


Length conversions and mass–length relationships of five forage-fish species in the California current ecosystem

Danial G. Palance^{1,2} | Beverly J. Macewicz² | Kevin Stierhoff² | David A. Demer² | Juan P. Zwolinski^{2,3} 

¹NOAA Commissioned Officer Corps, Assigned to SWFSC, La Jolla, California, USA

²NOAA Southwest Fisheries Science Center, La Jolla, California, USA

³University of California at Santa Cruz, Santa Cruz, California, USA

Correspondence

Juan P. Zwolinski, NOAA Southwest Fisheries Science Center, 8901 La Jolla Shores Dr, La Jolla, CA 92037, USA.

Email: jzwolins@ucsc.edu

Abstract

Length-measurement conversions and seasonal mass–length relationships (MLR) for Pacific herring *Clupea pallasii*, northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, Pacific mackerel *Scomber japonicus* and jack mackerel *Trachurus symmetricus* in the California Current are presented. The conversions between total (L_T), fork (L_F) and standard lengths (L_S) should facilitate comparisons of data across disciplines and institutions. These equations resulted from an analysis of measurements spanning 14 years and the western seaboard of North America, from the north end of Vancouver Island to the USA–Mexico border. Major-axis regressions were used to calculate reciprocal length-measurement conversions (e.g., L_T to L_S and L_S to L_T) and generalised linear models and ordinary least-squares models were used to create MLRs that account for seasonal variations. The MLR models indicated seasonal differences for all species except *C. pallasii*, for which there was no multi-season data. Discrepancies between these and published models were examined, along with the suitability and benefit of the various types of models used for length-measurement conversion and MLRs.

KEYWORDS

California current, generalised linear model, major-axis regression, mass-at-length, pelagic fishes

1 | INTRODUCTION

Indices of abundance by age or length obtained from fishery monitoring programmes and scientific surveys are essential for managing fish populations (Walters & Martell, 2004). For example, metrics of length, mass and age track patterns of productivity in fish stocks and, when applied in population models, become integral to the foundation of sustainable fishing strategies (Beverton & Holt, 1957). Accurate characterisations of these indices are therefore critical, particularly because even small errors in biological inputs can propagate through models, resulting in both hindcast and forecast errors (Carvalho *et al.*, 2017; Link *et al.*, 2012; Raimondo, 2012). For example, errors in fish length (L) or misspecification of mass–length relationships (MLRs) will

propagate from estimates of fish mass to derived quantities such as spawning stock biomass, stock–recruitment relationships, or harvest guidelines.

In the California Current ecosystem (CCE), which extends from southern British Columbia to the Baja California Peninsula, the forage-fish community is dominated by Pacific Herring *Clupea pallasii* Valenciennes 1847, northern anchovy *Engraulis mordax* Girard 1854, Pacific sardine *Sardinops sagax* (Jenyns 1842), Pacific mackerel *Scomber japonicus* Houttuyn 1782 and jack mackerel *Trachurus symmetricus* (Ayres 1855) (Zwolinski *et al.*, 2014). Variations in the abundances of these small pelagic fishes have inspired studies ranging in scope from the dynamics of single stocks to the entire assemblage of small pelagic fishes and their environment (Bakun & Parrish, 1982;

Jacobson *et al.*, 2005; Schwartzlose *et al.*, 1999). Although researchers from different institutions may study the same ecosystem, or even the same fish populations, they may use different standards for fishlength measurements. For example, in the USA and Mexico, standard length (L_S) is commonly measured for *S. sagax*, (Butler *et al.*, 1996; Cisneros-Mata *et al.*, 1995; Hill *et al.*, 2008), whereas fork length (L_F) is measured in Canada (Hargreaves *et al.*, 1994; McFarlane & MacDougall, 2001). In the USA, L_F is measured for *S. japonicus* and *T. symmetricus* (Crone *et al.*, 2009; Fitch, 1958; Knaggs & Parrish, 1973; Wine & Knaggs, 1975), but L_S is measured in Mexico (García-Franco *et al.*, 2001; Gluyas-Millán & Quiñonez-Velázquez, 1997). Elsewhere, total length (L_T) is the common measurement for small pelagic fishes (Barange *et al.*, 1996; Martins *et al.*, 2013). Therefore, collaborative, comparative or integrative research requires conversion equations for length measurements collected with different standards.

Representative MLRs are also necessary when fish populations are modelled in trophic (Christensen & Pauly, 1992), individual-based

(Dorman *et al.*, 2015), or statistical catch-at-age (Lee *et al.*, 2011) models. These model estimates may be sensitive to the MLRs, which may vary with time, seasonally or multi-annually (Mallicoate & Parrish, 1981; Zwolinski *et al.*, 2001), and across the spatial domain. Furthermore, fisheries pressure and environmental dynamics may induce phenotypic drift, which may induce temporal and spatial variation in MLRs (Eikeset *et al.*, 2016). Therefore, characterisation of broadly distributed stocks with varying abundances requires data collected over large scales of space and time.

Historically, MLRs for forage fishes in the CCE have been derived using data spanning small areas and short time-scales and therefore do not represent entire stocks and their seasonal dynamics. For example, MLRs for *S. sagax*, *C. pallasii* and *E. mordax* were derived from populations off southern California or San Francisco Bay and surrounding estuaries in summer (Childress *et al.*, 1980; Clark, 1928; Collins, 1969; Gartz, 2004; Harvey *et al.*, 2000; Howard & Nakatsu, 1978; Spratt, 1981). MLRs for *S. japonicus* and *T. symmetricus* were derived predominantly from samples off California in spring, but with

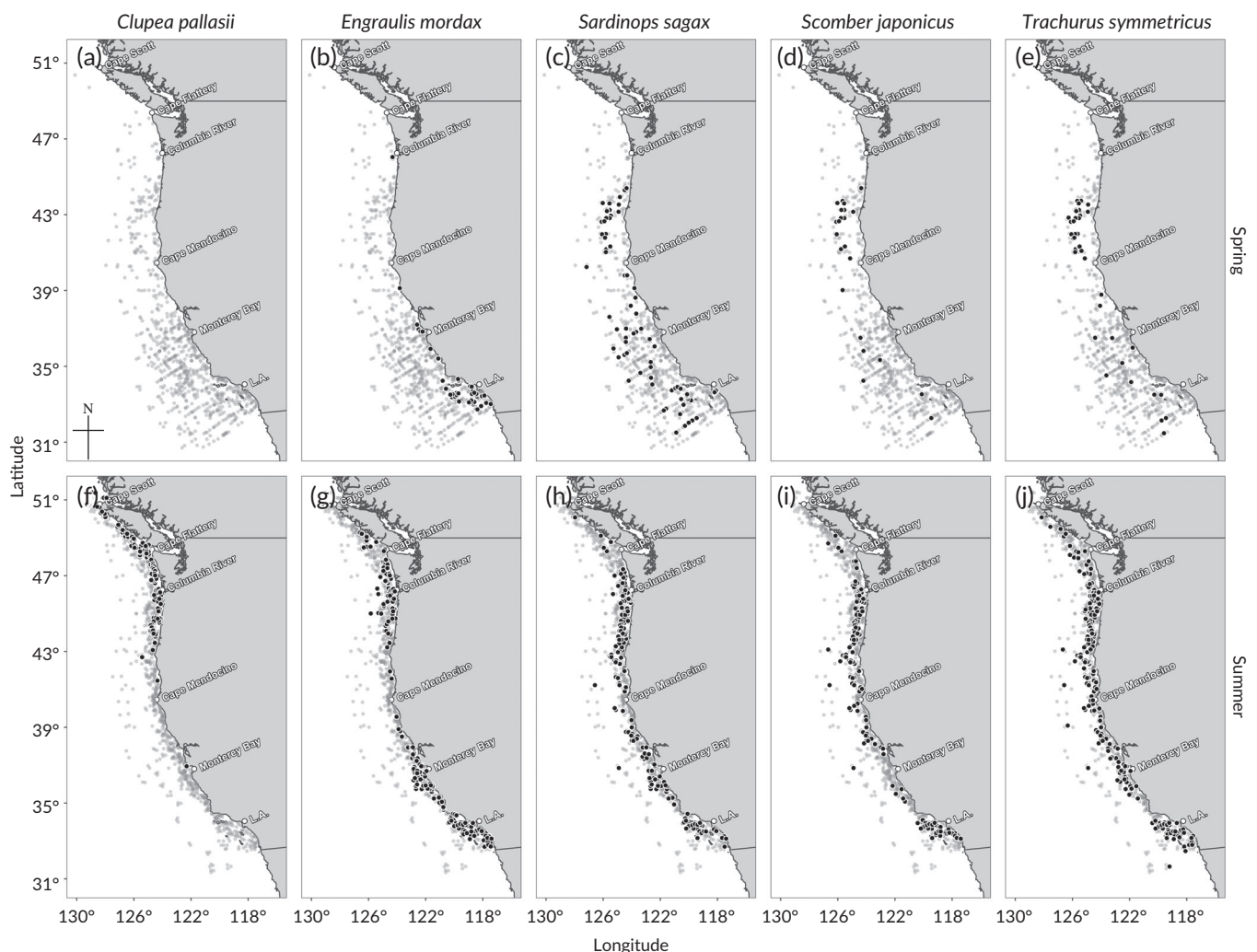


FIGURE 1 Locations of all trawls (○) and positive trawls (●) during (a–e) spring and (f–j) summer for (a) *Clupea pallasii*, (b) *Engraulis mordax*, (c) *Sardinops sagax*, (d) *Scomber japonicus* and (e) *Trachurus symmetricus* from surveys conducted in the California Current 2003–2017

some samples collected off Washington and Oregon in summer (Crone & Hill, 2015) and Baja California, Mexico in spring (MacCall *et al.*, 1980); population-level MLRs should result from data collected over much larger areas and throughout the year.

Here, major-axis regressions (MA), ordinary least-squares regressions (OLS) and generalised linear models (GLM) were used to derive new length-measurement conversions and seasonal MLRs from the most comprehensive contemporary data available on the dominant forage-fish species in the CCE. The merits of the proposed modelling methods and the validity of the long-term MLRs are discussed.

2 | MATERIALS AND METHODS

2.1 | Data collection

Measurements of fish length (L) and mass (M) were made on fresh specimens caught in 1678 surface trawls during 26 surveys conducted between 2003 and 2017 spanning 20° of latitude (c. 2220 km) off the west coast of North America from Vancouver Island to the USA–Mexico border (Figure 1). Length measurements were made in accordance with the definitions set forth by Anderson and Neumann (), incorporating an adjustment to the L_S definition, as illustrated (Figure 2) and summarised here: L_S , from the tip of the head (previously the anterior-most tip of the lower jaw) to the ventral end of the hypural bone; L_F , from the tip of the head to the end of the median caudal fin rays; L_T , from the tip of the head to the end of the dorso-ventrally compressed caudal fin rays. The lengths L_S , L_F and L_T of *S. sagax*, *C. pallasii* and *E. mordax*; and L_F and L_T of *C. pallasii*, *S. japonicus* and *T. symmetricus* were recorded to the nearest 1 mm. Not all length combinations were recorded every year for each species. Mass was measured to the nearest 0.5 g using a motion-compensated scale (Marel M1100 U2, PL2262; www.marel.com).

2.2 | Length-measurement conversions

Because the various measures of L have the same measurement units and are interchangeable on the ordinate (y) and abscissa (x), major-axis regression (Legendre & Legendre, 1998) was used to derive linear relationships between the various measurement types. The MA has the same structure as a two-term linear regression; *i.e.*, $y = \beta_0 + \beta_1 x$, where β_0 and β_1 are estimated parameters and y and x are any combination of the length measurements. In contrast to OLS, the MA equation is reciprocal in the sense that there is no dependency of one variable over the other and allows for error in both y and x (Laws & Archie, 1981). The MA models were fit using the package lmodel2 (Legendre, 2018) in R (www.r-project.org). The visual pattern of the scatterplots and the Pearson product-moment correlation coefficient (r) were used to assess the strength and validity of the linear relationships. For comparison with the MA, OLSs were fit to one set of the pairs of length data per species. The goal of this analysis was to test if MA resulted in more accurate predictions than OLS, particularly when performing the inverse prediction; *i.e.*, when the variable to be predicted was fit as a predictor in the model.

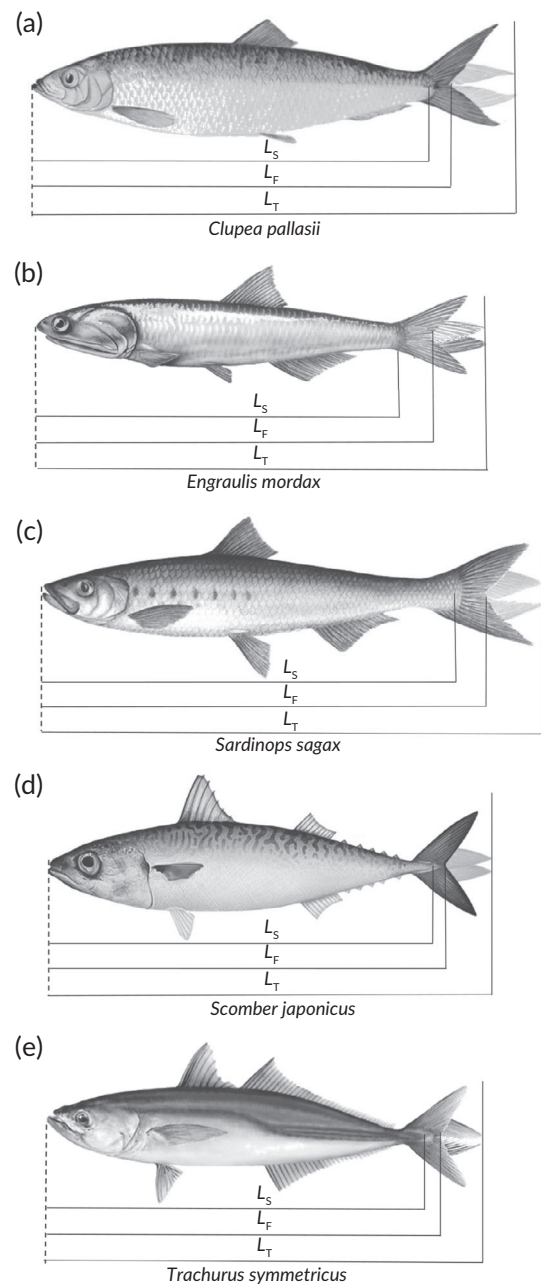


FIGURE 2 Measurement keys for standard (L_S), fork (L_F), and total length (L_T) for (a) *Clupea pallasii*, (b) *Engraulis mordax*, (c) *Sardinops sagax*, (d) *Scomber japonicus* and (e) *Trachurus symmetricus*

2.3 | Mass-length relationships

For fusiform fishes, models of MLR are generally expressed as $M = \beta_0 L^{\beta_1}$ (Schneider *et al.*, 2000), where β_0 and β_1 are species-specific parameters (see Table 1 for a review of model parameters for small pelagic species in the CCE). MLRs for each species were calculated by fitting both GLMs and linearised OLS regressions to M (g) and L_T (mm) using the base R functions *glm* and *lm*, respectively, and incorporating season (spring, March–May and summer, June–August) as an independent variable. Total lengths were calculated from L_S using the appropriate MA model for *S. sagax* and *E. mordax* and from L_F for

TABLE 1 Mass (M)–length (L) relationship models for *Clupea pallasii*, *Engraulis mordax*, *Sardinops sagax*, *Scomber japonicus*, and *Trachurus symmetricus*, where $M = \beta_0 L^{\beta_1}$ and length is expressed as standard length (L_S) for *S. sagax*, *E. mordax*, and *C. pallasii* and fork length (L_F) is used for *T. symmetricus* and *S. japonicus*. Measurement units and standards were converted as necessary. Body length (L_B) from Spratt (1981) was treated as L_S for comparison

Species	Study	L	β_0	β_1	Sex	Units L, M	Length range	Time of year	Location
<i>Clupea pallasii</i>	Gartz (2004)	L_S	8.372×10^{-6}	3.090	Both	mm, g	25–110	April–Dec	San Francisco Estuary
	Harvey et al. (2000)	L_S	4.400×10^{-03}	3.398	Both	cm, g	3.3–25.5	NS	WA, OR
	Spratt (1981)	L_S	4.278×10^{-06}	3.232	Both	mm, g	128–236	Dec–Mar	San Francisco Bay
	Spratt (1981)	L_S	2.125×10^{-05}	2.932	Both	mm, g	140–248	Dec–Mar	Tomales Bay
	Collins (1969)	L_S	1.093×10^{-05}	3.049	Female	mm, g	80–171	Sep–May	Southern CA
<i>Engraulis mordax</i>	Collins (1969)	L_S	8.056×10^{-06}	2.984	Male	mm, g	84–159	Sep–May	Southern CA
	Gartz (2004)	L_S	1.700×10^{-05}	2.922	Both	mm, g	45–165	Apr–Dec	San Francisco Bay
	Harvey et al. (2000)	L_S	4.850×10^{-02}	2.413	Both	cm, g	6.6–26.4	NS	CA
	Howard and Nakatsu (1978)	L_S	1.015×10^{-05}	3.000	Both	mm, g	80–171	NS	Southern CA
	Childress et al. (1980)	L_S	5.420×10^{-06}	3.070	Both	mm, g	NS–240	NS	Southern CA
<i>Sardinops sagax</i>	Clark (1928)	L_S	5.400×10^{-06}	3.150	Both	mm, g	69–288	Nov–May	Southern CA
	Gartz (2004)	L_S	1.400×10^{-05}	2.933	Both	mm, g	70–90	April–Dec	San Francisco Bay
	Hill et al. (2016)	L_S	7.524×10^{-06}	3.233	Both	cm, kg	9–28	Feb–Sep	California Current
	Keys (1928)	L_S	9.000×10^{-03}	3.100	Male	cm, g	NS	Jan–Dec	CA
	Crone and Hill (2015)	L_F	2.700×10^{-06}	3.400	Both	cm, kg	11–42	Jan–Dec	CA, WA, OR, Mexico
<i>Scomber japonicus</i>	Knaggs and Parrish (1973)	L_F	1.366×10^{-06}	3.393	Female	mm, g	NS	Apr–Aug	CA
	Leong (1984)	L_F	1.760×10^{-07}	3.757	Both	mm, g	243–450	NS	Captive fish
<i>Trachurus symmetricus</i>	MacCall et al. (1980)	L_F	1.234×10^{-05}	2.978	Both	mm, g	217–554	NS	CA, Mexico
	Wine and Knaggs (1975)	L_F	3.310×10^{-06}	3.223	Female	mm, g	NS	Jan–Dec	CA
	Wine and Knaggs (1975)	L_F	3.181×10^{-06}	3.237	Female	mm, g	NS	Jul–Aug	CA

NS: Not Specified; CA: California; OR: Oregon; WA: Washington state.

S. japonicus and *T. symmetricus*. Total length for *C. pallasii* was calculated from both L_S and L_F because the length protocol varied between surveys with only one of the two recorded concurrently with L_T . The GLMs have the following structure:

$$g(\hat{M}_i) = \beta_0 + \beta_1 l_{s,i} + \beta_2 \log_e(L_{T,i}) \quad (1)$$

where g is the log link function, M_i has a γ -distribution with mean $\hat{M}_i = e^{(\beta_0 + \beta_1 l_{s,i} + \beta_2 \log_e(L_{T,i}))}$ and variance $= \frac{\hat{M}_i^2}{v}$, where v is a dispersion parameter estimated during fitting. β_0 , β_1 and β_2 are coefficients to be estimated: β_0 is the intercept, β_1 is the parameter for the summer indicator variable l_s , and β_2 is the slope on the linear predictor scale. The γ -distribution is appropriate to model non-negative responses with constant coefficients of variation; i.e., the variance increases with the mean in a predictable way (McCullagh & Nelder, 1989). The global quality of the model fit is reported by the proportion of deviance explained, D^2 (Guisan & Zimmermann, 2000).

For the OLS models, L_T and M were first log-transformed:

$$\log_e(M_i) = \beta_0 + \beta_1 l_s + \beta_2 \log_e(L_{T,i}) + e_i, \quad (2)$$

where β_0 , β_1 and β_2 are analogous to the GLM and e is Gaussian random error with mean = 0 and constant variance = σ^2 . For the OLS models, the predicted values were output on the original scale by back-transforming the predicted value on the logarithmic scale and incorporating the log-normal bias correction ($0.5s^2$), as detailed by (Newman, 1993):

$$\hat{M} = e^{(\beta_0 + \beta_1 l_s + 0.5s^2)} * L^{\beta_2} \quad (3)$$

where $s^2 = \left(\sum_{i=1}^N e_i^2 / N - 3 \right)$. To assess the accuracy of the models, GLM and OLS predictions were compared with the empirical average mass calculated in 1 mm length bins. Furthermore, the predictions of the GLMs and linearised OLS MLRs for each species were compared with historical models using the percent difference (Δ_M , %) from the reference GLM for summer:

$$\Delta_M(\%) = 100 \left(\hat{M}_m - \hat{M}_{glm,s} \right) \hat{M}_{glm,s}^{-1} \quad (4)$$

where \hat{M}_m is the predicted mass-at-length calculated using any of the published models or our OLS model and $\hat{M}_{\text{glm},S}$ is the predicted mass-at-length from the summer GLM; i.e., our reference model. Residual diagnostics of each model type were also compared.

3 | RESULTS

3.1 | Length-measurement conversions

For each species, MA was used to estimate β_0 and β_1 for converting between L_S , L_F and L_T . *Scomber japonicus* and *T. symmetricus* had only paired measurements of L_F and L_T , and *C. pallasii* had pairs of L_F and L_T and L_S and L_T , but not L_F and L_S . The MA regressions were considered valid for the entire possible length range of each species because: (1) the models exhibited r^2 values in excess of 95%, indicating a strong global fit (Table 2 and Supporting Information Figures S1–S4); (2) all length-length correlations (r) were highly significant ($P < 0.01$); (3) there was no evidence of departure from

TABLE 2 Major-axis (MA) regression model equations describing conversions between total (L_T), fork (L_F), and standard lengths (L_S) for *Clupea pallasii*, *Engraulis mordax*, *Sardinops sagax*, *Scomber japonicus* and *Trachurus symmetricus*

Species	n	Equation (L in mm)	r^2
<i>Clupea pallasii</i>	1091	$L_T = 1.200L_S - 1.607$	0.996
	814	$L_T = 1.110L_F - 0.323$	0.994
<i>Engraulis mordax</i>	291	$L_T = 1.137L_S + 5.100$	0.995
	123	$L_T = 1.081L_F + 1.870$	0.982
	123	$L_S = 0.965L_F - 5.736$	0.975
<i>Sardinops sagax</i>	1604	$L_T = 1.157L_S + 0.724$	0.984
	1572	$L_T = 1.134L_F - 5.036$	0.992
	1731	$L_S = 0.980L_F - 5.243$	0.984
<i>Scomber japonicus</i>	583	$L_T = 1.115L_F - 4.114$	0.997
<i>Trachurus symmetricus</i>	704	$L_T = 1.100L_F + 0.896$	0.999

the linearity assumption. OLS length models for a subset of the data were also significant ($P < 0.01$, not shown). Despite the regression coefficients being different from those of the equivalent MA models (Supporting Information Table S1), the predictions of lengths, both direct and inverse using OLS, did not differ significantly from the MA model predictions. Moreover, no bias was detected when estimating fish lengths using the OLS models' inverse predictions (Supporting Information Figure S5).

3.2 | Mass-length relationships

For all species, the variance of M increased with L (Supporting Information Figures S6–S8), justifying the use of the γ -distribution for the errors. For all species with seasonal data, the intercept for the summer samples was consistently larger than that of the spring, indicating that fish were 7.1%–16% heavier in the summer, depending on the species (Table 3 and Supporting Information Figures S6, S7). All GLMs were statistically significant ($P < 0.01$), with the least deviance explained for *E. mordax* ($D^2 = 0.97$; Table 3). The models' fits were good or very good for most species throughout the length range, with some exceptions. Specifically, the models for *S. sagax* and *T. symmetricus* do not capture the relatively lower fish mass at the largest lengths: for the *S. sagax* MLR in spring, the average measured mass at $L_T > c. 285$ mm was c. 7.2% smaller than the predictions (Supporting Information Figure S6); similarly, the *T. symmetricus* MLR in summer overestimated the mass by c. 7% at $L_T > 500$ mm (Supporting Information Figure S7). In log scale, the patterns and distributions of residuals appear nearly identical for the GLM and OLS models (Supporting Information Figures S9–S13). However, in the linear domain, predictions of the OLS MLRs were consistently higher than those of the GLMs (Supporting Information Figure S14). In comparison with other studies, the majority of the MLR predictions were within c. 40% above or below our predicted weights (Figure 3).

TABLE 3 Mass (M)–length (L) relationship equations from ordinary least squares (OLS) regressions and general linear models (GLM) for *Clupea pallasii*, *Engraulis mordax*, *Sardinops sagax*, *Scomber japonicus* and *Trachurus symmetricus*

Species	n	Model type	(M in g, L_T in mm)	D^2	r^2
<i>Clupea pallasii</i>	1961	GLM	$M = \exp(-13.140)L_T^{3.253}$	0.987	0.992
		OLS	$M = \exp(-13.156 + 0.044)L_T^{3.256}$		
<i>Engraulis mordax</i>	5210	GLM	$M = \exp(-12.847 + I_S 0.087)L_T^{3.167}$	0.966	0.979
		OLS	$M = \exp(-13.043 + 0.071 + I_S 0.086)L_T^{3.206}$		
<i>Sardinops sagax</i>	13,239	GLM	$M = \exp(-12.475 + I_S 0.174)L_T^{3.121}$	0.970	0.981
		OLS	$M = \exp(-12.555 + 0.052 + I_S 0.172)L_T^{3.135}$		
<i>Scomber japonicus</i>	3519	GLM	$M = \exp(-12.631 + I_S 0.083)L_T^{3.165}$	0.973	0.976
		OLS	$M = \exp(-12.650 + 0.045 + I_S 0.082)L_T^{3.168}$		
<i>Trachurus symmetricus</i>	5340	GLM	$M = \exp(-12.108 + I_S 0.074)L_T^{3.069}$	0.994	0.996
		OLS	$M = \exp(-12.149 + 0.044 + I_S 0.072)L_T^{3.076}$		

I_S : Summer indicator variable.

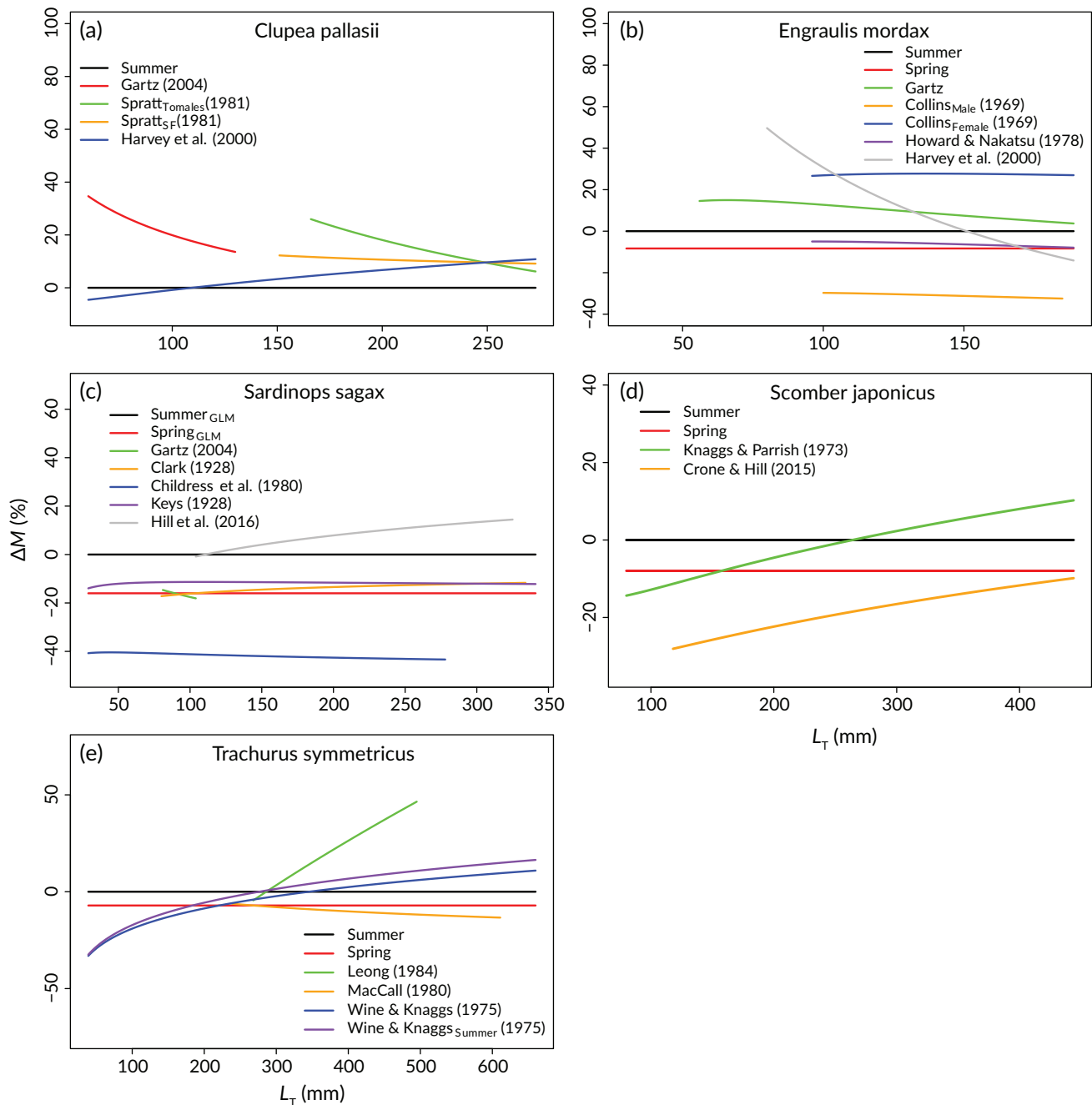


FIGURE 3 Percent difference in predicted mass (ΔM) between generalised linear model mass-total length (L_T) relationships from this study (both spring and summer) and published data for (a) *Clupea pallasii* (b) *Engraulis mordax*; (c) *Sardinops sagax*; (d) *Scomber japonicus*; (e) *Trachurus symmetricus*, using the summer GLM model from this study as a reference

4 | DISCUSSION

4.1 | Length-measurement conversions

In previous studies, length-measurement conversions were derived using OLS (Morato *et al.*, 2001; Moutopoulos & Stergiou, 2002; Petrakis & Stergiou, 1994; Sinovčić *et al.*, 2004), which assumes that the predictor length has no error and the dependent length includes all of the variability. This approach may not provide the best model if the predictor variable has measurement error (Laws & Archie, 1981;

Legendre & Legendre, 1998). Moreover, the OLS construction allows only unidirectional prediction. In contrast, MA finds the axis that minimises errors on both measured variables and allows bi-directional conversions. For these reasons, MA is theoretically more appropriate for conversions between lengths measured with different standards. Despite these theoretical considerations and the difference in model parameters, no bias was detected in the OLS length-measurement conversions, either direct (*i.e.*, predicting y from x), or inverse. Therefore, in situations like ours, on which both variables are measured with

small errors, it appears that OLS may be used without bias. More research is necessary to know if this is generally true.

For many species, L_S is prone to error due to several working definitions and difficulty in locating the hypural plate (Howe, 2002). For species with a well-defined tail fork, L_F may be less prone to error than L_S , but there are ambiguities in the location and deepness of the tail fork. L_T appears to be less susceptible to measurement error than L_S and L_F , except when there is damage to the caudal fin. We propose that L_T is measured for all species mentioned here. If L_T cannot be measured due to fin damage, then L_S or L_F should be made, followed by conversion to L_T . This approach would harmonise sampling protocols for these species and would remove the potential confusion from measuring different lengths during the processing of multi-specific trawl samples.

4.2 | Mass-length relationships

The MLRs derived using OLS of log-transformed data (Childress *et al.*, 1980; Clark, 1928; Harvey *et al.*, 2000; Hill *et al.*, 2016), predict median weight, not mean weight, if there is no account for transformation bias (Newman, 1993). There was no mention of such correction in the literature analysed for this paper. When the correction is applied however, there is the possibility of a positive bias in the linear-scale predictions if the distribution of the residuals in the log-scale does not follow a normal distribution (Hayes *et al.*, 1995; Zwolinski *et al.*, 2009). This might explain why our linearised OLS models predicted larger fish mass in comparison to the GLM models.

Here, GLMs with the γ -distribution and log-link function captured the underlying trends observed in fish sampled over more than a decade and were unaffected by the unbalanced design of the observations, with a couple exceptions. For example, the summer MLR models for *T. symmetricus* and *S. sagax* fit well throughout most of their length distribution, but overestimated mass towards the larger animals. Further analysis is required to ascertain if this behaviour is a characteristic of the species or instead an artefact of the small number of data points at larger sizes. If the observed pattern is in fact a real attribute of the fish, it may be the result of sarcopaenia; *i.e.*, the gradual loss of muscle mass with age (Demontis *et al.*, 2013). If this is true, it may be the first such observation for fishes.

The seasonal variations in MLRs are probably the result of the reproductive cycle, food availability, or both (Nebenzahl, 1997). An increase in mass from spring to summer was observed in all species for which seasonal data were available. Clark (1928) had noted that the fat content of *S. sagax* individuals peaked in December and declined through to April, which suggests that *S. sagax* increasingly store fat from summer through winter and then use it during spring spawning (Zwolinski & Demer, 2012, 2014). A similar seasonal pattern was observed for European Sardine *Sardina pilchardus* (Walbaum 1792), which showed the gonadosomatic index (I_G) and condition factor (K) of females to be in opposite phase of that of the maturity cycle (Zwolinski *et al.*, 2001). Mallicoate and Parrish (1981) also observed periodic fat accumulation in mature *E. mordax* from the central sub-population, *T. symmetricus* and *S. japonicus*. In those cases, mean

specimen weights peaked between July and September and decreased during the subsequent winter.

Our MLRs have some notable differences from those in the literature. For example, a model for *T. symmetricus* by Leong (1984) indicates larger increases in mass with length, probably because the model was derived with data from captive fish that were fed daily to satiation and not subjected to inconsistent food abundance and quality as in the wild. For *C. pallasii*, our MLR differs from one in the literature (Spratt, 1981) most probably because the two equations were derived from data collected using different length-measurement standards. We measured L_S , but Spratt (1981) had difficulty locating the hypural plate and therefore measured body length (L_B), from the tip of the snout to the end of the silvery part of the body. For *S. sagax*, our MLR predictions differ *c.* 40% from those of Childress *et al.* (1980), which we suspect is because their model is derived from only 21 individuals. For *E. mordax*, our MLR predictions differ most from Harvey *et al.* (2000), which may also be due to a small sample size ($n = 34$).

ACKNOWLEDGEMENTS

We thank the numerous people who sampled the fish comprising the 14-year data set and appreciate the efforts to collect these data by the captains and crews of many survey vessels. Critical reviews by Andrew Thompson and two anonymous reviewers during the acceptance process improved this manuscript.

ORCID

Juan P. Zwolinski  <https://orcid.org/0000-0002-8009-4910>

REFERENCES

- Anderson, R. O., & Neumann, R. M. (1996). Length, weight, and associated structural indices. In B. R. Murphy and D. W. Willis (Eds.), *Fisheries techniques* (2nd edn, pp. 447–482). Bethesda, Maryland: American Fisheries Society.
- Bakun, A., & Parrish, R. H. (1982). Turbulence, transport and pelagic fish in the California and Peru current systems. *California Cooperative Oceanic Fisheries Investigations Reports*, 23, 99–112.
- Barange, M., Hampton, I., & Soule, M. (1996). Empirical determination of in situ target strengths of three loosely aggregated pelagic fish species. *ICES Journal of Marine Science*, 53, 225–232.
- Beverton, R. J. H., & Holt, S. J. (1957). *On the Dynamics of Exploited Fish Populations Fishery investigations, series II*. London: Her Majesty's Stationery Office.
- Butler, J. L., Granados, M. L., Barnes, J. T., Yaremko, M., & Macewicz, B. J. (1996). Age composition, growth and maturation of the Pacific sardine (*Sardinops sagax*) during 1994. *California Cooperative Oceanic Fisheries Investigations Reports*, 37, 152–159.
- Carvalho, F., Punt, A. E., Chang, Y. J., Maunder, M. N., & Piner, K. R. (2017). Can diagnostic tests help identify model misspecification in integrated stock assessments? *Fisheries Research*, 192, 28–40.
- Childress, J. J., Taylor, S. M., Cailliet, G. M., & Price, M. H. (1980). Patterns of growth, energy utilisation and reproduction in some meso- and bathypelagic fishes off southern California. *Marine Biology*, 61, 27–40.

- Christensen, V., & Pauly, D. (1992). Ecopath-II – a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling*, 61, 169–185.
- Cisneros-Mata, M. A., Nevarez-Martinez, M. O., & Hammann, M. G. (1995). The rise and fall of the pacific sardine, *Sardinops sagax caeruleus girard*, in the Gulf of California, Mexico. *CalCOFI Report*, 36, 136–143.
- Clark, F. N. (1928). The weight-length relationship of the California sardine (*Sardina caerulea*) at San Pedro. *Fish Bulletin*, 12, 59.
- Collins, R. A. (1969). Size and age composition of northern anchovies, *Engraulis mordax*, in the California anchovy reduction fishery for the 1965–66, 1966–67 and 1967–68 season. In J. Messersmith (Ed.), *The northern anchovy, Engraulis mordax and its fishery 1965–1968* (pp. 56–63). Fishery Bulletin: California Department of Fish & Game.
- Crone, P. R. & Hill, K. T. (2015). Pacific mackerel (*Scomber japonicus*) stock assessment for USA management in the 2015–16 fishing year. p. 131. Pacific Fishery Management Council, 7700 NE Ambassador Place, Suite 101, Portland, Oregon 97220: Pacific Fishery Management Council.
- Crone, P. R., Hill, K. T., McDaniel, J. D. & Lo, N. C. H. (2009). Pacific mackerel (*Scomber japonicus*) stock assessment for USA management in the 2009–10 fishing year. p. 197pp: Pacific Fishery Management Council, Pacific Fishery Management Council, 7700 NE Ambassador Place, Suite 101, Portland, Oregon 97220. 197 p.
- Demontis, F., Piccirillo, R., Goldberg, A. L., & Perrimon, N. (2013). Mechanisms of skeletal muscle aging: insights from *Drosophila* and mammalian models. *Disease Models & Mechanisms*, 6, 1339–1352.
- Dorman, J. G., Sydemann, W. J., Bograd, S. J., & Powell, T. M. (2015). An individual-based model of the krill *Euphausia pacifica* in the California current. *Progress in Oceanography*, 138B, 504–520.
- Eikeset, A. M., Dunlop, E. S., Heino, M., Størvik, G., Stenseth, N. C., & Dieckmann, U. (2016). Roles of density-dependent growth and life history evolution in accounting for fisheries-induced trait changes. *Proceedings of the National Academy of Sciences*, 113, 15030–15035.
- Fitch, J. E. (1958). Age composition of the southern California catch of Pacific mackerel for the two seasons, 1955–56 and 1956–57. *California Department of Fish and Game, Fishery Bulletin*, 106, 19–26.
- García-Franco, W., Cota-Villavicencio, A., & Sánchez-Ruiz, F. J. (2001). Diagnóstico de la pesquería de peces pelágicos menores en la costa occidental de Baja California, México. *Ciencia Pesquera*, 15, 113–120. <https://www.inapesca.gob.mx/portal/documentos/publicaciones/cienciapesquera/CP15/CP15-04 LHC.pdf>
- Gartz, R. (2004). Length-weight relationships for 18 fish species common to the San Francisco Estuary. *IEP Newsletter*, 17, 49–57.
- Gluyas-Millán, M. G., & Quiñonez-Velázquez, C. (1997). Age, growth and reproduction of Pacific mackerel *Scomber Japonicus* in the Gulf of California. *Bulletin of Marine Science*, 61, 837–847.
- Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling*, 135, 147–186.
- Hargreaves, N. B., Ware, D. M., & McFarlane, G. A. (1994). Return of Pacific sardine (*Sardinops sagax*) to the British Columbia coast in 1992. *Canadian Journal of Fisheries and Aquatic Sciences*, 51, 460–463.
- Harvey, J. T., Loughlin, T. R., Perez, M. A. & Oxman, D. S. (2000). Relationship between fish size and otolith length for 63 species of fishes from the Eastern North Pacific Ocean. In NOAA technical report, p. 36: National Oceanic & Atmospheric Administration.
- Hayes, D. B., Brodziak, J. K. T., & O’Gorman, J. B. (1995). Efficiency and bias of estimators and sampling designs for determining length-weight relationships of fish. *Canadian Journal of Fisheries and Aquatic Science*, 52, 84–92.
- Hill, K. T., Crone, P. R., Dorval, E. & Macewicz, B. J. (2016). Assessment of the Pacific sardine resource in 2016 for USAA management in 2016–17. NOAA-TM-NMFS-SWFSC-562.
- Hill, K. T., Dorval, E., Lo, N. C. H., Show, C. & Felix-Uraga, R. (2008). Assessment of the Pacific sardine resource in 2008 for USA management in 2009. PFM, Nov 2008, Agenda Item G.2.b, 236 p.
- Howard, G. V., & Nakatsu, L. (1978). *Northern anchovy fishery final environmental impact statement and fishery management plan*. Portland, OR: National Oceanic & Atmospheric Administration & Pacific Fishery Management Council.
- Howe, J. C. (2002). Standard length: not quite so standard. *Fisheries Research*, 56, 1–7.
- Jacobson, L. D., Bograd, S. J., Parrish, R. H., Mendelssohn, R., & Schwing, F. B. (2005). An ecosystem-based hypothesis for climatic effects on surplus production in California sardine (*Sardinops sagax*) and environmentally dependent surplus production models. *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 1782–1796.
- Knaggs, E. H., & Parrish, R. H. (1973). Maturation and growth of Pacific mackerel, *Scomber japonicus* houttuyn. *Marine Technical Resources Report 3* (p. 21). Long Beach, CA: California Department of Fish & Game.
- Laws, E. A., & Archie, J. W. (1981). Appropriate use of regression-analysis in marine biology. *Marine Biology*, 65, 13–16.
- Lee, H. H., Maunder, M. N., Piner, K. R., & Methot, R. D. (2011). Estimating natural mortality within a fisheries stock assessment model: an evaluation using simulation analysis based on twelve stock assessments. *Fisheries Research*, 109, 89–94.
- Legendre, P. (2018). lmodel2: Model II Regression. www.semanticscholar.org/paper/MODEL-II-REGRESSION-USER%E2%80%99S-GUIDE%2C-R-EDITION-Legendre/f74004ceb124ddb8c1417f79cf77a8def0c8167
- Legendre, P., & Legendre, L. (1998). *Numerical ecology* (p. 853). Amsterdam, Netherlands: Elsevier.
- Leong, R. (1984). Growth of jack mackerel, *Trachurus symmetricus*, in captivity. *CalCOFI Reports*, 25, 146–150.
- Link, J. S., Ihde, T. F., Harvey, C. J., Gaichas, S. K., Field, J. C., Brodziak, J. K. T., ... Peterman, R. M. (2012). Dealing with uncertainty in ecosystem models: the paradox of use for living marine resource management. *Progress in Oceanography*, 102, 102–114.
- MacCall, A. D., Frey, H. W., Huppert, D. D., Knags, E. H., McMillan, J. A. & Stauffer, G. A. (1980). Biology and economics of the fishery for jack mackerel in the northeastern pacific. NOAA Technical Memorandum NMFS - SWFSC- 4, 85 p.
- Mallicoate, D. L., & Parrish, R. H. (1981). Seasonal growth patterns of California stocks of northern anchovy, *Engraulis mordax*, Pacific mackerel, *Scomber japonicus* and jack mackerel, *Trachurus symmetricus*. *CalCOFI Reports*, 22, 69–81.
- Martins, M. M., Skagen, D., Marques, V., Zwolinski, J., & Silva, A. (2013). Changes in the abundance and spatial distribution of the Atlantic chub mackerel (*Scomber colias*) in the pelagic ecosystem and fisheries off Portugal. *Scientia Marina*, 77, 551–563.
- McCullagh, P., & Nelder, J. A. (1989). *Generalised linear models*. London: Chapman & Hall.
- McFarlane, G. A., & MacDougall, L. A. (2001). Biological information for Pacific sardine (*Sardinops sagax*) captured during research cruises, 1992–2000. *Canadian Technical Report of Fisheries and Aquatic Sciences*, 2372, 149.
- Morato, T., Afonso, P., Lourinho, P., Barreiros, R. S., Santos, R. S., & Nash, R. D. M. (2001). Length-weight relationships for 21 coastal fish species of the Azores, North-Eastern Atlantic. *Fisheries Research*, 50, 297–302.
- Moutopoulos, D. K., & Stergiou, K. I. (2002). Length-weight and length-length relationships of fish species from the Aegean Sea (Greece). *Journal of Applied Ichthyology*, 18, 200–203.
- Nebenzahl, D. A. (1997). Age, growth and population structure of Jack Mackerel (*Trachurus symmetricus*) from the northeastern Pacific Ocean (Master Thesis). Available from <http://islandora.mlm.calstate.edu/islandora/object/islandora:1152>

- Newman, M. C. (1993). Regression analysis of log-transformed data: statistical bias and its correction. *Environmental Toxicology & Chemistry*, 12, 1129–1133.
- Petrakis, G., & Stergiou, K. I. (1994). Weight-length relationships for 33 fish species in Greek waters. *Fisheries Research*, 21, 465–469.
- Raimondo, S. (2012). Incorporating temperature-driven seasonal variation in survival, growth and reproduction into population models for small fish. *Marine Ecology Progress Series*, 469, 101–112.
- Schneider, J. C., Alexander, G. R., & Merna, J. W. (2000). Modules for lake and stream surveys. In J. C. Schneider (Ed.) *Manual of fisheries survey methods II: with periodic updates*. (Chapter 2). Ann Arbor, Michigan: Michigan Department of Natural Resources.
- Schwartzlose, R. A., Alheit, J., Bakun, A., Baumgartner, T. R., Cloete, R., Crawford, R. J. M., ... Zuzunaga, J. Z. (1999). Worldwide large-scale fluctuations of sardine and anchovy populations. *South African Journal of Marine Science-Suid-Afrikaanse Tydskrif Vir Seewetenskap*, 21, 289–347.
- Sinović, G., Franičević, M., Zorica, B., & Čikeš-Keč, V. (2004). Length-weight and length-length relationships for 10 pelagic fish species from the Adriatic Sea (Croatia). *Journal of Applied Ichthyology*, 20, 156–158.
- Spratt, J. D. (1981). Status of the pacific herring, *Clupea harengus pallasii*, resource in California. *Fish Bulletin* 171. Sacramento, CA: California Department of Fish and Wildlife.
- Walters, C., & Martell, S. J. D. (2004). *Fisheries ecology and management*. Princeton, NJ: Princeton University Press.
- Wine, V., & Knaggs, E. H. (1975). Maturation and growth of jack mackerel, *Trachurus symmetricus*. *Marine research technical Report* 3. Long Beach, CA: California Department of Fish and Game.
- Zwolinski, J., Fernandes, P. G., Marques, V., & Stratoudakis, Y. (2009). Estimating fish abundance from acoustic surveys: calculating variance due to acoustic backscatter and length distribution error. *Canadian Journal of Fisheries and Aquatic Sciences*, 66, 2081–2095.
- Zwolinski, J., Stratoudakis, Y., & Soares, E. (2001). Intra-annual variation in the batch fecundity of sardine off Portugal. *Journal of Fish Biology*, 58, 1633–1645.
- Zwolinski, J. P., & Demer, D. A. (2012). A cold oceanographic regime with high exploitation rates in the Northeast Pacific forecasts a collapse of the sardine stock. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 4175–4180.
- Zwolinski, J. P., & Demer, D. A. (2014). Environmental and parental control of Pacific sardine (*Sardinops sagax*) recruitment. *ICES Journal of Marine Science*, 71, 2198–2207.
- Zwolinski, J. P., Demer, D. A., Cutter, G. R., Jr., Stierhoff, K., & Macewicz, B. J. (2014). Building on fisheries acoustics for marine ecosystem surveys. *Oceanography*, 27, 68–79.

SUPPORTING INFORMATION

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

How to cite this article: Palance DG, Macewicz BJ, Stierhoff K, Demer DA, Zwolinski JP. Length conversions and mass-length relationships of five forage-fish species in the California current ecosystem. *J Fish Biol.* 2019;1–9. <https://doi.org/10.1111/jfb.14105>