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Length-Based Assessment of Hovsgol Grayling (*Thymallus nigrescens*), Lenok (*Brachymystax lenok*), and Burbot (*Lota lota*) Population Status in Lake Hovsgol, Mongolia

Монголын Хөвсгөл нуурын Хөвсгөл хадран (*Thymallus nigrescens*), шөвгөр хоншоорт зэвэг (*Brachymystax lenok*), гутаарь (*Lota lota*) загасны уртад суурилсан популяцийн төлөв байдал

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Keywords: data-limited stock assessment | inland fisheries | Lake Khuvsgul | LBSPR | length-based indicators

ABSTRACT

Despite the global importance of inland fisheries, data available for stock assessment is often limited. Data-limited methods that use length composition data offer a potential approach to assessing more inland fisheries. We assessed the population status of three fish species in Lake Hovsgol, Mongolia through length-based spawning potential ratio (LBSPR) analysis and evaluation of trends in eight length-based indicators of population status, catch-per-unit-effort (CPUE), and body size. Hovsgol grayling (*Thymallus nigrescens*) were not yet overfished, but CPUE and body size declined due to targeting of large, mature fish. Lenok (*Brachymystax lenok*) were experiencing overfishing, especially of small, immature fish, which contributed to size–structure truncation. The burbot (*Lota lota*) population was healthy according to most indicators, but the lack of local life history information exacerbated already large uncertainties. Continued monitoring and improved coordination among fishers, managers, and scientists will be critical to enhancing the sustainability of these fisheries.

This article has been corrected on [28 November 2024]: The foreign language abstract has been edited for clarity.

ХУРААНГУЙ
Эх газрын загас агнуурын дэлхийн ач холбогдлыг эс тооцвол загас агнуурын нөөцийн үнэлгээний мэдээлэл ихэвчлэн хязгаарлагдмал байдаг. Уртад суурилсан мэдээлэлд тулгуурладаг хязгаарлагдмал өгөгдөл бүхий аргаар эх газрын загас агнуурыг үнэлэх боломжтой. Бид Хөвсгөл нуурын гурван зүйл загасны популяцийн төлөв байдлыг уртад суурилсан үржлийн боломжит харьцаагаар (LBSPR) тодорхойлж, популяцийн төлөв байдлын үнэлгээний уртад суурилсан найман индикатор, нэгж барилт (CPUE), биеийн хэмжээ зэргийг үнэлж гаргасан. Хөвсгөл хадран (*Thymallus nigrescens*) загас нь хэт олборлолтонд өртөөгүй боловч нэгж барилт, биеийн хэмжээ зэрэг нь бие гүйцсэн, том загасыг агнаснаас үүдэлтэйгээр буурсан. Шөвгөр хоншоорт зэвэг (*Brachymystax lenok*) загасыг хэт их агнаж, ялангуяа жижиг, бие гүйцээгүй загасыг барьж байгаа нь хэмжээ-бүтцэд нь нөлөөлсөн. Гутаарь (*Lota lota*) загасны популяци ихэнх үзүүлэлтээрээ эрүүл байгаа ч бүс нутгийн амьдралын эргэлтийн мэдээлэл дутмаг байгаа нь тодорхойгүй байдлыг улам нэмэгдүүлж байна. Үргэлжилсэн мониторинг болон загасчид, удирдлагууд, эрдэмтдийн хоорондын уялдаа холбоог сайжруулах нь загас агнуурын тогтвортой байдлыг сайжруулахад чухал үүрэг гүйцэтгэнэ.

1 | Introduction

Inland fish stocks provide important socio-economic benefits, including economic value, employment, tourism, recreation, and food security (McIntyre, Reidy Liermann, and Revenga 2016; Smith, Khoa, and Lorenzen 2005). Food security is especially important for rural communities that rely on local fish for subsistence, although data for inland subsistence fisheries are generally lacking (Beard et al. 2011). In 2015, inland capture fisheries accounted for 7%–11.5% of global fish production, but this was thought to be a substantial underestimate (Bartley et al. 2015). Despite their importance, inland stocks remain largely unassessed due to challenges in collecting fisheries data in dispersed and often isolated fisheries (Lorenzen et al. 2016; Welcomme et al. 2010).

Improvement in the assessment and management of inland fisheries will likely depend on use of data-limited stock assessment methods. While gold-standard data-rich assessment methods require time series of catch and relative abundance, in addition to knowledge of species biology, data-limited methods tend to require only one of these data types and knowledge of only a few biological or life history parameters (Dowling et al. 2015). In general, data-limited assessment methods are categorized as either catch-only models or length-based approaches. Catch-only models use time series of catch data to inform assumptions of biomass, which allow for estimation of historical abundances and exploitation rates (Fitzgerald, Delanty, and Shephard 2018; Free et al. 2020). However, catch-only models rely heavily on prior assumptions and often perform poorly when assumptions are inaccurate (Free et al. 2020; Ovando et al. 2022; Pons, Cope, and Kell 2020; Thorson and Cope 2015). In contrast, length-based models require length–frequency data, but do not rely on historical catch and effort data. Instead, knowledge of life history strategies and an understanding of the expected length composition of a stock can be used to estimate stock status (Haddon 2011; Prince et al. 2015) and mortality rates (Hordyk, Ono, Valencia, et al. 2015). These characteristics make length-based models ideal candidates for assessment of small, data-poor fisheries in inland waters, which frequently lack reliable time series of reported catch (Babcock et al. 2013; Fitzgerald, Delanty, and Shephard 2018; Hommik et al. 2020; Hordyk, Ono, Sainsbury, et al. 2015).

While applications of length-based stock assessment methods to marine fisheries have grown rapidly, applications to inland fisheries are scarce (Lorenzen et al. 2016). In marine systems, length-based approaches for estimating the spawning potential ratio (SPR), which describes stock status as a proportion of unfished reproductive potential, have been especially common (Coscino et al. 2024; Cousido-Rocha et al. 2022; Lauden et al. 2024; Prince et al. 2015). This family of methods, known as LBSPR approaches, leverage basic life history parameters to predict the length composition and reproductive potential of an unfished population and use the observed length composition of the catch, which is shaped by fishing mortality, to estimate fisheries selectivity, relative fishing mortality, and stock status. For example, an assessment of Palauan coral reef fish populations using one such LBSPR model ultimately resulted in the implementation of minimum size limits for multiple species (Prince et al. 2015). Despite being more frequently used in marine fisheries, length-based methods have been applied to some inland fish stocks, including the use of an LBSPR model and other length-based indicators to assess fish stocks in a variety of aquatic inland habitats (Shephard et al. 2020). Later research used local ecological knowledge (LEK) from Guyanese fishermen to design monitoring surveys of target species using local gears (Shephard et al. 2023). Data from these surveys were used to evaluate status using an LBSPR model and other length-based indicators, which were themselves used to provide a baseline for future semi-quantitative LEK-based monitoring. A novel LBSPR model for fisheries exhibiting dome-shaped selectivity was used to generate SPR estimates for brown trout (*Salmo trutta*) in Irish lakes (Hommik et al. 2020).

Data required for length-based assessment models (length composition of the catch and basic life history information) can also be used to estimate indicators of stock condition and fishing intensity to support status estimates from length-based assessment models and provide further insights into population dynamics of a stock (Lorenzen et al. 2016). Examples of these indicators include measures of trends in relative abundance or CPUE, body size, and simple length-based indicators designed to provide insights into the extent to which the catch was likely to (a) avoid growth or recruitment overfishing and (b) optimize catch from within the most productive size classes (Cope and Punt 2009; Froese 2004; ICES 2015). Survey trends may help to identify the directionality of observed changes in stock status, while length-based indicators may provide insights into how fishery selectivity molded these impacts.

We used data-limited length-based stock assessment methods to evaluate the status of populations of three imperiled fish species in Lake Hovsgol, Mongolia, the Hovsgol grayling (*Thymallus nigrescens*), lenok (*Brachymystax lenok*), and burbot (*Lota*

lota). Lake Hovsgol, Mongolia's largest lake (318 km^3; Goulden et al. 2006) and the 19th largest lake in the world by volume (Herdendorf 1982), has been protected within Lake Hovsgol National Park since 1992 (MET 2019). Despite its protected status, low population density, and minimal development, Lake Hovsgol is facing synergistic pressures from climate change (Batima et al. 2005; Dagvadorj, Batjargal, and Natsagdorj 2014), pollution (Free et al. 2014; MET 2019), and fishing pressure (Free, Jensen, and Mendsaikhan 2015; Ocock et al. 2006a; Sideleva 2006). The impact of fishing is unknown but could be sizeable. Small-scale commercial fisheries for lenok and Hovsgol grayling operated before the park was established (Dulma 1979), recreational hook-and-line fishing remains legal, and illegal gill-net fishing and beach seining is common (Ahrenstorff et al. 2012; Free, Jensen, and Mendsaikhan 2015; Ocock et al. 2006a). Subsistence gillnet fishing is not strictly legal, but is generally tolerated and frequently targets Hovsgol grayling at river mouths during their spring upstream spawning migration (Free, Jensen, and Mendsaikhan 2015). For these reasons, the Mongolian Red List (Ocock et al. 2006b) currently identifies lenok and burbot as threatened and Hovsgol grayling as endangered. Hovsgol grayling is closely related to the Baikal grayling (*Thymallus baicalensis*), but is morphologically distinct (Knizhin and Weiss 2009; Olson et al. 2019) and has sometimes been considered a separate species despite low genetic divergence (Kaus et al. 2019; Koskinen et al. 2002; Roman et al. 2018; Weiss et al. 2021). Conservation status classifications for all three species are based on limited population and distribution data and lack the quantitative support necessary to guide sustainable and equitable management, especially for subsistence fisheries (Bartley et al. 2015; Dulmaa 1999).

We used length-based data-limited assessment methods and 5 years of fisheries-independent gillnet data collected between 2009 and 2022 to evaluate the status of Hovsgol grayling, lenok, and burbot stocks in Lake Hovsgol, Mongolia. We sought to determine if stocks of the three species were either overfished or experiencing overfishing to shed light on the need for potential management interventions. We evaluated status using: (1) LBSPR method to examine trends in reproductive potential; (2) length-based indicators of sustainable fishing to evaluate growth and recruitment overfishing risk; and (3) trends in relative abundance and body size to further understand trends and mechanisms of population change. Overall, we updated the evaluation of population status for Lake Hovsgol's three most abundant fish species to provide a new quantitative basis for guiding conservation and management decisions inside Lake Hovsgol National Park.

2 | Methods

2.1 | Study Area

Lake Hovsgol is an ultra-oligotrophic lake in the Baikal rift region of northern Mongolia, 1645 m above sea level (Figure 1;

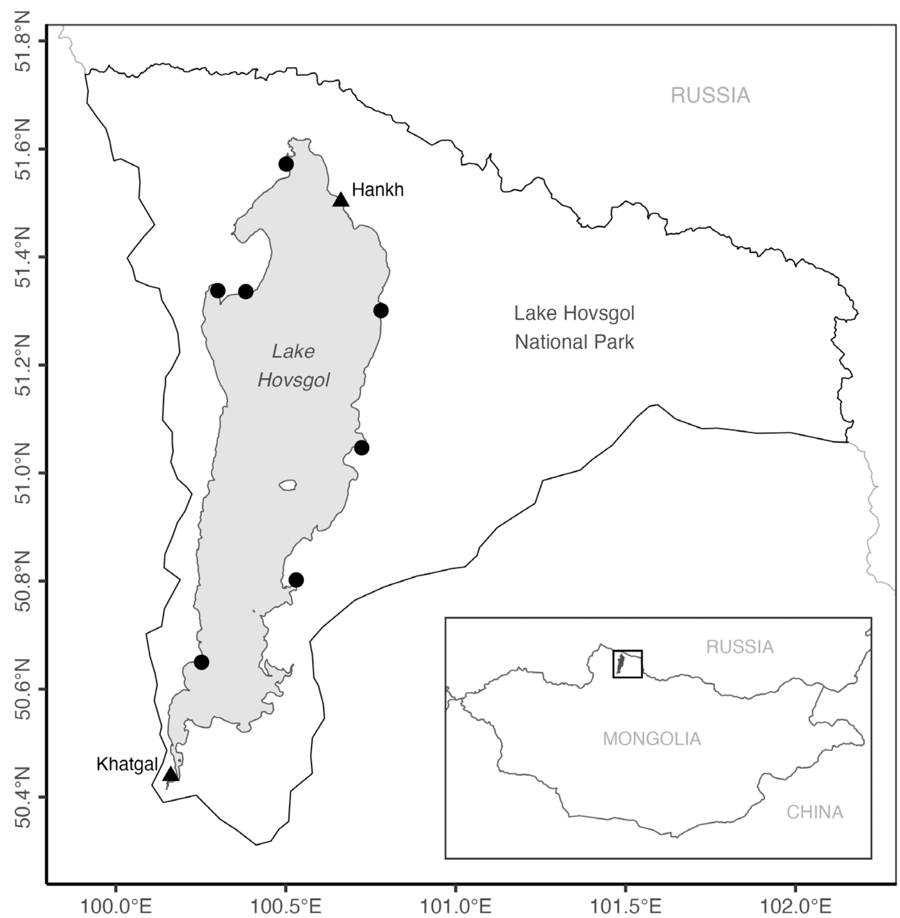

FIGURE 1 | Locations of gillnet surveys in Lake Hovsgol, Mongolia during 2009–2022. Black circles indicate survey locations, black triangles indicate the two towns on the lake, and the black line indicates the border of Lake Hovsgol National Park.

Dulma 1979). Lake Hovsgol is 135 km long and 40 km wide, with a maximum depth of 262 m (Goulden et al. 2006). Tributaries feed Lake Hovsgol from the northern, eastern, and western shores. The lake drains south through the Eg River, which flows into the Selenga River and ultimately into Lake Baikal (Dulma 1979; Tomilov and Dashidorzh 1965).

Lake Hovsgol is located in a dry climate with cold winters and mild summers (Batima et al. 2005; Goulden et al. 2006). Although flooding sometimes occurs, an overwhelming pattern of drying since the late 1800s is suspected to be a result of climate change (Tomilov and Dashidorzh 1965). Mongolia is experiencing a rate of warming almost three times greater than the global average (Dagvadorj, Batjargal, and Natsagdorj 2014), with a mean air temperature increase of 1.66°C over 60 years (Punsalmaa, Nyamsuren, and Buyndalai 2004). However, potential impacts of climate change on Lake Hovsgol's flora and fauna are unknown.

A large portion of the lake's watershed (1.2 million ha) is protected within Lake Hovsgol National Park (LHNP). Lake Hovsgol was designated as a Strictly Protected Area in 1992 and as a National Park in 1995 (MET 2019). The watershed has low human population density and is minimally developed, including the lakeshore (MEC 2013; Urabe et al. 2006). As of 2016, 5876 people resided in villages of Khankh on the northern shore and Hatgal on the southern shore (MET 2019). Tourists primarily use the southern end of the lake for recreation, including fishing, while residents graze livestock on the eastern and western shores. Herding families rely on livestock for sustenance and fish from the lake to supplement their subsistence rather than as a primary food resource (Urabe et al. 2006).

Most aquatic fauna reside in littoral and sublittoral zones of Lake Hovsgol (Ahrenstorff et al. 2012), which cover only 15% of the lake surface area (Tomilov and Dashidorzh 1965). Ten fish species are reported to inhabit the lake (Sideleva 2006), but extensive sampling with multiple gears from 2009 to 2022 found just nine species (Ahrenstorff et al. 2012; Free, Jensen, and Mendsaikhan 2015; Young et al. 2015; Olaf Jensen unpublished data). Omul (*Coregonus migratorius*), introduced to the lake in 1956–1957 and 1980 (Dulmaa 2003), were never found by our research team.

2.2 | Fish Sampling

Gillnets were used to sample nearshore areas in 5 years during 2009–2022, as described by Ahrenstorff et al. (2012) and Free, Jensen, and Mendsaikhan (2015). Seven sampling locations were surveyed once each year between mid and late July in 2009, 2011–2013, and 2022 (Figure 1), using horizontal multi-mesh gillnets anchored to the substrate. Nets were 20 m × 2.5 m, with five 4-m long monofilament panels of 2.54, 3.81, 5.08, 6.35, and 7.62 cm bar mesh sizes (whole- or half-inch measures), and strung in sequence. At each site, two nets were fished overnight (8.5–11.75 h) in water shallower than 10 m deep.

Captured fish were identified to species and total body length was measured (mm). For a random subsample of captured fish, body weight, sex, and gonadosomatic index (GSI) were also recorded. Otoliths were extracted from a random selection of lenok for age estimation (Table S1) as age and growth of this species was not well described before analysis of these otoliths (Tsogtsaikhan et al. 2017). No burbot otoliths were extracted as this species has a broad circumpolar distribution with existing age and growth studies (Fratt 1991; Devine 2002). Due to the endangered status of Hovsgol grayling, live individuals were released soon after capture, and data requiring invasive collection methods (i.e., otolith extraction, GSI) were only performed for Hovsgol grayling that were dead upon gear retrieval. While mortality within the net may be non-random with respect to fish size/age, because all fish (live and dead) were identified and measured, this does not bias the length–frequency data on which this analysis is based. This research was performed under approved animal care protocols (Rutgers University Animal Care and Facilities Committee 11-005 and University of Wisconsin-Madison L006317). Permission to conduct field research (Permit 6/445) was granted by the Mongolian Ministry of Environment and Green Development.

2.3 | LBSPR Assessment

A LBSPR model developed by Hordyk, Ono, Sainsbury, et al. (2015 and Hordyk et al. (2016); henceforth "LBSPR model") was implemented in the 'LBSPR' R package (Hordyk 2021) to assess stock status of Hovsgol grayling, lenok, and burbot in Lake Hovsgol. The model used basic life history parameters to predict the length composition and reproductive potential of an unfished population from sampled length compositions, which were shaped by fishing mortality, to estimate fishery selectivity, mortality ratio (F/M), and spawning potential ratio (SPR) for each species in each year of sampling (Hordyk, Ono, Sainsbury, et al. 2015). The mortality ratio, F/M, estimates the ratio between instantaneous fishing mortality (F) and natural mortality (M). Apical fishing mortality is an estimate of the highest F experienced by any age or length class. An F/M of 0.87 is often used as a target reference point for teleosts, in which larger values indicate stocks experiencing overfishing (Zhou et al. 2012). SPR is the ratio of fished to unfished egg production and represents a proportion or percentage of unfished reproductive potential. An SPR of 20% is considered a threshold above which stocks can sustain themselves (Goodyear 1993), and 40% is considered a proxy for the biomass associated with maximum sustainable yield (B_{MSY}) (Clark 2002; Lorenzen et al. 2016; Thorson et al. 2012).

The LBSPR model requires seven life history parameters, which we estimated from survey data or sourced from literature (Table 1). Estimates of von Bertalanffy growth parameters—age at length zero (a_0), asymptotic length (L_∞), and growth coefficient (K)—were from analysis of our sampling data for Hovsgol grayling and lenok (Tsogtsaikhan et al. 2017). For burbot, which lack local age-length information, von Bertalanffy growth parameters were derived as median values from FishBase (Froese and Pauly 2022) (Table 1 and Table S2). Length at which 50% (L_{50}) and 95% (L_{95}) of individual fish were mature were used to specify a logistic maturity ogive (Figure 3) using estimates by Sideleva (2006).

The LBSPR model also requires the ratio of natural mortality to the von Bertalanffy growth coefficient (M/K) for each species.

TABLE 1 | Growth and other life history parameters for Hovsgol grayling, lenok, and burbot.

Parameter	Definition	Hovsgol grayling	Lenok	Burbot
Age and growth				
α	Length–weight coefficient	0.0042[f]	0.0043[f]	0.0053[d,*]
B	Length–weight exponent	3.15[f]	3.19[f]	3.05[d]
a_0**	Age at which length equals zero (year)	−1.63[f]	0[f]	−1.98[b]
K**	von Bertalanffy growth coefficient (1/year)	0.19[f]	0.17[f]	0.14[b]
L_∞**	Asymptotic length (cm total length)	33.7[f]	76.1[f]	88.0[b]
$CV_{L\infty}$**	Coefficient of variation for L_∞ (cm total length)	0.07[f,*]	0.09[f,*]	
A	Maximum age (year)	17[f]	10[f]	24[a]
M**	Instantaneous natural mortality (1/year)	0.31	0.27	0.11
		0.36	0.59	0.22
		0.38		0.27
Maturity and fecundity				
L_{50}**	Length at 50% maturity (cm total length)	23.1[e]	35.0[e]	44.2[e,*]
L_{95}**	Length at 95% maturity (cm total length)	25.7[e,*]	41.0[e]	52.5[e,*]
A_{50}	Age at 50% maturity (year)	4.5[e,*]	5[e,*]	3[e]
GSI	Annualized gonadosomatic index	0.168[d]		0.059[c]

Note: For each species, up to three values of natural mortality (M), obtained through various methods (Table S2), were used to estimate F/M and SPR. Values assigned d, e, and f superscripts were estimated using data from Lake Hovsgol populations. ** marks parameters used in the LBSPR model.

Sources: For parameters obtained from FishBase, we used the median of the available estimates (Table S2). Where superscripts are followed by *, we used a related value from the indicated source to estimate the presented value through methods described elsewhere in this paper (e.g., for burbot, age at 50% maturity [Sideleva 2006] was converted to L_{50} using the von Bertalanffy equation for length at age).

[a]Chen (1968).

[b]FishBase (Froese and Pauly 2022).

[c]Fratt (1991).

[d]Free, Jensen, and Mendsaikhan (2015).

[e]Sideleva (2006).

[f]Tsogtsaikhan et al. (2017).

M was estimated for each species using “The Natural Mortality Tool” (NMT; Cope and Hamel 2022), which evaluates 14 methods to estimate M (Table S3). Of these, up to three estimates (Table 1 and Table S4) were selected to represent a range of plausible M values. We followed Free, Jensen, and Mendsaikhan (2015) for selecting methods identified to perform best within each class of life-history invariant method (t_{max}-, K-, or GSI-based) (Then et al. 2015). For Hovsgol grayling, M estimates differed slightly from those estimated by Free, Jensen, and Mendsaikhan (2015) due to our use of updated K and L_∞ estimates (Tsogtsaikhan et al. 2017) and an update to the Gunderson (1997) method of estimating M (Hamel 2015). Only the K- and t_{max}-based methods of M estimation were used for lenok given the lack of GSI data for this species. Of these two options, $M = 0.27$ was used as a baseline value, because it was identified from the K-based life invariant method identified to be best performing by Then et al. (2015). For Hovsgol grayling and burbot, median M estimates were used as baselines.

Length bin sizes were developed for use within the model. For each species, bin size was selected based on visual inspection of histograms of length–frequency distributions of the catches. The smallest interval that allowed smooth representation of size classes across the range of capture lengths was used (Figure 2).

2.4 | Validation of the LBSPR Selectivity Assumptions

The LBSPR model used here assumed logistic selectivity of catch by a gear (Hordyk, Ono, Sainsbury, et al. 2015). However, for passive gears like gillnets, selectivity is often geometric, where body size of a captured fish is proportional to the size of its capture mesh (Millar and Fryer 1999; Millar and Holst 1997). This means each mesh has a modal capture length for maximum retention, and the spread of catch sizes around the mode is dome-shaped. For such selectivity, a method of LBSPR that accounts for dome-shaped selectivity is often used in SPR estimation (Hommik et al. 2020). However, for gillnets composed of multiple mesh sizes, such as those used in our survey, the combined dome-shaped selectivities of all meshes can result in an overall net selectivity that follows a logistic curve. Confirmation of this expectation would validate the use of the Hordyk, Ono, Sainsbury, et al. (2015) model, which assumes logistic selectivity for the entire net.

To test if the combined selectivity of all meshes in experimental gillnets was logistic, selectivity outside of LBSPR was estimated using several different approaches (Millar 2009, p. 200, 1992; Millar and Fryer 1999; Millar and Holst 1997). Specifically,

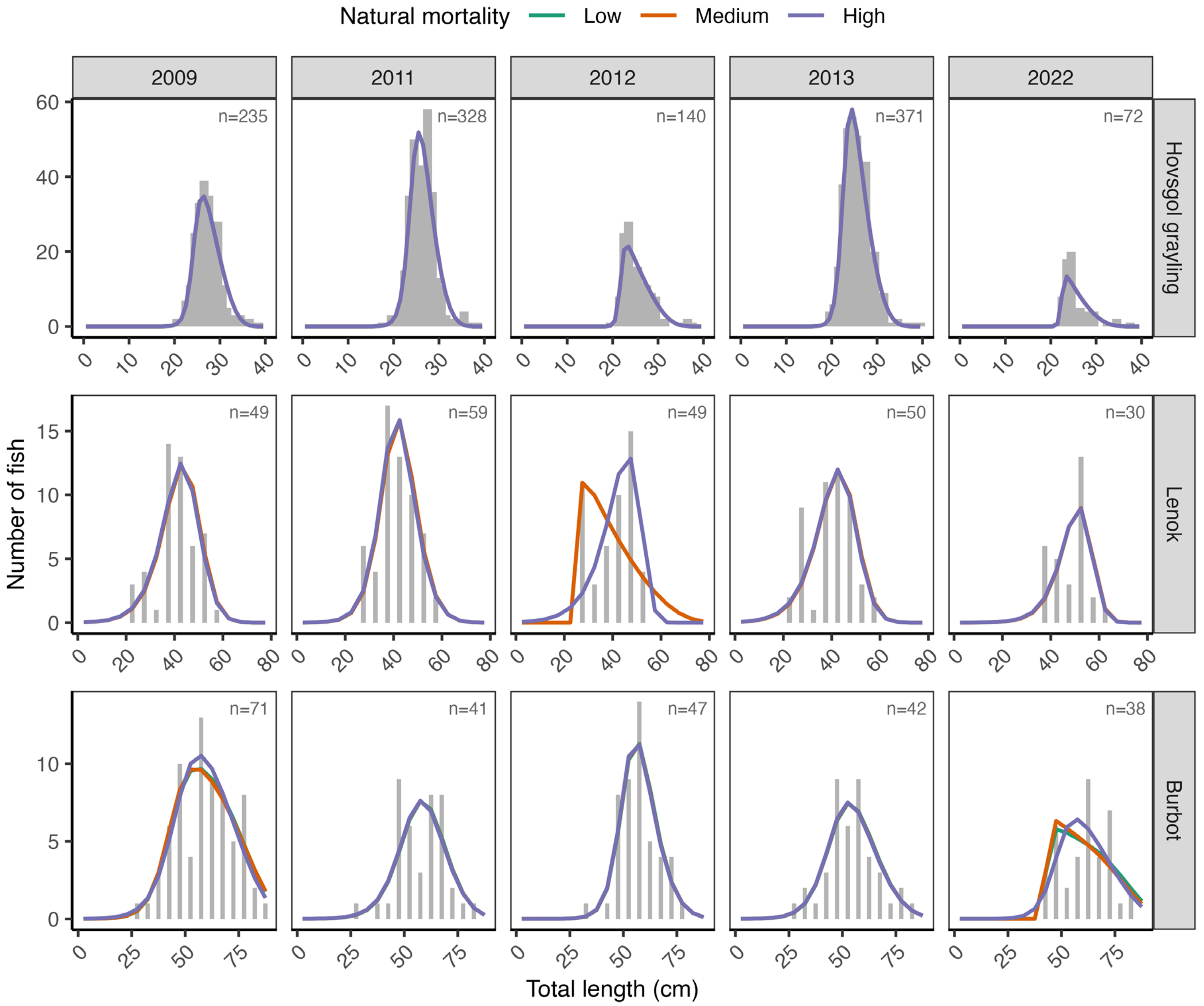

FIGURE 2 | Annual observed catch (bars) and expected size composition of catches based on models fit (lines) for Hovsgol grayling, lenok, and burbot in Lake Hovsgol, Mongolia, during 2009–2022. Line color differentiates unique estimates of natural mortality (*M*) for each species. In most cases, lines closely overlap. The sample size is printed in the top-right corner.

selectivity was estimated under conditions of normal and lognormal dome-shaped gear selection, and the model with the lowest deviance was used to evaluate net-wide (all meshes) selectivity for each species. Modal capture lengths from all meshes were used to estimate net-wide selectivity (Hommik et al. 2020). Although each mesh exhibited dome-shaped selectivity, overall net selectivity was indeed logistic across body sizes for lenok and burbot (Figure S1). This was further supported by the P_{obj} length-based metric (Figure 5), an indicator of selectivity type. As a result, LBSPR was used to internally estimate logistic selectivity across mesh sizes for these two species.

The assumption of geometric selectivity was not met for Hovsgol grayling, for which catches of most length classes were disproportionately high in the smallest mesh size (2.54 cm). This surprising selectivity may be attributed to grayling protruded dorsal fin rays, which violated both the dome-shaped selectivity assumption (Hommik et al. 2020) and logistic selectivity assumption (Hordyk, Ono, Sainsbury, et al. 2015; Hordyk et al. 2016). Because net-wide selectivity was logistic for lenok and burbot, we opted to use the LBSPR model to internally estimate logistic selectivity for Hovsgol grayling. This decision was also supported by the P_{obj} length-based indicator (Figure 5). This decision would lead the model to attribute an absence of larger, more fecund individuals to fishing mortality, rather than declining selectivity, and to overestimate *F/M* and underestimate SPR if selectivity was truly dome-shaped (Hordyk, Ono, Valencia, et al. 2015). Estimates of *F/M* and SPR for Hovsgol grayling would be unbiased if selectivity was truly logistic or conservative (SPR higher than estimated and *F/M* lower than estimated) if selectivity was truly dome-shaped.

2.5 | Length-Based Indicators

To supplement SPR estimates, eight other length-based indicators of fisheries status were evaluated. Four indicators evaluated whether catch successfully avoided growth overfishing by

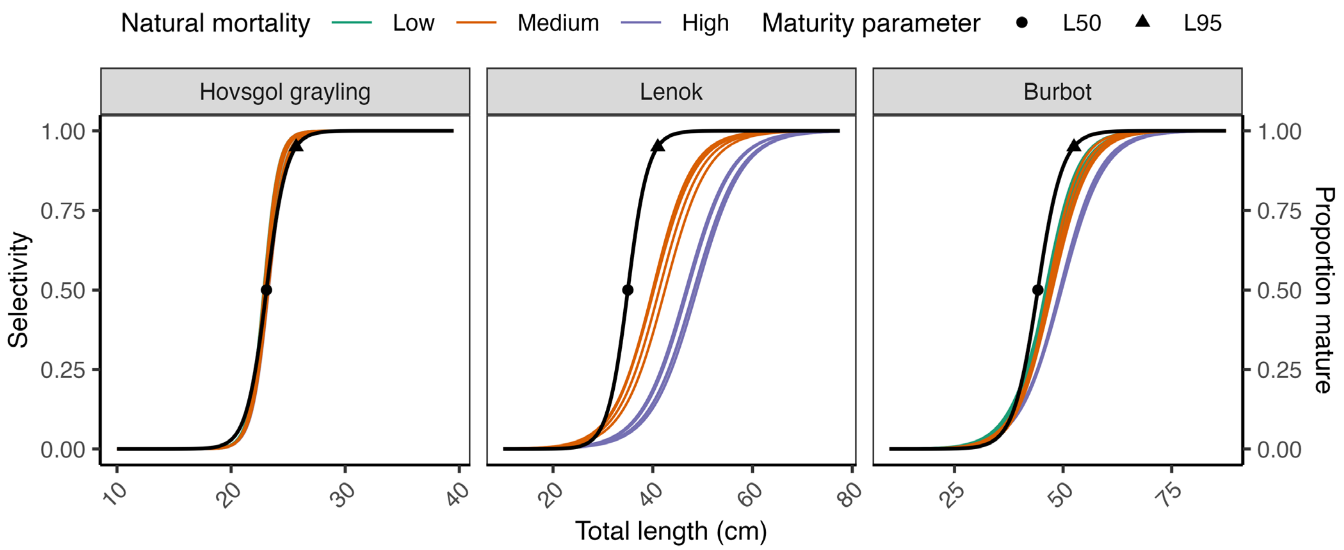

FIGURE 3 | Annual estimated selectivity curves at different levels of natural mortality (M) and assumed maturity ogive (black) for Hovsgol grayling, lenok, and burbot in Lake Hovsgol, Mongolia during 2009–2022. Lines of the same color indicate estimates for different years. Black points indicate L_{50} (circle) and L_{95} (triangle): The lengths at which 50% and 95% of individuals of each species are mature, respectively. These parameters are used to specify the maturity ogive.

avoiding capture of immature fish and recruitment overfishing by avoiding capture of the most fecund fish (Froese 2004; Cope and Punt 2009). Specifically, they measured the proportion of the catch composed of (1) mature individuals (P_{mat}) larger than L_{50}, where 100% is desirable; (2) highest yield of individuals (P_{opt}) in the length class where biomass was most concentrated (L_{opt}), where 100% is desirable; and (3) old, large, highly fecund individuals, or "mega-spawners" (P_{mega}), where 0% is desirable but <30% is acceptable. The sum of these three metrics (P_{obj}) was used in a decision tree to determine the type of selectivity by a fishery (Cope and Punt 2009). Two other indicators compared the ratios (Beverton 1992): (1) length at first capture (L_c) to the length at which 50% of individuals were mature (L_{50}), where values >1 are desirable because most individuals were able to spawn before capture; and (2) mean capture length of individuals larger than L_c (L_{mean}) and L_{opt}, where values close to 1 are desirable because it indicates that most fishing was at the optimal size. Two other indicators indicated if fishing pressure resulted in truncation (ICES 2015): (1) the ratio of L_{mean} to L_{50}, where values >1 are desirable; and (2) mean length of the largest 5% of the catch ($L_{max5\%}$) to the asymptotic length (L_∞), where values >0.8 are desirable. Length-based indicators may identify a potential need for intervention (Babcock et al. 2013), but are often limited in sensitivity to true stock status; thus, management based solely on these metrics may not prevent overfishing (Cope and Punt 2009). However, when paired with other estimates of status, like SPR, length-based indicators can provide mechanistic insights into effects of fishing (Cope and Punt 2009; Cousido-Rocha et al. 2022).

2.6 | Survey Trends in Catch-Per-Unit-Effort and Body Size

Trends in CPUE and body size were estimated during 2009–2022. CPUE was calculated for each species in number (n night^{-1}) and biomass (kg night^{-1}) caught by all gillnets per sampling night. Body size was measured in both weight (g) and total body length (cm). Temporal trends were estimated using linear mixed-effect models that treated sampling site as a random effect in the 'lme4' R package (Bates et al. 2015). Full and null models were compared using likelihood ratio tests to evaluate the statistical significance of detected trends (Free, Jensen, and Mendsaikhan 2015). In synthesizing results from LBSPR and survey trends analyses, a stock could be declining in abundance but not yet be overfished, as when CPUE declines but the stock remains above the target biomass reference point, just as a stock can be overfished but recovering, as when CPUE increases but the stock remains below the target reference point.

3 | Results

For Hovsgol grayling, the range of M estimates was narrow (0.07; Table 1), potentially due to use of population-specific life history parameters. The LBSPR model-estimated length composition of the survey catch did not vary across the range of M values and was similar to the sample length composition for all years (Figure 2). Selectivity of Hovsgol grayling was logistic ($1 < P_{obj} < 2$; Table S5). Selectivity-at-length was similar among years and estimates of M (Figure 3). Mean estimates of F/M and SPR were relatively similar across all estimates of M. Across years, mean F/M ranged 0.04–0.65, below the 0.87 target reference point, but did not differ among or between years at the 95% confidence level (Figure 4). The 95% confidence interval for mean SPR was above the 40% target reference point for all years and estimates of M (Figure 4; Table S4). Hovsgol grayling was at or above limit reference points for P_{mega}, L_{mean}/L_{50}, and $L_{max5\%}/L_\infty$ for all years, but L_{mean}/L_{50} declined toward the reference point over time (Table S5; Figure 5). L_{mean}/L_{opt} also declined over the survey period but did not reach the target reference point by 2022. Hovsgol grayling CPUE decreased in number ($p = 0.001$) and weight ($p < 0.001$) during 2009–2022 (Figure 6). Reduced biomass was explained by decreasing trends in body

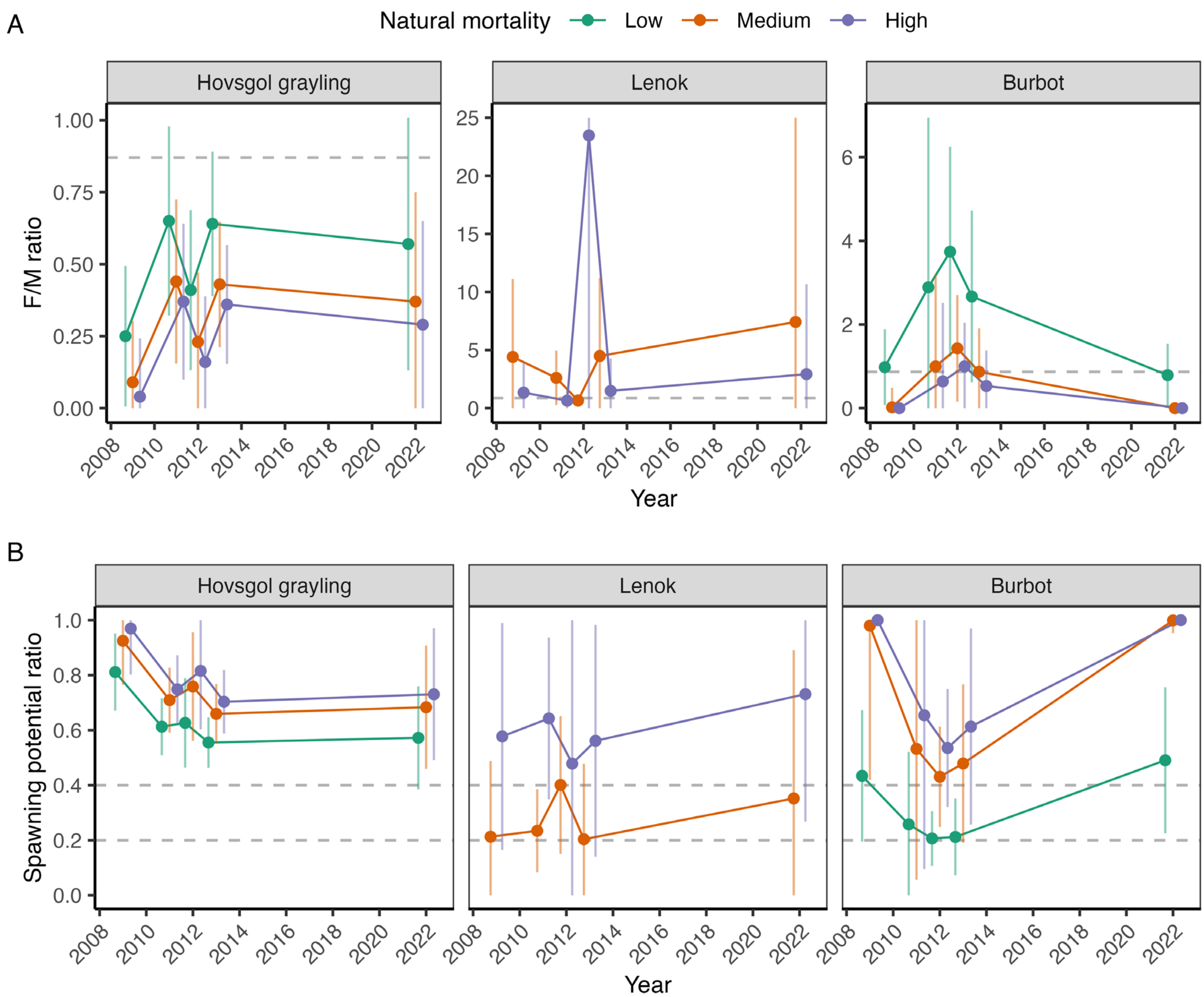

FIGURE 4 | Annual estimates of (A) *F/M* and (B) spawning potential ratio (SPR) at different levels of natural mortality (*M*) for Hovsgol grayling, lenok, and burbot in Lake Hovsgol, Mongolia during 2009–2022. Error bars denote 95% confidence intervals. In *F/M* plots, the dashed horizontal line indicates the $F/M = 0.87$ reference point for teleosts. In SPR plots, dashed horizontal lines indicate 20% limit and 40% target reference points. Upper confidence limits for *F/M* estimates of lenok are capped at 25 for clarity.

size of both length ($p < 0.001$) and weight ($p = 0.01$). Catches in 2022 were smaller in body length and weight ranges than in previous years, with larger minimum size and lower maximum size for both metrics (Figure 6).

For lenok, both M estimates (0.27 and 0.59; Table 1) produced LBSPR model estimates of the survey catch length composition that were similar among years (Figure 2), except in 2012, when peak length of the catch shifted from 27.5 cm ($M = 0.27$) to 57.5 cm total length ($M = 0.59$; Figure 2). Selectivity-at-length was higher at lower M (Figure 3; Table S4). For both estimates of M, a higher proportion of mid-sized individuals was estimated to be mature than were selected by the gear (Table S4). Mortality ratio (*F/M*) estimates were relatively constant during 2009–2022 (Figure 4). In 2012, mean *F/M* for $M = 0.59$ was much higher than for other years, but did not differ from other years because the confidence interval was wide (95% CI = 0, 120). For $M = 0.27$, SPR reached a maximum of 41% in 2012, but was closer to 20% in other years (Figure 4). For $M = 0.59$, SPR was higher overall (47%–72%), but had wide confidence intervals. Estimates of P_{mat}, L_{mean}/L_{opt}, and $L_{max5\%}/L_{\infty}$ were above management reference points in 2022, but not in other years (Table S5; Figure 5). L_{mean}/L_{50} was the only indicator above the reference point for all years. Length and weight both increased significantly during 2009–2022 (Figure 6). CPUE in numbers ($p = 0.12$) and biomass ($p = 0.86$) did not significantly trend through time (Figure 6). Proportionally fewer individuals of smaller size (< 35 cm total length) and lower weight (< 0.5 kg) were sampled in 2022, when the overall largest lenok were captured (Figure 6).

For burbot, all three estimates of M (0.11, 0.22, 0.27; Table 1) produced expected length compositions of survey catches that were similar for all years, with the largest difference in 2022 (Figure 2). For $M = 0.11$, similar proportions of burbot were estimated to be mature and selected by the gear (Figure 3). For $M = 0.22$ and $M = 0.27$, the proportion of mature mid-sized fish increased relative to fish that were susceptible to capture (Figure 3). In each year, *F/M* and SPR were similar for all estimates of M (Figure 4;

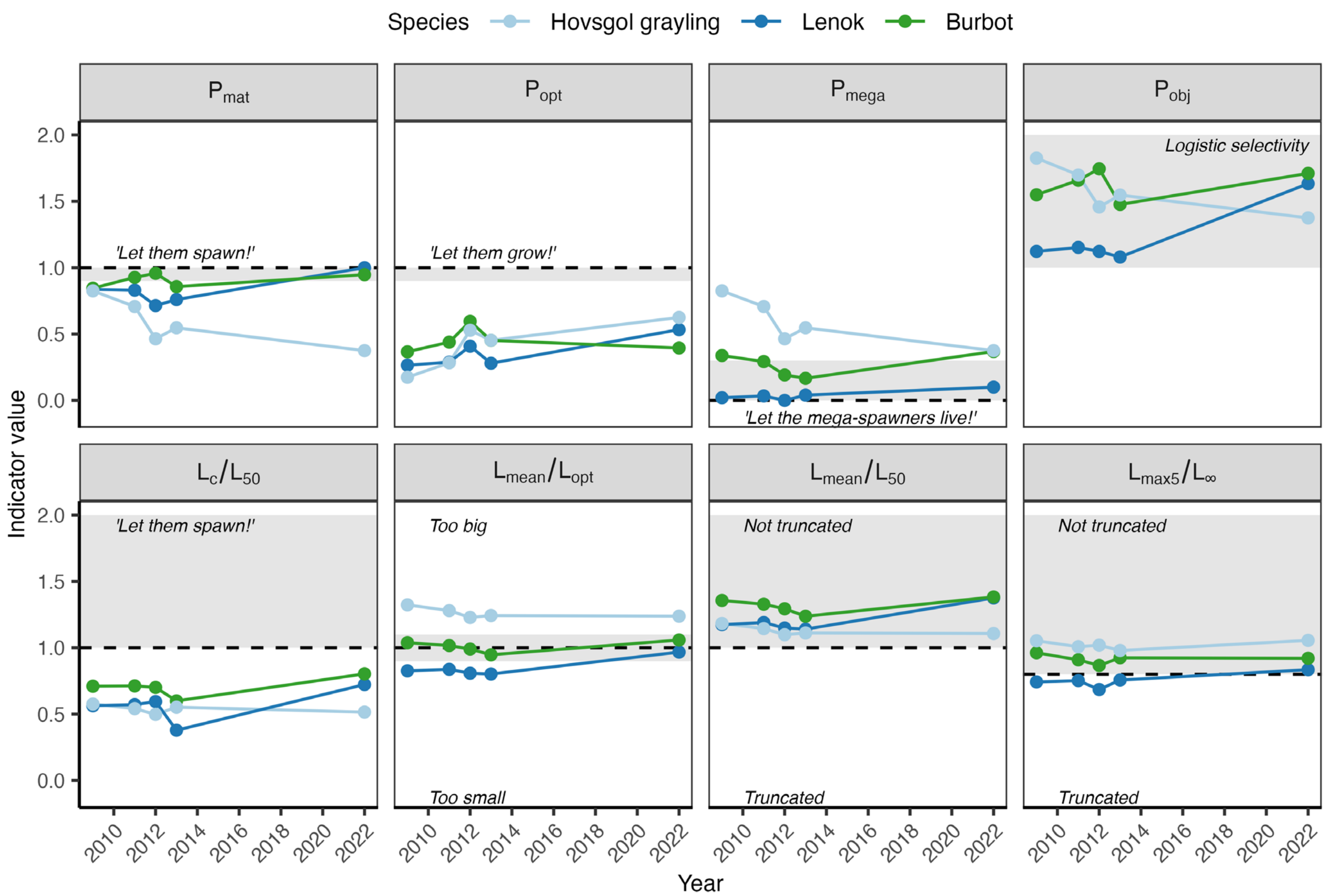

FIGURE 5 | Temporal trends in length-based indicators for Hovsgol grayling, lenok, and burbot in Lake Hovsgol, Mongolia during 2009–2022. For all but P_{obj}, dashed horizontal lines indicate target reference points and gray shading indicates the range of acceptable values. P_{obj} has no target reference point, but values between 1.0 and 2.0 support logistic selectivity. Italic labels against the reference line or within the gray shading indicate the interpretation of values within the acceptable range for that indicator. Other italic labels indicate interpretation of values outside the acceptable range. Italic labels in quotes are colloquial titles by Froese (2004).

Table S4). Mean SPR was at or above 20% for all estimates of M (Figure 4; Table S4). For $M = 0.22$ and $M = 0.27$, mean SPR was above 40%, with lower 95% confidence bounds above 20% in all years except 2011. For the same M estimates in 2009 and 2022, nearly all mortality was attributed to M, with little to no uncertainty (Figure 4). Burbot P_{mega} steadily declined through 2013, and exceeded the 30% reference point in 2009 and 2022 (Table S5; Figure 5), coinciding with high estimates of SPR in those years. L_{mean}/L_{50}, $L_{max5\%}/L_{\infty}$, and L_{mean}/L_{opt} suggested good stock status relative to management reference points in all years (Table S5; Figure 5). Burbot body size (length: $p = 0.35$; weight: $p = 0.25$) and CPUE (count: $p = 0.11$; mass: $p = 0.06$) did not significantly trend through time (Figure 6).

4 | Discussion

4.1 | Hovsgol Grayling Status

Hovsgol grayling is listed as an endangered species under assessment guidelines from the International Union for Conservation of Nature (IUCN), but this determination was not made on the basis of a formal stock assessment (Ocock et al. 2006a). The SPR and F/M estimates from our LBSPR analysis indicate that the stock is neither overfished nor experiencing overfishing. This suggests that a conservation status designation may have been premature or that the population has recovered since the 2006 designation. However, declining trends in abundance and body size are concerning. Length-based indicators suggest that fisheries too heavily target large, mature fish, including many mega-spawners, thereby driving a decline in body size. Declines in CPUE without concurrent declines in SPR could be explained by loss of spawning habitat (i.e., the steady drying of streams) due to climate change (Ocock et al. 2006b, 2006a), because loss of spawning habitat could reduce population size without changing length structure. Along with size selective fishing, warming lake temperatures could also contribute to observed declines in grayling body sizes.

The impact of fishing on Hovsgol grayling may be buffered by a mixture of inefficient targeting and availability of pelagic refugia away from fishing. Although our smallest mesh size (2.54 cm) was notably more efficient at catching Hovsgol grayling than other mesh sizes, this small mesh is uncommon in the Lake Hovsgol gillnet fishery (Free, Jensen, and Mendsaikhan 2015). Its near absence may spare Hovsgol grayling from more severe effects of gillnet fishing. Hovsgol grayling are largely targeted by an illegal gillnet fishery during spring spawning runs, which could exacerbate effects of fishing if most mature fish are captured before they reproduce. However, Hovsgol grayling

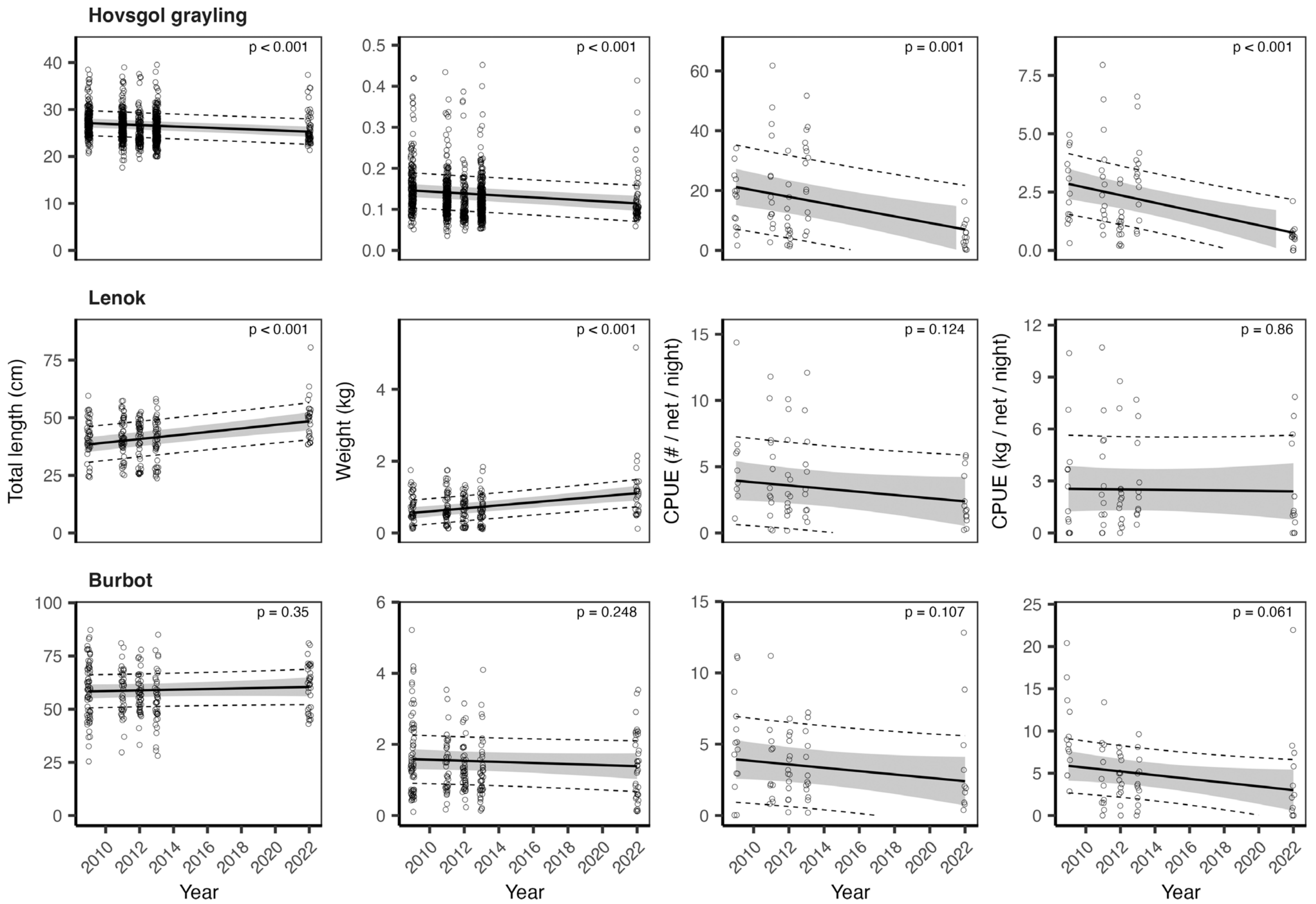

FIGURE 6 | Temporal trends in CPUE and body size for Hovsgol grayling, lenok, and burbot in Lake Hovsgol, Mongolia during 2009–2022. For body size, points represent total length (cm) or weight (g) measures of individual fish. Weights were either measured in the field or estimated based on body length. CPUE (# net^{-1} night^{-1}) is the number of fish collected and CPUE (kg net^{-1} night^{-1}) is for fish weight. Each point represents the CPUE of a single mesh size from a single sampling event. Trends were identified using linear mixed effects models wherein dark lines indicate the fitted trend, the shaded region indicates the 95% confidence interval, and dashed lines indicate the prediction interval.

captured in tributaries used for spawning runs or in the littoral zone, where most gillnets are set, may not be a large proportion of the population. Two Hovsgol grayling morphotypes, which correspond to littoral and pelagic feeding habits, have been identified (Ahrenstorff et al. 2012), but inshore-offshore migration patterns are unknown. Thus, Hovsgol grayling may utilize the pelagic as a refuge from fishing pressure, which could contribute to their stable status.

4.2 | Lenok Population Status

Lenok are experiencing overfishing—especially of small, immature fish—and may be overfished. The overfished designation of lenok is sensitive to the natural mortality estimate used in the LBSPR analysis, with the higher estimate leading to a "not overfished" designation and the lower estimate leading to an "overfished" designation. However, remaining indicators suggest that lenok could be overfished soon if overfishing is not curbed. *F*/*M* estimates from the LBSPR analysis indicate that lenok are experiencing overfishing, and length-based indicators suggest that this overfishing was concentrated on small, immature fish, which caused the truncation of the size structure and an apparent increase in body size (Table 2). Although increasing body size usually indicates improving stock status (Shin et al. 2005), such a conclusion would be incorrect in this case, as the apparent increase in body size was due to overharvest of small lenok. Thus, management measures that reduce targeting and mortality of smaller lenok are likely to prevent overfishing in this fishery.

4.3 | Burbot Population Status

Burbot population status was good according to most of the evaluated indicators, but large uncertainty was exacerbated by a lack of local life history information. The LBSPR analysis indicated that burbot were neither overfished nor experiencing overfishing for two of three natural mortality estimates. This finding aligned with indications that CPUE and body size were stable and that the catch was largely composed of mature fish that avoided mega-spawners and size–structure truncation. However, unlike Hovsgol grayling and lenok, age data were lacking for burbot, which increased uncertainty of growth and mortality parameters, especially because burbot growth and reproduction varies considerably by latitude and habitat (e.g., lakes, bays, rivers) (Chen 1968; Fratt 1991; Hewson 1955). Simulation testing has shown that LBSPR model estimates of

TABLE 2 | Summary and synthesis (bolded) of Hovsgol grayling, lenok, and burbot population status for multiple assessment methods in Lake Hovsgol, Mongolia during 2009–2022.

Indicator	Result
Hovsgol grayling	
LBSPR SPR estimate	Not overfished: SPR consistently above reference point
LBSPR F/M estimate	Not experiencing overfishing: F/M consistently below reference point
Length-based indicators	Catch heavily targets large, mature fish including mega-spawners
CPUE trend	Declining CPUE
Body size trend	Declining body size
Synthesis	**Hovsgol grayling are not yet overfished or experiencing overfishing but declining CPUE and declining body size due to targeting of large, mature fish including mega-spawners is concerning**
Lenok	
LBSPR SPR estimate	Potentially overfished: assessment depends on *M* value
LBSPR F/M estimate	Experiencing overfishing: F/M consistently above reference point
Length-based indicators	Catch avoids mega-spawners but catches to many small, immature fish leading to truncation
CPUE trend	Stable CPUE
Body size trend	Increasing body size
Synthesis	**Lenok population is experiencing overfishing, especially of small, immature fish, leading to truncation and apparent body size increases; if it's not overfished, it may be soon**
Burbot	
LBSPR SPR estimate	Likely not overfished: SPR above reference point for 2 of 3 *M* values
LBSPR F/M estimate	Likely not experiencing overfishing: F/M near or below reference point for 2 of 3 *M* values
Length-based indicators	Catch is largely composed of mature fish and avoids mega-spawners and truncation
CPUE trend	Stable CPUE
Body size trend	Stable body size
Synthesis	**Burbot population status is good according to nearly all indicators; however, its life history parameters are less certain given the lack of local age data, adding to already large uncertainty**

F/M and SPR are most sensitive to misspecification of *M/K*, L_∞, and the coefficient of variation of L_∞ ($CV_{L\infty}$; Hordyk, Ono, Valencia, et al. 2015), which highlights the importance of filling critical data gaps in the future. We used the median of available life history parameter estimates from across the burbot native range to account for this uncertainty (Table S2), but future stock assessments for Lake Hovsgol burbot would benefit from population-specific life history parameter estimates.

4.4 | Impact of Fishing on Population Status

Population status of these species should be considered within the context of both historical and recent fishing patterns. Historically, Lake Hovsgol supported commercial fisheries for lenok, burbot, and grayling (Dulmaa 1999; Tomilov and Dashidorzh 1965), though the scale of these fisheries was not well-quantified. Tomilov and Dashidorzh (1965) noted that lenok and Hovsgol grayling were taken in "significant quantities" by historical fisheries. Dulmaa (1999) reported catches of 250–400 tons from Lake Hovsgol in the mid-1970s (see table 24 in Dulmaa 1999) but this value is not internally consistent with other values stated in the report. For example, the report named lenok and grayling as the primary targets of historical commercial fisheries in Lake Hovsgol, followed secondarily by roach (*Rutilus rutilus*), perch (*Perca fluiviatilis*), and burbot (Dulmaa 1999). However, the report contradictorily stated that historical incidental catches of burbot (50 tons) doubled catches of lenok (24 tons) in a beach-seine fishery targeting lenok, and that there was "almost no commercial fishery" targeting grayling in Lake Hovsgol (Dulmaa 1999). The two reported catch volumes fall significantly short of the 250–400 ton total volume, the basis of which was not documented (Dulmaa 1999). A more detailed history of fishing on Lake Hovsgol would greatly improve understanding of the potential impact of historical fishing on Lake Hovsgol's fishes.

The establishment of Lake Hovsgol National Park in 1992 coincided with new fishing restrictions, but enforcement has been both difficult and limited (Free, Jensen, and Mendsaikhan 2015; Ocock et al. 2006b). Illegal commercial fishing is believed to occur with high frequency (Ocock et al. 2006b), as indicated by the observation of derelict gillnet fragments, active gillnet fishing, and grayling for sale by market and street-side vendors (Free, Jensen, and Mendsaikhan 2015). Although otherwise illegal, gillnetting during the spring spawning migration is generally tolerated by park rangers when classified as subsistence fishing. A recreational hook-and-line fishery of unknown size is also present (Sideleva 2006), although the illegal gillnet fishery is generally believed to be a larger source of fishing mortality (Ocock et al. 2006b). Despite relatively low human population density around Lake Hovsgol, estimates of fishing effort for the local resident population suggest that overexploitation is plausible (Free, Jensen, and Mendsaikhan 2015).

4.5 | Impact of Climate Change on Stock Status

Climate change may play an increasingly important role in the status of fish populations in Lake Hovsgol. Mongolia is experiencing a rate of warming almost 3-times greater than the global average (Dagvadorj, Batjargal, and Natsagdorj 2014), with mean air temperature increasing 1.66°C over 60 years (Punsalmaa, Nyamsuren, and Buyndalai 2004). Surface waters in Lake Hovsgol warmed 0.034°C each decade over the past 20 years (Fan et al. 2022). Furthermore, rising air temperatures and changing precipitation patterns have led to the drying of many grayling spawning streams in Lake Hovsgol, with only 20 of 96 permanent streams that once flowed into the lake carrying water year round today, and most drying between June and July (Ocock et al. 2006a). Hovsgol grayling may be especially sensitive to such changes, particularly loss of spawning habitat. The Hovsgol grayling is ecologically similar to the Baikal grayling and Arctic grayling (*Thymallus arcticus*), which have both been predicted to decrease in their distributions, abundance, and growth in response to warming, based on a study in the Eg-Uur River, Mongolia (Hartman and Jensen 2017). Therefore, we conclude that declining size, which is among the most rapid declines in salmonid body size globally (Solokas et al. 2023), and CPUE of Hovsgol grayling during the period of our study could have been partially caused by climate change.

Abundance and body size of Lake Hovsgol lenok also appear to have declined in recent years. CPUE and body size did not trend upward or downward during 2009–2013 (Free, Jensen, and Mendsaikhan 2015), but incorporation of data from 2022 indicated a pronounced shift to larger-bodied lenok, and a notable, although not statistically significant, decline in CPUE ($p=0.12$, compared to $p=0.98$ during 2009–2013; Free, Jensen, and Mendsaikhan 2015; Figure 6). Although likely due to size selective fisheries, these shifts may also be partially attributed to resource competition among lenok in response to a warming climate. Increased consumption, as a result of increased metabolic needs in warmer waters, has been predicted to reduce lenok abundance, as well as growth of surviving individuals, in Mongolian lotic systems (Hartman and Jensen 2017). Lenok in Lake Hovsgol may therefore be experiencing increased competition in response to warming temperatures that results in decreasing abundance. However, lenok may not experience a drastic increase in metabolic rate due to decreased energy expenditure required by a lentic system with low predation risk (Young et al. 2015) and relatively low flow velocity.

Burbot are noted to be particularly sensitive to anthropogenic impacts and have been proposed as an informative indicator species for identifying early warnings of climate change effects on cold-water species (Stapanian et al. 2010). Across much of their range, changes in abundance have been attributed to climate change (Stapanian et al. 2010). While we found no temporal trends in CPUE of the Lake Hovsgol population, effects of climate change may be visible through other metrics. Our extreme estimates of *F/M* may be evidence of recruitment variability (Hordyk, Ono, Valencia, et al. 2015), which is not modeled within LBSPR. Impacts of climate warming on burbot reproduction and successful egg development can result in fluctuations in abundance and catch through recruitment variability, as in Lithuanian commercial fisheries (Švagždys 2002). Future length-based assessments for burbot and other fishes in Lake Hovsgol may therefore benefit from using length-based approaches, such as LIME (Rudd and Thorson 2018), that can explicitly estimate annual recruitment variation with longer time series.

4.6 | Implications for Monitoring and Management

We used complementary data-limited length-based and descriptive methods to provide initial estimates of the status of Hovsgol grayling, lenok, and burbot populations in Lake Hovsgol. The estimates provided a useful baseline for tracking future population health, but continued monitoring is necessary to further assess how fish populations in Lake Hovsgol respond to the joint pressures of fishing and climate change. Even in the absence of resources for full quantitative stock assessments, continued assessment using data-limited methods and complementary measures, such as length-based indicator estimates and trend analyses, will be of value. In this way, our study adds to the growing list of instructive examples of the application of data-limited stock assessment methods commonly used in marine fisheries within an inland fisheries context (Hommik et al. 2020; Shephard et al. 2023, 2020).

Our results suggest that interventions are likely necessary to curb overfishing of the lenok population and reverse the concerning decline of the Hovsgol grayling population. The design of effective, equitable, and feasible management measures will require coordination among fishers, managers, and scientists, and could include measures such as gear restrictions (e.g., limits on gillnet mesh size, lengths, or soak times) or tightened regulations on fishing during the spring grayling spawning migration (which likely includes high lenok bycatch). Improved monitoring of catch and effort during the spring grayling spawning fishery would be relatively inexpensive to monitor (because it occurs during a short period in a limited number of streams) and would be highly informative to management because it likely constitutes most fishing effort. Information from such monitoring could be used to design management actions that allow the persistence of the subsistence fishery while also allowing enough spawners to escape harvest. Furthermore, sampling the catch length composition could support annual assessments of fish populations in Lake Hovsgol and evaluation of management effectiveness. This would instill a system of adaptive co-management that would make fisheries in Lake Hovsgol more resilient to the joint stressors of fishing and climate change (Wilson et al. 2018).

Despite the global importance of inland fisheries, freshwater fish stock status remains largely unassessed due to challenges in collecting fisheries data in dispersed and isolated fisheries (Lorenzen et al. 2016). The need for assessments is mounting as freshwater systems experience the steepest declines in biodiversity (WWF 2024) with threats coming from, in order of decreasing frequency, invasive species, climate change, habitat loss, pollution, and overexploitation (Arthington et al. 2016). Although overexploitation currently ranks as the least common threat, catches from global inland fisheries are increasing (FAO 2024), and expert opinion suggests that 13% of inland fisheries are experiencing high fishing pressure, 40% are under moderate pressure, and 47% are under low pressure (Stokes et al. 2021). The wider use of the length-based stock assessment methods exemplified in this study presents a promising pathway to guiding improved management of inland stocks with an empirical understanding of stock status. Compared to time series of catch and relative abundance, length composition data are relatively easy to collect and even 1 year of data can identify whether and why (e.g., growth or recruitment overfishing) a stock is overfished and or experiencing overfishing. This empowers managers with the information needed to determine whether an intervention is needed, the magnitude of the required intervention, and what the intervention should target. Our study provides a useful template for expanding the use of length-based assessment stock assessment methods to manage important inland fisheries.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

References

Ahrenstorff, T. D., O. P. Jensen, B. C. Weidel, B. Mendsaikhan, and T. R. Hrabik. 2012. "Abundance, Spatial Distribution, and Diet of Endangered Hovsgol Grayling (*Thymallus nigrescens*)." *Environmental Biology of Fishes* 94: 465–476. https://doi.org/10.1007/s10641-011-9961-5.

Arthington, A. H., N. K. Dulvy, W. Gladstone, and I. J. Winfield. 2016. "Fish Conservation in Freshwater and Marine Realms: Status, Threats and Management." *Aquatic Conservation: Marine and Freshwater Ecosystems* 26: 838–857. https://doi.org/10.1002/aqc.2712.

Babcock, E. A., R. Coleman, M. Karnauskas, and J. Gibson. 2013. "Length-Based Indicators of Fishery and Ecosystem Status: Glover's Reef Marine Reserve, Belize." *Fisheries Research* 147: 434–445. https://doi.org/10.1016/j.fishres.2013.03.011.

Bartley, D. M., G. J. De Graaf, J. Valbo-Jørgensen, and G. Marmulla. 2015. "Inland Capture Fisheries: Status and Data Issues." *Fisheries Management and Ecology* 22: 71–77. https://doi.org/10.1111/fme.12104.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 1–48. https://doi.org/10.18637/jss.v067.i01.

Batima, P., L. Natsagdorj, P. Gombluudev, and B. Erdenetsetseg. 2005. "Observed Climate Change in Mongolia." *AIACC Working Papers*: 1–25.

Beard, T. D., R. Arlinghaus, S. J. Cooke, et al. 2011. "Ecosystem Approach to Inland Fisheries: Research Needs and Implementation Strategies." *Biology Letters* 7: 481–483. https://doi.org/10.1098/rsbl.2011.0046.

Beverton, R. J. H. 1992. "Patterns of Reproductive Strategy Parameters in Some Marine Teleost Fishes." *Journal of Fish Biology* 41: 137–160. https://doi.org/10.1111/j.1095-8649.1992.tb03875.x.

Chen, L. C. 1968. "The Biology and Taxonomy of the Burbot, *Lota lota* Leptura, in Interior Alaska." *Biological Papers of the University of Alaska* 11: 1–53.

Clark, W. G. 2002. "$F_{35\%}$ Revisited Ten Years Later." *North American Journal of Fisheries Management* 22: 251–257. https://doi.org/10.1577/1548-8675(2002)022<0251:FRTYL>2.0.CO;2.

Cope, J. M., and O. S. Hamel. 2022. "Upgrading From *M* Version 0.2: An Application-Based Method for Practical Estimation, Evaluation and Uncertainty Characterization of Natural Mortality." *Fisheries Research* 256: 106493. https://doi.org/10.1016/j.fishres.2022.106493.

Cope, J. M., and A. E. Punt. 2009. "Length-Based Reference Points for Data-Limited Situations: Applications and Restrictions." *Marine and Coastal Fisheries* 1: 169–186. https://doi.org/10.1577/C08-025.1.

Coscino, C. L., L. Bellquist, W. J. Harford, and B. X. Semmens. 2024. "Influence of Life History Characteristics on Data-Limited Stock Status Assertions and Minimum Size Limit Evaluations Using Length-Based Spawning Potential Ratio (LBSPR)." *Fisheries Research* 276: 107036. https://doi.org/10.1016/j.fishres.2024.107036.

Cousido-Rocha, M., S. Cerviño, A. Alonso-Fernández, et al. 2022. "Applying Length-Based Assessment Methods to Fishery Resources in the Bay of Biscay and Iberian Coast Ecoregion: Stock Status and Parameter Sensitivity." *Fisheries Research* 248: 106197. https://doi.org/10.1016/j.fishres.2021.106197.

Dagvadorj, D., Z. Batjargal, and L. Natsagdorj. 2014. *Mongolia Second Assessment Report on Climate Change 2014*. Ulaanbaatar: Ministry of Environment and Green Development of Mongolia.

Devine, J. A. 2002. *A Food Web Analysis of the Fishery in Chequamegon Bay, Lake Superior*. Master's thesis, Stevens Point, WI: University of Wisconsin.

Dowling, N. A., C. M. Dichmont, M. Haddon, D. C. Smith, A. D. M. Smith, and K. Sainsbury. 2015. "Empirical Harvest Strategies for Data-Poor Fisheries: A Review of the Literature." *Fisheries Research* 171: 141–153. https://doi.org/10.1016/j.fishres.2014.11.005.

Dulma, A. 1979. "Hydrobiological Outline of the Mongolian Lakes." *Internationale Revue der Gesamten Hydrobiologie und Hydrographie* 64: 709–736. https://doi.org/10.1002/iroh.19790640602.

Dulmaa, A. 1999. "Fish and Fisheries in Mongolia." In *Fish and Fisheries at Higher Altitudes: Asia*, edited by T. Petr. Rome, Italy: Food and Agriculture Organization of the United Nations.

Dulmaa, A. 2003. "Mongolian Limnology and Ichthyology." In *Mongolia Today*, edited by D. Badarch and R. A. Zlinskas, 312. London: Routledge.

Fan, C., K. Liu, S. Luo, et al. 2022. "Detection of Surface Water Temperature Variations of Mongolian Lakes Benefiting From the Spatially and Temporally Gap-Filled MODIS Data." *International Journal of Applied Earth Observation and Geoinformation* 114: 103073. https://doi.org/10.1016/j.jag.2022.103073.

FAO. 2024. *The State of World Fisheries and Aquaculture 2024—Blue Transformation in Action*. Rome: FAO. https://doi.org/10.4060/cd0683en.

Fitzgerald, C. J., K. Delanty, and S. Shephard. 2018. "Inland Fish Stock Assessment: Applying Data-Poor Methods From Marine Systems." *Fisheries Management and Ecology* 25: 240–252. https://doi.org/10.1111/fme.12284.

Fratt, T. W. 1991. *Trophic Ecology of Burbot and Lake Trout in Green Bay and Lake Michigan With Information for Burbot on Fecundity, Gonadosomatic Index, Sea Lamprey Marks, and Intestinal Acanthocephalans*. Master's thesis, Stevens Point, WI: University of Wisconsin.

Free, C. M., O. P. Jensen, S. C. Anderson, et al. 2020. "Blood From a Stone: Performance of Catch-Only Methods in Estimating Stock Biomass Status." *Fisheries Research* 223: 105452. https://doi.org/10.1016/j.fishres.2019.105452.

Free, C. M., O. P. Jensen, S. A. Mason, M. Eriksen, N. J. Williamson, and B. Boldgiv. 2014. "High-Levels of Microplastic Pollution in a Large, Remote, Mountain Lake." *Marine Pollution Bulletin* 85: 156–163. https://doi.org/10.1016/j.marpolbul.2014.06.001.

Free, C. M., O. P. Jensen, and B. Mendsaikhan. 2015. "A Mixed-Method Approach for Quantifying Illegal Fishing and Its Impact on an Endangered Fish Species." *PLoS One* 10: e0143960. https://doi.org/10.1371/journal.pone.0143960.

Froese, R. 2004. "Keep It Simple: Three Indicators to Deal With Overfishing." *Fish and Fisheries* 5: 86–91. https://doi.org/10.1111/j.1467-2979.2004.00144.x.

Froese, R., and D. Pauly. 2022. "FishBase [WWW Document]." www.fishbase.org.

Goodyear, C. 1993. "Spawning Stock Biomass Per Recruit in Fisheries Management: Foundation and Current Use." In *Canadian Special Publication of Fisheries and Aquatic Sciences*, edited by S. J. Smith, J. J. Hunt, and D. Rivard, 67–81. Ottawa, Ontario: Fisheries and Oceans Canada.

Goulden, C., O. Tumurtogoo, E. Karabanov, and A. Mongontsetseg. 2006. "The Geological History and Geography of Lake Hovsgol." In *The Geology, Biodiversity and Ecology of Lake Hovsgol (Mongolia)*, edited by C. E. Goulden, T. Sitnikova, J. Gelhaus, and B. Boldgiv, 1–19. Leiden, The Netherlands: Backhuys Publishers.

Haddon, M. 2011. *Modelling and Quantitative Methods in Fisheries*. 2nd ed. New York: Chapman and Hall/CRC. https://doi.org/10.1201/9781439894170.

Hamel, O. S. 2015. "A Method for Calculating a Meta-Analytical Prior for the Natural Mortality Rate Using Multiple Life History Correlates." *ICES Journal of Marine Science* 72: 62–69. https://doi.org/10.1093/icesjms/fsu131.

Hartman, K. J., and O. P. Jensen. 2017. "Anticipating Climate Change Impacts on Mongolian Salmonids: Bioenergetics Models for Lenok and Baikal Grayling." *Ecology of Freshwater Fish* 26: 383–396. https://doi.org/10.1111/eff.12282.

Herdendorf, C. E. 1982. "Large Lakes of the World." *Journal of Great Lakes Research* 8: 379–412.

Hewson, L. C. 1955. "Age, Maturity, Spawning and Food of Burbot, *Lota lota*, in Lake Winnipeg." *Journal of the Fisheries Research Board of Canada* 12: 930–940. https://doi.org/10.1139/f55-049.

Hommik, K., C. J. Fitzgerald, F. Kelly, and S. Shephard. 2020. "Dome-Shaped Selectivity in LB-SPR: Length-Based Assessment of Data-Limited Inland Fish Stocks Sampled With Gillnets." *Fisheries Research* 229: 105574. https://doi.org/10.1016/j.fishres.2020.105574.

Hordyk, A. 2021. "LBSPR: Length-Based Spawning Potential Ratio. R Package Version 0.1.6." https://CRAN.R-project.org/package=LBSPR.

Hordyk, A., K. Ono, K. Sainsbury, N. Loneragan, and J. Prince. 2015. "Some Explorations of the Life History Ratios to Describe Length Composition, Spawning-Per-Recruit, and the Spawning Potential Ratio." *ICES Journal of Marine Science* 72: 204–216. https://doi.org/10.1093/icesjms/fst235.

Hordyk, A., K. Ono, S. Valencia, N. Loneragan, and J. Prince. 2015. "A Novel Length-Based Empirical Estimation Method of Spawning Potential Ratio (SPR), and Tests of Its Performance, for Small-Scale, Data-Poor Fisheries." *ICES Journal of Marine Science* 72: 217–231. https://doi.org/10.1093/icesjms/fsu004.

Hordyk, A. R., K. Ono, J. D. Prince, and C. J. Walters. 2016. "A Simple Length-Structured Model Based on Life History Ratios and Incorporating Size-Dependent Selectivity: Application to Spawning Potential Ratios for Data-Poor Stocks." *Canadian Journal of Fisheries and Aquatic Sciences* 73, no. 12: 1787–1799. https://doi.org/10.1139/cjfas-2015-0422.

ICES. 2015. "Report of the Fifth Workshop on the Development of Quantitative Assessment Methodologies Based on Life-History Traits, Exploitation Characteristics, and Other Relevant Parameters for Data-Limited Stocks (WKLIFE V)." ICES Expert Group Reports (Until 2018). https://doi.org/10.17895/ICES.PUB.19283927.

Kaus, A., S. Michalski, B. Hänfling, D. Karthe, D. Borchardt, and W. Durka. 2019. "Fish Conservation in the Land of Steppe and Sky: Evolutionarily Significant Units of Threatened Salmonid Species in Mongolia Mirror Major River Basins." *Ecology and Evolution* 9: 3416–3433. https://doi.org/10.1002/ece3.4974.

Knizhin, I. B., and S. J. Weiss. 2009. "A New Species of Grayling *Thymallus svetovidovi* Sp. Nova (Thymallidae) From the Yenisei Basin and Its Position in the Genus *Thymallus*." *Journal of Ichthyology* 49: 1–9. https://doi.org/10.1134/S0032945209010019.

Koskinen, M. T., I. Knizhin, C. R. Primmer, C. Schlötterer, and S. Weiss. 2002. "Mitochondrial and Nuclear DNA Phylogeography of *Thymallus* Spp. (Grayling) Provides Evidence of Ice-Age Mediated Environmental Perturbations in the World's Oldest Body of Fresh Water, Lake Baikal." *Molecular Ecology* 11: 2599–2611. https://doi.org/10.1046/j.1365-294X.2002.01642.x.

Lauden, H. N., X. Xu, S. Lyu, K. Lin, N. Chen, and X. Wang. 2024. "Assessment of the Fish Stock Status Using LBSPR With Its Implications on Fisheries Management: A Case Study of *Nemipterus virgatus*, *Priacanthus macracanthus*, and *Saurida undosquamis* in the Northern South China Sea." *Journal of Applied Ichthyology* 2024: 6808795. https://doi.org/10.1155/2024/6808795.

Lorenzen, K., I. G. Cowx, R. E. M. Entsua-Mensah, et al. 2016. "Stock Assessment in Inland Fisheries: A Foundation for Sustainable Use and Conservation." *Reviews in Fish Biology and Fisheries* 26: 405–440. https://doi.org/10.1007/s11160-016-9435-0.

McIntyre, P. B., C. A. Reidy Liermann, and C. Revenga. 2016. "Linking Freshwater Fishery Management to Global Food Security and

Biodiversity Conservation." *Proceedings of the National Academy of Sciences of the United States of America* 113: 12880–12885. https://doi.org/10.1073/pnas.1521540113.

MEC. 2013. *Lake Hovsgol National Park General Management Plan 2013 Foundation Document*. Ulaanbaatar, Mongolia: Mongol Ecology Center.

MET. 2019. *Mongolia: Sustainable Tourism Development Project: Initial Environmental Examination, Project Number: 50013-002*. Mongolia: Ministry of Environment and Tourism of Mongolia.

Millar, R. B. 1992. "Estimating the Size-Selectivity of Fishing Gear by Conditioning on the Total Catch." *Journal of the American Statistical Association* 87: 962–968. https://doi.org/10.1080/01621459.1992.10476250.

Millar, R. B. 2009. "SELECT: R Functions for Trawl and Net (or Hook) Selectivity." https://www.stat.auckland.ac.nz/~millar/selectware/code.html.

Millar, R. B., and R. J. Fryer. 1999. "Estimating the Size-Selection Curves of Towed Gears, Traps, Nets and Hooks." *Reviews in Fish Biology and Fisheries* 9: 89–116. https://doi.org/10.1023/A:1008838220001.

Millar, R. B., and R. Holst. 1997. "Estimation of Gillnet and Hook Selectivity Using Log-Linear Models." *ICES Journal of Marine Science* 54: 471–477. https://doi.org/10.1006/jmsc.1996.0196.

Ocock, J., G. Baasanjav, J. E. M. Baillie, et al. 2006a. *Summary Conservation Action Plans for Mongolian Fishes*, 1–41. London: Zoological Society of London.

Ocock, J., G. Baasanjav, J. E. M. Baillie, et al. 2006b. *Mongolian Red List of Fishes*, 1–72. London: Zoological Society of London.

Olson, K. W., T. J. Krabbenhoft, T. R. Hrabik, B. Mendsaikhan, and O. P. Jensen. 2019. "Pelagic–Littoral Resource Polymorphism in Hovsgol Grayling *Thymallus nigrescens* From Lake Hovsgol, Mongolia." *Ecology of Freshwater Fish* 28: 411–423. https://doi.org/10.1111/eff.12464.

Ovando, D., C. M. Free, O. P. Jensen, and R. Hilborn. 2022. "A History and Evaluation of Catch-Only Stock Assessment Models." *Fish and Fisheries* 23: 616–630. https://doi.org/10.1111/faf.12637.

Pons, M., J. M. Cope, and L. T. Kell. 2020. "Comparing Performance of Catch-Based and Length-Based Stock Assessment Methods in Data-Limited Fisheries." *Canadian Journal of Fisheries and Aquatic Sciences* 77: 1026–1037. https://doi.org/10.1139/cjfas-2019-0276.

Prince, J., S. Victor, V. Kloulchad, and A. Hordyk. 2015. "Length Based SPR Assessment of Eleven Indo-Pacific Coral Reef Fish Populations in Palau." *Fisheries Research* 171: 42–58. https://doi.org/10.1016/j.fishres.2015.06.008.

Punsalmaa, B., B. Nyamsuren, and B. Buyndalai. 2004. "Trends in River and Lake Ice in Mongolia." Assessments of Impacts and Adaptations to Climate Change (AIACC) Working Paper.

Roman, I., Y. Bourgeois, J. Reyes-Velasco, O. P. Jensen, J. Waldman, and S. Boissinot. 2018. "Contrasted Patterns of Divergence and Gene Flow Among Five Fish Species in a Mongolian Rift Lake Following Glaciation." *Biological Journal of the Linnean Society* 125: 115–125. https://doi.org/10.1093/biolinnean/bly083.

Rudd, M. B., and J. T. Thorson. 2018. "Accounting for Variable Recruitment and Fishing Mortality in Length-Based Stock Assessments for Data-Limited Fisheries." *Canadian Journal of Fisheries and Aquatic Sciences* 75: 1019–1035. https://doi.org/10.1139/cjfas-2017-0143.

Shephard, S., K. Edwards, S. George, et al. 2023. "Community-Based Monitoring, Assessment and Management of Data-Limited Inland Fish Stocks in North Rupununi, Guyana." *Fisheries Management and Ecology* 30: 121–133. https://doi.org/10.1111/fme.12604.

Shephard, S., J. Valbo-Jørgensen, J. Abadía, et al. 2020. *Size-Based Assessment of Data-Limited Inland Fish Stocks—Review and applications (FAO Fisheries and Aquaculture Circular No. 1214)*. Rome: FAO. https://doi.org/10.4060/cb1594en.

Shin, Y.-J., M.-J. Rochet, S. Jennings, J. G. Field, and H. Gislason. 2005. "Using Size-Based Indicators to Evaluate the Ecosystem Effects of Fishing." *ICES Journal of Marine Science* 62: 384–396. https://doi.org/10.1016/j.icesjms.2005.01.004.

Sideleva, V. G. 2006. "Fish Fauna of Lake Hovsgol and Selenga River in Comparison With Ichthyofauna of Lake Baikal." In *The Geology, Biodiversity and Ecology of Lake Hövsgöl (Mongolia)*, edited by C. E. Goulden, T. Sitnikova, J. Gelhaus, and B. Boldgiv, 357–378. Leiden, Netherlands: Backhuys Publishers.

Smith, L. E. D., S. N. Khoa, and K. Lorenzen. 2005. "Livelihood Functions of Inland Fisheries: Policy Implications in Developing Countries." *Water Policy* 7: 359–383. https://doi.org/10.2166/wp.2005.0023.

Solokas, M. A., Z. S. Feiner, R. Al-Chokachy, et al. 2023. "Shrinking Body Size and Climate Warming: Many Freshwater Salmonids Do Not Follow the Rule." *Global Change Biology* 29: 2478–2492. https://doi.org/10.1111/gcb.16626.

Stapanian, M. A., V. L. Paragamian, C. P. Madenjian, et al. 2010. "Worldwide Status of Burbot and Conservation Measures." *Fish and Fisheries* 11: 34–56. https://doi.org/10.1111/j.1467-2979.2009.00340.x.

Stokes, G. L., A. J. Lynch, S. Funge-Smith, et al. 2021. "A Global Dataset of Inland Fisheries Expert Knowledge." *Scientific Data* 8: 182. https://doi.org/10.1038/s41597-021-00949-0.

Švagždys, A. 2002. "Growth and Abundance of Burbot in the Curonian Lagoon and Determinatives of Burbot Abundance." *Acta Zoologica Lituanica* 12: 58–64. https://doi.org/10.1080/13921657.2002.10512487.

Then, A. Y., J. M. Hoenig, N. G. Hall, and D. A. Hewitt. 2015. "Evaluating the Predictive Performance of Empirical Estimators of Natural Mortality Rate Using Information on Over 200 Fish Species." *ICES Journal of Marine Science* 72: 82–92. https://doi.org/10.1093/icesjms/fsu136.

Thorson, J. T., and J. M. Cope. 2015. "Catch Curve Stock-Reduction Analysis: An Alternative Solution to the Catch Equations." *Fisheries Research* 171: 33–41. https://doi.org/10.1016/j.fishres.2014.03.024.

Thorson, J. T., J. M. Cope, T. A. Branch, and O. P. Jensen. 2012. "Spawning Biomass Reference Points for Exploited Marine Fishes, Incorporating Taxonomic and Body Size Information." *Canadian Journal of Fisheries and Aquatic Sciences* 69: 1556–1568. https://doi.org/10.1139/f2012-077.

Tomilov, A. A., and A. Dashidorzh. 1965. "Lake Khuvsgul and the Possibilities of Its Use for Commercial Fishing." In *Limnologicheskie Issledovaniya Baikala I Nekotorykh Ozer Mongolii*, edited by G. I. Galazii, 164–180. Moscow, Russia: Nauka.

Tsogtsaikhan, P., B. Mendsaikhan, G. Jargalmaa, et al. 2017. "Age and Growth Comparisons of Hovsgol Grayling (*Thymallus nigrescens* Dorogostaisky, 1923), Baikal Grayling (*T. baicalensis* Dybowski, 1874), and Lenok (*Brachymystax lenok* Pallas, 1773) in Lentic and Lotic Habitats of Northern Mongolia." *Journal of Applied Ichthyology* 33: 108–115. https://doi.org/10.1111/jai.13247.

Urabe, J., T. Sekino, Y. Hayami, et al. 2006. "Some Biological and Chemical Characteristics of Lake Hovsgol." In *The Geology, Biodiversity and Ecology of Lake Hövsgöl (Mongolia)*, edited by C. E. Goulden, T. Sitnikova, J. Gelhaus, and B. Boldgiv, 387–402. Leiden, Netherlands: Backhuys Publishers.

Weiss, S. J., D. V. Gonçalves, G. Secci-Petretto, et al. 2021. "Global Systematic Diversity, Range Distributions, Conservation and Taxonomic Assessments of Graylings (Teleostei: Salmonidae; *Thymallus* Spp.)." *Organisms, Diversity and Evolution* 21: 25–42. https://doi.org/10.1007/s13127-020-00468-7.

Welcomme, R. L., I. G. Cowx, D. Coates, et al. 2010. "Inland Capture Fisheries." *Philosophical Transactions of the Royal Society of London.*

Series B, Biological Sciences 365: 2881–2896. https://doi.org/10.1098/rstb.2010.0168.

Wilson, J. R., S. Lomonico, D. Bradley, et al. 2018. "Adaptive Comanagement to Achieve Climate-Ready Fisheries." *Conservation Letters* 11: e12452. https://doi.org/10.1111/conl.12452.

WWF. 2024. *Living Planet Report 2024—A System in Peril*. Gland, Switzerland: WWF.

Young, T., O. P. Jensen, B. C. Weidel, and S. Chandra. 2015. "Natural Trophic Variability in a Large, Oligotrophic, Near-Pristine Lake." *Journal of Great Lakes Research* 41: 463–472. https://doi.org/10.1016/j.jglr.2015.02.010.

Zhou, S., S. Yin, J. T. Thorson, A. D. M. Smith, M. Fuller, and C. J. Walters. 2012. "Linking Fishing Mortality Reference Points to Life History Traits: An Empirical Study." *Canadian Journal of Fisheries and Aquatic Sciences* 69: 1292–1301. https://doi.org/10.1139/f2012-060.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.