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Estimates of natural mortality for flatfish in the Northwest Atlantic: A comparison of model predicted estimates

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ABSTRACT

The main motivation of this paper is to compare empirical estimates of M and compare it with the current estimate used for natural mortality (*M* of 0.2 yr^{-1}) for the Georges Bank yellowtail flounder stock assessment. We examined a database of direct estimates of *M*, maximum age (t_{max}), von Bertalanffy growth parameters *K* and L_∞, as described by Then et al. (2014), for flatfishes (Order Pleuronectiformes). A total of six flatfish species (Family Pleuronectidae) were available from Northwest Atlantic and Northeast Pacific ocean basins, with literature *M* estimates ranging from 0.18 to 0.39 yr^{-1}. We applied the original and updated equations of four empirical estimators based on t_{max} and on the von Bertalanffy growth parameters presented in Then et al. (2014) to the flatfish dataset to obtain empirical estimates of *M* and bootstrap-derived standard errors. With the exception of one species, the range of the empirical *M* estimates encompassed the literature *M* estimates. The t_{max}-based *M* estimates more closely matched the literature values than the growth-based *M* estimates. However, all the empirical estimates derived using bootstrap resampling suggested that *M* for the Georges Bank yellowtail flounder is greater than 0.2 yr^{-1}. Empirical *M* estimates derived using both historical and recent growth estimates for the Georges Bank stock also provided evidence for $M > 0.2$. Based on a non-exhaustive literature survey, sexual dimorphism in growth and lifespan is prevalent in flatfish; for the stocks that exhibit such sex-specific differences, the females are typically the larger and longer-lived. Sex-specific empirical *M* estimates suggest that males experience higher natural mortality than females. Although the oldest fish in a comprehensive review of databases was 14, this was a male fish; the bulk of data, however, suggests that females survive in greater numbers to older ages than males. Considering all of the data, and patterns for other flatfish, it is not unreasonable to expect that M is greater for males than for females.

Introduction

This working paper explores the use of an existing dataset described in Then et al. (2014) to examine estimates of natural mortality rate, *M*, as well as other pertinent life history parameters for flatfishes (order Pleuronectiformes). The dataset was originally collated for the purpose of providing a comprehensive comparison of the predictive performances of a number of widely used empirical estimators of *M*. These estimators included Alverson and Carney (1975), Pauly (1980). Hoenig (1983), and Jensen (1996). Then et al. (2014) showed that prediction errors for maximum age-based estimators were approximately half that of the von Bertalanffy *K*-based estimators. They also provided updated predictive equations for a number of recommended estimators as well as estimates of uncertainty in the parameters of the equations.

The parameter *M* is known to be a highly important and influential stock parameter but a difficult one to estimate reliably by any means. Although a direct estimate of *M* is almost always preferred over an indirect or empirical estimate, the latter can potentially be used to cross-validate and determine the reasonableness of an existing direct *M* estimate. For the Georges Bank yellowtail flounder, the estimate of *M* used in current stock assessments is 0.2. The use of various empirical estimators can help shed light on whether this estimate is appropriate or should be revised.

Another important issue for consideration is the use of the *M* estimate of 0.2 across both male and female yellowtail flounder. This is of relevance as this fish appears to display sexual dimorphism in growth (Lux and Nichy, 1969; Legault, 2010). In addition, there is evidence of sex-specific differences in the lifespan of the yellowtail flounder, with more females reaching older ages than males.

This work was motivated by the Terms of Reference for the empirical benchmark of Georges Bank yellowtail flounder. Namely, to examine all available data related to this stock to determine whether the information in the data support the findings of the current assessment (Legault, 2013) and how that information might be used to inform management about appropriate catch levels. In the current assessment model (ADAPT Virtual Population Analysis; Parrack 1986; Gavaris 1988; Conser and Powers 1990), a value for natural mortality is assumed rather than estimated. This approach is standard in most stock assessments, regardless of the model. We evaluate how the model estimators reviewed in Then et al. (2014) compare with the current assumed value for *M* of 0.2.

The objectives of this working paper are to: (1) compare *M* estimates of flatfish from the literature to derived *M* estimates using updated empirical estimators recommended in Then et al. (2014), (2) compare empirical estimates of *M* of flatfish using both the original and the updated equations, (3) derive estimates of uncertainty for the empirical *M* estimates, (4) compare empirical estimates of *M* for yellowtail flounder using age and growth estimates from two different time periods (historic versus recent studies) (5) determine if sex-specific empirical estimates of *M* are preferred to that of estimates based on combined sexes, and (6) provide recommendations for reasonable *M* estimate for the Georges Bank yellowtail flounder based on the best available data for the stock.

Methods

Dataset of natural mortality (*M*) estimates

The dataset in Then et al. (2014) comprises estimates of natural mortality rate *M* (yr^{-1}), maximum age (t_{max}), von Bertalanffy parameters *K* (yr^{-1}) and L_∞ (mm), as well as mean water temperature *T* (ºC) for 201 unique fish species. The most important criteria for the inclusion of *M* estimates in the dataset is that the *M* estimate must be derived using a direct method, i.e., any estimates based on existing indirect or empirical methods, such as Pauly (1980) and Hoenig (1983), were rejected. Direct methods include age-based and length-based catch curve analyses, tagging, and regression of total mortality rate versus effort.

Many of the species in the full dataset were evaluated to be unexploited or lightly exploited based primarily on information or assessments provided by the authors of the mortality and (or) the growth studies. The species included in the dataset are primarily marine stocks from the North American, Australian and European continents and their surrounding water bodies. The von Bertalanffy growth *K* estimates ranged from 0.012 to 2.56 yr^{-1}, L_∞ from 49 to 3164 mm, and t_{max} from 38 weeks to 205 years. Mean *T* of stocks ranged from 4.6 to 30ºC after accounting for physiological adjustments (as described in Pauly, 1980).

Then et al. (2014) evaluated the performance of a number of widely used empirical estimators. Many of these estimators were derived from regression analysis which assumes, among other things, independence of observations. The inclusion of multiple M estimates for a single species (stocks from multiple locations or separate male and female estimates) very likely violates that assumption. Then et al. (2014) dealt with that issue by using only a single observation for a given species. They selected the best set of estimates for a species based primarily on the aging method, validation of the ages and sample size of the study. For studies where sex-specific estimates for both *M* and other life history parameters were available, either the estimates for male or for females were included when there is strong evidences of sexual dimorphism in growth. The choice of sex to be reported depended on the quality of the growth estimates (i.e., estimate of t_0, adequacy of sampling of young fish, sample size). Further details of the dataset compilation and criteria for inclusion of estimates are outlined in Then et al. (2014).

The dataset in Then et al. (2014) contained a total of 6 flatfish species from the family Pleuronectidae. Table 1 provides estimates of *M* and the matching life history parameters of these flatfishes, as well as the original sources of these estimates. The six species are the American plaice from St. Mary's Bay, Newfoundland, the petrale sole from Queen Charlotte Sound, British Columbia, the English sole from Puget Sound, Washington, the Pacific halibut from the North Pacific and the Bering Sea, the winter flounder from St Mary's Bay, Nova Scotia, and the yellowtail flounder from Southern New England and Georges Bank. Hence, these flatfish stocks are either from Northwest Atlantic (3) or Northeast Pacific waters (3). Literature *M* estimates ranged from 0.18 to 0.39 yr^{-1} and were derived using catch curve analyses and tagging experiments.

A few things are worth noting for these individual stocks. The American plaice in St Mary Bay are considerably smaller in length at age compared to other adjacent stocks of plaice (Pitt, 1967). For the petrale sole, the growth study conducted by Ketchen and Forrester (1966) using whole otoliths yielded a maximum age of 22, but the maximum age recorded for this stock is 35 (Munk, 2001). The growth estimates for winter flounder were given by Beverton and Holt (1959), based on the study by Dickie and McCracken (1955). The latter study directly estimated the von Bertalanffy weight-at-age parameters, but Beverton and Holt (1959) likely used the length-at-age data to estimate L_∞ and *K*. Estimates of *M* for the English sole were averaged across sex, mesh size and fishing trips (Table 13 in Van Cleve and El-Sayed, 1969) and the von Bertalanffy growth estimates likewise were averaged although the growth is sexually dimorphic. For yellowtail flounder, the pooled growth parameters were estimated although the females appeared to grow faster than males (Lux and Nichy, 1969).

Aging methods for these flatfishes vary from using scales, sectioned otoliths, break-and burn technique on otoliths, and interopercular bone (Table 2). A common finding for a number of aging studies is that ages determined from scales and whole otoliths tended to be smaller than that from otoliths subjected to break and burn procedure or sectioning (e.g., Pacific halibut in Forsberg, 2001). If ageing errors were present, this would also affect the von Bertalanffy parameters. For example, if ages are underestimated, then t_{max} would be underestimated. This would overestimate *M* for the t_{max} model, but would underestimate *M* for the $Hoenig_{nls}$ estimator. Underaging could also produce bias in the estimate of the von Bertalanffy parameters, most likely overestimating *K* and subsequently overestimating *M* (following equations in Table 1).

In the case of Georges Bank yellowtail flounder, scales are used to determine age. Two validation studies have been conducted that lend confidence in the accuracy of this technique (Lux and Nichy, 1969; Alade, unpub. results). In both studies, scales from tagged fish were compared to scales of the same fish at the time of recapture, and the number of new growth rings corresponded very well with the amount of time the fish were at liberty. One caveat is that the oldest fish where scales were read was 7 (Table 3; Lux and Nichy, 1969). Thus, readability and reliability of scales from older fish has not been validated to the same extent as for younger fish. A study by Stone and Perley (2002) examined thin sections of otoliths for Georges Bank yellowtail flounder and concluded that reading annuli was difficult due to " the presence of weak, diffuse or split opaque zones and strong checks." Furthermore, there was great difficulty in identifying the second annulus, which impacted assigned ages and contributed to weak inter-age reader agreement (Stone and Perley, 2002). Thus, although sectioned otoliths are generally preferred to scales for age determination, it cannot be concluded that they are necessarily better for yellowtail flounder.

Empirical estimators of *M*

Table 1 provides the original and updated predictive equations for the recommended empirical estimators based on maximum age (t_{max}), and von Bertalanffy growth parameters *K* and L_∞. These estimators were evaluated and ranked based on the cross-validation prediction errors (CVPE). In addition, they were also recommended (or otherwise) based on model residuals, model parsimony principle and biological considerations. Figure 1 shows the CVPE and rank for each updated estimator. The two best t_{max}–based estimators were the one-parameter t_{max} and the two-parameter t_{max} estimators (also known as the $\text{Hoenig}_{\text{nls}}$ model). The two best growth-based estimators were the one-parameter model and the Pauly model refitted without temperature (also known as $\text{Pauly}_{\text{nls-}T}$). The original and updated versions of the four models are used to estimate M of the six flatfish species based on life history parameters in Table 2.

The original regression estimators of Pauly (1980) and Hoenig (1983) were derived from age and growth studies that were conducted at least 30 years ago. The updated empirical estimators in Then et al. (2014) incorporated both older as well as newer studies of age and growth. Given that all studies of M for the six flatfish stocks were conducted during the 1950s to 1970s, with the exception of the Pacific halibut (in the early 2000s), we estimated M using both the 'original' and updated equations in Table 1 for comparison.

For both the Grand Banks and Georges Bank stocks of yellowtail flounder, estimates of age and growth were available from an earlier period and more recent times for comparison (see Table 3). The updated empirical equations were used to derive M values from these two sets of growth estimates.

Sexual dimorphism in growth of flatfish

We did a non-exhaustive literature survey of flatfish growth studies to determine the prevalence of sexual dimorphism. For each of these studies, we determined which sex exhibited a larger size (either via the estimate of L_∞ or the size-at-age at older ages), had a longer lifespan (t_{max}), and had higher von Bertalanffy growth coefficient of K.

Calculation of uncertainty in *M* estimates

The calculation of uncertainty of an empirically-derived M estimate assumes that the assumptions of the fitted model are met, e.g., an ordinary least-squares regression model assumes no errors in the measurements of the independent variables and errors are distributed normally. Another important assumption is that the model being fitted is the true model. Since we do not know the true values of M, calculation of uncertainties of predicted M may be underestimated if we rely on model-derived estimates of variance or confidence intervals.

The approach we took to provide confidence intervals was to use a non-parametric bootstrap method to calculate the uncertainty in the resulting M estimates by resampling from the 201 data points in the dataset of Then et al. (2014), which we will term as the full dataset. Specifically, we fitted each model listed in Table 1 to 10000 bootstrap samples of the full dataset. The fitted equation was then used to predict M for the six flatfish stocks (Table 2). For each flatfish stock, we calculated the cross-validation root mean squared error of the bootstrap M estimates, henceforth referred to as the bootstrap standard error (SE). All analyses and plotting were conducted using the R statistical programming language (R Development Core Team, 2011).

Results

Out of 66 families in the Then et al. (2014) data set, Pleuronectidae had the 19th lowest mean *M* estimates of stocks by family (mean *M* = 0.25). Table 4 summarizes the estimates of *M* and the bootstrap SE derived from using the four preferred empirical estimators of *M*. All four updated empirical estimates of *M* are lower than the literature *M* values for the Pacific halibut, and they are all higher than the literature *M* values for *Limanda ferruginea*, the yellowtail flounder. Literature *M* estimates of the Pacific halibut and the yellowtail flounder were derived using tagging methods. More recent studies of Georges Bank yellowtail flounder suggest some movement between stock areas, and it is difficult to know to what extent movement was accounted for in these earlier studies, and how that might have affected those M estimates.

With the exception of *Hippoglossus stenolepis*, the Pacific halibut, the literature *M* estimates fall within the range of the *M* estimates derived from both original and updated estimators (Figure 2). The range of empirical *M* estimates from the updated models appeared to encompass that of the original equations (Figure 2). Model residual plots indicated that the *M* estimates from the updated equations are more variable than that from the original equations, particularly for the one-parameter *K* model (Figure 3). Based on the model residuals, the updated $\text{Pauly}_{\text{nls-}T}$ model tended to yield lower *M* estimates than that of the literature values. On the other hand, the updated one-parameter *K* model tended to yield more variable and higher *M* estimates than the literature *M* values (Figure 3). Residuals of the updated t_{max}–based estimators appeared to be more evenly distributed.

Bootstrap estimates of *M* and SE for all six flatfish species indicated that *M* estimates from the updated one-parameter t_{max} model were less variable than that of the $\text{Hoenig}_{\text{nls}}$; likewise the updated one-parameter *K* model yielded less variable *M* estimates than the $\text{Pauly}_{\text{nls-T}}$ model (Table 4; Figures 4 to 9). For most of these flatfish species, the disagreement between the literature and empirical *M* estimates was considerably greater for the t_{max}–based than the growth-based *M* estimates (Figures 4 to 9). The most obvious and consistent disagreement between the literature and empirically-derived *M* estimates is for the yellowtail flounder (Figure 9); all the latter estimates suggested that M is > 0.2 for the yellowtail flounder.

The empirical estimators in Then et al. (2014) were applied to historic and recent literature values for life history parameters of two stocks of yellowtail flounder in the Northwest Atlantic Ocean (the Grand Banks and Georges Bank, Figure 10). Based on the 'older' age and growth estimates from Pitt (1974) for the Grand Banks yellowtail flounder, the t_{max}–based M estimates generally coincided for both males and females (Figure 11). On the other hand, the growth-based M estimates suggested that the M of males were higher than the females, although the discrepancies between the M estimates of one-parameter K and $\mathrm{Pauly}_{\mathrm{nls\text{-}T}}$ were large. When estimating M using the recent growth estimates for the Grand Banks stock from Dwyer et al. (2003), there appeared to be considerable agreement between the t_{max}–based and growth-based estimators in terms of both the range of estimates and the directionality of sex-specific differences in M where the males were predicted to have higher M than the females (Figure 12). The t_{max}–based M estimates were more closely matched with the direct M estimate available from a recent tagging study (Cowen et al., 2009) than the growth-based M estimates.

For the Georges Bank yellowtail flounder, the t_{max}–based M estimates using an older age and growth study (Lux and Nichy, 1969) were about two times higher than those based on more recent age and growth estimates (Brooks, pers. comm.). This is because the oldest age in the study by Lux and Nichy (1969) was 7, whereas age 14 was the oldest fish in a recent examination of data (Brooks, pers. comm.). In contrast, the growth-based empirical M estimates using the estimates from Lux and Nichy (1969) suggested that M was lower than that based on the recent age and growth study (Figure 13). This is because the estimate of the von Bertalanffy K in the study by Lux and Nichy (1969) was smaller (0.335) than the K estimated in a recent examination of data (0.46-0.63; Brooks, pers. comm.). Lux and Nichy (1969) combined the first quarter commercial fishery data from southern New England with the third quarter data from Georges Bank, and only estimated the von Bertalanffy curve for ages 2 to 7. The recent von Bertalanffy estimation was based on both spring and fall data from the NEFSC bottom trawl surveys. The lack of young fish in the Lux and Nichy (1969) study likely influenced their estimate of

K compared to the recent work (Brooks, pers. comm.). The t_{max}–based and growth-based *M* estimates disagreed with respect to the directionality of sex-specific differences in the Georges Bank yellowtail flounder. For the recent data exploration, the maximum age of males was 14 (survey data) and for females it was 13 (commercial fishery data), so the t_{max}–based *M* estimate for males was slightly lower than for females. A recent study of sex-specific von Bertalanffy *K* estimated a value of 0.46 for females and 0.63 for males, so in this case the growth-based *M* estimates were larger for males than females.

Literature survey of eleven flatfish species showed that sexual dimorphism is fairly ubiquitous in the flatfish group, with the exception of the single tropical species of toothed flounder. While there appeared to be discordance as to which sex exhibited higher growth rates, it was generally clear for the sexually-dimorphic flatfish species that the females are larger and longer-lived between the two sexes (Table 5). This suggested that the males would be predicted to have higher *M* than the females when using the empirical estimators. The ambiguity in sex-specific differences in growth rates were mainly due to the close similarity in *K* estimates for both sexes. In addition, the t_0 estimates for the flatfish in Table 5 tended to deviate considerably from 0, suggesting that young flatfish were poorly sampled and hence the *K* estimates may be poorly characterized.

Discussion

The current assessment for Georges Bank yellowtail flounder is a VPA model for combined sexes and assumes M = 0.2. For the single stock of yellowtail flounder examined in this paper, no sex-specific estimates of M or von Bertalanffy growth parameters were available when the database was compiled in Then et al. (2014), even though the authors of the growth study that was included had established that growth is sexually dimorphic (Lux and Nichy, 1969). Hence it is difficult to ascertain if empirically derived sex-specific M estimates would be more accurate. Wood and Cadrin (2013) noted from tagging studies that estimated survival for females of yellowtail flounder were higher than the males, although this could be due to sex differences in catchability.

The updated empirical equations in Then et al. (2014) were developed based on various fish species of different life history strategies and ecological habits. It is possible that a taxonomic-specific regression may improve predictions of M for that given taxonomic group. For example, Ralston (1987) and Pauly and Binohlan (1996) developed empirical estimators of M for groupers and snappers. We did explore the option for developing flatfish-specific estimators of M; however, given the small sample size and narrow range of observations for the independent variables, we did not pursue this further.

One important consideration is to interpret the life history parameters available for this stock in light of the aging method used. Historically, scales have been used as the primary aging structure for the Georges Bank stock as well as for adjacent stocks (Stone and Perley, 2002). Although early validation studies demonstrated the accuracy of aging with scales, there were no fish older than age 7 in the study (Lux and Nichy, 1969; Alade, pers. comm.). Undoubtedly, interpretation of annuli of older fish is difficult, and a number of studies have demonstrated that sectioned otoliths are superior to whole otoliths (e.g., Dwyer et al. 2003). On the other hand, Stone and Perley (2002) noted the difficulty and uncertainty associated with reading sectioned otoliths for yellowtail flounder. If underaging is an issue for the Georges Bank yellowtail flounder stock, the derived estimates of the von Bertalanffy growth parameters would also likely biased, thus affecting the basis for an assumed value for M. With respect to the assessment, we expect that the model input (catch at age, survey indices at age) would be unaffected if underaging of older fish was occurring because the VPA assessment model has a plus group at age 6. This means that any fish that are older than age 6 are assigned to the age 6 category and plus group calculations are carried out for these fish.

The *M* estimate of 0.2 for the southern New England and Georges Bank yellowtail flounder based on tagging data from Lux (1969) is considerably lower than the empirical estimates (Figure 12). Based on an older age and growth study (Lux & Nichy, 1969), the t_{max}-based *M* estimates suggest that $M > 0.7$ (given their t_{max} of 7) but the growth-based *M* estimates suggest that $M < 0.6$ (given their *K* estimate of 0.335), using the updated equations in Table 1. However, using more recent age and growth information (Table 4), the empirical tmax-based *M* estimates are approximately 0.4 (t_{max} of 14) while the growth-based *M* estimates are > 0.6 (*K* range from 0.46-0.63). Sex-specific estimates from growth-based estimators suggest that *M* of the female yellowtail flounder is considerably lower than that of the male while the growth-based *M* estimates for combined sexes is intermediate to the sex-specific estimates.

A recent multistate mark-recapture study on tagging data of the Grand Banks yellowtail flounder from years 2000 to 2004 yielded an *M* estimate of 0.256 (Cowen et al., 2009). Corresponding exploitation rates were low during that period, ranging from 0.000 to 0.047. This suggests that the *M* of the Grand Banks stock, at least in the more recent times, is likely higher than 0.2. The empirically estimated *M* also appeared to suggest that $M = 0.2$ for the Grand Banks stock is possibly the lower limit of *M*.

A recent examination of three databases for yellowtail flounder (research surveys, 1963-present; commercial fishery data, 1973-present; observer data, 1992-present) found that the maximum observed age for males and females was 14 (1975) and 11 (1970, 1974, 2001), respectively, in the research surveys; 13 (1986) and 13 (1986) in the commercial landings; and 10 (2003) and 11 (2003) in the observer database. The fact that fish at ages 10 and 11 were observed as recently as 2003, despite heavy exploitation, suggest that a possible upper bound for a combined-sex estimate might be around 0.5. Considering the difference in growth patterns and sex-specific estimates of *K*, one could probably expect an upper bound slightly above 0.5 for males and somewhat below 0.5 for females. Combined with the literature-based direct estimate of 0.2, we feel that the available data and empirical estimates support bounds between about 0.2 and 0.6. This range is supported by the empirical bootstrap estimates for the t_{max}-based estimators (Figures 8 and 12), which had the smallest CVPE and were overall the preferred methods identified in Then et al. (2014).

It is difficult to specify what the best point estimate should be, particularly since there is evidence in literature to suggest that it may be sex-specific, whereas the assessment model is not sex-specific. Several studies note that males and females have similar size at age until age 2, but beyond that age females are larger than males (Lux and Nichy, 1969; Stone and Perdy, 2002). This could suggest that *M* is similar for age 1 and 2 males and females, but for fish age 3 and older there may be a difference in male and female natural mortality. If a new value is assumed for the VPA assessment, careful consideration will need to be given to the sex composition of the catch (if that can be determined) and whether there are sufficient samples in the surveys to determine the sex-ratio at age. In addition, the *M* value assumed in the assessment will need to be consistent with the approach taken to specify reference points and rebuilding projections.

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Table 1. Select original and updated equations of preferred empirical estimators of natural mortality *M* (based on Then et al. 2014). Variables: Natural mortality rate *M*, maximum age t_{max}, von Bertalanffy growth parameters *K* and L_∞, mean water temperature *T*. All length measurements are in mm.

Model	Original equation	Author	Updated equation
one-parameter t_{max}	$M = 4.22/\ t_{max}$	Hewitt and Hoenig (2005)	$M = 5.075/\ t_{max}$
Hoenig	$\log M = 1.44 - 0.982 \log t_{max}$	Hoenig (1983)	$\mathrm{M} = 4.895\ t_{max}^{-0.922}$
one-parameter *K*	$M = 1.5\ K$	Jensen (1996)	$M = 1.684\ K$
Pauly	$\log_{10} M = -0.0066 - 0.279 \log_{10} L_\infty + 0.6543 \log_{10} K + 0.4634 \log_{10} T$	Pauly (1980)	$M = e^{1.461} K^{0.741} L_\infty^{-0.347}$

Table 2. Estimates of natural mortality rate M (yr^{-1}), maximum age t_{max} (yr) von Bertalanffy growth parameters K (yr^{-1}) and L_∞ (mm) for six species of flatfish. Methods for deriving M estimates: catch curve analysis (caa), tagging (tag). Aging structures used: sectioned otoliths (sot), otoliths subject to break and burn technique (bot), scale (sca), other hard parts (hpt), and undetermined (un). Sex: female (f), male (m), combined sexes (c).

Genus	Species	Common Name	Location	Sex	M	M method	M Reference	K	L_∞	Growth Reference	t_{max}	t_{max} Method	t_{max} Reference
Hippoglossoides	*platessoides*	American plaice	St Mary Bay, Newfoundland	f	0.18	caa	Pitt, 1973	0.07	600	Pitt, 1967	32	sot	Pitt, 1973
Eopsetta	*jordani*	petrale sole	Queen Charlotte Sound, British Columbia	c	0.23	caa	Ketchen & Forrester, 1966	0.17	538	Ketchen & Forrester, 1966	35	un	Munk, 2001
Hippoglossus	*stenolepis*	Pacific halibut	North Pacific & the Bering Sea	c	0.2	tag	Chen & Xiao, 2006	0.08	1345	Martell et al, 2013	55	bot	Forsberg, 2001
Pseudopleuronectes	*americanus*	winter flounder	St Mary Bay, Nova Scotia	c	0.37	tag	Dickie & McCracken, 1955	0.26	469	Beverton & Holt, 1959	11	un	Dickie & McCracken, 1955
Parophrys	*vetulus*	English sole	north Puget Sound, Washington	c	0.39	caa	Van Cleve & El-Sayed, 1969	0.31	372	Van Cleve & El-Sayed, 1969	16	hpt	van Cleve & El-Sayed, 1969
Limanda	*ferruginea*	yellowtail flounder	Southern New England and Georges Bank	c	0.2	tag	Lux, 1969	0.34	500	Lux & Nichy, 1969	14	sca	Lux & Nichy, 1969

Table 3. Estimates of sex-specific von Bertalanffy growth parameters K (yr^{-1}) and L_∞ (mm) and maximum age t_{max} (yr) for yellowtail flounder. res.: research samples; com.: commercial samples. m: male; f: female; c: combined sexes. Table adapted from Dwyer et al. (2003).

Location	Type	Sex	K	L_∞	t_{max}	Source
Grand Bank	res.	m	0.41	42.07	11	Pitt, 1974
Grand Bank	res.	f	0.29	48.12	12	Pitt, 1974
Grand Bank	com.	m	0.32	46.40	12	Pitt, 1974
Grand Bank	com.	f	0.24	52.96	10	Pitt, 1974
New England	com.	c	0.34	50.00	7	Lux and Nichy, 1969
Grand Bank	res.	m	0.19	48.80	21	Dwyer et al., 2003
Grand Bank	res.	f	0.16	55.60	25	Dwyer et al., 2003
Georges Bank	res.	c	0.49	44.26	14	Brooks (pers. comm.)
Georges Bank	res.	m	0.63	38.92	14	Brooks (pers. comm.)
Georges Bank	res.	f	0.46	46.82	11	Brooks (pers. comm.)

***** Estimates of maximum age from NOAA research surveys are 14 for a male in 1975 and 11 for three females caught in 1970, 1974, and 2001. Based on commercial catch data, the maximum age estimates are 13 for a female in 1986 and 12 for a male in 1986.

Table 4. Estimates of *M* (in bold) for flatfish based on literature values and derivation using updated empirical estimators of one-parameter t_{max} (abbreviated as Onetmax), $Hoenig_{nls}$ (Hoenig), one-parameter *K* (OneK), and $Pauly_{nls\text{-}T}$ (Pauly). Bootstrap estimates of standard error (SE) of the *M* estimates are given in italics below each empirical *M* estimate. Sources of literature values are given in Table 2. *Empirical *M* estimates applicable to females. Model and bootstrap SE estimates for the one-parameter t_{max} coefficient are 0.1 and 0.23 respectively. Model and bootstrap SE estimates for the one-parameter *K* are 0.08 and 0.17 respectively.

Genus	Species	***M* estimates** (*SE*)				
		Literature	Onetmax	Hoenig	OneK	Pauly
**Hippoglossoides*	*platessoides*	**0.18**	**0.16**	**0.20**	**0.12**	**0.07**
			0.03	*0.05*	*0.06*	*0.06*
Eopsetta	*jordani*	**0.23**	**0.15**	**0.18**	**0.29**	**0.13**
			0.09	*0.03*	*0.06*	*0.08*
Hippoglossus	*stenolepis*	**0.20**	**0.09**	**0.12**	**0.13**	**0.05**
			0.11	*0.06*	*0.07*	*0.09*
Pseudopleuronectes	*americanus*	**0.37**	**0.46**	**0.54**	**0.44**	**0.19**
			0.08	*0.20*	*0.08*	*0.07*
Parophrys	*vetulus*	**0.39**	**0.32**	**0.38**	**0.52**	**0.23**
			0.08	*0.03*	*0.14*	*0.12*
Limanda	*ferruginea*	**0.20**	**0.36**	**0.43**	**0.57**	**0.22**
			0.15	*0.26*	*0.36*	*0.27*

Table 5. Presence of sexual dimorphism in various species of flatfish. The sex that has the larger size, higher maximum age estimate and higher von Bertalanffy *K* parameter is given as well. m: male; f: female; na: not applicable; ?: result was ambiguous.

Scientific name	Common name	Sexual dimorphism	*Larger sex	Higher t_{max}	Higher *K*	Source
Hippoglossoides platessoides	American plaice	y	f	f	?	Pitt, 1967
Eopsetta jordani	petrale sole	y	f	f	f	Ketchen & Forrester, 1966
Hippoglossus stenolepis	Pacific halibut	y	f	f	?	Martell et al, 2013
Pseudopleuronectes americanus	winter flounder	y	f	?	?	Howe & Coates, 1975
Parophrys vetulus	English sole	y	f	f	m	Van Cleve & El-Sayed, 1969
Limanda ferruginea	yellowtail flounder	y	f	f	?	Lux & Nichy, 1969; Dwyer et al., 2003
Microstomus pacificus	Dover sole	y	f	f	f	Brodziak & Mikus, 2000
Cyclopsetta querna	toothed flounder	n	na	f	na	Amezcua et al., 2006
Atheresthes stomias	arrowtooth flounder	y	f	f	m	Turnock et al., 2003; Wilderbuer & Turnock, 2009
Glyptocephalus cynoglossus	witch flounder	?	?	f	?	Bowering, 1989
Reinhardtius hippoglossoides	Greenland halibut	?	f	f	?	Bowering, 1983

* Determined from a larger estimate of L_∞ or length-at-age.

For the Greenland halibut, mean size at age similar between males and females up to ages 7-11 (depending on area); difference in growth patterns only observed after ages 8-12.

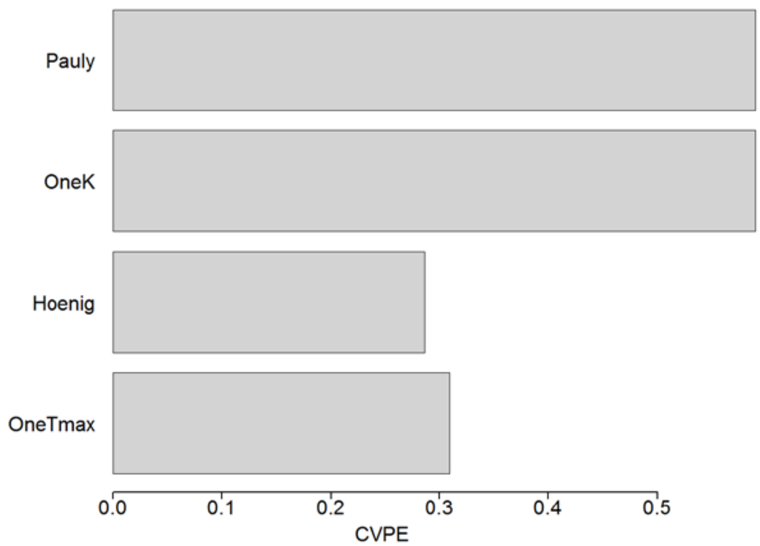

Figure 1. Barchart of cross-validation prediction errors (CVPE) for the empirical estimators of one-parameter t_{max} (abbreviated as Onetmax), $\text{Hoenig}_{\text{nls}}$ (Hoenig), one-parameter K (OneK), and $\text{Pauly}_{\text{nls-}T}$ (Pauly). Results from Then et al. (2014).

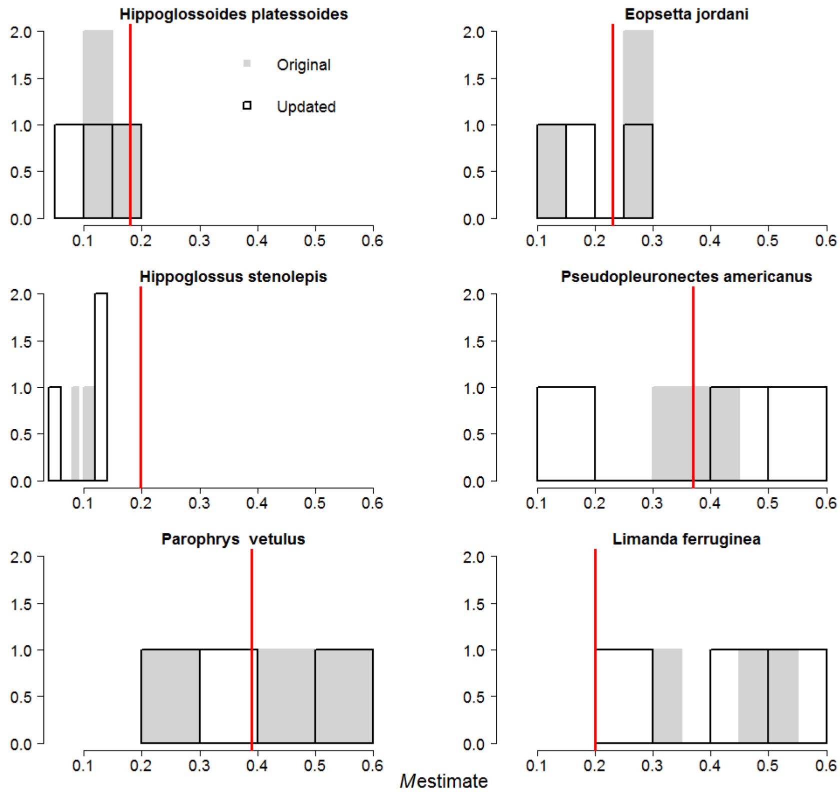

Figure 2. Histogram of natural mortality (*M*) estimates for six flatfish species derived from four original (gray shaded) and four updated (unshaded with black border) empirical models, namely the one-parameter t_{max}, Hoenig, one-parameter *K*, and Pauly. The empirical equations are given in Table 1. The vertical red line denotes the *M* estimate from literature.

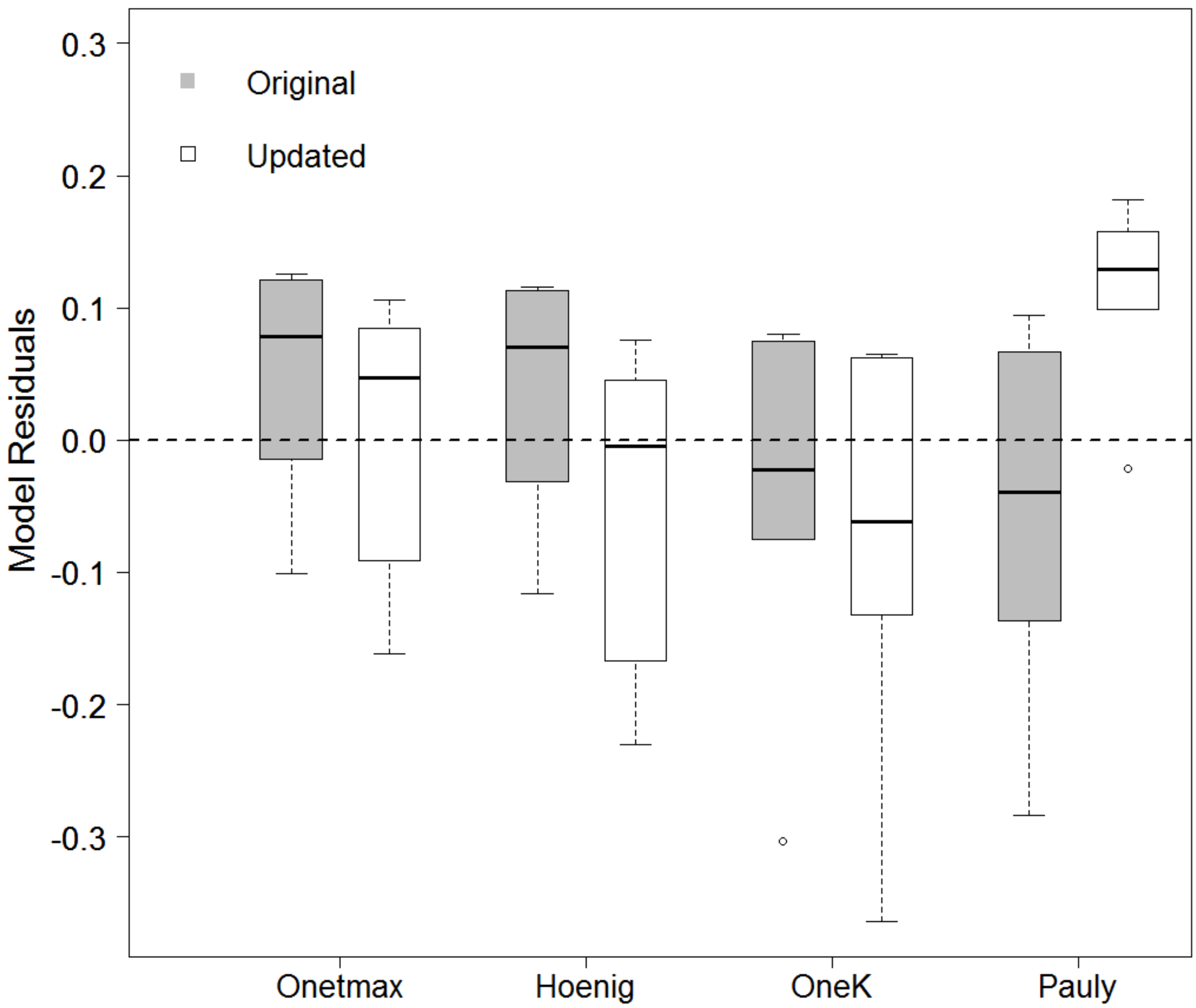

Figure 3. Box-and-whisker plot of model residuals (literature – predicted *M* estimates) of six flatfish species (see Table 2 for species list) for four original (gray shaded) and updated (unshaded) models, namely one-parameter t_{max} (abbreviated as Onetmax), one-parameter *K* (OneK), and Pauly. Table 1 provides the predictive equations for each model. The solid bold line in each box-and-whisker denotes the median residual.

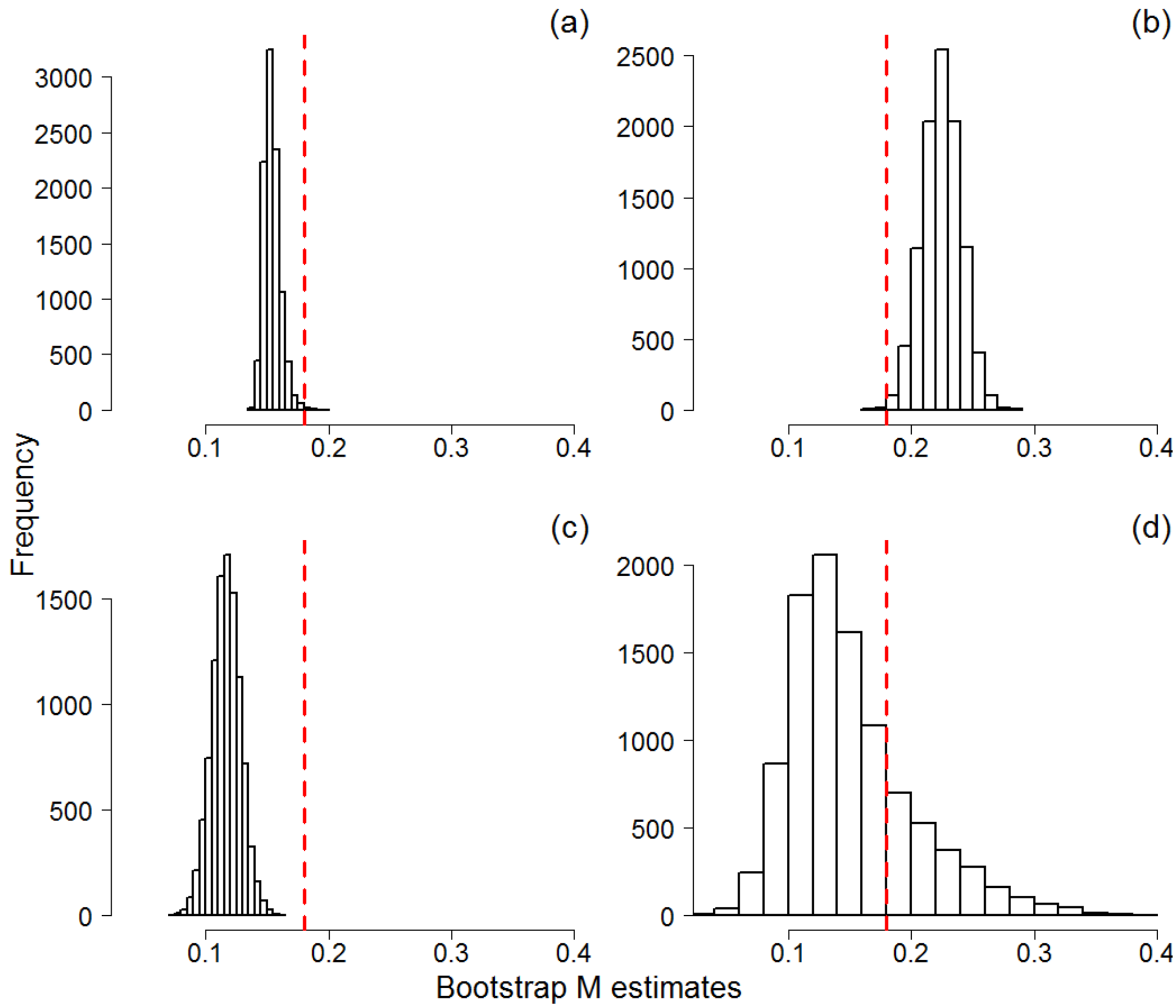

Figure 4. 10000 bootstrap estimates of M for *Hippoglossoides platessoides* for the updated empirical models of (a) one-parameter t_{max}, (b) Hoenig$_{nls}$, (c) one-parameter K, and (d) Pauly$_{nls\text{-}T}$. Dashed red line indicate a direct M estimate (= 0.18) for this species. Parameters used for the estimation of M are listed in Table 3.

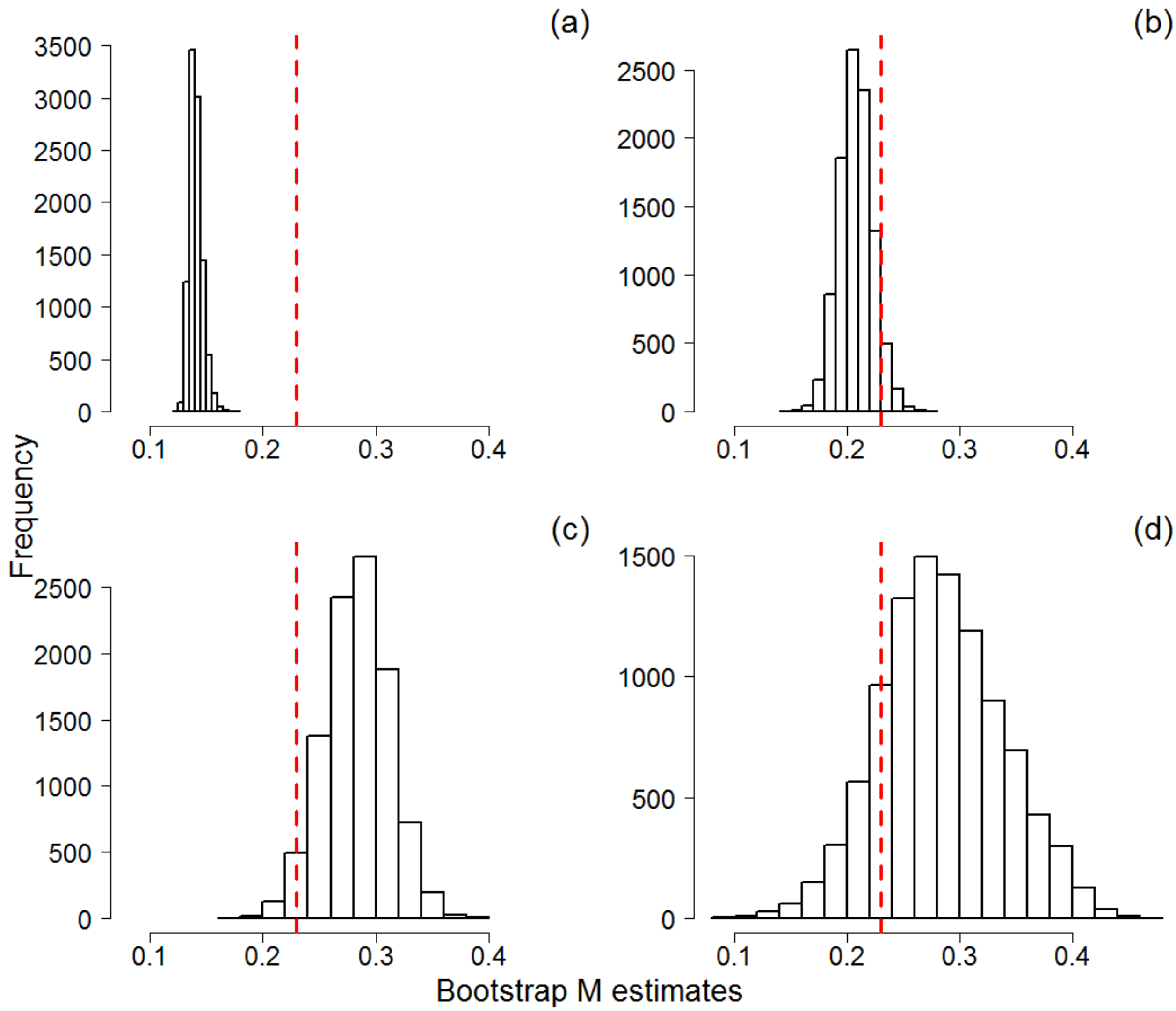

Figure 5. 10000 bootstrap estimates of *M* for *Eopsetta jordani* for the updated empirical models of (a) one-parameter t_{max}, (b) $\text{Hoenig}_{\text{nls}}$, (c) one-parameter *K*, and (d) $\text{Pauly}_{\text{nls-T}}$. Dashed red line indicate a direct *M* estimate (= 0.23) for this species. Parameters used for the estimation of *M* are listed in Table 3.

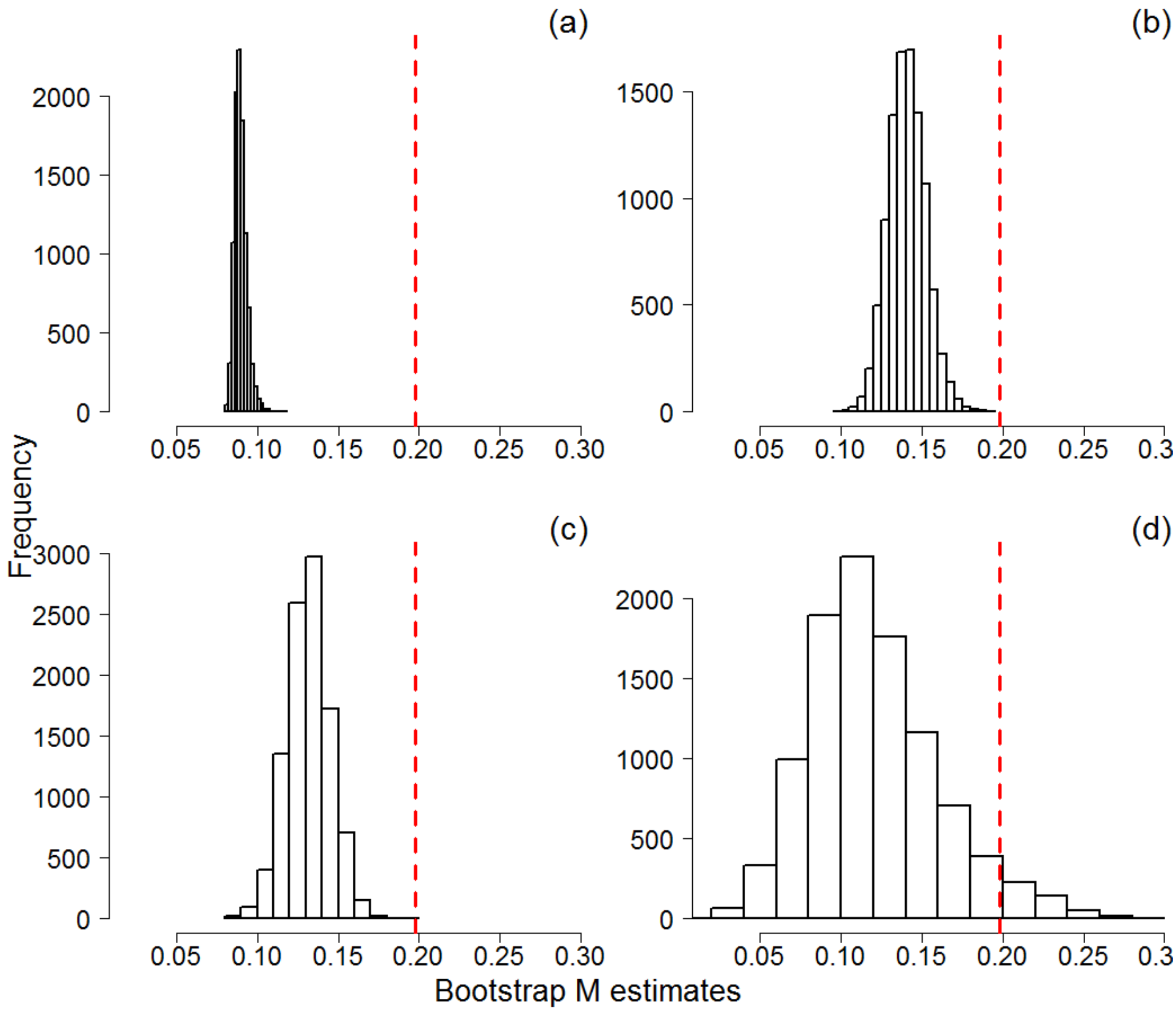

Figure 6. 10000 bootstrap estimates of M for *Hippoglossus stenolepis* for the updated empirical models of (a) one-parameter t_{max}, (b) Hoenig_{nls} , (c) one-parameter K, and (d) $\text{Pauly}_{nls\text{-}T}$. Dashed red line indicate a direct M estimate (= 0.2) for this species. Parameters used for the estimation of M are listed in Table 3.

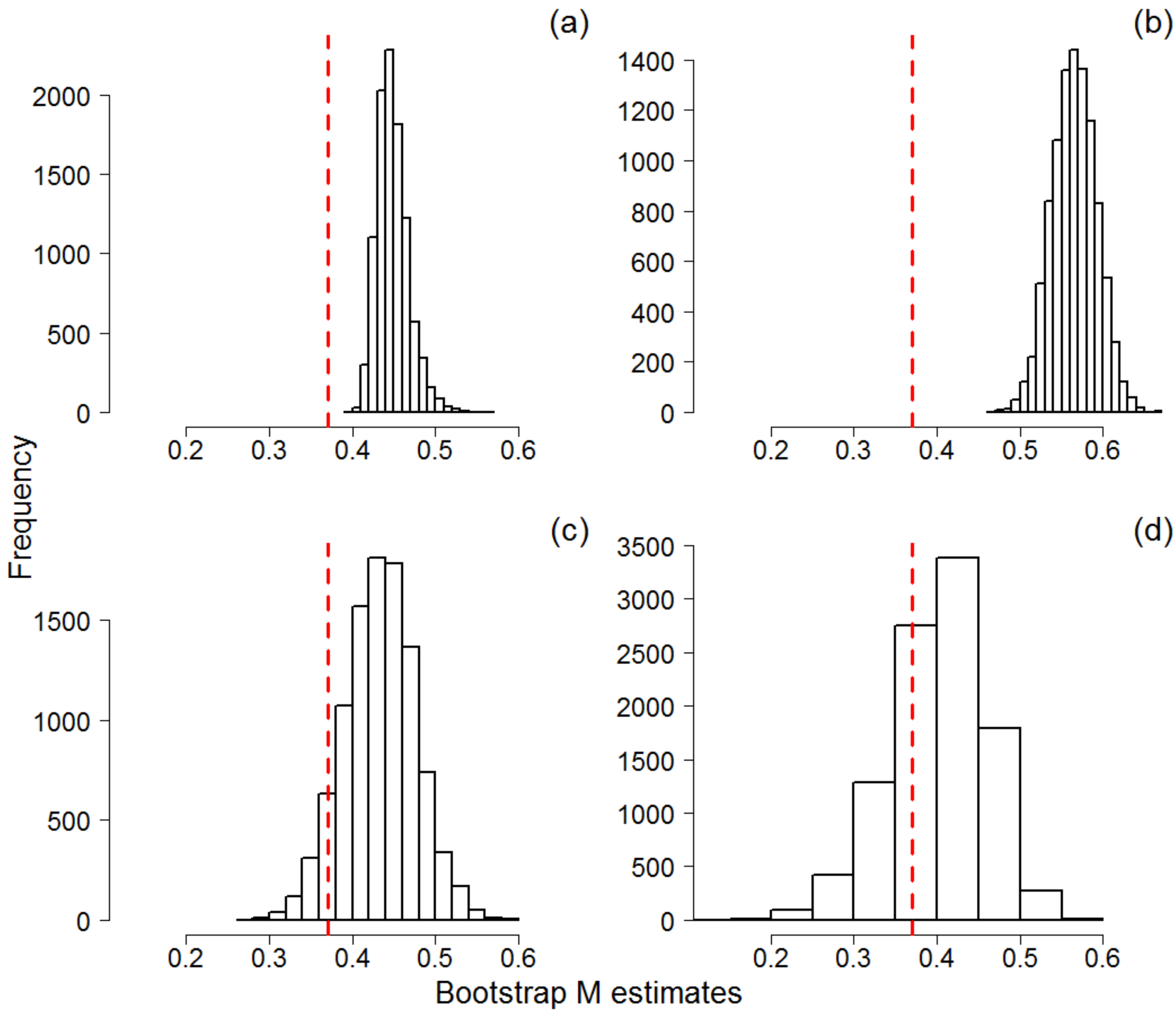

Figure 7. 10000 bootstrap estimates of *M* for *Pseudopleuronectes americanus* for the updated empirical models of (a) one-parameter t_{max}, (b) Hoenig$_{nls}$, (c) one-parameter *K*, and (d) Pauly$_{nls\text{-}T}$. Dashed red line indicate a direct *M* estimate (= 0.37) for this species. Parameters used for the estimation of *M* are listed in Table 3.

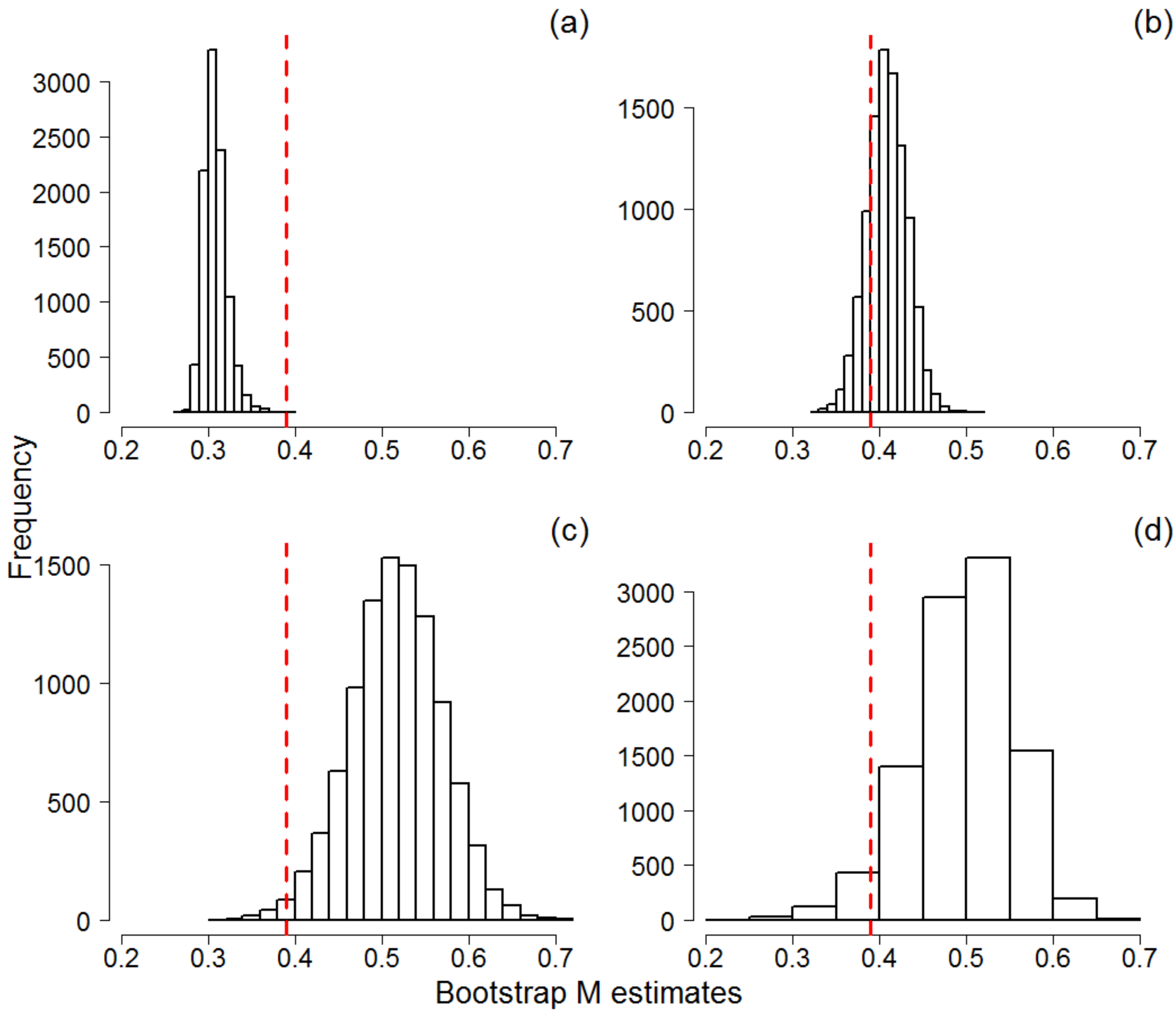

Figure 8. 10000 bootstrap estimates of *M* for *Parophrys vetulus* for the updated empirical models of (a) one-parameter t_{max}, (b) Hoenig$_{nls}$, (c) one-parameter *K*, and (d) Pauly$_{nls\text{-}T}$. Dashed red line indicate a direct *M* estimate (= 0.39) for this species. Parameters used for the estimation of *M* are listed in Table 3.

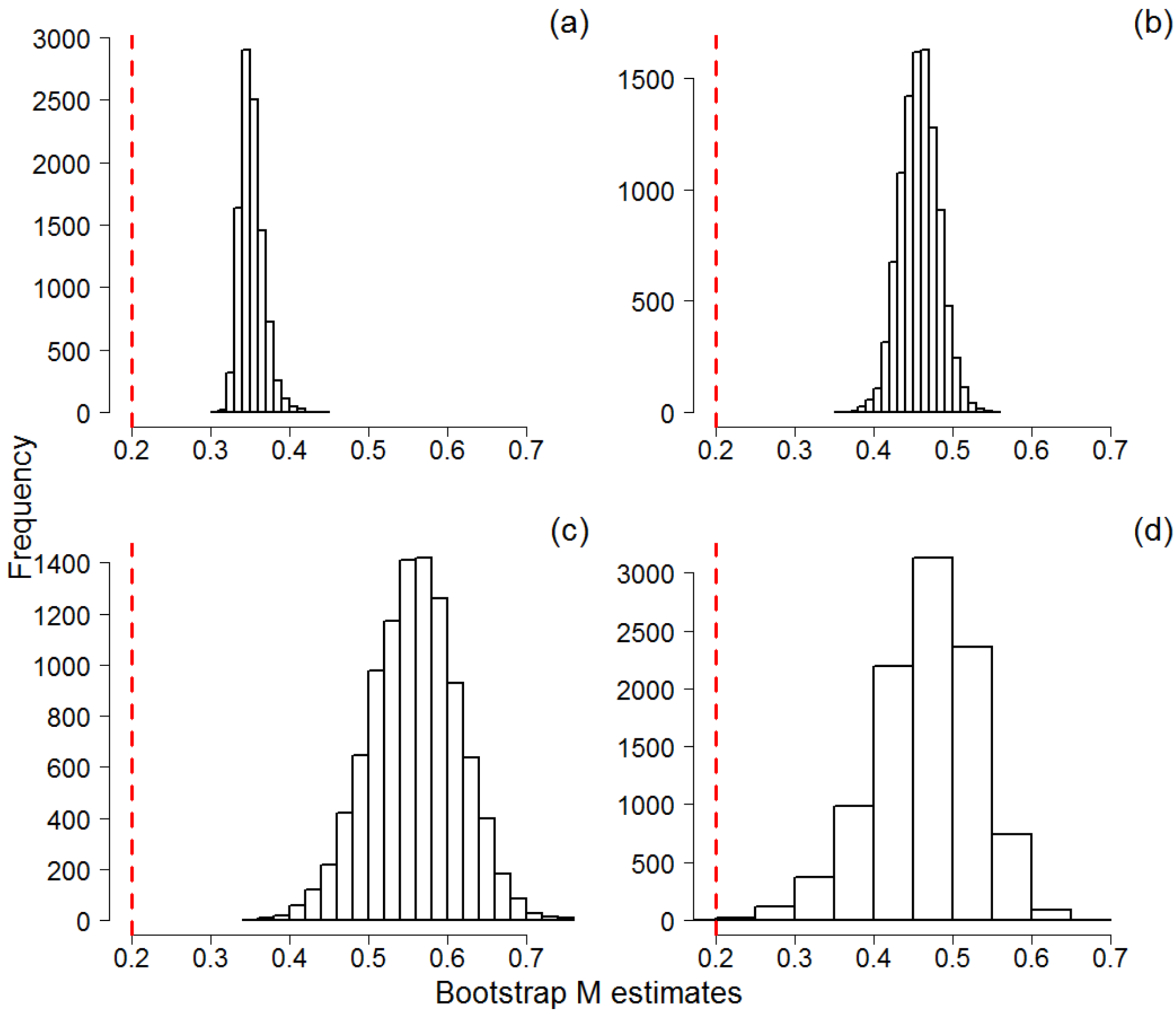

Figure 9. 10000 bootstrap estimates of *M* for *Limanda ferruginea* for the updated empirical models of (a) one-parameter t_{max}, (b) $\text{Hoenig}_{\text{nls}}$, (c) one-parameter *K*, and (d) $\text{Pauly}_{\text{nls-T}}$. Dashed red line indicate a direct *M* estimate (= 0.2) for this species. Parameters used for the estimation of *M* are listed in Table 3.

Figure 10. Map showing the geographic location of Georges Bank and the Grand Banks, where two stocks of yellowtail flounder are found.

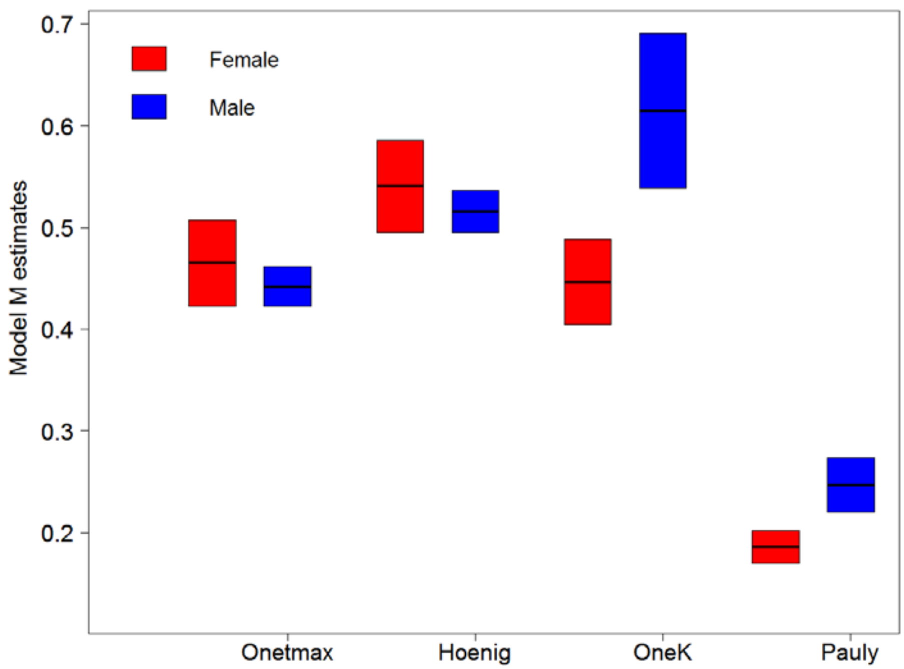

Figure 11. Box-and-whisker plot of model estimates of *M* for Grand Banks yellowtail flounder, based on growth estimates from Pitt (1974). Updated empirical models used are one-parameter t_{max} (abbreviated as Onetmax), $\text{Hoenig}_{\text{nls}}$ (Hoenig), one-parameter *K* (OneK), and $\text{Pauly}_{\text{nls-}T}$ (Pauly). Parameters used for the estimation of *M* are listed in Table 4.

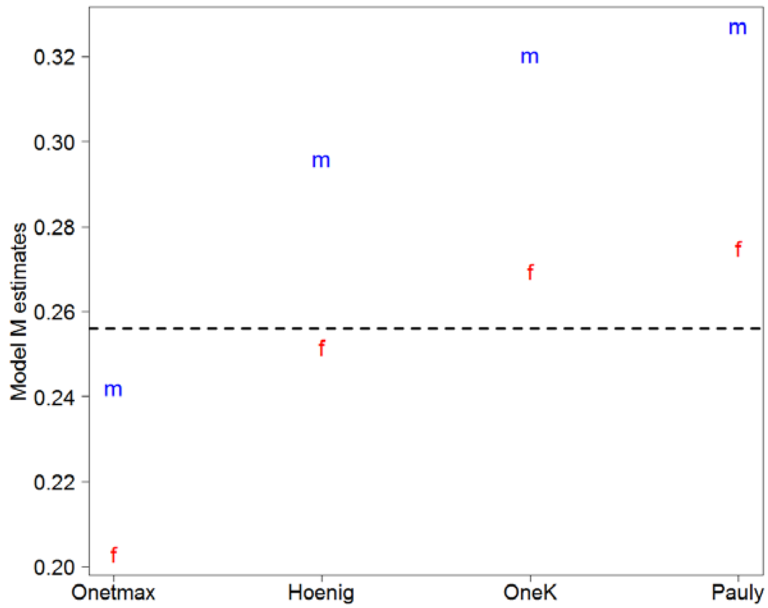

Figure 12. Plot of model estimates of *M* for the Grand Banks yellowtail flounder, based on growth estimates from Dwyer et al. (2003). Empirical models used are one-parameter t_{max} (abbreviated as Onetmax), $\text{Hoenig}_{\text{nls}}$ (Hoenig), one-parameter *K* (OneK), and $\text{Pauly}_{\text{nls-}T}$ (Pauly). Dashed line indicate a direct *M* estimate (= 0.256) for the Grand Bank yellowtail flounder from Cowen et al. (2009), based on mark-recapture data. Parameters used for the estimation of *M* are listed in Table 4.

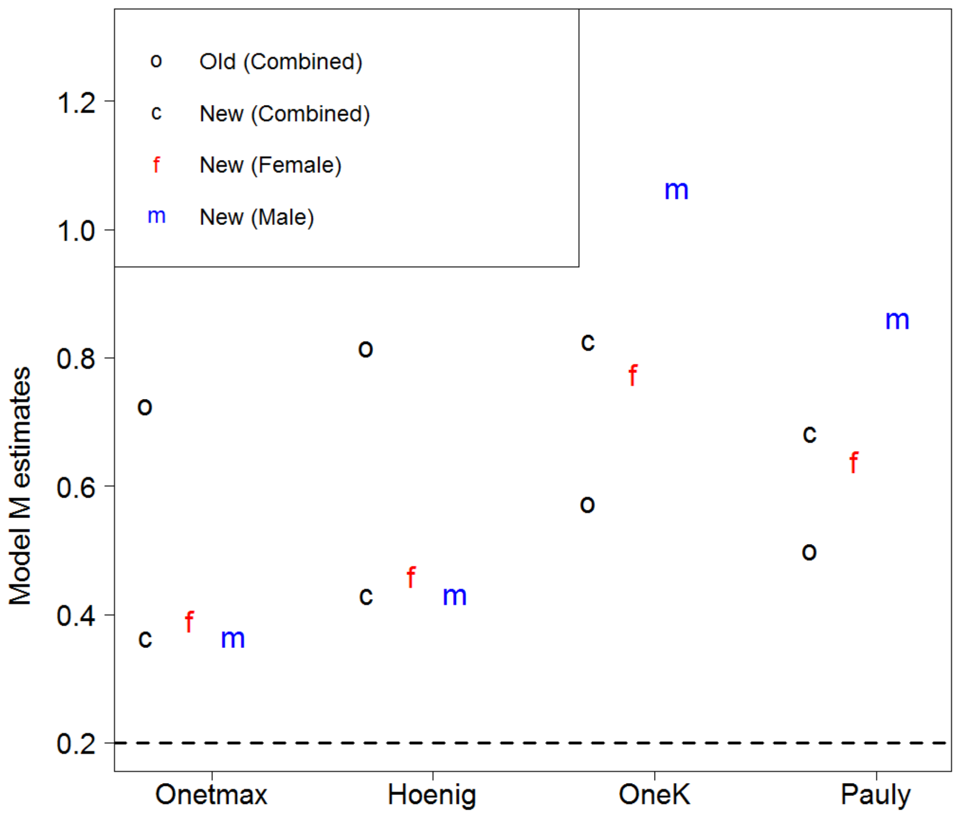

Figure 13. Plot of model estimates of *M* for the New England and Georges Bank yellowtail flounder based on growth estimates from Lux and Nichy (1969) and Brooks (pers. comm.), denoted as old and new study respectively. Growth estimates from Brooks are based on survey data from years 1963 to 2013. Empirical models used are one-parameter t_{max} (abbreviated as Onetmax), $\text{Hoenig}_{\text{nls}}$ (Hoenig), one-parameter *K* (OneK), and $\text{Pauly}_{\text{nls-T}}$ (Pauly). Dashed line indicate a direct *M* estimate (= 0.2) from Lux (1969), based on tagging data. Parameters used for the estimation of *M* are listed in Table 4.