INTRODUCTION

Growth patterns of fish result from their energy allocation strategy, life stages and the environmental conditions in which they reside. Temperature, for example, can potentially drive size-dependent metabolic energy rates, which then influence physiological functions such as food consumption rates, leading to growth variation (Barneche & Allen, 2018; Madenjian et al., 2018). Previous studies suggest that common temperature-related growth patterns and reproductive traits in various fish populations, for example, faster
growth, earlier maturation, shorter life span and smaller body size, are often associated with warmer temperature (Angilletta et al., 2004; Atkinson, 1994; van Rijn et al., 2017); see also nonlinear temperature effects whereby decreased growth occurs when exceeding optimal temperature (Matthias et al., 2018). Variations in both somatic and gonadic growth rates hence shape different life-history characteristics amongst individuals, even within the same species, and underpin the diversity of marine fish communities. Changes in environmental conditions may alter these rates, which prompt shifts in fish abundance, composition and geographical distribution as a whole (Damuth, 1981; Oindo et al., 2001). Thus, better quantification of fish growth patterns, and consequently, their energy allocation mechanisms, in relation to those driving factors, will provide new and practical insights into the conservation and management of marine fish.

Mathematical models play a pivotal role in describing the extent to which the rates of somatic and gonadic growth vary over a lifetime, specifying the energy flow that determines the growth patterns of fish. The growth model is often expressed in the form of either body mass or length; these are a power transformation of one another. Successful examples include variants of the von Bertalanffy–Püttter model (Püttter, 1920; von Bertalanffy, 1934) delineating a monophasic growth curve with time-independent parameters. However, these monophasic models offer little theoretical explanation regarding reproductive energy allocation at the post-maturation stage (Boukal et al., 2014). Therefore, recent studies (Mollet et al., 2010; Quince, Abrams, et al., 2008; Quince, Shuter, et al., 2008) have advanced diphasic (biphasic) growth models, accommodating the pre- and post-maturation phases, between which reproductive energy allocation differs, and thus, interrelated changes in growth patterns and maturation (Honsey et al., 2016; Lester et al., 2004) can be modelled. For a chronological summary of diphasic growth models, see Wilson et al. (2017).

Notwithstanding such a promising feature of diphasic growth models, considerable challenges often emerge when estimating model parameters via numerical methods. The model takes a nonlinear differential form that may be analytically intractable; the model parameters therein involve a change point, and their estimators are potentially correlated with each other. These challenges mainly stem from the two aspects: the nonlinear nature of growth models and the type of data available. The parameter estimation task becomes particularly challenging when it relies on fisheries data (fish population data), the most common data type collected—which are essentially a one-time observation of age and body size measurement for each individual. As opposed to longitudinal growth data that contain repeated observations from the same individual over its lifetime, fisheries data do not provide vital individual information, such as consecutive growth measures or the time points of maturity and spawning. Yet, both mathematical growth models and numerical techniques heavily rely upon such information, and this lack of information in data consequently hinders standard parameter estimation algorithms.

To cope with these challenges, much of the previous research adopts a predetermined value for some model parameters (Mollet, Dieckmann & Rijnsdorp, 2016; Mollet et al., 2010; Mollet, Poos & Rijnsdorp, 2016; Quince, Abrams, et al., 2008; Quince, Shuter, et al., 2008). Doing so, however, introduces implicit assumptions that may limit model interpretation; in particular, the energy allocation suggested by those parameters entirely depends on such assumptions. The emerging recognition that models and data are tightly connected and inseparable in parameter estimation (Wilson et al., 2017) heightens the need to understand the nature of the challenges and to investigate potential modelling approaches in a constructive manner. Such comprehension would offer crucial bases for developing estimable and interpretable growth models that advance biological insight into the underlying energy allocation mechanism. Yet, to date, this seems to have received little attention in practice.

Here, the present study develops a suite of diphasic allometric scaling growth models that generalise the modelling framework studied by West et al. (2001) and Quince, Shuter, et al. (2008). The modelling process identifies three typical challenges (Sections 3.2.1–3.2.3) arising from parameter estimation based on fisheries data. An effective parameter estimation procedure is then proposed to reconcile these challenges as well as to enhance model interpretation. A simulation study undertaken supports that the procedure can provide accurate model parameter estimates. The present study illuminates the fact that the relative energy allocation to reproduction can be specified as a time-delay factor in the growth model. Using fisheries data for subtropical cutlassfish Trichiurus japonicus collected from the northern and southern coasts of Taiwan (Wang & Heino, 2018), the proposed model highlights the intraspecific extent to which energy allocation strategies vary for two sites with different conditions.

## 2 DATA

The fisheries data for subtropical cutlassfish Trichiurus japonicus were collected from monthly samplings of trawl fisheries at two landing sites in Taiwan (Tsukuan and Kengfang at latitudes of 22 and 24°N, hereafter referred to as sites T and K respectively) from 2013 to 2015; a total of 254 (site K) and 150 (site T) individuals were sampled for the study. The same stratified random sampling design was used with the consistent sampling months, the boat size and the range of mesh sizes in both sites; see Wang et al. (2017) and Wang and Heino (2018) for more details about the sampling methods.

For the $i$-th individual cutlassfish of age $t$, the total ($w_t$) and gonadic ($g_t$) weights were measured; the individual age here was the average value of otolith annuli reported by two independent readers, which recorded age resulted in 6-month time-scales.
The somatic weight \( w_t \) was then calculated as the difference between the total and gonadic weights, \( w_t = v_t - g_t \). The data include individuals up to 6 years in age, which is a relatively narrow range, partly due to the exploitation and rapid life history of this species. See Wang and Heino (2018) for a detailed description of biological measurements and age estimation.

The fish population data analysed here form a triplet \( \{ v_t, w_t, g_t \} \) for individual fish, \( i = 1, 2, \ldots, n \). Strictly speaking, a time point \( t \) in the data solely depends on individual \( i \); the precise notation for observations should therefore be \( v_i(t_i) \), since only a one-time observation can be made for each specimen in fisheries data. For simplicity, however, it is denoted throughout the manuscript in the simpler notation, that is, \( v_t \), unless stated otherwise. This aspect is a distinctive feature of fisheries population data as opposed to longitudinal growth records.

The study species, \( T. \ japonicus \), is a common benthopelagic fish distributed in coastal waters of the western North Pacific (Munekiyo, 1990; Tzeng et al., 2016). Most adult fish spawn in neritic shelf water, and their larvae stay in near-shore coastal areas. Their juveniles and subadults will then subsequently inhabit the mid-shelf zones (Martins & Haimovici, 2000). They are restricted in dispersal ability, and thus, large-scale cross-basin migration by juveniles and adults will be less likely (Tzeng et al., 2016). They display different life-history patterns between the study sites, for example, slower growth rates during the juvenile stage, older age at maturation and larger length at age at the adult stage in the north-eastern coast (site K) compared with the southwestern coast (site T). Such spatial differences in their life histories are considered as an adaptive response to local environmental conditions or exploitation (Wang & Heino, 2018). The level of genetic differentiation seems low between these study sites (He et al., 2014; Tzeng et al., 2016), and the likelihood of migration between the sites is unknown. The average (standard deviation) body weight and length of the fish samples are, respectively, 162.6 (124.2) g and 215.5 (56.5) mm for site K, 140.5 (78.9) g and 212.4 (43.7) mm for site T.

### 3 | MODEL DEVELOPMENT AND CHALLENGES

#### 3.1 | The model

Although growth models are often expressed in a single differential form, consider here differential equation models that describe fish body weights \( v_t \) of age \( t \) which consists of somatic \( (w_t) \) and gonadic \( (g_t) \) weights, namely,

\[
\begin{align*}
v_t &= dv_t + dg_t, \quad (1a) \\
w_t &= aw_t^\alpha dt - dg_t. \quad (1b)
\end{align*}
\]

The indicator function \( I_{(t \geq t_s)} \) here returns 1, if age \( t \) is older than the age of maturity \( r \) or returns 0 if otherwise. Most individual fish spawn multiple times, say \( r_k, k = 1, 2, \ldots \), over the lifetime. For such a case, the models here are considered for the time range after the most recent \( k \)-th spawning time, \( t > r_k \) and promise that the gonadic weight reduces to some weight \( c \) at spawning times, that is, \( g_t = c \) for \( t \in \{ r_k \} \).

Equation (1a) states a trivial sum constraint between the somatic and gonadic weights—that is, the sum of these weights must equal the total weight, \( v_t = w_t + g_t \). Equations (1b)–(1c) determine the energy allocation mechanism. In Equation (1b), the first term, \( aw_t^\alpha \), expresses a rate at which energy is available for body growth with the unknown constants \( a \) and \( \alpha \); the second term, \( dg_t \), represents the reproduction energy cost apportioned after maturity, as defined by Equation (1c). The gonadic growth rate is specified to be analogous to the somatic weight but with another set of unknown coefficients, \( b \) and \( \beta \). These constants, \( a, \alpha, b, \) and \( \beta \), together determine a trajectory of body growth and thus will be estimated from observed data in the later sections. For instance, the body mass linearly increases if \( a = 0 \) and exhibits an exponential increase if \( a > 0 \). The parameter \( a \) represents the mass-independent rate of energy allocation, for which higher values will shorten the amount of time to double the body mass from age \( t \). Such a qualitative interpretation can be similarly applied to the parameters \( b \) and \( \beta \), regarding gonadic growth.

The relative energy allocated to gonadic growth can then be defined by taking the ratio between Equation (1c) and (1a), as,

\[
r_t = \frac{dg_t}{dv_t} = \frac{b}{a} \omega_t^{\alpha-\beta} I_{(t \geq r_s)}.
\]

The rate here, \( 0 \leq r_t < 1 \), represents the instantaneous relative reproductive investment, which becomes applicable after maturity is reached. Furthermore, by integrating Equation (4) over a lifetime, it yields,

\[
R_t = \int_r^t r_t ds.
\]

The quantity of \( R_t \geq 0 \) expresses the relative energy spent on reproduction up to age \( t \).

These two quantities, \( r_t \) and \( R_t \), are purely model based and cannot be obtained from fisheries data because no consecutive growth observations for each individual, equivalent quantities such as \( dv_t \) and \( dg_t \), are available. However, once the model parameters—namely \( a, b, \alpha, \) and \( \beta \)—are estimated from data, the energy allocated to reproduction can be quantified through Equations (2) or (3). Since the parameter estimation is often challenging, previous studies have had to assume specific values a priori for the exponents \( a \) and \( \beta \) (Mollet, Dieckmann, et al., 2016; Mollet et al., 2010; Mollet, Poos, et al., 2016; Quince, Abrams, et al., 2008; Quince, Shuter, et al., 2008). The idea of the growth models here generalises the diphasic model studied...
by West et al. (2001); Quince, Abrams, et al. (2008), Quince, Shuter, et al. (2008); Mollet et al. (2010) and represents a simple instance of the dynamic energy budget theory (Kooijman, 1986), allowing all model parameters to be estimable from observed fisheries data.

### 3.2 | The three challenges in parameter estimation

Unlike the present models (1a–1c), growth models are often expressed in a single differential form (1b), through which all the parameters therein are simultaneously estimated. In practice, the maturity time, \( r \), is either specified a priori or treated as another parameter. The model is then regarded as an average (or expected) growth pattern within the population caught, when fisheries data are employed for parameter estimation.

Typical challenges in parameter estimation are threefold and will be discussed in the following subsections. First, no analytically closed form for the differential Equation (1b) means fitting an unknown curve to data, which requires additional numerical means. Second, the age of maturity and the time points of spawning generally differ amongst individuals; these types of information are missing in fisheries data. Third, simultaneously estimating four or five parameters from a single nonlinear model (1b) induces a correlation amongst the parameter estimators that may lead to parameter convergence problems. The following subsections explore and identify these three potential challenges in more detail.

#### 3.2.1 | Non-closed form

To illustrate the mathematical nature of the challenge, consider here a reparameterised model (1b), namely,

\[
dw_t = (1 - r_t) aw_t^2 dt, \tag{1b'}
\]

where \( r_t \) is defined in Equation (2). The trajectory of somatic weight, \( w_t \), can then be described in a non-closed form, which still involves a non-integrable term. With the method of separation of variables, it becomes \( \int w_t^{-a} dw_t = a \int (1 - r_t) dt \) and yields

\[
w_t = \left\{ w_0^{1-a} + a (1-a) (t - R_t) \right\} ^{\frac{1}{1-a}}, \tag{4}
\]

where the first integral \( R_t \) is the cumulative relative reproductive investment (Equation 3), which is the non-integrable term as in Equation (3), and \( w_0 \) is the initial somatic weight at age \( t = 0 \). The function is nonlinear in terms of age \( t \). If the rate \( r_t \) is assumed to be constant (time-independent), \( r_t = r \), and hence \( a = \frac{1}{r} \) as in Quince, Shuter, et al. (2008), Equation (3) is simplified to \( R_t = r \int_0^t ds = r (t - r) \). The solution of (1b') can then be explicitly expressed in the closed form

\[
w_t = \left\{ w_0^{1-a} + a (1-a) \{ t - r(t - r) \} \right\} \frac{1}{(1-a)}.
\]

Equation (4) delineates the function form of somatic growth, which appears to be a power function, but does not provide an analytically explicit form as the non-integrable term, \( R_t \), is involved. Note that only for the pre-maturity period, \( t < r \), there exists an explicit analytical solution as \( R_t = 0 \) (Equation 4). This is a situation in which a standard parameter estimation technique, such as the nonlinear least-squares method (trajectory matching), cannot easily be applied and requires some extra numerical means. The present study will suggest an alternative numerical approach to estimate model parameters without solving the differential equation (see Section 4).

#### 3.2.2 | Age of maturity and multiple spawning times

Data-oriented challenges here stem from the fact that neither the age of maturity nor the multiple spawning time points of individuals are available in fisheries data. Given that the cumulative relative reproductive investment \( R_t \) plays a pivotal role in Equation (4) as a time-delay factor, \( (t - R_t) \), the relative time of somatic growth slows down owing to the amount of energy invested in reproduction. Although the age of maturity \( r \) and thus the quantity of \( R_t \), vary amongst individuals even within the same population, they must be assumed as constant in the model because observations cannot be obtained for individuals in fisheries data. In practice, the age at 50% maturity is a tacit choice as an assumed value for \( r \) (Minte-Vera et al., 2016; Wootton et al., 2020). If \( r \) is also to be estimated with other parameters, the estimation process faces some technical difficulties caused by the non-differentiable nature of the objective function with respect to the change point \( r \). The classic statistical theory fails to work for the inference of \( r \) as such. Furthermore, for fish that spawn multiple times over the lifetime, it requires the record of the spawning times \( \{ r_k \} \) of each individual, since the gonadic weight is obtained by integrating model (1c) from the most recent \( k \)-th spawning time \( r_k \) to the current time \( t \) as

\[
g_t = \int_{r_k}^t dg_t.
\]

However, the spawning time \( r_k \) is usually unknown in fisheries data.

The present study offers a practical approach that circumvents such data-oriented challenges, embedding the probability of maturity up to \( t \) into the parameter estimation algorithm that does not require observations \( \{ r_k \} \) (see Section 4.2).

#### 3.2.3 | Correlation in parameter estimators

While taking a common nonlinear fitting approach, such as the nonlinear least-squares method (trajectory matching), the simultaneous estimation of four or five parameters from a single model such as Equation (4) induces a correlation amongst the estimators because the model is also nonlinear in terms of the parameters. This may
cause problems in parameter convergence, as mentioned in a previous study (Wilson et al., 2017) in the body length modelling context, which represents a general case of growth models. The source of correlation relies on the fact that the asymptotic covariance matrix of parameter estimators, for example, \( \hat{\theta} = (\hat{a}, \hat{a}, \hat{b}, \hat{\rho})^T \), is given as:

\[
\text{var}(\hat{\theta}) = \text{E}\left( (\theta - \hat{\theta})(\theta - \hat{\theta})^T \right)^{-1} = \sigma^2 (J^T J)^{-1},
\]

(5)

where \( \theta \) is the vector of true parameter values and \( \sigma^2 \) is the error variance. Here, \( J \) is the derivative (Jacobian) matrix of size \( n \times 4 \) (the number of observations times the number of parameters). Its \( (i,j) \)-element is

\[
J_{ij} = \frac{\partial w_i(\hat{\theta})}{\partial \theta_j},
\]

where \( w_i(\theta) = w(t_i; \theta) \) to be precise as mentioned in Section 2; the notation here emphasises that the \((i,j)\)-element is a value calculated from, with the parameter estimates \( \hat{\theta} \) substituted, the first-order partial derivative of Equation (4) with respect to parameter \( j \) at the age \( t \) of specimen \( i \) in fisheries data. Since the nonlinear nature of the model, each column vector of matrix \( J \) likely involves the other parameters in its partial differential form, and thus, \( J^T J \) is unlikely a diagonal matrix. This fact induces a correlation in parameter estimators. Note that Equation (5) relies on the first-order Taylor approximation for the model errors as

\[
w(\theta) - w(\hat{\theta}) \approx \frac{\partial w(\hat{\theta})}{\partial \theta} (\theta - \hat{\theta}) = J(\theta - \hat{\theta}).
\]

See Bates and Watts (1988) for more theoretical details.

In contrast, the present models (1a)–(1c) illuminate the fact that the parameters \((a, a) (b, \beta)\) can be separately estimated if the total \((v_t)\) and gonadic \((g_t)\) weights are observed (see Section 4). This is a unique feature of body mass modelling and, of course, not straightforward in the body length modelling context because the body length cannot easily be dissected into somatic- and gonadic-related lengths; see Section 7 for further discussion.

**4 | PARAMETER ESTIMATION**

Standard techniques for estimating the parameters of nonlinear differential equations follow one of two approaches. One is the nonlinear least-squares method (Bates & Watts, 1988; Seber & Wild, 1989), also known as nonlinear regression or trajectory matching; the other is the two-stage least-squares method, so-called gradient matching (Ramsay, 1996; Ramsay & Hooker, 2017; Varah, 1982). The former fits the solution of differential equations to data by minimising the squared errors and appears to be almost exclusively used in previous growth modelling studies. If the analytical solution is unavailable, as in the present study, an additional step is required. That is, the procedure must solve the differential equations numerically first and then estimate the parameters. These steps are iteratively repeated until the parameters converge. The process takes a relatively long time and may have some undesirable consequences for parameter estimation (Ramsay et al., 2007). For the present study, in particular, the former approach is inconvenient, as discussed in Sections 3.2.1–3.2.3. In contrast, the latter approach that will be implemented here minimises the squared errors in gradients (derivatives) and can thus overcome all the challenges addressed.

Here, the parameter estimation procedure is implemented on the gradient matching approach that consists of two steps: (a) estimate expected processes \( \hat{v}_t \), \( \hat{w}_t \), and \( \hat{g}_t \) from data via a smoothing technique, specifically the locally weighted regression (Cleveland, 1979; Cleveland & Devlin, 1988); and (2) estimate the parameters by minimising the squared errors in the gradients (derivatives) of the growth models.

First, consider the observed data \( \{v_t, w_t, g_t\}_{t=1}^n \) as noisy realisations from the processes, \( v_t \), \( w_t \) and \( g_t \) governed by the differential Equations (1a)–(1c). Each observed component with noise can be specified as

\[
v_t = v_t + \nu_t,
\]

\[
w_t = w_t + \omega_t,
\]

\[
g_t = g_t + \gamma_t,
\]

(6a)

(6b)

(6c)

where \( \nu_t, \omega_t \) and \( \gamma_t \) are the noise terms describing a discrepancy of observation \((i = 1, 2, ..., n)\) from the model, and their (ensemble) means are zero, that is, \( \nu_t = E[v_t] = 0 \). These noise terms constrain each other, \( \nu_t = \omega_t = \gamma_t \), maintaining the sum constraint for the observations from the same individual, \( v_t = w_t + g_t \). Although the analytical form of the processes is unknown (Section 3.2.1), Equations (6a)–(6c) here suggest that the function forms can still be non-parametrically obtained from data, taking their expectation; that is, \( \hat{v}_t = E[v_t] \). The calculation of these expectations, \( \hat{v}_t \), \( \hat{w}_t \), and \( \hat{g}_t \), will be carried out by the locally weighted regression in Section 4.1.

Second, given the constraint (1a), the models required for parameter estimation can be reduced to a set of stochastic differential equations written in a conventional way, namely,

\[
dv_t = aw_t^0 dt + \sigma v_t dt,
\]

\[
dg_t = bw_t^0 dt + \sigma g_t dt,
\]

(7a)

(7b)

where \( v_t \) and \( g_t \) represent a stochastic divergence over time, white noise, with their (time) means being also zero, \( E[v_t] = E[g_t] = 0 \). Substituting the expectation of the processes from the first step above to Equations (7a)–(7b), the overall expected growth of total and gonadic weights within a population then becomes.
\[ \frac{dv_t}{dt} = a \hat{v}_t \, dt, \quad (8a) \]

\[ \frac{d\hat{v}_t}{dt} = b_p \hat{v}_t \, dt, \quad (8b) \]

where \( p_t = P(\tau \leq t) = E \left[ I_{\{t \geq \tau\}} \right] \) that is, the probability of fish being mature by age \( t \). Notably, the multiplicative term \( b_p \) in Equation (8b) is time varying. The diphasic model can thus resemble a smooth monophasic model sensu the overall average growth pattern at a population level. The parameter estimation will be conducted by minimising the squared errors in the gradients (Equations 7a and 7b), in other words, matching the gradients—both sides of Equations (8a) and (8b); see Section 4.2.

The following subsections discuss some technical details of the parameter estimation procedure regarding these two steps introduced above. See the discussion (Section 7) for a more detailed explanation of how the proposed procedure here reconciles all the challenges discussed in Section 3.2.

### 4.1 | Locally weighted regression

For illustration purposes, consider Equation (6a) of which the analytical form is unknown. The locally weighted regression technique locally approximates the value of \( v_t \) for an arbitrary point \( t \) by a polynomial function of order \( p \) (Fan & Gijbels, 1996; Simonoff, 1996). The local polynomial approximation relies on a Taylor expansion for a neighbourhood of \( t \) as.

\[
v_t = \sum_{j=0}^{p} \frac{1}{j!} \frac{dv_t}{dt} (t_t - t)^j + v_{it},
\]

where \( v_{it} \) represents the higher order terms, higher than the order \( p \), of the expansion and is thus the error term. Recalling Equation (6a), the approximation here suggests that the curve estimation of \( v_t \) from data \( v_{it} \) becomes a task of estimating local coefficients \( \lambda_t = (\lambda_{0t}, \lambda_{1t}, \ldots, \lambda_{pt})^T \) that depend on age \( t \); this is why the approximation needs to be carried out locally (around an age point \( t \)) in a sequential manner rather than (globally) fitting a single polynomial function to the whole data at once. This estimation can be achieved by sequentially applying the weighted least-squares method to the error term \( v_{it} \) (Equation 9) with an appropriate neighbourhood, \( h \). The coefficient estimates are obtained as

\[
\hat{\lambda}_t = \arg\min_n \sum_{i=1}^{n} k \left( \frac{t_t - t}{h} \right) v_{it}^2
\]

\[
= \arg\min_n \sum_{i=1}^{n} k \left( \frac{t_t - t}{h} \right) \left\{ v_{it} - \sum_{j=0}^{p} \lambda_{jt} (t_t - t)^j \right\}^2
\]

\[
= \left( X_t^T K_t X_t \right)^{-1} X_t^T K_t v_t,
\]

where \( k (\cdot) \) is a kernel function that assigns a weight to each observed age point \( t_t \). The weight decreases as point \( t_t \) becomes distant from an arbitral age \( t \). The choice of kernel function characterises each smoothing technique. The matrix notation here is

\[
K_t = \text{diag} \left\{ k \left( \frac{t_t - t}{h} \right), \ldots, k \left( \frac{t_n - t}{h} \right) \right\},
\]

\[
v = \begin{bmatrix} v_{1t} \\ v_{2t} \\ \vdots \\ v_{nt} \end{bmatrix}, \quad X_t = \begin{bmatrix} 1 & (t_t - t) & \ldots & (t_t - t)^p \\
1 & (t_1 - t) & \ldots & (t_1 - t)^p \\
\vdots & \vdots & \ddots & \vdots \\
1 & (t_n - t) & \ldots & (t_n - t)^p \end{bmatrix}.
\]

The estimate of the total weight at age \( t \), \( \hat{v}_t \), is then obtained as the estimated local regression coefficient \( (j = 0) \),

\[
\hat{v}_t = \hat{\lambda}_{0t},
\]

and the first derivative of total weight is given by the first derivative of the local polynomial function (Equation 9), that is, the linear coefficient \( (j = 1) \),

\[
\frac{dv_t}{dt} = \hat{\lambda}_{1t}.
\]

The local regression method employed here is loess (Cleveland & Devlin, 1988; Cleveland et al., 1991) that adopts a tri-cube weight as a kernel function,

\[
k (u) = (1 - |u|^3)^3, \quad (0 \leq u < 1).
\]

A crucial choice for loess is the size of the neighbourhood—namely, bandwidth, equivalent to \( h \). Although there are several different criteria suggested, one based on cross-validation (Loader, 1999) would be a simple option and is used in the present study; that is,

\[
CV (h) = \frac{1}{n} \sum_{i=1}^{n} (v_{it} - \hat{v}_{i..})^2,
\]

where \( \hat{v}_{i..} \) denotes the leave-\( i \)-out estimate of total weight. The optimal size of the neighbourhood that achieves the minimum \( CV (h) \) is chosen. The order of local polynomial \( p \) is set as \( p = 1 \) as it is sufficient for such a smooth function (Equation 4).

The same approach is applied to gonadic weight, \( \hat{g}_t \), to obtain \( \hat{\hat{g}_t} \) and \( d \hat{g}_t / dt \); the estimate of somatic weight is then obtained from

\[
\hat{\hat{v}_t} = \hat{\hat{g}_t} - \hat{g}_t.
\]

### 4.2 | Minimising squared errors in gradients

Given all the overall expected body weights and their derivatives (Equations 10–12), the parameters \((a, a)\) and \((b, b)\) are estimated separately by minimising the squared errors in the gradients (Equations 7a and 7b), in other words, matching the gradients as.
\[(\hat{a}, \hat{a}) = \arg\min \int \gamma^2 dt = \arg\min \left( \frac{d\gamma}{dt} - a\hat{\omega}_t \right)^2 dt. \quad (13a)\]

\[\left(\hat{b}, \hat{\beta} \right) = \arg\min \int \gamma^2 dt = \arg\min \left( \frac{d\gamma}{dt} - b\hat{\omega}_t \right)^2 dt. \quad (13b)\]

The first derivatives of \(\hat{\gamma}_t\) and \(\hat{\omega}_t\) in the integrand above are estimated by the linear coefficient of the local polynomial (Equation 11) and \(\hat{\omega}_t\) is due to Equation (12). Although Equations (13a) and (13b) are stated in an integral form because time \(t\) is continuous, the integrations must be discretised and performed numerically via numerical techniques such as the trapezium method with appropriate intervals. The present study chose the time increment of \(dt = 1/120\).

Here, the probability of maturity \(p_t = P(r \leq t)\) in Equation (13b) can be modelled at a fish population level through the generalised additive model (GAM, Cleveland et al., 1991; Hastie & Tibshirani, 1990) as:

\[\logit \{P(r \leq t)\} = \log \left( \frac{p_t}{1-p_t} \right) = \eta_t,\]

where \(\eta_t\) is a smooth function of age \(t\) estimated by the local regression technique (Section 4.1). The estimated probability of maturity is then obtained as

\[\hat{\beta}_t = \left\{1 + \exp \left( -\hat{\eta}_t \right) \right\}^{-1}, \quad (14)\]

and is substituted to Equation (13b). Importantly, Equation (13b) does not require any spawning time data \(\{r_k\}\) as they minimise the error in the gradient (Equation 7b).

### 5 | SIMULATION STUDY

To illustrate the performance of the approach proposed in Section 4, a simulation study was conducted for a total of 1,000 runs, mimicking fisheries data. In each run, simulation data \(\{v_t, w_t, g_t\}\) were generated for 250 individual fish of age between 0 and 6 years by 6-month scales based on the models (7a)–(7b) with the initial values \(v_0 = 7\) and \(g_0 = 0\). A wider standard deviation was assumed for the error term of total weight, \(\sigma = 10\), and a narrower one for gonadic weight, \(\sigma = 1\). The maturation probability \(p_t\) assumed a logistic function form.

\[p_t = \left[1 + \exp \left\{ - (\eta_0 + \eta_1 t) \right\} \right]^{-1}, \quad (15)\]

for which the parameter values, \(\eta_0\) and \(\eta_1\), were predetermined to make the age at 50% maturity 2 years. Note that the probability (Equation 15) here is a parametric expression of Equation (14), adopting the two parameters \(\eta_0\) and \(\eta_1\) instead of \(\eta_t\), a smooth function of age \(t\). Whether a simulated individual of age \(t\) was mature (\(g_t > 0\)) or immature (\(g_t = 0\)) was then decided by a Bernoulli random variable governed by the probability (Equation 15). All the predefined parameters used for the simulation study are listed in the first row of Table 1.

The overall simulation results suggest that the proposed approach can provide accurate parameter estimates. Table 1 summarises the simulation results, the mean and standard deviation values from the 1,000 replicates for each parameter. The bias here simply reports an empirical bias, the difference between the mean of the 1,000 estimates and the predetermined parameter value. The level of this bias is relatively small and will be inconsequential for most practical purposes. Note that the case for the parameters \(\eta_0\) and \(\eta_1\) is a standard simulation exercise of generalised linear models (GLMs, McCullagh & Nelder, 1989)—Equation (15), as the model, generated the maturity data (0 or 1), from which the parameters were directly estimated. The level of bias for the other parameters, \(a, a, b\) and \(\beta\), appears smaller than that of \(\eta_0\) and \(\eta_1\).

Figure 1 illustrates the boxplots of the parameter estimates from the 1,000 simulation runs. The red dots superposed correspond to the true parameter values from which the simulation data are generated. All the median values (the solid lines in the box) locate near the true values (the red dots), suggesting that the proposed framework offers an effective parameter estimation procedure.

### 6 | RESULTS

The estimated parameters facilitate a better understanding of intraspecific energy allocation strategy for the two different sites, K (Kengfeng) and T (Tsukan), in Taiwan. Table 2 shows the estimated parameters, with their 95% bootstrap confidence intervals constructed by the bootstrap bias-correction method (Efron & Tibshirani, 1994) with 2000 bootstrap samples, based on the subset data of different age ranges up to 3 (\(t \leq 3\)) and 4 (\(t \leq 4\)) years. Note that there are only a few data points after the age of 4 years at site K and after 3 years at site T (see Figure 2), meaning that the extrapolation beyond these age points requires extra care.

| Parameter | Value | Mean estimates | Standard deviation | Bias |
|-----------|-------|----------------|--------------------|------|
| \(a\)     | 4.20  | 4.39           | 0.64               | 0.19 |
| \(\alpha\)| 0.60  | 0.59           | 0.03               | < -0.01 |
| \(b\)     | 0.02  | 0.02           | 0.01               | 0.01 |
| \(\beta\) | 1.14  | 1.16           | 0.09               | 0.09 |
| \(\eta_0\)| -6.20 | -6.58          | 1.30               | 1.30 |
| \(\eta_1\)| 3.10  | 3.40           | 0.65               | 0.65 |

**TABLE 1** Summary of parameter estimates for the 1,000 simulation runs. The first row represents the predetermined (true) values used in the simulation study.
The difference between the two sites is reflected in these parameter estimates. The nonlinear nature of body growth becomes apparent at site K by comparing the difference in each exponent, $\hat{a}$ and $\hat{b}$, being estimated from the two different age ranges; a larger exponent value indicates stronger nonlinearity. Such nonlinearity is muted for site T, owing to fewer observations after 3 years and/or site-dependent characteristics. Interestingly, each parameter estimate for $t \leq 3$ is more or less similar, particularly somatic weight, between these two sites, accounting for a broader overlap in its 95% confidence interval. This fact captures the subtle differences in growth patterns up to 3 years and indicates a plausible divergence afterwards between the sites.

The panels in the top three rows of Figure 2 illustrate the estimated growth curves of the total, somatic and gonadic weights for each site with observations. The superposed growth curves are obtained by numerically solving Equations (1a)–(1c) with the estimated parameters (Table 2) and the initial values: $v_0 = w_0 = 6.84$ (site K) and 4.31 (site T)—these are the average value of the observations at age $t = 0$. The black lines are calculated based on the parameter estimates for $t \leq 3$, and the green ones are for $t \leq 4$; the dashed segments indicate an extrapolation. For reference, a commonly adopted exponent value $a$ is $2/3 \approx 0.66$, close to the estimate of site K for $t \leq 4$.
The probability of maturity (the bottom panels in Figure 2) reaches 100% within a relatively early period (2–3 years). It demonstrates a sharper increase for site T with warmer water temperature, suggesting that the fish here mature earlier than those at site K. The age at 50% maturity is approximately 1 year for site T, whereas it is older for site K; see Wang and Heino (2018) for more details.

The instantaneous and cumulative relative reproductive investments, \( r_t \) and \( R_t \), represent the extent to which the reproductive energy allocation relative to total weight changes over a lifetime, taking a larger value when more energy is invested towards gonadic growth. The latter plays a time-delay effect (Equation 4), that is, somatic growth slows down. Figure 3 contrasts the energy allocation strategies to gonadic growth between the two sites, illustrating the estimated \( \hat{r}_T \) and \( \hat{R}_T \). The curves here are calculated with either the estimates for \( t \leq 3 \) (site T) or \( t \leq 4 \) (site K) because of only few observations after these age points for each site. The \( \hat{r}_T \) curve (the top panel) for site T illustrates that the instantaneous relative reproductive investment stops increasing and becomes nearly around 6%–7% after the age of 2, at which the probability of maturity reaches 100% (the right-bottom panel in Figure 2). On the contrary, \( \hat{r}_K \) for site K keeps increasing over the lifetime. This fact highlights that, for site T, there is a higher relative reproductive investment than site K up to the age of 3, after which that of site K becomes higher towards older ages. Roff (1983) suggests a constant ratio of gonadic to somatic weight for various species. The contrast between the two curves \( \hat{r}_T \) and \( \hat{R}_T \) here clearly demonstrates the variability in the intraspecific age-dependent reproductive investment for the two sites.

7 | DISCUSSION AND CONCLUSIONS

The present study has developed a modelling approach that depicts the energy allocation mechanisms between somatic and gonadic growth without assuming any model parameter values a priori. Although the generalisation offers excellent potential for flexible and biologically interpretable modelling, at the same time, it faces some challenges in estimating model parameters from field data such as fisheries data. The study here has highlighted the three challenges that arise and has addressed a unified modelling framework to disentangle these issues.

First, the gradient matching (two-stage least squares) approach offers an effective parameter estimation procedure even when the consecutive growth information of individuals is missing. This attractive feature is appropriate for situations in which the non-closed
model form is obtained, as in the present case (Section 3.2.1). In contrast, the trajectory matching (nonlinear least-squares) method is convoluted by unstable and intensive computation because it must solve all three Equations (1a)–(1c) numerically and iteratively fits the data until the parameter estimates converge. Furthermore, given that relatively large and mature individuals are often underestimated in fisheries data, the trajectory matching method becomes more challenging in identifying an accurate age of maturation as discussed in Honsey et al. (2016) and Wootton et al. (2020). Another alternative for alleviating the challenges is, for example, a priori assigning a fixed value to the exponents of the model as in Quince, Abrams, et al. (2008), Quince, Shutler, et al. (2008), Mollet et al. (2010), Mollet, Dieckmann, et al. (2016) and Mollet, Poos, et al. (2016). Unfortunately, however, such a conditional approach induces a significant shortcoming that limits the interpretability of the model regarding energy allocation mechanisms.

Second, the proposed approach has demonstrated that the age of maturity can be naturally accommodated in a probabilistic manner (Equation 8b) and does not require spawning time data for individuals while minimising the squared errors in the gradient. This expression can be obtained only in the differential form (Equations 8a and 8b) because the differential form (1c) is independent of the spawning times \( \{ t_k \} \). Importantly, the multiplicative term \( b_P \) is a time-varying effect that initiates a smooth transition between the pre- and post-maturation phases, since the probability of maturity \( (0 \leq P \leq 1) \) exhibits a smooth and monotonic increase over time (the bottom panels in Figure 2). The estimated overall average growth pattern thus illustrates a smooth trajectory at the population level. On the contrary, the trajectory matching method must deal with spawning times, \( \{ t_k \} \), and the age of maturity, \( r \), as a specific change point at which the trajectory switches, because its minimisation is carried out in the integral form. If \( r \) were also a parameter, its objective function to be minimised becomes non-differentiable with respect to \( r \); for such a situation, Wilson et al. (2017) recommend a profile method. Together with the gradient matching method, the proposed modelling framework naturally avoids these technical difficulties.

Third, maintaining the sum constraint between somatic and gonadic weights is crucial, that is, \( v_t = w_t + g_t \) and \( a_{it} = v_{it} - y_{it} \) for observations. The sum constraint here expresses the interdependency (induced correlation) between the three weights, \( v_t, w_t \) and \( g_t \), reflecting that these weights are observed from the same individual. The proposed parameter estimation procedure through the equations in differential forms (Equations 7a and 7b) ensures the error structure that underpins the theoretical bases. Adopting an inappropriate error structure and introducing unnecessary data transformation may thus limit model interpretability. This fact may not be much appreciated if modelling focuses, as commonly done in the previous literature, solely upon a single growth model as in Equation (1b). However, the present study has dealt with such interdependency and partially disentangled the correlation structure amongst the parameter estimators due to the model nonlinearity, expressing the suite of growth models (1a)–(1c) that account for the sum constraint. This is because neither of Equation (7a) or Equation (7b) used for parameter estimation shares the same parameters, and the model can therefore be fitted separately if total and gonadic weights are available. This fact illuminates an aspect of the inseparability between model complexity and data. The present study has successfully resolved the issue at the data collection stage, measuring total and gonadic weights.

Growth models often focus on body length, \( y_t \), rather than body mass. To convert between these two measures, a cubic transformation is commonly used: \( w_t = m y_t^3 \), where \( m \) is another parameter that is a product of specific gravity, a conversion factor and a space factor representing the fraction of a cube that an individual of length \( y_t \) would occupy when isometric growth is assumed (Beverton & Holt, 1954; Matthias et al., 2018). Of course, as body length measurement cannot be split into somatic and gonadic segments, the growth model cannot be fitted separately. Rather, the focus on body length negates the need for multiple spawning times when estimating model parameters and may explain modelling body length appears to have been more widely studied, on top of the convenience in field data collection; measuring body length is more effortless than weight. However, the challenges of parameter estimation share the same root in terms of model complexity. The reparameterised models (1b') and (4) may provide a convenient expression that eases such challenges and is worthy of future investigation.
In addition, using an approximated analytical form for Equation (4) offers another possibility for easing parameter estimation. Given that the explicit form can be obtained for the pre-maturity period, it could be used as a proxy if \( R_t \) remains small and negligible relative to age \( t \) in Equation (4). According to the present results, the value of \( R_t \approx 0.35 \) at the largest for the species of age \( t = 6 \) (the bottom panel in Figure 3).

The interplay between model complexity and data availability leads to more case-specific modelling tasks. However, comprehending the nature of challenges and investigating unified approaches for parameter estimation together potentially enhance the interpretability of the model, as the present study has demonstrated. This study offers new advances to gain insight into intraspecific differences in energy allocation between growth and reproduction under different conditions, enabling the model parameters to capture the differences. More importantly, the proposed model illuminates body size dependency through the exponential parameters, indicating a further potential to explore size-dependent phenomena such as behaviour or growth costs (Barneche et al., 2019; Pauli et al., 2019).

Clearly, developing and interpreting a suite of diphasic growth models would not only advance our understanding of intraspecific life-history strategies but also broaden our perspectives and raise further questions on the maintenance of diverse fish communities in the marine realm.

COMPETING INTERESTS
The authors declare that there are no competing interests.

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AUTHORS’ CONTRIBUTIONS
H.-Y.W. designed the sampling and collected data; H.S. carried out data analysis and modelling. All the authors equally contributed to the writing of the manuscript and gave the final approval for publication and agreed to be held accountable for the work performed therein.

DATA AVAILABILITY STATEMENT
Data and all R code are available from GitHub: https://github.com/hshimadzu/GrowthModelling and also deposited on Shimadzu and Wang (2021).

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