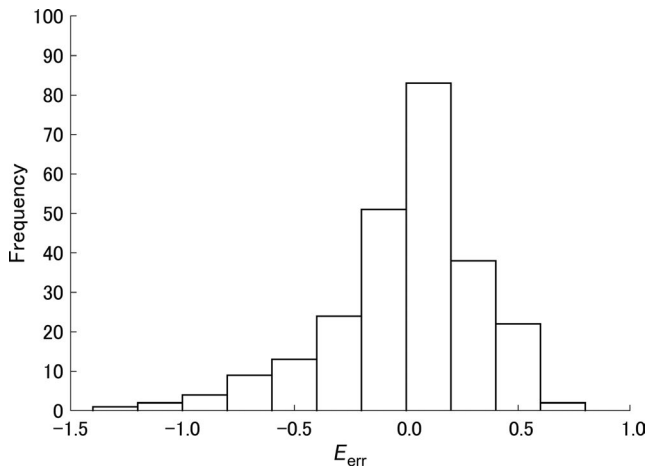


FIGURE 5 Frequency of the estimation error of respiration rate ($E_{err}/100\%$)

Compared with No.1-5, mass-specific $\dot{M}O_2$ and COT at 14°C from No.6-9 were lower, which could basically explained by the mass dependence, as well as the individual difference of the body shape, such as the relationship of fish mass with cross-sectional area (Figure 6). At the same mass, the higher cross-sectional area (e.g., No.5) means higher water drag effect on the individual, which could result in higher mass-specific $\dot{M}O_2$ and COT. To eliminate this effect, we considered the equation:

$$R' = a'W^{b_R} \left(\frac{A_i}{A} \right)^q \quad (6)$$

where R' was the corrected mass-specific $\dot{M}O_2$ ($\text{mg } O_2 \text{ min}^{-1} \text{ kg}^{-1}$), a' was content, b_R was the mass dependence parameter (-0.490), A_i was cross-sectional area (cm^2) of each individual, and A was the estimated cross-sectional area at the same mass which was calculated by power regression of the relationship of fish mass and cross-sectional area:

$$A = 0.291W^{0.724} \quad (7)$$

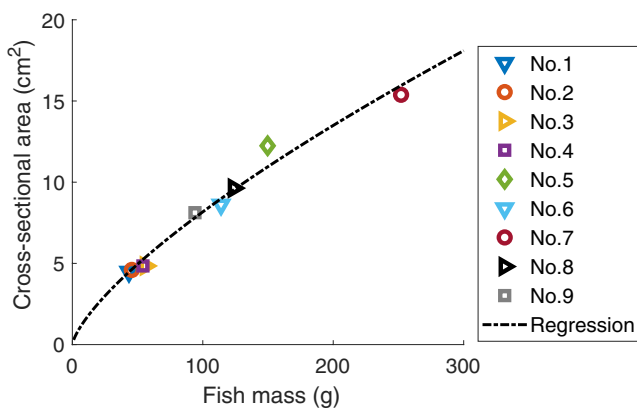


FIGURE 6 Relationship between fish mass and fish cross-sectional area at 14°C. The broken line represents the power regression of fish mass (W , g) and fish cross-sectional area (A , cm^2): $A = 0.291W^{0.724}$ ($r^2 = .977$, $p < .005$)

with $r^2 = .977$, $p < .005$ (Figure 6). Factor q was the correction parameter for the ratio of A_i and A . When $a' = 61.7$ and $q = 1.83$, the multivariate non-linear regression of R' , A_i and W obtained the minimum RMSE (Figure 7). This correction was only applied on the individual tested at 14°C in this study because cross-sectional area data were not recorded from previous studies; however, the effect of fish shape may need to be included into the IBM as an important explanatory variable in the future work.

4.2 | Respiration equation for bioenergetics modelling

In bioenergetics modelling, the swimming dependence parameter (d_R) can be used to assess swimming ability; a low d_R means low oxygen consumption while swimming at a certain speed or high swimming efficiency. Ito et al. (unpublished) estimated d_R for Cape Anchovy *Engraulis capensis* as 0.0553 based on the experiments conducted by James and Probyn (1989), while Megrey et al. (2007) concluded that the d_R of Pacific Herring *Clupea harengus pallasii* adults was 0.0300 based on Klumb, Rudstam, and Mills (2003).

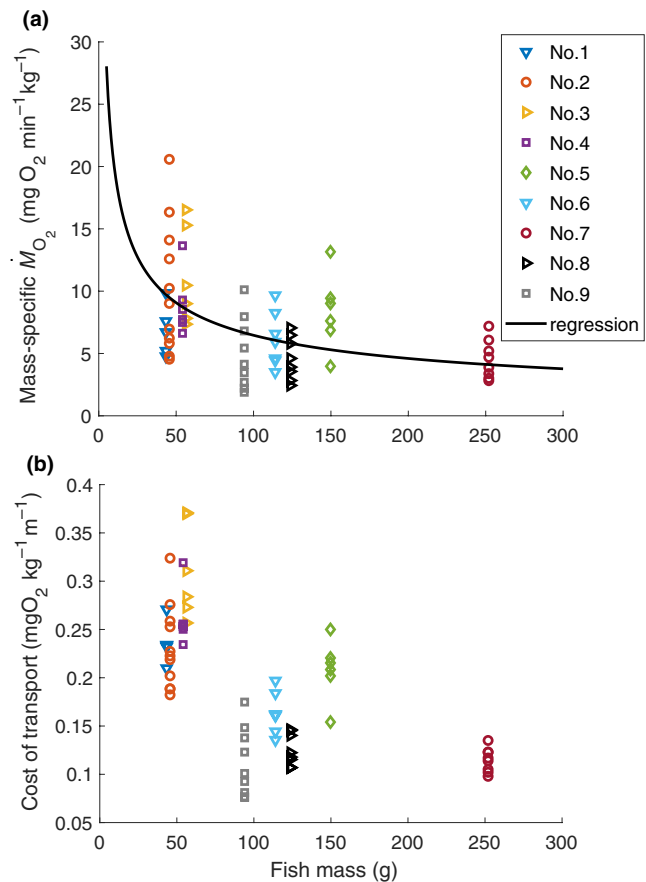


FIGURE 7 Relationship between fish mass and corrected (a) mass-specific $\dot{M}O_2$ and (b) cost of transport for the nine Pacific Chub Mackerel tested in this study at 14°C. The solid line in (a) represents of corrected mass-specific $\dot{M}O_2$ (R' , $\text{mg } O_2 \text{ min}^{-1} \text{ kg}^{-1}$) as a function of W with standard cross-sectional area (following Equation (7)): $R' = 61.7W^{-0.490}$

Compared to those values, the d_R of chub mackerel (0.0231) is the lowest (Figure 8a). This comparison suggests that, among these three small pelagic fish species, which all experience changes in biomass associated with regime shifts or climate change, the chub mackerel is the most efficient swimmer. In most previous bioenergetics modelling studies (e.g., Ito et al., 2004; Megrey et al., 2007), d_R was set as a fixed value that was applied to individuals throughout their entire life history. However, in this study, d_R showed a negative relationship with fish size. Therefore, replacing a fixed d_R with a function incorporating size dependence might have to be considered in the application of IBMs for chub mackerel and other species.

Similarly, the dependence of oxygen consumption rate on body mass (b_R) of chub mackerel (-0.490) was the lowest among

these small pelagic species (Figure 8b). For the European Anchovy *Engraulis encrasicolus ponticus*, b_R was estimated to be -0.34 (Oguz, Salihoglu, & Fach, 2008), whereas for Pacific Herring the value was -0.227 (Megrey et al., 2007). Therefore, compared to Pacific Herring and European Anchovy, mass-specific oxygen consumption rate of chub mackerel decreased more with fish mass, at least for the size range of mackerel examined in this study. Generally, the scaling coefficient of teleost oxygen consumption rate with body size varies between 0.67 and 1.0, as shown for 89 teleost species from various ecological lifestyles (Killen, Atkinson, & Glazier, 2010). Thus, the mass dependence of mass-specific oxygen consumption rate ranges from -0.33 to 0. Among the 89 teleost species examined by Killen et al. (2010), pelagic species with high locomotor requirements tended to have higher metabolic

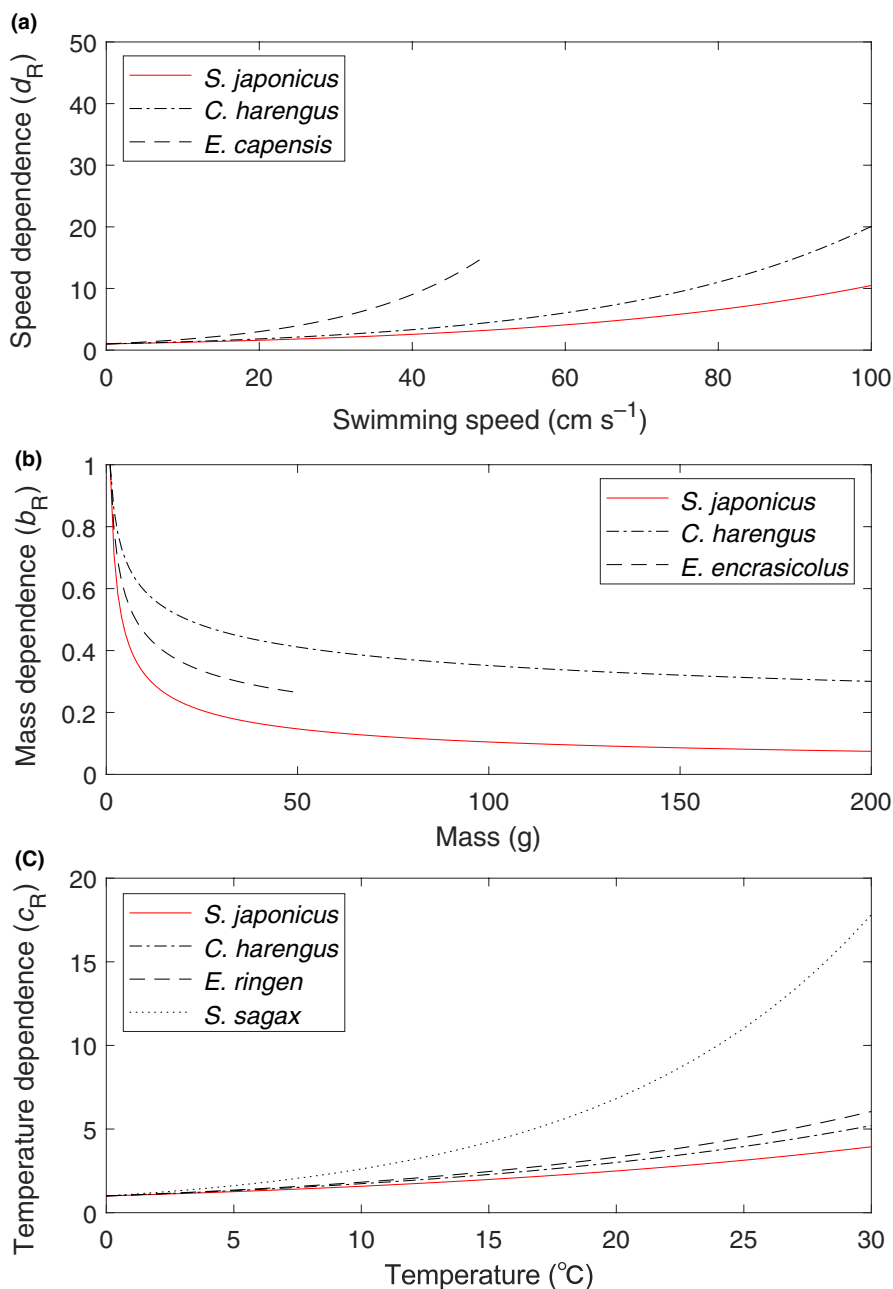


FIGURE 8 Comparisons between Pacific Chub Mackerel and other small pelagic species for (a) swimming speed dependence based on d_R , (b) mass dependence based on b_R and (c) temperature dependence based on c_R [Colour figure can be viewed at wileyonlinelibrary.com]

requirements for a given body size, but a lower b_R than bathyal and benthic species. However, the b_R value of chub mackerel is outside the normal range; it is less than -0.33 , which may reflect the limited size range of mackerel examined in this study and the need for future comparative metabolic data from both smaller and larger individuals. This need is further highlighted by the higher scaling exponent of mass-specific gill surface area with body mass (-0.032) for a wider size range of *S. japonicus* (95.2–740 g) (Wegner, Sepulveda, Bull, & Graham, 2010), which would be expected to scale closely with mass-specific oxygen consumption rate (Wegner, 2011).

In addition to b_R and d_R , fish $\dot{M}O_2$ also varies with temperature, as represented by c_R , which = $\ln(Q_{10})/10$; the higher the c_R or the Q_{10} value, the more sensitive $\dot{M}O_2$ is to temperature changes. Van der Lingen (1995) measured the Q_{10} of the southern African Pilchard *Sardinops sagax* to be 1.82 ± 0.35 ($c_R = 0.060$) at temperatures between 10 and 22°C. Megrey et al. (2007) assumed c_R of Pacific Herring adults to be 0.0548, based on laboratory studies conducted by Klumb et al. (2003). Blaxter and Hunter (1982) assumed c_R of Peruvian Anchoveta *Engraulis ringen* to be 0.0956, which is much higher than values for other small pelagic species. The c_R of chub mackerel determined in this study (0.0419) was the lowest of all of these species, suggesting that, as temperature increases, oxygen consumption rate of chub mackerel increases less than it does in the above species of the same size, indicating that chub mackerel metabolism is less affected by changes in temperature (Figure 8c).

4.3 | Optimal swimming speed

If fish maximize efficiency during routine swimming and migration, they might swim at the lower U_{opt} rather than U_{max} because U_{opt} represents the most efficient swimming speed based on the minimum energetic cost per distance travelled. For oceanodromous species like chub mackerel, which ontogenetically migrate throughout broad areas, swimming at the speeds at which COT is minimal for prolonged periods potentially allows a greater proportion of ingested energy to be allocated for growth and reproduction. Like U_{max} , U_{opt} has also been reported to be affected by fish size and temperature (e.g., Claireaux, Couturier, & Groison, 2006; Videler, 1993), but this was not the case in our study. Within the limited size range of chub mackerel compiled in this study, U_{opt} was 42.5 cm/s regardless of temperature and fish size. This value falls in the minimum COT range of chub mackerel at 14°C, being similar to the estimate of U_{opt} of 44.2 cm/s (2.0 FL/s in 22.1 cm FL) *S. japonicus* at 24°C (Dickson, Donley, Hansen, & Peters, 2012), and much higher than the voluntary swimming speed of 1.2 FL/s by a group of *S. japonicus* of 22–26 cm (26.4–31.2 cm/s) swimming in a tank at temperatures of 12–23°C (Schaefer, 1986). The lower voluntary swimming speed in a tank (when fish are not trying to cover a required migratory distance at the most efficient cruising speed) likely represents the minimum speed required to efficiently

maintain hydrostatic equilibrium and, while less efficient per unit distance travelled, requires less overall energy than swimming at U_{opt} . Besides, while applying U_{opt} as the migration speed in IBM, for the individual outside the size range of chub mackerel in this study, especially for fish larvae or young juveniles (<15 cm FL), the relative value (1.5–3.0 FL/s) may be more reasonable because the absolute value could be too high to reach.

For the interspecific comparison with other pelagic teleosts of similar size, the COT of *S. japonicus* at U_{opt} was calculated by substituting same FL (or TL) and temperature into Equation (1), where the FL was estimated from the fork length–mass relationship of *S. japonicus* tested at varies speed: $W = 0.005FL^{3.2}$ ($r^2 = .961$, $p < .001$). At 24°C, 22.1 cm of mean FL, the U_{opt} of *S. japonicus* was 1.9 FL/s with a COT of 0.24 mg O₂ kg⁻¹ m⁻¹, lower than that of Kawakawa *E. affinis* at 5.0 FL/s with a COT of 0.44 mg O₂ kg⁻¹ m⁻¹ (Dickson et al., 2012). *S. japonicus* also had lower U_{opt} and COT (2.1 FL/s, 0.22 mg O₂ kg⁻¹ m⁻¹) compared to California Yellowtail *S. dorsalis* (19.3 ± 1.4 cm TL) at 3.7 TL/s with a COT of 0.29 mg O₂ kg⁻¹ m⁻¹ (Wegner, Drawbridge, & Hyde, 2018). The lower U_{opt} and COT of chub mackerel suggests they may migrate at a lower swimming speed with higher efficiency compared to these other pelagic fishes. Chub mackerel also had a lower U_{opt} , but a higher COT (0.27 mg O₂ kg⁻¹ m⁻¹), compared to Green Jack *C. caballus* (22.1 ± 2.2 cm, 3.8 FL/s with a COT of 0.16 mg O₂ kg⁻¹ m⁻¹) at 27.2°C. As an active tropical teleost species, *C. caballus* was tested at 27.2°C, which was within the typical temperature range of their distribution (Smith-Vaniz, Robertson, Dominici-Arosemena, & Molina, 2010). Since *S. japonicus* was also tested within its typical thermal range, the higher COT of *S. japonicus* may be attributed to swimming interspecific differences, such as the higher aspect ratio and lower slip (estimates of propeller efficiency) (Dickson et al., 2012), but this needs further verification.

In conclusion, this study first measured both aerobic swimming performance and oxygen consumption rates of chub mackerel at 14°C, a relatively low temperature within the thermal range of this species. By combining these new data with data from previous studies, a more complete data set was constructed to estimate swimming and respiration parameters needed for chub mackerel bioenergetics and individual-based modelling. Although chub mackerel had lower U_{opt} values than similarly sized carangids, they also had lower dependence of oxygen consumption rate on body mass, temperature and swimming speed while compared to other small pelagic fishes which biomass fluctuates heavily with climate variability shifts like PDO. This indicates the relatively high swimming efficiency and lower susceptibility of chub mackerel to environmental temperature variation.

While the estimated parameters offer a qualitative assessment of the high swimming capacity of chub mackerel collected in the California Current area within the size range of 14.0–33.0 cm, additional experiments are required for accurate application of the bioenergetic parameters established here to stocks that are distributed in different regions or are outside of this body size range. Therefore, future work should focus on oxygen consumption measurements of chub mackerel from different stocks and

over a wider size range. In particular, data from chub mackerel larvae and small juveniles should be obtained because of differences in growth characteristics between life stages and the importance of early life stages to the success of strong year-classes. Furthermore, chub mackerel often school for migration, feeding and to reduce predation (Olst & Hunter, 1970; Watanabe, 1970), and it would be valuable to incorporate potential decreases in oxygen consumption rates due to reductions in fluid friction resistance and stress that result from schooling (Herskin & Steffensen, 1998; Takagi, Ito, Torisawa, & Inada, 2015) when evaluating these bioenergetic parameters.

ACKNOWLEDGEMENTS

This work was supported by KAKENHI (Grant-in-Aid for Scientific Research on Innovative Areas) Grant Number JP15H05823 (OMIX project) and JP18H03956. We thank the University of Tokyo Ocean Alliance with the financial support of Nippon Foundation for sponsoring the overseas internship for C. Guo at the NOAA Southwest Fisheries Science Center (SWFSC), which produced some of the new metabolic data. We would also like to thank Patrick Appel and Kathy Swiney, NOAA SWFSC, for their assistance with fish care. We thank Drs. Barbara Javor and Andrew Leising, NOAA SWFSC, for their advice on this manuscript. We appreciate the invaluable suggestions from the editor and anonymous reviewers. KAD was supported to work on this paper while serving at the U.S. National Science Foundation (NSF). Any opinion, findings and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the NSF.

CONFLICT OF INTEREST

The authors have no conflict of interest related to the present study.

AUTHOR CONTRIBUTION

Chenyang Guo and Shin-ichi Ito devised the project, the main conceptual ideas and proof outline. Chenyang Guo, Nicholas C. Wegner and Emmanis Dorval conceived and planned the experiments at 14°C, and Chenyang Guo and Laura N. Frank carried out the experiments. Kathryn A. Dickson planned the experiments at 24°C and 18°C. Dane H. Klinger planned the experiments at 20°C and 15°C. Chenyang Guo and Shin-ichi Ito processed the experimental data, performed the analysis and designed the figures. Chenyang Guo wrote the manuscript with input from all authors. All authors discussed the results and commented on the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author, upon reasonable request.

ORCID

Chenyang Guo  <https://orcid.org/0000-0001-8111-4883>

Shin-ichi Ito  <https://orcid.org/0000-0002-3635-2580>

Kathryn A. Dickson  <https://orcid.org/0000-0002-6714-4776>

REFERENCES

- Beamish, F. W. H. (1964). Respiration of fishes with special emphasis on standard oxygen consumption: II. Influence of weight and temperature on respiration of several species. *Canadian Journal of Zoology*, 42(2), 177–188. <https://doi.org/10.1139/z64-016>
- Beauchamp, D. A., Stewart, D. J., & Thomas, G. L. (1989). Corroboration of a bioenergetics model for Sockeye Salmon. *Transactions of the American Fisheries Society*, 118(6), 597–607. [https://doi.org/10.1577/1548-8659\(1989\)118<0597:COABMF>2.3.CO;2](https://doi.org/10.1577/1548-8659(1989)118<0597:COABMF>2.3.CO;2)
- Bell, W., & Terhune, L. (1970). *Water tunnel design for fisheries research*. In Fisheries Research Board of Canada Technical Report 195 (pp. 1–69).
- Blaxter, J. H. S., & Hunter, J. R. (1982). The Biology of the Clupeoid Fishes. *Advances in Marine Biology*, 20, 1–223. [https://doi.org/10.1016/S0065-2881\(08\)60140-6](https://doi.org/10.1016/S0065-2881(08)60140-6)
- Brett, J. R. (1964). The respiratory metabolism and swimming performance of Young Sockeye Salmon. *Journal of the Fisheries Research Board of Canada*, 21, 1183–1226. <https://doi.org/10.1139/f64-103>
- Buckley, B. C. (2000). Interactive multimedia and model-based learning in biology. *International Journal of Science Education*, 22(9), 895–935. <https://doi.org/10.1080/095006900416848>
- Claireaux, G., Couturier, C., & Groison, A. L. (2006). Effect of temperature on maximum swimming speed and cost of transport in juvenile European sea bass (*Dicentrarchus labrax*). *Journal of Experimental Biology*, 209(17), 3420–3428. <https://doi.org/10.1242/jeb.02346>
- Clarke, A., & Johnston, N. M. (1999). Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of Animal Ecology*, 68(5), 893–905. <https://doi.org/10.1046/j.1365-2656.1999.00337.x>
- Collette, B. B., Acero, A., Canales Ramirez, C., Cardenas, G., Carpenter, K. E., Chang, S. K., Yeh, S. (2011). *Scomber japonicus*. *The IUCN Red List of Threatened Species 2011: e.T170306A6737373*, 8235.
- Crone, P. R., Hill, K. T., Zwolinski, J. P., & Kinney, M. J. (2019). *Pacific mackerel (Scomber japonicus) stock assessment for U.S. management in the 2019–20 and 2020–21 fishing years*. Portland, OR: Pacific Fishery Management Council.
- DeAngelis, D. L., & Grimm, V. (2014). Individual-based models in ecology after four decades. *F1000Prime Reports*, 6, 6–39. <https://doi.org/10.12703/P6-39>
- Dewar, H., & Graham, J. (1994). Studies of tropical tuna swimming performance in a large water tunnel. III. kinematics. *The Journal of Experimental Biology*, 192, 45–59.
- Dickson, K. A., Donley, J. M., Hansen, M. W., & Peters, J. A. (2012). Maximum sustainable speed, energetics and swimming kinematics of a tropical carangid fish, the green jack *Caranx caballus*. *Journal of Fish Biology*, 80(7), 2494–2516. <https://doi.org/10.1111/j.1095-8649.2012.03302.x>
- Dickson, K., Donley, J., Sepulveda, C., & Bhoopat, L. (2002). Effects of temperature on sustained swimming performance and swimming kinematics of the chub mackerel *Scomber japonicus*. *The Journal of Experimental Biology*, 205, 969–980.
- FAO (2018). *Fishery and aquaculture statistics. Global aquaculture production 1950–2016 (FishstatJ)*. FAO Fisheries and Aquaculture Department. Rome, Italy: FAO.
- Gibson, G. A., Stockhausen, W. T., Coyle, K. O., Hinckley, S., Parada, C., Hermann, A. J., ... Ladd, C. (2018). An individual-based model for sablefish: Exploring the connectivity between potential spawning and nursery grounds in the Gulf of Alaska. *Deep Sea Research Part II: Topical Studies in Oceanography*, 165, 89–112. <https://doi.org/10.1016/j.dsr2.2018.05.015>
- Grimm, V., & Railsback, S. F. (2004). *Individual-based modeling and ecology*. Princeton, NJ: Princeton University Press.
- Guderley, H. (2004). Metabolic responses to low temperature in fish muscle. *Biological Reviews of the Cambridge Philosophical Society*, <https://doi.org/10.1017/S1464793103006328>
- Herskin, J., & Steffensen, J. F. (1998). Energy savings in sea bass swimming in a school: Measurements of tail beat frequency and oxygen

- consumption at different swimming speeds. *Journal of Fish Biology*, 53(2), 366–376. <https://doi.org/10.1006/jfbi.1998.0708>
- Huse, G., & Giske, J. (1998). Ecology in Mare Pentium: An individual based spatio-temporal model for fish with adapted behaviour. *Fisheries Research*, 37, 163–178. [https://doi.org/10.1016/S0165-7836\(98\)00134-9](https://doi.org/10.1016/S0165-7836(98)00134-9)
- Ito, S., Kishi, M. J., Kurita, Y., Oozeki, Y., Yamanaka, Y., Megrey, B. A., & Werner, F. E. (2004). Initial design for a fish bioenergetics model of Pacific saury coupled to a lower trophic ecosystem model. *Fisheries Oceanography*, 13, 111–124. <https://doi.org/10.1111/j.1365-2419.2004.00307.x>
- Ito, S., Rose, K. A., Megrey, B. A., Schweigert, J., Hay, D., Werner, F. E., & Aita, M. N. (2015). Geographic variation in Pacific herring growth in response to regime shifts in the North Pacific Ocean. *Progress in Oceanography*, 138, 331–347. <https://doi.org/10.1016/j.pocean.2015.05.022>
- James, A. G., & Probyn, T. (1989). The relationship between respiration rate, swimming speed and feeding behaviour in the cape anchovy *Engraulis capensis gilchristi*. *Journal of Experimental Marine Biology and Ecology*, 131(2), 81–100. [https://doi.org/10.1016/0022-0981\(89\)90001-4](https://doi.org/10.1016/0022-0981(89)90001-4)
- Kaneko, H., Okunishi, T., Seto, T., Kuroda, H., Itoh, S., Kouketsu, S., & Hasegawa, D. (2019). Dual effects of reversed winter–spring temperatures on year-to-year variation in the recruitment of chub mackerel (*Scomber japonicus*). *Fisheries Oceanography*, 28(2), 212–227. <https://doi.org/10.1111/fog.12403>
- Kawai, H., Yatsu, A., Watanabe, C., Mitani, T., Katsukawa, T., & Matsuda, H. (2002). Recovery policy for chub mackerel stock using recruitment-per-spawning. *Fisheries Science*, 68(5), 963–971. <https://doi.org/10.1046/j.1444-2906.2002.00520.x>
- Killen, S. S., Atkinson, D., & Glazier, D. S. (2010). The intraspecific scaling of metabolic rate with body mass in fishes depends on life-style and temperature. *Ecology Letters*, 13(2), 184–193. <https://doi.org/10.1111/j.1461-0248.2009.01415.x>
- Kitchell, J. F., Stewart, D. J., & Weininger, D. (1977). Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). *Journal of the Fisheries Research Board of Canada*, 34(10), 1910–1921. <https://doi.org/10.1139/f77-258>
- Klinger, D. H., Dale, J. J., Machado, B. E., Incardona, J. P., Farwell, C. J., & Block, B. A. (2015). Exposure to Deepwater Horizon weathered crude oil increases routine metabolic demand in chub mackerel, *Scomber japonicus*. *Marine Pollution Bulletin*, 98(1–2), 259–266. <https://doi.org/10.1016/j.marpolbul.2015.06.039>
- Klumb, R. A., Rudstam, L. G., & Mills, E. L. (2003). Comparison of alewife young-of-the-year and adult respiration and swimming speed bioenergetics model parameters: Implications of extrapolation. *Transactions of the American Fisheries Society*, 132(6), 1089–1103. <https://doi.org/10.1577/T03-038>
- Letcher, B. H., Rice, J. A., Crowder, L. B., & Rose, K. A. (1996). Variability in survival of larval fish: Disentangling components with a generalized individual-based model. *Canadian Journal of Fisheries and Aquatic Sciences*, 53(4), 787–801. <https://doi.org/10.1139/f95-241>
- Megrey, B. A., Rose, K. A., Klumb, R. A., Hay, D. E., Werner, F. E., Eslinger, D. L., & Smith, S. L. (2007). A bioenergetics-based population dynamics model of Pacific herring (*Clupea harengus pallasii*) coupled to a lower trophic level nutrient-phytoplankton-zooplankton model: Description, calibration, and sensitivity analysis. *Ecological Modelling*, 202(1–2), 144–164. <https://doi.org/10.1016/j.ecolmod.2006.08.020>
- Meliá, P., Schiavina, M., Gatto, M., Bonaventura, L., Masina, S., & Casagrandi, R. (2013). Integrating field data into individual-based models of the migration of European eel larvae. *Marine Ecology Progress Series*, 487, 135–149. <https://doi.org/10.3354/meps10368>
- Oguz, T., Salihoglu, B., & Fach, B. (2008). A coupled plankton-anchovy population dynamics model assessing nonlinear controls of anchovy and gelatinous biomass in the Black Sea. *Marine Ecology Progress Series*, 369(1997), 229–256. <https://doi.org/10.3354/meps07540>
- Oligny-Hébert, H., Senay, C., Enders, E. C., & Boisclair, D. (2015). Effects of diel temperature fluctuation on the standard metabolic rate of juvenile Atlantic salmon (*Salmo salar*): Influence of acclimation temperature and provenience. *Canadian Journal of Fisheries and Aquatic Sciences*, 72(9), 1306–1315. <https://doi.org/10.1139/cjfas-2014-0345>
- Pacific Fishery Management Council (2017). *Status of the pacific coast coastal pelagic species fishery and recommended acceptable biological catches. Stock assessment and fishery evaluation for 2016*. Portland, OR: Pacific Fishery Management Council.
- Patterson, K. R., Pitcher, T. J., & Stokes, T. K. (1993). A Stock collapse in a fluctuating environment: The chub mackerel *Scomber japonicus* (Houttuyn) in the eastern central Pacific. *Fisheries Research*, 18, 199–218. [https://doi.org/10.1016/0165-7836\(93\)90153-X](https://doi.org/10.1016/0165-7836(93)90153-X)
- Peck, M. A., & Moyano, M. (2016). Measuring respiration rates in marine fish larvae: Challenges and advances. *Journal of Fish Biology*, 88(1), 173–205. <https://doi.org/10.1111/jfb.12810>
- Railsback, S. F., & Rose, K. A. (1999). Bioenergetics modeling of stream trout growth: Temperature and food consumption effects. *Transactions of the American Fisheries Society*, [https://doi.org/10.1577/1548-8659\(1999\)128<0241:BMOSTG>2.0.CO;2](https://doi.org/10.1577/1548-8659(1999)128<0241:BMOSTG>2.0.CO;2)
- Robert, D., Castonguay, M., & Fortier, L. (2009). Effects of preferred prey density and temperature on feeding success and recent growth in larval mackerel of the southern Gulf of St. Lawrence. *Marine Ecology Progress Series*, 377, 227–237. <https://doi.org/10.3354/meps07833>
- Rose, K. A., Fiechter, J., Curchitser, E. N., Hedstrom, K., Bernal, M., Creekmore, S., ... Agostini, V. (2015). Demonstration of a fully-coupled end-to-end model for small pelagic fish using sardine and anchovy in the California Current. *Progress in Oceanography*, 138, 348–380. <https://doi.org/10.1016/j.pocean.2015.01.012>
- Rose, K. A., Rutherford, E. S., Mcdermot, D. S., Forney, J. L., & Mills, E. L. (1999). Individual-based model of yellow perch and walleye populations in Oneida Lake. *Ecological Monographs*, 69(2), 127–154. <https://doi.org/10.2307/2657234>
- Sassa, C., & Tsukamoto, Y. (2010). Distribution and growth of *Scomber japonicus* and *S. australasicus* larvae in the southern East China Sea in response to oceanographic conditions. *Marine Ecology Progress Series*, 419, 185–199. <https://doi.org/10.3354/meps08832>
- Schaefer, K. M. (1986). Lethal temperatures and the effect of temperature change on volitional swimming speeds of chub mackerel, *Scomber Japonicus*. *Copeia*, 1986(1), 39. <https://doi.org/10.2307/1444885>
- Sepulveda, C., & Dickson, K. A. (2000). Maximum sustainable speeds and cost of swimming in juvenile kawakawa tuna (*Euthynnus affinis*) and chub mackerel (*Scomber japonicus*). *The Journal of Experimental Biology*, 203(20), 3089–3101.
- Smith-vaniz, B., Robertson, R., Dominici-Arosemena, A., & Molina, H. (2010). *Caranx caballus*. *The IUCN Red List of Threatened Species 2010: e.T183579A8138427*. Retrieved from <https://doi.org/http://dx.doi.org/10.2305/IUCN.UK.2010-3.RLTS.T183579A8138427.en>
- Takagi, T., Ito, S., Torisawa, S., & Inada, Y. (2015). Energy-saving in schooling Japanese mackerel (*Scomber japonicus*) and the effect of induced velocity of wake vortices. *Journal of Aero Aqua Bio-Mechanisms*, 4(1), 78–82. <https://doi.org/10.5226/jabmech.4.78>
- Van Der Lingen, C. D. (1995). Respiration rate of adult pilchard *Sardinops sagax* in relation to temperature, voluntary swimming speed and feeding behaviour. *Marine Ecology Progress Series*, <https://doi.org/10.3354/meps129041>
- van Olst, J. C., & Hunter, J. R. (1970). Some Aspects of the Organization of Fish Schools. *Journal of the Fisheries Research Board of Canada*, <https://doi.org/10.1139/f70-145>
- Videler, J. J. (1993). *Fish swimming. Fish and fisheries series* (Vol. 10). London, UK: Chapman & Hall.

- Watanabe, C., & Yatsu, A. (2004). Effects of density-dependence and sea surface temperature on interannual variation in length-at-age of chub mackerel (*Scomber japonicus*) in the Kuroshio-Oyashio area during 1970–1997. *Fishery Bulletin*, 102(1), 196–206.
- Watanabe, T. (1970). Morphology and ecology of early stages of life in Japanese common mackerel, *Scomber japonicus* Houttuyn, with special reference to fluctuation of population. *Bulletin Tokai Regional Fisheries Research Laboratory*, 62, 1–283.
- Weber, E. D., & McClatchie, S. (2012). Effect of environmental conditions on the distribution of Pacific mackerel (*Scomber japonicus*) larvae in the California Current system. *Fishery Bulletin*, 110, 85–97.
- Wegner, N. C. (2011). Gill respiratory morphometrics. In A. P. Farrell (Ed.), *Encyclopedia of fish physiology: From genome to environment*, Vol. 2 (pp. 803–811). San Diego, CA: Elsevier Press.
- Wegner, N. C., Drawbridge, M. A., & Hyde, J. R. (2018). Reduced swimming and metabolic fitness of aquaculture-reared California Yellowtail (*Seriola dorsalis*) in comparison to wild-caught conspecifics. *Aquaculture*, 486, 51–56. <https://doi.org/10.1016/j.aquaculture.2017.11.041>
- Wegner, N. C., Sepulveda, C. A., Bull, K. B., & Graham, J. B. (2010). Gill morphometrics in relation to gas transfer and ram ventilation in high-energy demand teleosts: Scombrids and billfishes. *Journal of Morphology*, 271(1), 36–49. <https://doi.org/10.1002/jmor.10777>
- Yatsu, A., Watanabe, T., Ishida, M., Sugisaki, H., & Jacobson, L. D. (2005). Environmental effects on recruitment and productivity of Japanese sardine *Sardinops melanostictus* and chub mackerel *Scomber japonicus* with recommendations for management. *Fisheries Oceanography*, 14(4), 263–278. <https://doi.org/10.1111/j.1365-2419.2005.00335.x>
- Yoneda, M. (2017). Keys to fluctuating the stock biomass of chub mackerel *Scomber japonicus*: temperature and maternal effects on early life history traits. *Nippon Suisan Gakkaishi*, 83(5), 837. <https://doi.org/10.2331/suisan.WA2447-3>. (in Japanese).
- Yukami, R., Nishijima, S., Imasu, K., Watanabe, C., Kamimura, Y., & Furuichi, S. (2019). Stock assessment and evaluation for the Pacific stock of chub mackerel (fiscal year 2018). In: *Marine fisheries stock assessment and evaluation for Japanese waters (fiscal year 2018/2019)* (pp. 163–208). Tokyo, Japan: Fisheries Agency and Fisheries Research Agency of Japan. (in Japanese).

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Guo C, Ito S-I, Wegner NC, et al. Metabolic measurements and parameter estimations for bioenergetics modelling of Pacific Chub Mackerel *Scomber japonicus*. *Fish Oceanogr*. 2020;29:215–226. <https://doi.org/10.1111/fog.12465>