

BRIEF COMMUNICATIONS

Fish length exclusively determines sexual maturation in the European whitefish *Coregonus lavaretus* species complex

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The probability that a fish matures at a certain age and length (the so-called probabilistic maturation reaction norm, PMRN) was analysed for a European whitefish *Coregonus lavaretus* species complex population living in the Austrian pre-alpine Lake Irrsee. Fish length was found to be the only relevant determinant of maturation probability, and females matured at slightly smaller sizes than males.

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To optimally manage stocks and to ensure sustainable population development, fishers need to understand how fish life-history traits affect reproduction, growth and mortality (Roff, 1992; Stearns, 1992; Wootton, 1998). Life-history traits of major relevance are those that alter the maturation schedule. Many studies investigated a relation of age at maturity to growth parameters, including a correlation with asymptotic length (Jensen, 1985; Froese & Binohlan, 2000) or growth rate (Berrigan & Charnov, 1994; Jonsson *et al.*, 2013). Some authors also discussed the idea that in certain species, maturation may occur at a length threshold (De Roos *et al.*, 2003; Marty *et al.*, 2011), but no clear empirical evidence for this hypothesis has been presented. In fact, traditional methods of analysis make it difficult to arrive at such a conclusion, as they leave the process of maturation entangled with survival and growth. The probabilistic maturation reaction norm (PMRN) approach, building on work by Stearns & Crandall (1984), Stearns & Koella (1986) and Heino *et al.* (2002), overcomes this problem.

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Whitefish (Salmoniformes: Coregonidae) are important for commercial and recreational freshwater fisheries in northern temperate regions (Arlinghaus *et al.*, 2002; Thomas & Eckmann, 2007; Ebener *et al.*, 2008). It has been shown that the onset of maturation in coregonids varies over time and among stocks, usually accompanied by variations in coregonids growth (Edsall, 1960; Jensen, 1981, 1985; Beauchamp *et al.*, 2004; Eckmann *et al.*, 2007; Wang *et al.*, 2008). It is established that maturation in coregonids depends primarily on age and length (Jensen, 1985; Beauchamp *et al.*, 2004; Heikinheimo & Mikkola, 2004).

To estimate the age and length at which maturation occurs, several methods are widely used, all of which are based on maturity status of sampled fish (*i.e.* immature or mature) *v.* age or length. The traditional approach is to perform a logistic regression on these data, obtaining a so-called maturity ogive, and to heuristically define maturation as occurring at the age and length at which 50% of fish are mature (A_{50} or L_{50}), foregoing any mechanistic explanation of how A_{50} and L_{50} relate to the age and length at which a single fish matures. By contrast, the modern PMRN approach considers the probability that a fish matures at a certain age and length. Thus, it not only describes the dependence of the maturation process on age and length but also accounts for the various sources of microenvironmental and genetic variance affecting maturation (Heino *et al.*, 2002; Grift *et al.*, 2003). In the PMRN framework, onset of maturation is defined by the length-at-age at which the probability of maturing is 50% ($L_{p50,A}$).

The only detailed study on the maturation schedule of coregonids using the PMRN approach was conducted for Great Lake whitefish *Coregonus clupeaformis* (Mitchill 1818) in several North American populations by Wang *et al.* (2008). While this study revealed differences among study sites, the dependence of PMRN midpoints on age ($L_{p50,A}$) remained unclear due to the paucity of data. This study improves on this *status quo* by analysing the PMRN of the *Coregonus lavaretus* (L. 1758) species complex population of Lake Irrsee, Austria.

Coregonus lavaretus was stocked in Lake Irrsee (47° 53' N; 13° 18' E) for the first time in 1968. This stocked fish originated from the Baltic area (Lake Miedwie) and was classified as belonging to the *C. lavaretus* species complex (Gassner & Wanzenböck, 2007). The *C. lavaretus* population of Lake Irrsee has been subject to an intensive recreational fishery with annual angling catches between 761 and 4739 fish, or 1.6 and 7.2 kg ha⁻¹, in 2000 to 2009.

Since 2000, the population has been studied by gillnet sampling carried out annually in October, before the spawning season starts in late November. Prior to sampling, hydroacoustic surveys were conducted in most of the sampling years. The echograms indicated that *C. lavaretus* were equally distributed throughout the lake and that the preferred vertical habitat during the night was at a depth of *c.* 12–15 m (H. Gassner, unpubl. data). Consequently, gillnets with mesh sizes from 15 to 70 mm were set over night in part of the lake at a depth of 12–15 m (Gassner *et al.*, 2004; Gassner & Wanzenböck, 2007). The sampling gear covered the whole size range of Lake Irrsee *C. lavaretus* and was not selective with respect to maturity status. Individual total length (L_T), sex and maturity status were determined for all the *C. lavaretus* caught ($n = 2000$). The age (A) of each individual was identified by scale reading according to the method used by Devries & Frie (1996). Fish older than 5 years were omitted in the analysis to avoid unreliable estimates. The analysed data were compiled by pooling data collected from 2000 to 2009, and the

following analyses were carried out using the statistical software R (R Core Team; www.r-project.org).

Average somatic growth was described by a biphasic growth model that assumed linear growth during the first year, when all individuals were immature, and growth according to a von Bertalanffy growth function for older fish, which gives length-at-age as $L(A) = L_{\infty} \left\{ 1 - e^{-k(A-A_0)} \right\}$. The parameters, asymptotic length (L_{∞}), growth coefficient (k) and age offset (A_0), were obtained by fitting this function to sampled length-at-age data of mature *C. lavaretus* through a non-linear least-squares method. Average growth functions were estimated both for the whole population and for males and females separately. Annual average growth increments $\Delta L(A)$ were calculated from size differences between ages.

The PMRN calculation uses maturity ogive functions. Using logistic regression, four ogive models, describing maturity as a linear function of age and L_T , were statistically compared (Table I). On basis of the results of this analysis, the two ogive models $A+L_T$ (age and length as predictor variables) and $L_T|A$ (length as predictor variable with age as factor) were selected for the following PMRN calculations due to the minimal AIC and BIC values found for the logistic regression models $A+L_T$ and L_T describing maturity status (Table I). The probability $m(A, L_T)$ of maturing at a given age and length was calculated as $m(A, L_T) = \{o(A, L_T) - o[A-1, L_T - \Delta L_T(A)]\} \{1 - o[A-1, L_T - \Delta L_T(A)]\}^{-1}$ (Heino *et al.*, 2002; Barot *et al.*, 2004). Lower (2.5%) and upper (97.5%) confidence bounds for the midpoints ($L_{p50,A}$) were estimated by resampling the original data 1000 times. This procedure was carried out both for the whole population and for males and females separately. For the latter, the sex ratio of immature individuals as a function of age and length was estimated by simulating growth of a sample cohort according to the estimated sex-specific growth functions.

As a result, the following growth parameters \pm s.e. were obtained for the analysed *C. lavaretus* population: $L_{\infty} = 44.38 \pm 0.88$ cm, $k = 0.40 \pm 0.03$ year⁻¹ and $A_0 = -0.28 \pm 0.14$ year⁻¹. The PMRN midpoints for age 1–5 years

TABLE I. Statistical analyses of logistic regression models of maturity ogives. The four tested models are shown in the first column, where c_x is coefficient, A represents age and L_T represents L_T . For model selection, the Akaike information criterion (AIC) and the Bayesian information criterion (BIC), which penalizes additional model parameters more strongly than the AIC, were calculated. The models that minimize these criteria were investigated more closely. The small variance inflation factors (VIFs) indicate that the degree of correlation between predictor variables was acceptable for the $A + L_T$ model (conventionally, VIF values of up to 10 are considered unproblematic) Values in bold are the two models used in PMRN calculations due to minimal BIC, respectively, AIC values.

Maturity ogive model	Short name	AIC	BIC	VIF		
				A	L_T	AL
logit ($o(A)$) = $c_0 + c_1A$	A model	912.36	923.18	–	–	–
logit ($o(L_T)$) = $c_0 + c_1L_T$	L_T model	811.80	822.62	–	–	–
logit ($o(A, L_T)$) = $c_0 + c_1A + c_2L$	$A + L$ model	811.78	828.01	3.61	3.61	–
logit ($o(A, L_T)$) = $c_0 + c_1A + c_2L + c_3AL$	$A \times L$ model	812.67	834.31	40.54	7.06	60.58

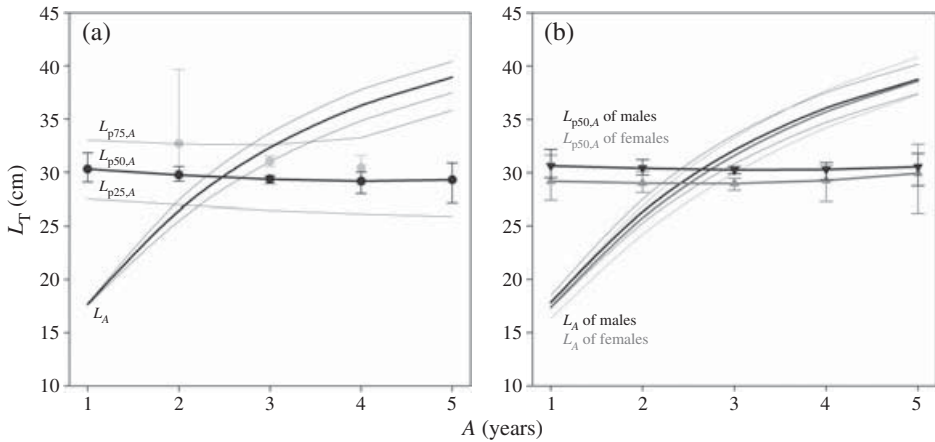


FIG. 1. Onset of maturation in Lake Irrsee *Coregonus lavaretus*. Points indicate the length (L)-at-age (A) at which the probability of maturing is 50% ($L_{p50,A}$) for (a) the whole population and (b) males (\blacktriangledown) and females (\blacktriangle) separately. Values of $L_{p50,A}$ estimated by the $A + L_T$ ogive model are shown for discrete ages 1–5 years (\bullet), with connecting lines only illustrating the trend. Values of $L_{p50,A}$ estimated by the $L_T|A$ ogive model are shown for discrete ages 2–4 years (\bullet) and could not be reliably estimated outside this range. In (a), the L -at- A at which the probability of maturing is 25 or 75% ($L_{p25,A}$ or $L_{p75,A}$) is shown by thin lines. In (a) and (b), the error bars of the $L_{p50,A}$ values and the thin lines around the average growth trajectories L_A , shown as thick lines, indicate confidence bounds between 2.5 and 97.5%.

calculated with the $A + L_T$ ogive model showed little age-dependent variation: $L_{p50,A} = 30.30, 29.74, 29.36, 29.17$ and 29.29 cm [Fig. 1(a)]. The intersection of the growth function and the regression of the PMRN midpoints determined the onset of maturation, which occurred at an age of $c. 2.5$ years when *C. lavaretus* reached an L_T of $c. 29.5$ cm [Fig. 1(a)]. The PMRN midpoints estimated for ages separately with the $L_T|A$ ogive model were slightly higher and suffered from a higher degree of uncertainty [Fig. 1(a)].

The estimation of growth parameters \pm s.e. for males and females separately showed a lower asymptotic length and a higher growth coefficient for males than for females [males $L_\infty = 44.49 \pm 0.86$ cm, $k = 0.38 \pm 0.02$ year $^{-1}$ and $A_0 = -0.33 \pm 0.06$ year $^{-1}$; females $L_\infty = 46.97 \pm 1.14$ cm, $k = 0.33 \pm 0.02$ year $^{-1}$ and $A_0 = -0.35 \pm 0.06$ year $^{-1}$; Fig. 1(b)]. For males, PMRN midpoints ($L_{p50,A}$) for the $A + L_T$ ogive model were on average 0.86 cm higher than the $L_{p50,A}$ values calculated for the whole population [males: 30.63, 30.42, 30.26, 30.30 and 30.56 cm; Fig. 1(b)]. For females, $L_{p50,A}$ values for the $A + L_T$ ogive model were on average 0.28 cm lower than the $L_{p50,A}$ values calculated for the whole population [females: 29.20, 29.03, 28.99, 29.27 and 29.94 cm; Fig. 1(b)]. Accordingly, $L_{p50,A}$ values for males were slightly larger than for females. The intersections of the linearly interpolated sex-specific $L_{p50,A}$ values with the sex-specific growth functions showed that the onset of maturation occurred at an age of $c. 2.65$ years in males and $c. 2.50$ years in females and hence was very similar in both sexes [Fig. 1(b)]. Sex-specific PMRN midpoints estimated with the $L_T|A$ ogive model were again slightly higher and again suffered from a higher degree of uncertainty.

The differences between the $A + L_T$ ogive model and the $L_T|A$ ogive model in the PMRN midpoint estimation resulted mostly from higher uncertainties in the

calculation of the latter, owing to the smaller sample sizes within single age classes. Moreover, PMRN calculations based on the $L_T|A$ ogive model always involve two subsequent age classes. Fluctuations among cohorts in the onset of sexual maturity may consequently lead to less accurate estimations of the PMRN. This makes the $L_T|A$ ogive model generally problematic for PMRN analysis of pooled data, compared to the analysis of individual cohorts.

Compared to *C. clupearformis*, which is suggested to be a form of *C. lavaretus* (Sajdak & Phillips, 1997), the most striking difference with the present findings was that Lake Irrsee *C. lavaretus* matured at a substantially smaller L_T (c. 30 cm in Lake Irrsee compared to c. 40–50 cm in the Great Lakes; Wang *et al.*, 2008). Also, the L_T at maturation appeared to be relatively independent of age in the Lake Irrsee population, indicating that a purely length-based model of maturation is a good approximation. This might not be true for the Great Lake populations, although there were not enough data points reported in the study of Wang *et al.* (2008) to conclude this with certainty. Regarding sex-specific maturation schedules, Leskelä *et al.* (2004) and Wang *et al.* (2008) observed that female *C. lavaretus* reach sexual maturity later in life and at larger sizes, a trend found more generally for larger fish in a synoptic study by Froese & Binohlan (2000). In contrast to Froese & Binohlan (2000) and Wang *et al.* (2008), the study population exhibits reversed sexual differences in age and length at maturation. In Lake Irrsee, females tended to mature at smaller sizes and slightly younger ages than males.

It was hypothesized for Lake Constance *C. lavaretus* by Thomas *et al.* (2009) that intensive size-selective fishing could favour females that mature at younger ages and smaller sizes. The observed sex-specific maturation schedules in Lake Irrsee are compatible with this expectation and thus may be due to intensive size-selective fishing by sport anglers.

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