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ARTICLE

Long-term changes in body condition and gillnet selectivity in Lake Constance pelagic spawning whitefish (*Coregonus wartmanni*)

J. Tyrell DeWeber, Roland Rösch, Jan Baer, and Alexander Brinker

Abstract: The body condition of Lake Constance pelagic spawning whitefish (*Coregonus wartmanni*) has changed substantially during the past century and altered the length-based selectivity of gillnets. Linked hierarchical models using Bayesian inference and error propagation were used to estimate the monthly body condition of whitefish from 1932 to 2018 and condition-dependent gillnet selectivity from 1964 to 2018. As expected, body condition followed past trends in nutrient dynamics and was highest in summer months. Body condition was clearly linked to gillnet selectivity, with a weight increase of a 300 mm whitefish from 205 to 260 g predicted to reduce the mean (from 374 to 330 mm) and standard deviation (from 30.8 to 25.1 mm) of lengths selected by a 38 mm mesh gillnet. Simulations demonstrate that such changes can reduce the mean age in harvest by over 1 year and greatly bias population age distribution estimates if selectivity changes are ignored. Similar variation in gillnet selectivity is expected where trophic conditions or other factors cause body condition differences, and accounting for these changes could reduce biases to inform fishery management.

Résumé : L'embonpoint du corégone (*Coregonus wartmanni*) à reproduction pélagique du lac de Constance a considérablement changé au cours des cent dernières années et a significativement modifié la sélectivité basée sur la longueur des filets maillants. Des modèles hiérarchiques liés faisant appel à l'inférence bayésienne et à la propagation des erreurs ont été utilisés pour estimer l'embonpoint mensuel des corégones de 1932 à 2018 et la sélectivité de filets maillants dépendante de l'embonpoint de 1964 à 2018. Comme prévu, l'embonpoint suit les tendances de dynamique des nutriments et est plus grand durant les mois d'été. L'embonpoint est manifestement relié à la sélectivité des filets maillants, et une augmentation de 205 à 260 g de la masse des corégones de 300 mm devrait réduire la moyenne (de 374 à 330 mm) et l'écart-type (de 30,8 à 25,1 mm) des longueurs sélectionnées par un filet à mailles de 38 mm. Des simulations démontrent que de tels changements peuvent abaisser l'âge moyen dans les prises par plus d'un an et biaiser considérablement les estimations de la distribution des âges de populations si les variations de la sélectivité ne sont pas prises en compte. Des variations semblables de la sélectivité des filets maillants sont à prévoir là où des conditions trophiques ou d'autres facteurs causent des variations de l'embonpoint, et la prise en compte de ces variations pourrait réduire les biais dans l'information utilisée pour la gestion de la pêche. [Traduit par la Rédaction]

Introduction

Differences in fish morphology due to changes in relative weight at length or body condition are likely to influence gillnet contact selectivity, with clear implications for harvest and fishery management. In this paper gillnet selectivity refers to contact selectivity, or the probability of a given length fish being captured in a specific mesh given that it has come into contact with a net (Millar and Fryer 1999). It has long been documented that the capture of fish in gillnets through wedging or gilling depends upon the ratio of maximum fish girth to mesh size (Baranov 1914; Hamley 1975; Millar and Fryer 1999), with maximum selectivity at a ratio of 1–1.2 (McCombie and Berst 1969; Reis and Pawson 1999). The exact location of capture can vary among fish based on body morphology, but girth at capture location is highly correlated to maximum girth (Reis and Pawson 1999). Fish girth is seldom measured, however, and consequently gillnet selectivity is more often estimated using fish length (Millar and Fryer 1999). Since length and girth within a given population, species, or even group of fishes with a common morphology type are highly correlated, length-based selectivity can provide a reliable estimate of the underlying girth-based process (Reis and Pawson 1999). If fish condition and the girth to length relationship are not constant across space and time, however, length-based selectivity will likely change as well. If unaccounted for, such changes are likely to bias estimates of gillnet selectivity and dependent estimates such as population age or length distributions or fishery selectivity.

Many factors affect length–weight relationships and the body condition of a given fish taxa, including differences in ecosystem productivity, competition for food resources, reproduction, or phenotypic variation (Htun-Han 1978; Irons et al. 2007; Casini et al. 2016). For example, decreases in body condition of whitefish species (*Coregonus* spp.) have been linked to decreasing productivity related to nutrient management and invasive species (Herbst et al. 2013; Rösch et al. 2018). These changes are likely to influence length-based estimates of selectivity, as fish with higher weights and girth at the same length are more likely to be captured in smaller mesh sizes. For example, Kurkilahti et al. (2002) showed that gillnet selectivity of perch varied among lakes and that these differences were well explained by Fulton's condition factor (*K*; Ricker 1975). In addition, Kurkilahti et al. (2002) noted that *K*

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J.T. DeWeber, R. Rösch, and J. Baer. Fisheries Research Station Baden-Württemberg (LAZBW), Argenweg 50/1, 88085 Langenargen, Germany.
A. Brinker. Fisheries Research Station Baden-Württemberg (LAZBW), Argenweg 50/1, 88085 Langenargen, Germany; University of Constance, Institute for Limnology, Mainaustraße 252, 78464 Konstanz, Germany.

Corresponding author: J. Tyrell DeWeber (email: tyrell.deweber@lazbw.bwl.de).

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could provide a suitable surrogate for girth in length-based selectivity models, since weight is expected to be proportional to the cubed root of girth. Regardless of the exact measure used to represent body condition, assuming that length-based gillnet selectivity is constant when in fact it varies across time or space with body condition could result in biased estimates of selectivity. Such biases could be reduced by accounting for potential changes in length-based selectivity caused by differences in body condition among and within populations.

The goal of this study is to demonstrate how changes in body condition during a period of changing ecosystem productivity are linked to changes in length-based gillnet selectivity. Models predicting fish condition and selectivity are fit using long-term monitoring data for pelagic spawning whitefish (*Coregonus wartmanni*) from Upper Lake Constance. First, length–weight relationships are estimated using a mixed-effects model that accounts for temporal autocorrelation among years and months. The model is used to estimate month-specific fish condition, measured as the posterior predicted weight of a 300 mm individual (*w*300). Second, length-based gillnet selectivity is estimated through the use of multimesh samples available from 1964 to 2019, and the effect of *w*300 on selectivity parameters is estimated. A simulation approach is used to explore how changes in selectivity of the magnitude estimated here can affect estimation of underlying age distributions and characteristics of fish harvested in gillnets. The implications of body condition changes for gillnet selectivity, harvest, and fishery management are then discussed in the context of ecosystem changes.

Methods

Study area and species

Lake Constance is a large pre-alpine lake on the borders of Germany, Austria, and Switzerland at a mean elevation of 395 m that is divided into a large (472 km^2), deep (254 m) Upper Lake and a small (63 km^2), shallow (maximum depth = 16 m) Lower Lake. This paper deals solely with the better-documented Upper Lake Constance and its pelagic spawning whitefish (referred to as whitefish throughout unless clarity is needed). Two other extant forms of whitefish that primarily inhabit the littoral and benthic zones are not considered here, as they are less important for the local economy, cuisine, and heritage. The pelagic spawning whitefish has historically supported the most important commercial fishery in the lake, though its importance has varied throughout the last century due to nutrient-driven ecosystem changes in multispecies fishery yield (Baer et al. 2017). Upper Lake Constance went through pronounced eutrophication in the 20th century owing to nutrient inputs from municipal and agricultural runoff. Phosphorous concentrations increased from 7 $\mu\mathrm{g}\cdot\mathrm{L}^{-1}$ in 1951 to $>$80 $\mu\mathrm{g}\cdot\mathrm{L}^{-1}$ around 1980 and decreased to below 10 $\mu\mathrm{g}\cdot\mathrm{L}^{-1}$ again by 2006 following wastewater management (Stich and Brinker 2010). Mainly due to trophic dynamics, the growth, condition, and fishery yield has changed during the past 100 years (Thomas and Eckmann 2007; Baer et al. 2017). More recently, further reductions in weight at age, abundance indices, and fishery yield have been linked to a pelagic invasion by the three-spined stickleback (*Gasterosteus aculeatus*; Rösch et al. 2018).

Monitoring data

Fish sampling data has been collected through different methods by the Fisheries Research Station and other regional agencies to support fisheries management in Lake Constance for more than a century. This study utilizes long-term monitoring records beginning in 1932 that stem from three periods of fishery monitoring. Prior to 1963, monitoring was conducted in fishery-independent surveys using two gear types allowed in the fishery (cotton gillnets, purse seines) or by subsampling fisher catch. During this period, individual fish measurements were recorded, but the size of nets fished or other sample-specific information was not always recorded. Following 1963, only nylon gillnets were used in the fishery, and fishery-independent surveys using one or more meshes were conducted monthly or more often. Sampling information (e.g., net area, mesh size, total catch) and measurements of subsampled fish (e.g., length, weight, sex, age) were recorded for these samples. Whitefish scales were archived with auxiliary fish and sample data from 1932 to 1991. Beginning in 1991, standardized sampling has been conducted by the Fisheries Research Station of Baden-Wuerttemberg, the Nonnenhorn State Fishery Hatchery of Bavaria, and the Office of Nature, Hunting, and Fisheries of the Canton of St. Gallen, Switzerland. The modern dataset includes sample information and fish measurements for a subsample of fish in each mesh, which in most cases is 20 individual fish per mesh size or all fish if fewer than 20 are captured.

Length–weight dataset

Individual fish measurements from the scale archive dataset were used for all samples from 1932 to 18 September 1991, and the modern dataset was used thereafter. From the available data, 142 583 individual fish records had date, length, and weight recorded. Error measurements and clear outliers were identified and removed by visually analyzing interannual and annual length–weight plots (n = 405 records). Next, records without age or sex were removed, including 815 juveniles. Finally, a small number (n = 2608) of records after 1963 that did not record mesh size were removed. For 1963 and earlier, 73.3% of the records (17 190 of 23 449) did not record mesh size, but these samples are known to have been captured with the legal-sized mesh size (38–40 mm), multiple mesh sizes, or with a relatively non-size-selective pelagic seine. Rather than removing these records, the mesh size for these years was set to the average mesh size across the entire study period (38.6 mm). Imputing the average value should not affect mean parameter estimates unless the true mesh size fished was generally much higher or lower, but is likely to increase uncertainty of the mesh size effect. The effect of imputing the mean mesh size on the mesh size slope parameter was quantified by comparing with parameter estimates fit with a subset of 108 487 records where mesh size was recorded. Age was measured in years, sex was coded as 0 (male) and 1 (female), and mesh size was measured to the nearest millimetre. Age was assigned based on scales, which can underestimate age for slow-growing populations of coregonids (Muir et al. 2008), but aging error is ignored because age estimates from other structures or associated aging error estimates are unavailable. The total number of fish used for modeling was 128 285 collected between 1932 and 2019, with the number of fish per year and month varying greatly from 0 to 1000 (mean = 127; see online Supplementary material, Table S1[1]). The model was developed with this imbalance in mind and can provide plausible estimates of weight at length when data are lacking or very limited. Specifically, the random walk for year effects interpolates among years, and the hierarchical structure for month effects (see section on Length–weight modeling for details) borrows information from across the study period when data are missing or limited.

Selectivity dataset

Data for modeling selectivity included records from 1964 to 2018 of multiple mesh nylon gillnet samples with recorded date, mesh size, net area, total number of fish captured, and individual length measurements recorded per mesh. Samples between 1964 and 18 September 1991 were collected almost completely by or under the supervision of a single fishery scientist working at the Institute for Lake Research and recorded in field notebooks. Records between 18 September 1991 and October 2018 are from the modern sampling dataset described above. Sampling events

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[1] Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2020-0231.

from January to March (n = 328) were not used because gillnets were often set for more than one night during these months, but the number of nights was not always recorded and effective fishing effort was unknown. Only samples from nylon gillnets fished for one night were included in this study, but nets had variable twine diameters, colours, and areas. The effect of area on contact probability is accounted for as detailed below, but effects of diameter or colour were not included, as they were not always recorded. All samples within a given year, month, and mesh were considered one sampling event, for which the total number of individuals captured, total number measured, and total net area were calculated. Fish were grouped into 10 mm length bins ranging from 160 to 450 mm and nine smaller and larger length bins that had very sparse records (n = 25 fish combined) were not included. Data from 287 sampling months that had at least three mesh sizes fished were used for modeling. The modeling dataset had 56 620 records of fish length captured in 1544 sampling events. The mesh sizes and number of mesh sizes fished per month varied throughout the study period as summarized in Supplementary Fig. S1[1].

Length–weight modeling

Length, age, and mesh size were z-score-normalized to mean 0 and unit variance by subtracting the mean and dividing by the standard deviation prior to modeling to assist convergence and reduce computation time. The corresponding means ± standard deviations used for normalization were 1.514 ± 0.0495 for $\log_{10}$-transformed length, 3.1405 ± 0.9558 for age, and 38.6916 ± 5.5851 for mesh size. To aid interpretation, we also report these effects in the Results on the unnormalized scale, which is obtained by dividing the estimated posterior distribution by the appropriate standard deviation above.

In the full model, the $\log_{10}$-transformed weight of fish i in year y and month m, $\log(W_{iym})$, was modeled as a function of the effects $\beta.\mathrm{len}$ of $\log_{10}$-transformed length L_i, $\beta.\mathrm{age}$ of age A_i, $\beta.\mathrm{sex}_m$ of sex S_i, $\beta.\mathrm{mesh}$ of mesh M_i, deviations for each month month_{ym} and year year_y, and error ε_i:

$$(1)\qquad \log(W_{iym}) = \alpha + \mathrm{month}_{ym} + \mathrm{year}_y + \beta.\mathrm{len}_t \times \log(L_i) + \beta.\mathrm{age} \times A_i + \beta.\mathrm{sex}_m \times S_i + \beta.\mathrm{mesh} \times M_i + \varepsilon_i, \quad \text{with } \varepsilon_i \sim \mathrm{N}(0, \sigma)$$

The length coefficient $\beta.\mathrm{len}_y$ was allowed to vary annually, being drawn from a prior distribution with hyper priors for the overall mean effect μ^{len} and its standard deviation σ^{len}:

$$(2)\qquad \beta.\mathrm{len}_y \sim \mathrm{Normal}\left(\mu^{\mathrm{len}}, \sigma^{\mathrm{len}}\right)$$

where μ^{len} had prior distribution N(0,10) and σ^{len} had a uniform prior distribution between 0 and 1.

$\beta.\mathrm{sex}_m$ was allowed to vary among the 12 calendar months m since weight differences between sexes are likely to be greater in the months before and after spawning, with its month-specific effect having a prior distribution defined by hyper priors μ^{sex} and σ^{sex}:

$$(3)\qquad \beta.\mathrm{sex}_m \sim \mathrm{Normal}(\mu^{\mathrm{sex}}, \sigma^{\mathrm{sex}})$$

The year effect year_y was modeled as a random walk:

$$(4)\qquad \mathrm{year}_y = 0 \text{ for } y = 1 \text{ and } \mathrm{year}_y \sim \mathrm{year}_{y-1} + \mathrm{year.dev}_y \text{ for } y > 1$$

where each annual deviation had prior distribution:

$$(5)\qquad \mathrm{year.dev}_y \sim \mathrm{Normal}\left(0, \sigma^{\mathrm{Year}}\right)$$

The month_{ym} effect for a specific month and year was drawn from prior distribution:

$$(6)\qquad \mathrm{month}_{ym} \sim \mathrm{Normal}\left(\mu_m^{\mathrm{Month}}, \sigma_m^{\mathrm{Month}}\right)$$

The mean month effect μ_m^{Month} was estimated as

$$(7)\qquad \mu_1^{\mathrm{Month}} = 0 \text{ for } m = 1 \text{ and } \mu_m^{\mathrm{Month}} = \mu_{m-1}^{\mathrm{Month}} + \mathrm{dev}_m \text{ for } m \text{ from 2 to 12}$$

where the mean monthly deviations dev_m had uninformative prior distributions with mean 0 and standard deviation of 10.

This model formulation allows the length–weight coefficient $\beta.\mathrm{len}_y$ and the intercept (alpha in a standard length–weight regression) to vary with time and as a function of other factors. The intercept is associated with the typical body shape of a species or population (e.g., fusiform, eel-like; see Froese et al. 2014), and its variation means that condition changes across all lengths in the population in a similar manner (e.g., individuals of all lengths are similarly heavier when alpha is higher). Variation in beta allows for differing levels of allometric growth in weight at length throughout the study (e.g., individuals may become relatively lighter or heavier as they grow in length, and this may vary among months).

The full model (eq. 1) was compared with the following four submodels to determine which effects were best supported by the data: (*i*) a base model with only the terms α, month_{ym}, year_y, and $\beta.\mathrm{len}_y$; (*ii*) an age model, which was the base model plus $\beta.\mathrm{age}$; (*iii*) a mesh size model, which is the base model plus $\beta.\mathrm{mesh}$; and (*iv*) a sex effect model, which is the base model plus $\beta.\mathrm{sex}_m$. Model comparisons were made using the widely applicable information criterion (WAIC; Watanabe 2010), which was estimated in the R package loo (Vehtari et al. 2017).

The final model was used to predict the weight of a 300 mm whitefish individual in each month and year ($w300_{ym}$). As noted in the results, the effects of age, sex, and mesh size were supported and included in the final model. To predict weight at length for a standard mesh size that includes uncertainty across ages and sexes, $w300_{ym}$ was predicted for a 38 mm mesh net and averaged across both sexes and ages 3–6. This was accomplished by first predicting weight at length for both sexes at ages 3–6 for all years and months in the study region, with one prediction for each posterior draw. The mean and standard deviation of the predicted distribution of $w300_{ym}$ was then summarized for each year and month to define a normally distributed covariate in the selectivity model. Although weights at length are expected to have a lognormal distribution, the distributions of $w300_{ym}$ had very little skew as represented by low standard deviations on the log-scale (max. = 0.1) and were thus well approximated by a normal distribution. Weight at a fixed length was used because the length coefficient $\beta.\mathrm{len}_t$ was allowed to vary with time and may differ from isometric growth (i.e., not equal 3), which means that condition factors and relative weights are length-dependent (Cone 1989). It is also easier for managers and fishers to conceive changes in weight at fixed length, and 300 mm length was used because it is the minimum length target in the lake. To determine whether changes in condition at other lengths and associated effects on selectivity were similar for other lengths, the weight of 250 mm ($w250_{ym}$) and 350 mm ($w350_{ym}$) fish were also predicted as described for $w300_{ym}$.

Selectivity modeling

This study estimates selectivity using a multinomial approach similar to the SELECT methodology proposed by Millar (1992). The proportions π_{ymlj} of length l fish measured in mesh size j are multinomial-distributed with probabilities φ_{ymlj} and trial size equal to the total number of fish captured across all j in length l, $n_{yml\cdot}$:

$$(8)\qquad \pi_{ymlj} \sim \text{Multinomial}(\varphi_{ymlj}, n_{yml\cdot})$$

$$(9)\qquad \varphi_{ymlj} = \frac{p_{ymj} r_{ymj}(l) Q_{ymj}}{n_{yml\cdot}}$$

where p_{ymj} is the relative fishing intensity, $r_{ymj}(l)$ is the gillnet selectivity curve, and Q_{ymj} is the proportion of fish captured in gear j that were measured. The proportion Q_{ymj} is necessary for linking the subset of fish measured to the total number captured and relative fishing intensity. The term p_{ymj} was modeled as a function of total area of mesh size j (netarea$_{ymj}$) and a randomly distributed error term e^{p}_{ymj}:

$$(10)\qquad \text{logit}(p_{ymj}) = a^{p} + \text{b.area} \times \text{netarea}_{ymj} + e^{p}_{ymj}$$

where

$$(11)\qquad e^{p}_{ymj} \sim \text{Normal}(0, s^{p})$$

There is no information available in comparative selectivity study data to estimate a^{p}, so this value was set to −10. To determine whether estimates were sensitive to this assumption, we also compared results with models with a^{p} fixed to −5 and −15.

Normal, gamma, and binormal gillnet selectivity curves were compared using a subset of data to identify the best supported. All three curves followed the assumption of geometric similarity (i.e., length selected is assumed proportional to mesh size) to reduce the number of parameters (Baranov 1914; Millar and Fryer 1999). Formulas for the normal and gamma curves are found in table 1 of Millar and Fryer (1999). The formula for the binormal selectivity curve, which is a mixture of two normal distributions, is provided below (eq. 12). Alternative curves were compared assuming time-invariant selectivity parameters using June–October samples from 2005 to 2015 when weight at length was relatively stable and at least five mesh sizes were fished in most months. Selectivity curves were compared using WAIC, and the curve with the lowest value was used for further modeling. Curves were compared using a data subset to reduce computational demands (calculating WAIC requires monitoring the log-density for each observation) and enable subsequent modeling and presentation to focus on the best supported curve.

The binormal selectivity curve was clearly better supported by available data (see Results) and is defined as

$$(12)\qquad r_{ymj}(l) = \exp\left[-\frac{(l - k1_{ym} \times S_{ymj})^2}{2k2^2_{ym} \times S^2_{ymj}}\right] + c \times \exp\left[-\frac{(l - k3_{ym} \times S_{ymj})^2}{2k4^2_{ym} \times S^2_{ymj}}\right]$$

where $k1_{ym}$ and $k2_{ym}$ are the first modal mean and standard deviation, respectively, $k3_{ym}$ and $k4_{ym}$ are the second modal mean and modal standard deviation, respectively, c is the relative proportional height of the second mode, S is the mesh size fished, and l is the midpoint of the length bin. A decrease in $k1$ results in the selection of shorter fish by a given mesh, while a decrease in $k2$ reduces the range of lengths selected. Increases in the body condition of fish as measured by $w300_{ym}$ was hypothesized to reduce the mean parameters $k1$ and $k3$ (i.e., capture of shorter fish in the same mesh) and potentially also alter the range selected through changes in scale parameters $k2$ and $k4$. To test for these potential effects, the parameters $k1_{ym}$ and $k2_{ym}$ were modeled with an intercept ($a.k1$ or $a.k2$) and body condition effect ($b.k1$ or $b.k2$):

$$(13)\qquad k1_{ym} = a.k1 + b.k1 \times \hat{w}300_{ym}$$

$$(14)\qquad k2_{ym} = a.k2 + b.k2 \times \hat{w}300_{ym}$$

The linear formulation was chosen here for simplicity, but it is worth noting that a different form may be better supported given that girth is not linearly related to weight (Kurkilahti 2002). The values of $\hat{w}300_{ym}$ were drawn from a normal distribution with mean and standard deviation of predicted $w300_{ym}$ to propagate prediction uncertainty:

$$(15)\qquad \hat{w}300_{ym} \sim \text{Normal}\left[\text{mean}(w300_{ym}), \text{SD}(w300_{ym})\right]$$

To reduce computation times, the $\hat{w}300_{ym}$ values were z-score-normalized within the model using the overall mean and standard deviations of predicted $w300_{ym}$ from the study period.

The parameters $k3_{ym}$ and $k4_{ym}$ were defined as

$$(16)\qquad k3_{ym} = k1_{ym} + k1.\text{diff}$$

and

$$(17)\qquad k4_{ym} = k2 + k2.\text{diff}$$

where $k1$.diff and $k2$.diff are constant offsets from the primary selectivity parameters. To determine whether effects of $\hat{w}300_{ym}$ on $k1$ and $k2$ were supported by the data, we compared this model with a simpler model with $k1$ and $k2$ held constant using WAIC. In addition, similar models were also fit using $w250_{ym}$ and $w350_{ym}$ instead of $w300_{ym}$ to determine whether estimates of $b.k1$ and $b.k2$ were sensitive to the length used in defining relative condition.

Parameter estimation

Model parameters were estimated using JAGS 4.3.0 (Plummer 2017) run on three processors using dclone (Solymos 2010) in the R statistical environment (R Core Team 2019). Priors were chosen to be uninformative within reasonable bounds for each parameter as described with the full model code in Supplementary material[1]. Posterior chains were monitored and models were considered to have converged when the Gelman–Rubin diagnostic (Rhat) was less than 1.1 for all parameters (Gelman and Rubin 1992) as implemented in the coda package (Plummer et al. 2005). Autocorrelation at the thinned interval and effective sample size were also monitored using coda. Length–weight models were run on three chains with an adaptation period of 1000 iterations, after which the first 10 000 iterations were discarded and every 50th iteration from a further 50 000 iterations were saved for a total of 3000 posterior draws. It is worth noting that centering predictors (z-score normalization) allowed much faster convergence, as the noncentered version required 400 000 iterations to converge. The selectivity models were run on three chains with an adaptation period of 1000 iterations, after which the first 10 000 iterations were discarded and every 160th iteration from a further 80 000 iterations was saved for a total of 1500 posterior draws.

Implications for harvest and age distribution estimation

A simulation approach was taken to demonstrate the potential implications of body condition and gillnet selectivity changes on fishery harvest and estimation of population age distributions using three scenarios. The simulation model was based on a whitefish-type species and is described fully in Appendix A. Briefly, the simulation started with a stable age distribution with 10 age classes, and length at age followed von Bertalanffy growth with an asymptotic length of 400 mm that was fixed throughout all scenarios. The proportions of mature fish in the 10 age classes were {0, 0.4, 0.7, 1, 1, 1, 1, 1, 1, 1}, so that all age 4 and older fish were mature. Beverton–Holt recruitment, probability of capture, and age-specific natural mortality parameters were chosen to maintain an approximate population size of 80 000 individuals under scenario 1.

In scenario 1, selectivity and mesh size used for harvest were held constant over the 100-year period. In scenario 2, mesh size was held constant but gillnet selectivity changed throughout the simulation period in a manner and magnitude similar to changes estimated for Lake Constance whitefish due to changes in body condition. In scenario 3, selectivity changed as in scenario 2 but mesh size was changed to represent a potential management action taken to minimize harvest of immature fish (full maturity at age 4; see Appendix A). Specifically, during the first 50 years, mesh sizes were increased by 2 mm when the average age of fish harvested for 5 consecutive years dropped below 3.5 years. During the last 50 years, mesh size was decreased by 2 mm when the average age of fish harvested for 5 consecutive years was above 4 years.

In each scenario, the mean age in harvest, proportion of juveniles in harvest, and the Frec/Fbar selectivity metric recently suggested by Vasilakopoulos et al. (2020) were used to understand potential implications for changing gillnet selectivity on harvest. Frec/Fbar is calculated as the ratio of harvest mortality of the first age class recruited (here age 2) to the mean harvest mortality of fully recruited age classes (here ages 3–5). The metrics were calculated using the simulated population data to enable a simple presentation of implications without delving into the nuances of alternative sampling designs and stock assessment estimation. In addition to the harvest metrics, the effects of incorrectly assuming constant gillnet selectivity on population age distribution estimates are shown for scenario 2.

Results

Length–weight modeling

Posterior chains converged with Rhat below 1.05 for all parameters in all five models compared. Posterior samples for all parameters had absolute autocorrelations below 0.1 at the thinning rate of 100 and effective sample sizes of at least 2000. The full model with age, sex, and mesh size effects was much more supported based on WAIC. The increase in WAIC from the full model was 7148 for the sex effect only model, 8697 for the mesh size effect only model, 14 949 for the age effect only model, and 15 536 for the base model without sex, mesh size, or age effects.

The mean length coefficient (μ^{len}) was 0.1340 ± 0.0010 on the normalized scale, which corresponds to 2.7067 ± 0.0206 on the more often used $\log_{10}$ scale. The $\beta.\text{len}_y$ coefficients varied throughout the study period with standard deviation of 9.10e-3 ± 7.53e-4 (0.1838 ± 0.0152 on the $\log_{10}$ scale) from a minimum of 0.1126 ± 0.0026 (2.2767 ± 0.0516) in 1986 to a maximum of 0.1539 ± 0.0025 (3.1081 ± 0.0506) in 1936. The $\beta.\text{len}_y$ coefficients were relatively high from 1932 to 1960, decreased to lowest values in the 1980s, and increased to moderate values before declining again in the last few years (Supplementary Fig. S2[1]). The length–weight intercept also varied throughout the study due to year effects and among years due to month effects (Table 1; Supplementary Fig. S2[1]). Annual effects on the length–weight intercept (year.dev_y) were relatively low from 1932 to 1955, increased to highest values in the early 1960s, and then gradually declined to the lowest values in the last 5 years (Supplementary Fig. S2[1]). The annual slope $\beta.\text{len}_y$ and intercept effect year.dev_y had a small negative correlation (Pearson's $r = -0.185$). The intercept on the $\log_{10}$ scale was calculated for comparison with other length–weight studies and had an interannual mean of −1.67 with very strong annual correlations to $\beta.\text{len}_y$ (Supplementary Fig. S2[1]).

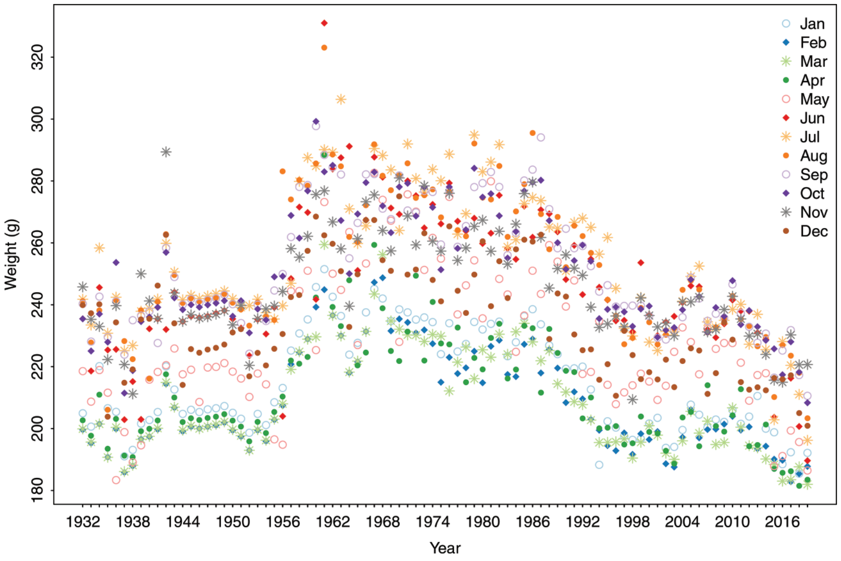
Table 1. Parameter estimates from the length–weight model summarized from posterior distributions as mean, standard deviation (SD), median, and 2.5 and 97.5 percentiles.

Parameter	Mean	SD	Median	2.50%	97.50%
α	2.41844	0.00815	2.41839	2.40264	2.43432
μ^{len}	0.13398	0.00102	0.13397	0.13200	0.13601
σ^{len}	0.00910	0.00075	0.00904	0.00777	0.01069
$\beta.\text{age}$	0.00303	0.00017	0.00303	0.00271	0.00336
$\beta.\text{mesh}$	0.01424	0.00017	0.01424	0.01392	0.01458
μ^{sex}	0.00915	0.00520	0.00917	−0.00101	0.01960
σ^{sex}	0.01755	0.00443	0.01671	0.01147	0.02867
$\beta.\text{sex}_1$	−0.00356	0.00116	−0.00358	−0.00589	−0.00125
$\beta.\text{sex}_2$	−0.01138	0.00102	−0.01138	−0.01342	−0.00939
$\beta.\text{sex}_3$	−0.01084	0.00092	−0.01083	−0.01262	−0.00908
$\beta.\text{sex}_4$	−0.00405	0.00085	−0.00404	−0.00574	−0.00240
$\beta.\text{sex}_5$	0.00411	0.00071	0.00412	0.00272	0.00547
$\beta.\text{sex}_6$	0.00837	0.00063	0.00837	0.00716	0.00957
$\beta.\text{sex}_7$	0.01004	0.00068	0.01003	0.00870	0.01134
$\beta.\text{sex}_8$	0.01132	0.00065	0.01131	0.01006	0.01262
$\beta.\text{sex}_9$	0.01544	0.00059	0.01545	0.01430	0.01656
$\beta.\text{sex}_{10}$	0.02181	0.00058	0.02181	0.02071	0.02296
$\beta.\text{sex}_{11}$	0.03658	0.00065	0.03660	0.03530	0.03788
$\beta.\text{sex}_{12}$	0.03193	0.00067	0.03193	0.03064	0.03322
μ_2^{Month}	−0.00772	0.00353	−0.00768	−0.01493	−0.00082
μ_3^{Month}	−0.00763	0.00351	−0.00754	−0.01490	−0.00100
μ_4^{Month}	−0.00551	0.00395	−0.00551	−0.01333	0.00223
μ_5^{Month}	0.02254	0.00449	0.02265	0.01362	0.03122
μ_6^{Month}	0.05328	0.00408	0.05328	0.04508	0.06082
μ_7^{Month}	0.06463	0.00371	0.06464	0.05716	0.07195
μ_8^{Month}	0.06201	0.00354	0.06203	0.05472	0.06894
μ_9^{Month}	0.05946	0.00326	0.05950	0.05287	0.06570
μ_{10}^{Month}	0.05337	0.00327	0.05339	0.04668	0.05970
μ_{11}^{Month}	0.03901	0.00353	0.03894	0.03216	0.04577
μ_{12}^{Month}	0.02090	0.00373	0.02094	0.01329	0.02786
σ_1^{Month}	0.01462	0.00276	0.01431	0.01006	0.02086
σ_2^{Month}	0.01114	0.00209	0.01101	0.00732	0.01556
σ_3^{Month}	0.01301	0.00175	0.01291	0.00988	0.01683
σ_4^{Month}	0.01874	0.00196	0.01860	0.01537	0.02297
σ_5^{Month}	0.02767	0.00254	0.02753	0.02311	0.03302
σ_6^{Month}	0.02348	0.00214	0.02337	0.01962	0.02812
σ_7^{Month}	0.01827	0.00178	0.01813	0.01516	0.02207
σ_8^{Month}	0.01618	0.00164	0.01608	0.01329	0.01975
σ_9^{Month}	0.01082	0.00137	0.01077	0.00831	0.01374
$\sigma_{10}^{\text{Month}}$	0.01088	0.00129	0.01084	0.00856	0.01356
$\sigma_{11}^{\text{Month}}$	0.01591	0.00159	0.01585	0.01303	0.01923
$\sigma_{12}^{\text{Month}}$	0.01829	0.00181	0.01819	0.01493	0.02215
σ	0.03532	0.00007	0.03532	0.03518	0.03546
σ^{Year}	0.01177	0.00133	0.01170	0.00938	0.01458

The effects of age, sex, and mesh size were unsurprisingly much smaller than length but were supported, and 95% credible intervals did not overlap 0 (Table 1). With other predictors held at their mean values, a 6 mm increase in mesh size was associated with an approximate 8.3 g mean weight increase and an increase in 1 year of age was associated with only a 1.7 g mean increase in weight. The difference between sexes depended upon the month, with age 3 females expected to weigh up to 20.8 g more than a male of similar length and age in November (spawning period is in early December) but 5.5 g less in March (Table 1). Imputing the mean mesh size had a small effect on the mesh size slope estimate, which was 3.2% higher when the subset of data with known mesh size was used.

The predicted weight of a 300 mm ($w300_{ym}$) fish captured in 38 mm mesh shows strong differences in body condition among years and months (Fig. 1). Body condition was low in the 1930s, increased to a maximum in the 1960s, and gradually decreased to relatively stable values relatively similar in magnitude to those in early years by around the mid-1990s. Since 2012, these values further decreased to the lowest values estimated during the study period (Fig. 1). In general, trends in $w300_{ym}$ closely followed the estimated annual offsets in the length–weight intercept year.dev_y (Supplementary Fig. S2[1]). On average, $w300_{ym}$ was lowest in

Fig. 1. Mean predicted weight of a 300 mm whitefish captured in a 38 mm mesh ($w300_{ym}$) per month and year from 1930 to 2019. [Colour online.]



February and increased to a maximum in July before decreasing again starting in November (Table 1; Fig. 1). However, there was substantial interannual variation in month effects (σ_m^{Month}), which was evident in plots for years with sufficient data (Table 1; Fig. 1). The interannual variation in month effects was highest in the spring (May and June) when temperature-dependent fish growth begins. The low variation in month and annual estimates from 1943 to 1950 is due to very limited or no data (see Supplementary Table S1[1]), resulting in the hierarchical model interpolating annual effects and using mean month effects.

Selectivity modeling

Posterior chains for selectivity curve comparisons and the final selectivity models converged and Rhat was below 1.05 for all parameters. Model comparisons of the three selectivity curves showed that the binormal selectivity model was much more supported (WAIC = 18 827) than the gamma (WAIC = 20 771) or normal (WAIC 20 620) selectivity models. The final binormal selectivity model fit with the full dataset had low absolute values of autocorrelation in posterior chains (≤0.15) at the thinned interval of 160 and effective sample sizes greater than 1058 for all parameters. In addition, the model allowing for selectivity parameters $k1$ and $k2$ to vary as a function of $w300_{ym}$ was much more supported (WAIC = 37 818) than the model with $k1$ and $k2$ held constant (WAIC = 39 197). Parameter estimates for the varying selectivity model were not sensitive to the value chosen for the contact intercept a^p, and almost all mean estimates varied by less than 1% (Supplementary Table S2[1]). The single exception was the slope b.area, which unsurprisingly changed more (by up to 5.5%), since it is correlated with the intercept. Nearly all parameter estimates were similar when $w250_{ym}$ and $w350_{ym}$ were used instead of $w300_{ym}$ (Supplementary Table S2[1]). The parameter $b.k1$ was negative for all models, and 95% credible intervals did not include 0, but the mean was 8% lower with $w250_{ym}$ and 19.5% higher with $w350_{ym}$. Similarly, the mean of parameter $b.k2$ was similar but 1.5% lower with $w250_{ym}$ and 9.2% higher with $w350_{ym}$. Given that negative effects were supported by all and had a similar magnitude, parameter estimates are reported below for the model using the intermediate $w300_{ym}$ and a^p set to −10.

Changes in body condition were clearly linked to changes in selectivity, with both $b.k1$ and $b.k2$ supporting decreases in $k1$ and $k2$ with increasing $w300_{ym}$ (Table 2). A roughly 2 standard deviation increase in $w300_{ym}$ from 205 to 260 g was associated with a decrease in $k1$ from 9.85 to 8.68, which corresponds to a decrease in peak selectivity of a 38 mm net from approximately 374 to 330 mm (Fig. 2). The same increase in weight was also expected to decrease $k2$ from 0.81 to 0.66, which corresponds to a decrease in the standard deviation of selected lengths of a 38 mm mesh net from 30.78 to 25.08 mm. The combination of changes results in shorter selected lengths with narrower curves and more pronounced bimodality for fish with higher condition. Similar changes in selected lengths were supported when $w250_{ym}$ and $w350_{ym}$ were used (Supplementary Figs. S3–S4[1]).

Table 2. Parameter estimates from the binormal selectivity model summarized from posterior distributions as mean, standard deviation (SD), median, and 2.5 and 97.5 percentiles from the posterior distributions.

Parameter	Mean	SD	Median	2.50%	97.50%
b.area	0.5259	0.0237	0.5262	0.4777	0.5727
e^p_{ymj}	0.7017	0.0181	0.7011	0.6672	0.7392
$a.k1$	9.2360	0.0138	9.2363	9.2087	9.2633
$b.k1$	−0.5679	0.0130	−0.5678	−0.5919	−0.5426
$k1$.diff	1.8724	0.0449	1.8717	1.7839	1.9672
$a.k2$	0.7316	0.0069	0.7317	0.7183	0.7452
$b.k2$	−0.0717	0.0066	−0.0719	−0.0849	−0.0586
$k2$.diff	1.1101	0.0234	1.1099	1.0654	1.1592
c	0.1569	0.0086	0.1570	0.1405	0.1745

The second mode was estimated to account for the capture of a small proportion ($c = 0.158 \pm 0.009$) of longer than expected individuals, which may represent capture through non-gilling, such as tangling (Table 2). As expected, net area had a positive effect on contact probability (b.area = 0.526 ± 0.024), and there was substantial unexplained variation in contact probability ($e^p_{ymj} = 0.702 \pm 0.018$). An increase in 1 standard deviation of net (2507 m^2) was associated with an approximately 70% relative increase in contact probability (from 0.000045 to 0.000077). The standard deviation e^p_{ymj} on the logit scale corresponds approximately to a coefficient of variation of 1 in contact probabilities, so that 95% of contact probabilities at a given net area were estimated to vary greatly around the mean approximately ±200%.

Implications for harvest and age distribution estimation

The changes in gillnet selectivity simulated to mirror increases in body condition under scenario 2 substantially decreased the

Fig. 2. Estimated selectivity of a 38 mm gillnet for relatively thin and fat whitefish. Thin and fat correspond to average predicted weights of a 300 mm fish ($w300_{ym}$) of values 205 and 260 g, respectively, which are roughly equal to 1 standard deviation below and above the average $w300_{ym}$.

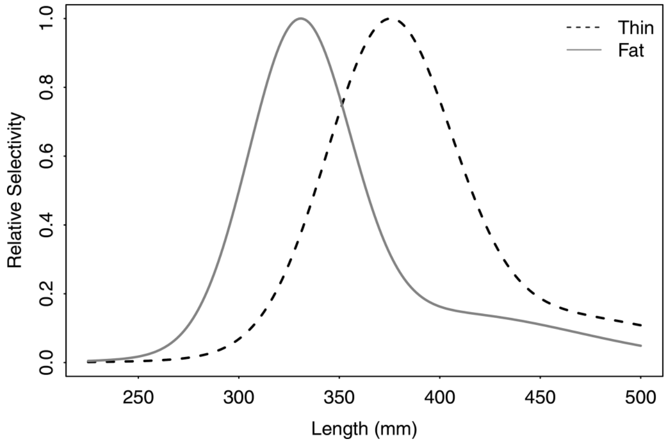
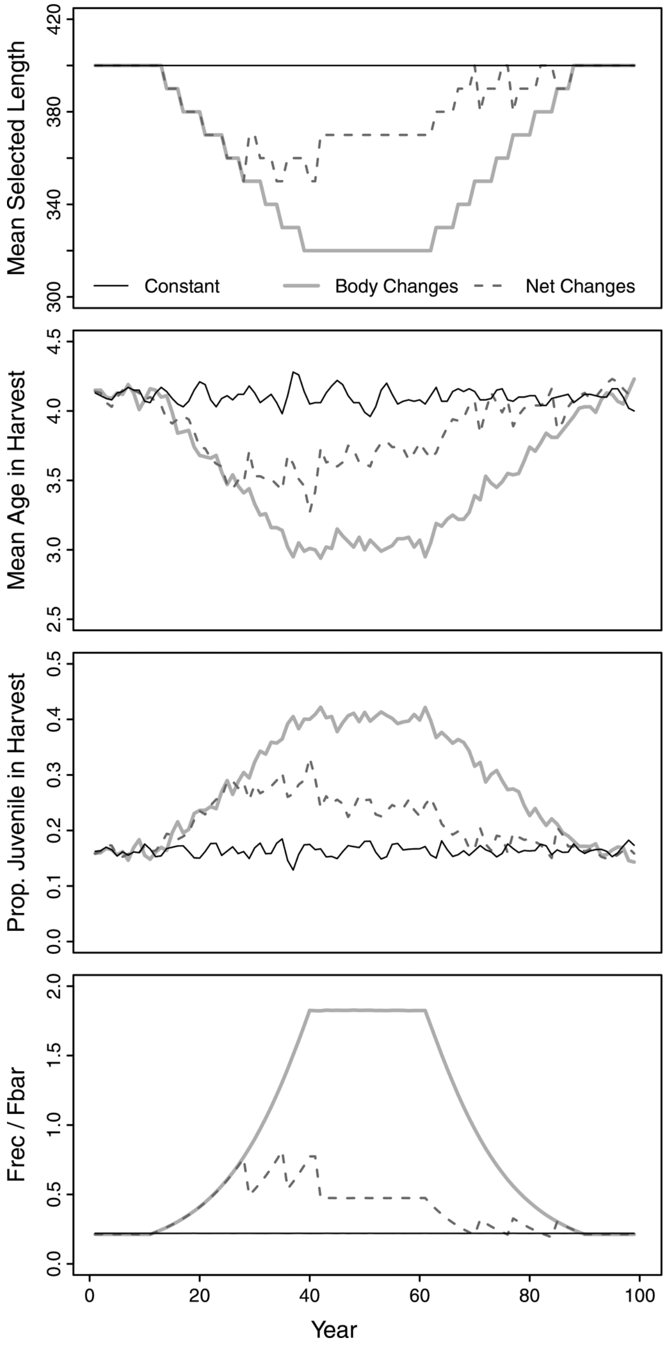


Fig. 3. Changes in the mean selected length, mean age in harvest, proportion of juveniles in harvest, and Frec/Fbar selectivity metric from a simulation model with three scenarios.



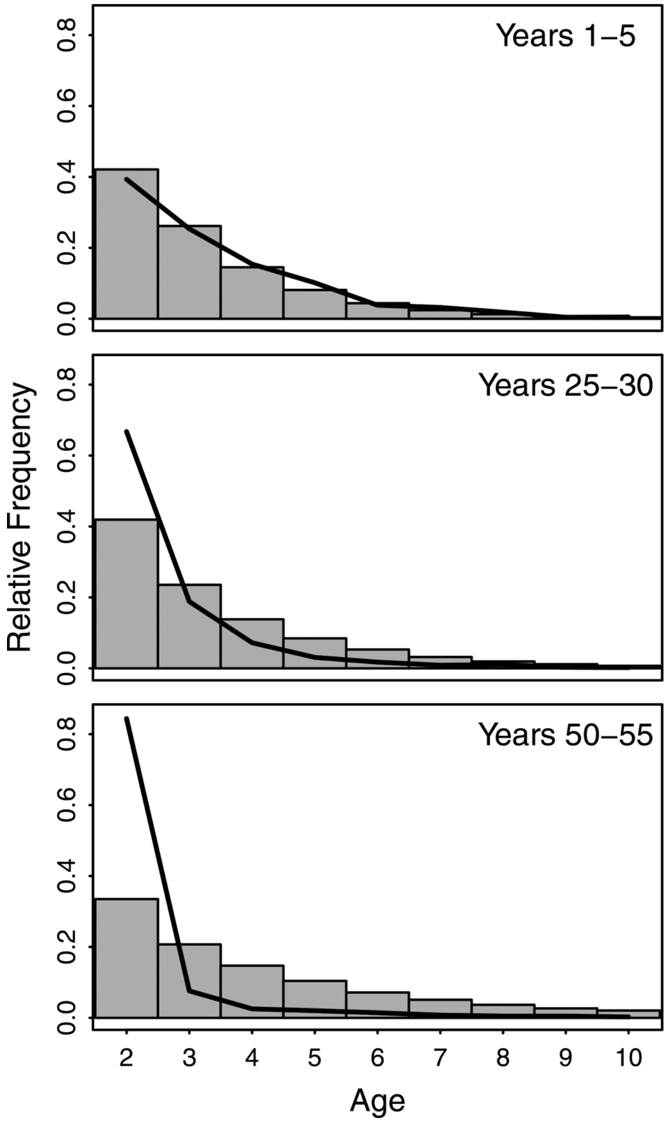
mean age harvested from 4.1 to slightly under 3 years and increased the proportion of juveniles in harvest from 0.15 to over 0.4 (Fig. 3). The Frec/Fbar selectivity metric tracked changes in selectivity and increased from approximately 0.2 to 1.8 (Fig. 3). Under scenario 3, gill net mesh size increased by 2 mm on three occasions (to 42, 44, and 46 mm around years 31, 37, and 43) when the prior 5-year average age in harvest dropped below 3.5 years and then returned to the starting mesh size of 40 mm by year 85. Increases in mesh size as simulated here kept the proportion of immature fish in harvest below 0.3 in most years, but did not eliminate all effects of gillnet selectivity changes. Under simulation conditions, keeping the proportion of immature fish in harvest near starting values around 0.15 would require increasing the mesh size more often to a largest mesh of 52 mm. As expected, assuming that selectivity was constant under changing conditions of scenario 2 resulted in greatly biased estimates of population age distribution (Fig. 4). When selectivity differences were greatest in years 50–55, the relative abundance of age class 2 was overestimated by 147%, while those of ages 3–10 were underestimated by 78%–88% (Fig. 4).

Discussion

This study clearly shows that body condition of whitefish in Lake Constance underwent dramatic changes and resulted in the selectivity of shorter fish by gillnets of the same mesh size. These results were supported regardless of whether the average weights at 250, 300, or 350 mm were used to represent body condition and estimate selectivity changes. Under simulation conditions designed around whitefish, increased body condition alone could have reduced the mean age harvested by over 1 year and increased the percentage of juveniles in harvest by 25%. The simulations held length at age constant to focus on effects of body condition changes, but it is very likely that growth rate would also increase with body condition (e.g., Thomas and Eckmann 2007). Thus, the reductions in age and maturity level of harvested fish are likely to be much greater than simulated results. Managers can respond to selectivity changes by changing mesh sizes, but these are unlikely to sufficiently mitigate effects on the population unless management is very responsive.

In Lake Constance, increased growth and body condition of whitefish resulted in the harvest of large numbers of immature, 1-year-old fish in the early 1960s (Nümann 1972). Managers responded by increasing the mesh size from 38 to 44 mm, which helped to reduce the harvest of immature fish, but larger increases would have been required to protect all immature fish (Nümann 1972). As re-oligotrophication gradually reduced fish growth and body condition, managers gradually reduced legal mesh sizes from 44 mm in 1995 to mostly 38 mm by 2017 to continue targeting mature fish with similar efficiency (M. Kugler and C. Friedl, 2018, Annual Report to IBKF: Whitefish fishery, monitoring and spawning fishery report for 2017). However, body condition has been at record low values since 2015 (Fig. 1), corresponding with reductions in relative abundance and growth following the invasion of the pelagic zone by three-spined stickleback (Rösch et al. 2018). Some fishers stress that smaller mesh sizes should be allowed, but managers are awaiting further information from stock assessments to

Fig. 4. True 5-year average population age distribution (bars) and estimated age distributions made under an incorrect assumption of constant gillnet selectivity (lines) at three time periods from a scenario with changing selectivity (scenario 2).



assess the effects of further mesh size reductions. At present, managers in Lake Constance set mesh size restrictions to protect young, immature fish based on monthly monitoring data, but predictive modeling tools have not been regularly applied. The changes in body condition and gillnet selectivity identified more accurately characterize harvested fish, which can be combined with a suite of stock assessment models to better understand historical population dynamics and provide improved predictive tools for comparing management alternatives.

The long-term datasets enabled estimating body condition and gillnet selectivity changes over several decades, but this also means that there was variation in other potential confounding factors. First, it is possible that reported and actual mesh sizes varied throughout the time period due to differing measurement practices or net manufacturers. Mesh size has been measured using a similar methodology (measuring across 10 knots while applying pressure to soaked nets) throughout the study period, however, so substantial variation in actual mesh sizes seems unlikely. Second, the twine diameter underwent a small and gradual change from 0.15 mm in early years to 0.12 mm, which has been the only diameter used since the early 1990s. While some studies suggest that twine diameter or material can alter relative selectivity (Yokota et al. 2001; Ayaz et al. 2011), others have concluded that twine diameter only affected the fishing power of the net and not the selectivity curve (Holst et al. 2002; Gray et al. 2005). Given that the differences in mesh sizes were only 0.03 mm in this study compared with 0.12 mm in Yokota et al. (2001) and 0.11 mm in Ayaz et al. (2011), it is expected that twine diameter had little or no effect on selectivity changes. Third, gillnet hanging ratio likely varied throughout the study period and may increase harvested fish lengths through tangling (Samaranayaka et al. 1997), although other studies have found no effect (Gray et al. 2005). Lastly, the mesh sizes fished in each month varied throughout the study, and this would have biased monthly estimates of condition since larger mesh size were estimated to catch heavier individuals, and these biases would have been carried over into effects on selectivity if unaccounted for. For this reason, mesh size was included in the length–weight modeling and mesh size-corrected estimates of condition were used in the selectivity modeling. In any case, results were similar to those reported here when using only the contemporary dataset (after 1991) when these factors were mostly constant, further confirming the role of body condition changes in altering gillnet selectivity.

The length–weight estimates in this study were based primarily on fish collected using gillnets, which can produce underestimates of the length–weight slope (β.len) of the population when an insufficient range of mesh sizes are fished (Froese 2006). In most years this should not be an issue because fish were captured using a large range of mesh sizes and a nonselective pelagic seine was also used for many records prior to 1958. However, the interannual mean length slope estimate was 2.7, and several annual estimates were below 2.5, which are lower than length–weight slopes reported for 14 populations of the closely related *Coregonnus lavaretus* from Fishbase (mean = 3.07, max. = 2.86, min. = 3.53; Froese and Pauly 2020). Since many of the very low β.len were estimated between 1977 and 1988 when only a narrow range of relatively large meshes (44–48 mm) was fished, it is possible that these coefficients are biased low. Slopes below 2.6 have also been estimated in the last 4 years when a very wide range of mesh sizes have been fished, however, which suggests that relatively low slopes have some support. It is also likely that selective harvest of more corpulent individuals flattened the length–weight relationship in the fished population relative to an unfished state, especially since higher slopes are more common prior to 1960 before the use of nylon gillnets greatly increased size-selective harvest mortality in Lake Constance (Nümann 1972). Regardless, plots of length–weight relationships showing low, mean, and high slope coefficients show that the effects of any potential biases within the relevant length range (nearly all are captured between 20 and 40 cm) are likely small (Supplementary Fig. S5[1]). It is worth cautioning that extrapolating to very small (<15 cm) or large fish (>50 cm) could lead to biased weight estimates.

The body condition of fish varies across populations and with time depending upon many factors, including ecosystem productivity, competition, temperature-dependent growth, and reproductive investment. Eutrophication caused by human activities is likely the most common cause of freshwater ecosystem changes that can improve growth conditions for some species (Smith and Schindler 2009; Colby et al. 1972), which could result in body condition changes similar to those shown here for Lake Constance whitefish. Where gillnets or other size-selective harvest techniques are used (e.g., trawls), eutrophication is thus likely to increase the harvest pressure on shorter, more corpulent individuals unless mesh sizes are adjusted. The effects of these selectivity changes on the population depend upon many factors, but are likely to lead to biased estimates if ignored (Linton and Bence

2011; Nielsen and Berg 2014). In systems like Lake Constance where most available data span a period of continuous ecosystem changes, identifying selectivity changes and their causes (e.g., changes in growth or body condition) can provide a better understanding of population dynamics in the available time series. In addition to informing population selectivity by a fishery, contact selectivity estimates are often used to estimate population age or length distributions of both harvested and nonharvested species from gillnet catches (Spangler and Collins 1992; Millar and Fryer 1999; Shoup and Ryswyk 2016). If body condition differs among time periods or populations, assuming invariant length-based selectivity would result in biased population estimates as demonstrated in simulation results.

Size-selective harvest has been shown to cause fishery-induced evolution in several cases, which is likely exacerbated when fast-growing fish are removed prior to spawning. These studies have often focused on the potential role of selecting fish that have faster growth in length from the population, potentially leading to slower skeletal growth over time (Enberg et al. 2012). The relatively strong effects of body condition on selectivity found in this study suggests that the removal of more corpulent fish at younger ages may also play a role in fishery-induced evolution by gillnets and other size-selective gears (Enberg et al. 2012). This potential effect depends upon the role that genetics plays in body condition differences within a population and remains to be tested. Thomas and Eckmann (2007) suggested that Lake Constance pelagic whitefish growth may have been reduced as a result of fishery-induced evolution but the role of selection on body condition has not been explored. However, Gum et al. (2014) did not find a reduction in genetic variation in the same population that would be consistent with strong fishery selection. Since females have greater body condition prior to spawning and reproductive investment may vary, more corpulent and fecund females may also recruit to a fishery and be harvested at younger ages (Handford et al. 1977; Huse et al. 2000). Identifying the role of body condition in fishery-induced evolution requires further research but may be difficult due to the likely confounding relationship with skeletal growth rates.

Based on the results here, it seems prudent that studies using length-based selectivity estimates account for the potential role of changing body condition. Many stock assessment frameworks estimate population selectivity separately and allow for temporal variation (Dichmont et al. 2016; Xu et al. 2018), which could presumably capture underlying variation in selectivity caused by changing body condition or other factors. However, in some cases fishery selectivity is informed by estimates of length-based contact selectivity, which may be drawn from selectivity studies at one or more time steps (Crone and Valero 2014; Sampson 2014). When body condition changes alter selectivity, these estimates must be updated periodically to avoid biases in stock assessment models and management parameters (Linton and Bence 2011; Ichinokawa et al. 2014). Regardless, knowing that changing body condition has altered selectivity could help to improve understanding of population responses to changing ecosystem conditions and harvest to inform fisheries management. Co-variation in contact selectivity and body condition could be accounted for through using girth-based selectivity estimates or tracking changes in body condition. Since girth measurements require more effort and are much less common, it is likely more feasible to estimate body condition from commonly collected length and weight measurements and then link these to selectivity as was done in this study.

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References

Ayaz, A., Altınağaç, U., Ozekinci, U., Ozen, O., Altın, A., and İşmen, A. 2011. Effect of twine thickness on selectivity of gillnets for bogue, *Boops boops*, in Turkish waters. Mediterr. Mar. Sci. **12**: 358–368. doi:10.12681/mms.37.

Baer, J., Eckmann, R., Rösch, R., Arlinghaus, R., and Brinker, A. 2017. Managing Upper Lake Constance fishery in a multi-sector policy landscape: beneficiary and victim of a century of anthropogenic trophic change. *In* Inter-sectoral governance of inland fisheries. *Edited by* A.M. Song, S.D. Bower, P. Onyangon, S.J. Cooke, and R. Chuenpagdee. Too Big To Ignore-WorldFish, St. Johns, Canada. pp. 32–47. Available from http://toobigtoignore.net/research-highlights-1/e-book-inter-sectoral-governance-of-inland-fisheries/ [accessed 23 June 2020].

Baranov, F.I. 1914. The capture of fish by gillnets. Mater. Pozn. Russ. Rybolov. **3**(6): 56–99.

Casini, M., Käll, F., Hansson, M., Plikshs, M., Baranova, T., Karlsson, O., et al. 2016. Hypoxic areas, density-dependence and food limitation drive the body condition of a heavily exploited marine fish predator. R. Soc. Open Sci. **3**(10): 160416. doi:10.1098/rsos.160416. PMID:27853557.

Colby, P.J., Spangler, G.R., Hurley, D.A., and McCombie, A.M. 1972. Effects of Eutrophication on Salmonid Communities in Oligotrophic Lakes. J. Fish. Res. Board Can. **29**(6): 975–983. doi:10.1139/f72-141.

Cone, R.S. 1989. The Need to Reconsider the Use of Condition Indices in Fishery Science. Trans. Am. Fish. Soc. **118**(5): 510–514. doi:10.1577/1548-8659(1989)118<0511:TNTRTU>2.3.CO;2.

Crone, P.R., and Valero, J.L. 2014. Evaluation of length- vs. age-composition data and associated selectivity assumptions used in stock assessments based on robustness of derived management quantities. Fish. Res. **158**: 165–171. doi:10.1016/j.fishres.2014.02.034.

Dichmont, C.M., Deng, R.A., Punt, A.E., Brodziak, J., Chang, Y.-J., Cope, J.M., et al. 2016. A review of stock assessment packages in the United States. Fish. Res. **183**: 447–460. doi:10.1016/j.fishres.2016.07.001.

Enberg, K., Jørgensen, C., Dunlop, E.S., Varpe, Ø., Boukal, D.S., Baulier, L., et al. 2012. Fishing-induced evolution of growth: concepts, mechanisms and the empirical evidence. Mar. Ecol. **33**(1): 1–25. doi:10.1111/j.1439-0485.2011.00460.x.

Froese, R. 2006. Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. J. Appl. Ichthyol. **22**(4): 241–253. doi:10.1111/j.1439-0426.2006.00805.x.

Froese, R., and Pauly, D. (*Editors*). 2020. FishBase: length–weight parameters for *Coregonus lavaretus*. Available from https://www.fishbase.de/summary/Coregonus-lavaretus.html [accessed 18 December 2020].

Froese, R., Thorson, J.T., and Reyes, R.B. 2014. A Bayesian approach for estimating length–weight relationships in fishes. J. Appl. Ichthyol. **30**(1): 78–85. doi:10.1111/jai.12299.

Gelman, A., and Rubin, D.B. 1992. Inference from iterative simulation using multiple sequences. Stat. Sci. **7**(4): 457–472. doi:10.1214/ss/1177011136.

Gray, C.A., Broadhurst, M.K., Johnson, D.D., and Young, D.J. 2005. Influences of hanging ratio, fishing height, twine diameter and material of bottom-set gillnets on catches of dusky flathead *Platycephalus fuscus* and non-target species in New South Wales, Australia. Fish. Sci. **71**(6): 1217–1228. doi:10.1111/j.1444-2906.2005.01086.x.

Gum, B., Geist, J., Eckenfels, S., and Brinker, A. 2014. Genetic diversity of upper Lake Constance whitefish *Coregonus* spp. under the influence of fisheries: a DNA study based on archived scale samples from 1932, 1975 and 2006. J. Fish Biol. **84**(6): 1721–1739. doi:10.1111/jfb.12393. PMID:24787479.

Hamley, J.M. 1975. Review of gillnet selectivity. J. Fish. Res. Board Can. **32**(11): 1943–1969. doi:10.1139/f75-233.

Handford, P., Bell, G., and Reimchen, T. 1977. A gillnet fishery considered as an experiment in artificial selection. J. Fish. Res. Board Can. **34**(7): 954–961. doi:10.1139/f77-148.

Herbst, S.J., Marsden, J.E., and Lantry, B.F. 2013. Lake whitefish diet, condition, and energy density in Lake Champlain and the lower four great lakes following *Dreissenid* invasions. Trans. Am. Fish. Soc. **142**(2): 388–398. doi:10.1080/00028487.2012.747991.

Holst, R., Wileman, D., and Madsen, N. 2002. The effect of twine thickness on the size selectivity and fishing power of Baltic cod gill nets. Fish. Res. **56**(3): 303–312. doi:10.1016/S0165-7836(01)00328-9.

Htun-Han, M. 1978. The reproductive biology of the dab *Limanda limanda* (L.) in the North Sea: gonosomatic index, hepatosomatic index and condition factor. J. Fish Biol. **13**(3): 369–378. doi:10.1111/j.1095-8649.1978.tb03445.x.

Huse, I., Løkkeborg, S., and Soldal, A.V. 2000. Relative selectivity in trawl, longline and gillnet fisheries for cod and haddock. ICES J. Mar. Sci. **57**(4): 1271–1282. doi:10.1006/jmsc.2000.0813.

Ichinokawa, M., Okamura, H., and Takeuchi, Y. 2014. Data conflict caused by model mis-specification of selectivity in an integrated stock assessment model and its potential effects on stock status estimation. Fish. Res. **158**: 147–157. doi:10.1016/j.fishres.2014.02.003.

Irons, K.S., Sass, G.G., McClelland, M.A., and Stafford, J.D. 2007. Reduced condition factor of two native fish species coincident with invasion of non-native Asian carps in the Illinois River, U.S.A. Is this evidence for competition and reduced fitness? J. Fish Biol. **71**(sd): 258–273. doi:10.1111/j.1095-8649.2007.01670.x.

Kurkilahti, M., Appelberg, M., Hesthagen, T., and Rask, M. 2002. Effect of fish shape on gillnet selectivity: a study with Fulton's condition factor. Fish. Res. **54**(2): 153–170. doi:10.1016/S0165-7836(00)00301-5.

Linton, B.C., and Bence, J.R. 2011. Catch-at-age assessment in the face of time-varying selectivity. ICES J. Mar. Sci. **68**(3): 611–625. doi:10.1093/icesjms/fsq173.

McCombie, A., and Berst, A. 1969. Some effects of shape and structure of fish on selectivity of gillnets. J. Fish. Res. Board Can. **26**(10): 2681–2689. doi:10.1139/f69-260.

Millar, R.B. 1992. Estimating the size-selectivity of fishing gear by conditioning on the total catch. J. Am. Stat. Assoc. **87**(420): 962–968. doi:10.1080/01621459.1992.10476250.

Millar, R.B., and Fryer, R.J. 1999. Estimating the size-selection curves of towed gears, traps, nets and hooks. Rev. Fish Biol. Fish. **9**(1): 89–116. doi:10.1023/A:1008838220001.

Muir, A.M., Sutton, T.M., Peeters, P.J., Claramunt, R.M., and Kinnunen, R.E. 2008. An evaluation of age estimation structures for Lake Whitefish in Lake Michigan: selecting an aging method based on precision and a decision analysis. N. Am. J. Fish. Manage. **28**(6): 1928–1940. doi:10.1577/M08-014.1.

Nielsen, A., and Berg, C.W. 2014. Estimation of time-varying selectivity in stock assessments using state-space models. Fish. Res. **158**: 96–101. doi:10.1016/j.fishres.2014.01.014.

Nümann, W. 1972. The Bodensee: effects of exploitation and eutrophication on the salmonid community. J. Fish. Res. Board Can. **29**(6): 833–847. doi:10.1139/f72-127.

Plummer, M. 2017. JAGS Version 4.3.0 user manual. Available from https://sourceforge.net/projects/mcmc-jags/ [accessed 23 June 2020].

Plummer, M., Best, N., Cowles, K., and Vines, K. 2005. CODA: Convergence diagnosis and output analysis for MCMC. R News 6: 7–11. Available from https://cran.r-project.org/doc/Rnews/Rnews_2006-1.pdf#page=7 [accessed 23 June 2020].

R Core Team. 2019. R: a language and environment for statistical computing. R Foundation of Statistical Computing, Vienna, Austria. Available from https://www.R-project.org.

Reis, E.G., and Pawson, M.G. 1999. Fish morphology and estimating selectivity by gillnets. Fish. Res. **39**(3): 263–273. doi:10.1016/S0165-7836(98)00199-4.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Bd. Can. 191. Dept. of the Environment, Fisheries and Marine Service, Ottawa, Ont.

Rösch, R., Baer, J., and Brinker, A. 2018. Impact of the invasive three-spined stickleback (*Gasterosteus aculeatus*) on relative abundance and growth of native pelagic whitefish (*Coregonus wartmanni*) in Upper Lake Constance. Hydrobiologia, **824**(1): 243–254. doi:10.1007/s10750-017-3479-6.

Samaranayaka, A., Engås, A., and Jørgensen, T. 1997. Effects of hanging ratio and fishing depth on the catch rates of drifting tuna gillnets in Sri Lankan waters. Fish. Res. **29**: 1–12. doi:10.1016/S0165-7836(96)00524-3.

Sampson, D.B. 2014. Fishery selection and its relevance to stock assessment and fishery management. Fish. Res. **158**: 5–14. doi:10.1016/j.fishres.2013.10.004.

Shoup, D.E., and Ryswyk, R.G. 2016. Length selectivity and size-bias correction for the North American standard gill net. N. Am. J. Fish. Manage. **36**(3): 485–496. doi:10.1080/02755947.2016.1141809.

Smith, V.H., and Schindler, D.W. 2009. Eutrophication science: where do we go from here? Trends Ecol. Evol. **24**(4): 201–207. doi:10.1016/j.tree.2008.11.009. PMID:19246117.

Solymos, P. 2010. Dclone: data cloning in R. R J. **2**: 29–37. doi:10.32614/RJ-2010-011.

Spangler, G.R., and Collins, J.J. 1992. Lake Huron fish community structure based on gill-net catches corrected for selectivity and encounter probability. N. Am. J. Fish. Manage. **12**(3): 585–597. doi:10.1577/1548-8675(1992)012<0585:LHFCSB>2.3.CO;2.

Stich, H.B., and Brinker, A. 2010. Oligotrophication outweighs effects of global warming in a large, deep, stratified lake ecosystem. Global Change Biol. **16**(2): 877–888. doi:10.1111/j.1365-2486.2009.02005.x.

Thomas, G., and Eckmann, R. 2007. The influence of eutrophication and population biomass on common whitefish (*Coregonus lavaretus*) growth — the Lake Constance example revisited. Can. J. Fish. Aquat. Sci. **64**(3): 402–410. doi:10.1139/f07-019.

Vasilakopoulos, P., Jardim, E., Konrad, C., Rihan, D., Mannini, A., Pinto, C., et al. 2020. Selectivity metrics for fisheries management and advice. Fish Fish. **21**(3): 621–638. doi:10.1111/faf.12451.

Vehtari, A., Gelman, A., and Gabry, J. 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Stat. Comput. **27**(5): 1413–1432. doi:10.1007/s11222-016-9696-4.

Watanabe, S. 2010. Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. J. Mach. Learn. Res. **11**.

Xu, H., Thorson, J.T., Methot, R.D., and Taylor, I.G. 2018. A new semi-parametric method for autocorrelated age- and time-varying selectivity in age-structured assessment models. Can. J. Fish. Aquat. Sci. **76**(2): 268–285. doi:10.1139/cjfas-2017-0446.

Yokota, K., Fujimori, Y., Shiode, D., and Tokai, T. 2001. Effect of thin twine on gill net size-selectivity analyzed with the direct estimation method. Fish. Sci. **67**(5): 851–856. doi:10.1046/j.1444-2906.2001.00332.x.

Appendix A. Description of simulation model

As described in the manuscript, a simulation model was used to understand how changes in body condition and gillnet selectivity alter harvest, estimates of population age distributions, and fishery management. The starting population size consisted of 80 000 individuals from a stable age distribution across 10 age classes from 1 to 10+ with the following proportions, after rounding to four decimals for presentation: {0.7256, 0.1453, 0.0545, 0.0337, 0.1888, 0.0103, 0.0057, 0.0031, 0.0017, 0.0013}. Across the 10 age classes, the proportion of mature fish was defined deterministically as {0, 0.4, 0.7, 1, 1, 1, 1, 1, 1, 1} and natural mortality followed a binomial process with probabilities as {0.8, 0.6, 0.2, 0.2, 0.2, 0.2, 0.2, 0.2, 0.5, 0.8}. Mean fish growth followed a von Bertalanffy curve with time measured in months and parameters used to represent whitefish growth data from the early 1990s in Lake Constance (L_∞ = 400 mm, t_0 = 7.2 months, and K = 0.06). Individual fish length was assumed to be normally distributed around the mean estimated value with a coefficient of variation equal to 10%. Recruitment (R) was simulated to follow a Beverton–Holt curve parameterized as $R = (a \times S)/(1 + a/b \times S)$, where a = 20, b = 10 000, and S is the number of spawners (number of surviving, mature fish). A coefficient of variation of 0.1 was used to introduce stochasticity into the number of recruited fish.

The number of fish harvested in a given age–length bin followed a deterministic process combining gillnet selectivity and probability of gear contact. Contact probability was set to 0.5 for all age classes, which resulted in approximate harvest mortality probability of 0.3 on age 4 and older fish under starting conditions. The starting legal mesh size was set to 40 mm, and starting selectivity parameters were chosen to ensure that gillnets were targeting mostly adult fish with a mean selectivity equal to the L_∞ of 400 mm ($k1$ = 10) and standard deviation equal to the estimated value for thin fish in the study ($k2$ = 0.78). Other selectivity parameters were set at their estimated values ($k1$.diff = 1.9, $k2$.diff = 1.1, and c = 0.15) in all scenarios. The simulated population went through each process in the following order using an annual time step: natural mortality, harvest, recruitment, and aging. Lengths were assigned to the aged fish using the growth curve described earlier at the start of each year.

The following three scenarios were run for 100 years.

Scenario 1: Gillnet selectivity and mesh size were held constant at reference values across the 100-year simulation period.

Scenario 2: Mesh size was constant, while gillnet selectivity changed throughout the simulation period in a manner and magnitude similar to changes estimated for Lake Constance whitefish due to changes in body condition. The magnitude in changes of $k1$ and $k2$ were 2 and 0.22, respectively, which would be expected to occur if body condition changed 4 standard deviations. Years 1–10 had starting values ($k1$ = 10, $k2$ = 0.78), followed by a gradual decrease over 30 years, a 20-year period of low selected lengths ($k1$ = 8, $k2$ = 0.56), a 30-year gradual increase in selected lengths, and finally another 10 years at starting values.

Scenario 3: Selectivity changed as in scenario 2, but mesh size was changed to represent a potential management intervention taken to minimize harvest of immature fish (i.e., targeting harvest of age 4 and older fully mature age classes). During the first half of the simulation when selected sizes were decreasing, the size of gillnet was increased by 2 mm when the average age of fish harvested for 5 consecutive years dropped below 3.5 years. In the second half when selected sizes were increasing, the size of gillnet fished was decreased by 2 mm when the average age of fish harvested for 5 consecutive years was above 4 years.

The mean age in harvest, proportion of juveniles in harvest, and the Frec/Fbar selectivity metric recently suggested by Vasilakopoulos et al. (2020) were calculated for each year in each simulation. Frec/Fbar is calculated as the ratio of harvest mortality of the first age class recruited (here age 2) to the mean harvest mortality of fully recruited age classes (here ages 3–5). The metrics were calculated using the simulated population data to enable a simple presentation of implications without delving into the nuances of alternative sampling designs and (or) stock assessment estimation.

The effect of incorrectly assuming constant gillnet selectivity on population age distribution estimates were also investigated using three 5-year time periods from scenario 2. In each 5-year time period, the average proportion of individuals in each age class was estimated by assuming that gillnet selectivity stayed constant at starting values. These estimates were compared with the known age class distribution from the simulated population.