The generalization of Gulland’s method: how to estimate maturity ogives when juvenile data are missing while spawner demography is known

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Abstract

The proportions of mature individuals at age or length, collectively known as the maturity ogive, are a key population characteristic and serve as critical input to age-disaggregated stock assessments. John Gulland showed in 1964 that it is possible to estimate maturity ogives even when representative data on immature individuals are not available, provided that one can distinguish newly mature individuals (first-time spawners) from those that had matured earlier (repeat spawners). Gulland’s method offers a valuable tool for obtaining information on an unobserved part of a population and is also applicable to other ontogenetic transitions, such as metamorphosis, smolting, ontogenetic niche shifts, and sex change. Here we present a full derivation of Gulland’s method from first principles, applicable to the general case in which the survival of immature, first-spawning, and repeat-spawning individuals may differ. Better observation methods, in particular in sclerochronology and histology, are expected to make meeting this method’s data requirements—i.e., the separation of first-time and repeat spawners—more often achievable, and estimating maturity ogives could serve as an additional incentive for allocating resources to enhanced data collection. With the generalization presented here, we hope to make Gulland’s method better known and more widely accessible.

Keywords: maturity ogives, life-history transitions, reproductive potential, stock dynamics

1. Introduction

Maturity ogives measure the proportions of mature individuals at age or length and serve as a key characteristic of populations, directly impacting their reproductive potential (Murua and Saborido-Rey, 2003; ICES, 2008; Flores et al., 2015). The demographic structure of the mature part of a population has profound consequences for recruitment and population dynamics (Trippel et al., 1997; Ottersen et al., 2006; Köster et al., 2013; Hixon et al., 2014). At the same
time, fish maturation is a highly plastic process that is influenced by an array of environmental factors such as food availability and temperature (Stearns and Crandall, 1984; Trippel, 1995). This implies that it is important to see maturity ogives as dynamic, rather than static, population characteristics and that an accurate understanding of stock dynamics necessitates the regular updating of a stock’s maturity ogive.

When representative measurements of both immature and mature individuals are available, it is straightforward to estimate a population’s maturity ogive as the proportions of mature individuals among all individuals, mature and immature, across all age or length classes. Indeed, it would seem obvious that data on both immature and mature individuals were always needed for estimating maturity ogives. However, John Gulland has shown, already more than 50 years ago, that this is not necessary: age-dependent maturity ogives can be calculated based on age-specific proportions of first-time spawning individuals among all spawning individuals (Gulland, 1964). This is potentially a very important methodological discovery, because obtaining representative samples of both immature and mature individuals can be difficult. A number of challenges are evident: immature and mature fish may be spatially segregated, sampling gear may have reduced catchability for smaller sizes, and—when obtaining data from commercial fisheries—fishermen often face regulations specifically designed to reduce catching juvenile fish that may end up being discarded. Gulland’s method therefore offers considerable promise in the many situations in which only the mature part of a population is amenable to quantitative sampling.

In reality, Gulland’s method has seen only sporadic use, probably because it is rare that first-time and repeat spawners are separated as part of routine stock monitoring. However, in some fish populations, the age at first spawning can be estimated from scales or otoliths based on so-called spawning checks. This is the case for Northeast Arctic cod (Gadus morhua), for which spawning checks can be identified in otoliths (Rollefsen, 1933; Zuykova et al., 2009).
Indeed, Northeast Arctic cod is the stock for which Gulland first devised his method. Since then, the method has recurrently been applied to this commercially and economically important stock (Jørgensen, 1990; Heino et al., 2002; Svåsand et al., 2003; Zuykova et al., 2009; Yaragina, 2010) and contributes to the maturity ogives used in the official stock assessment (Zuykova et al., 2009; ICES, 2017). Another important example of such applications is Norwegian spring-spawning herring (Clupea harengus), for which scales can be used to identify first-time spawners (Lea, 1928; Runnström, 1936; Engelhard et al., 2003). Gulland’s method has been applied to this stock in a few publications (Engelhard and Heino, 2004a, 2004b) and, since 2010, in the official stock assessment (ICES, 2016). Species for which Gulland’s method has not yet been used, even though first spawning can be identified from otoliths or scales, are as diverse as shortnose sturgeon (Acipenser brevirostrum; Taubert, 1980), steelhead trout (Oncorhynchus mykiss; Narver, 1969), Atlantic halibut (Hippoglossus hippoglossus; Devold, 1938), and orange roughy (Hoplostethus atlanticus; Francis and Horn, 1997). Future developments in sclerochronology could make this list much longer.

Gulland (1964) presented his method through a worked example rather than in terms of general equation(s). He also noted that differential survival between immature and mature fish will bias the results, but considered this bias unimportant and did not present a correction. Terje Jørgensen (1990) was the first to express Gulland’s method as a general equation. He also presented a way to account for the difference in survival between mature and immature fish, albeit indirectly, by adjusting the counts of repeat spawners. However, he did not present the derivation of the equations, nor did he allow for the survival of first-time spawners to differ from the survival of repeat spawners. Here we present a full derivation of Gulland’s method from first principles, applicable to the general case in which the survival of immature, first-spawning, and repeat-spawning individuals may differ. With this generalization, we hope to make Gulland’s method better known and more widely accessible.
2. Logic of Gulland’s method

We first describe the general idea underlying Gulland’s method. When survival of all types of individuals of the same age is equal, the method is straightforward and can easily be illustrated graphically (Fig. 1). This simplifying assumption is then relaxed in the next section.

The goal of Gulland’s method is to estimate the age-specific proportions $o_t$ of mature individuals for the population’s cohorts at each age $t$ from the observed (sampled) numbers of first-spawning and repeat-spawning fish, $n^F_t$ and $n^R_t$, respectively. Since we are dealing with each cohort separately, the index $t$ can be interpreted as either age or time (both measured in numbers of spawning seasons), whichever is more convenient. An individual is born as a juvenile (life stage $J$), then matures and becomes a first-time spawner (F), before turning into a repeat spawner (R) for the rest of its life. Thus, the generalized ontogeny is of type $J \rightarrow \cdots \rightarrow J \rightarrow F \rightarrow R \rightarrow \cdots \rightarrow R \rightarrow \dagger$, with each arrow corresponding to a time step, typically one year. As appropriate, other conventions for naming the successive stages can be adopted, as long as the distinction between juveniles, newly mature individuals, and individuals that were newly mature during earlier observation steps is maintained.

Gulland’s method is iterative, progressing backward in time. The estimation is started from the earliest age at which a cohort is fully mature. In the absence of data on juveniles, this can be identified as the latest age at which the samples contain first-time spawners. We therefore take this as the reference time and denote it by $T$ (Fig. 1). At time $T$, the maturity ogive, by definition, has the value $o_T = 1$. We can then work backward in time by noting that the proportion $o_{T-1}$ of mature individuals among all individuals one time step earlier, i.e., at time $T - 1$, equals the proportion $r_T$ of repeat spawners among all mature individuals at time $T$,

$$o_{T-1} = r_T.$$

The latter proportion is known directly from the sampling, $r_T = n^R_T / (n^F_T + n^R_T)$. For time $T - 2$, the proportion $o_{T-2}$ of mature individuals among all individuals likewise equals the proportion of repeat spawners among all individuals at time $T - 1$ (Fig. 1). This proportion
is not known from the outset. However, the proportion $o_{T-1}$ of mature individuals among all individuals in the cohort is known from the previous step, and the proportion $r_{T-1}$ of repeat spawners among all mature individuals is again known from the sampling. We can multiply these two proportions to determine $o_{T-2} = o_{T-1}r_{T-1}$ (Fig. 1). This equation is readily generalized for any time $t$. Thus, we obtain the general iterative equation for Gulland’s method under uniform survival probabilities,

$$o_{t-1} = o_tr_t,$$

or equivalently, $o_t = o_{t+1}r_{t+1}$. Accumulating all iterations, the maturity ogive can be expressed as an explicit closed-form function of time $t$,

$$o_t = \prod_{\tau=t+1}^{T} r_{\tau}. \quad (1b)$$

3. Generalization of Gulland’s method

We now derive Gulland’s method from first principles. This allows considering the role of survival, and of differences in survival between life stages, in a rigorous way.

Changes in the abundances of fish in a cohort over one time step are described as follows,

$$N^J_{t+1} = s^J_{t+1}N^J_{t}(1 - m_t), \quad (2a)$$

$$N^F_{t+1} = s^F_{t+1}N^J_{t}m_t, \quad (2b)$$

$$N^R_{t+1} = s^{FR}_{t}N^F_{t} + s^{RR}_{t}N^R_{t}, \quad (2c)$$

where $N^J_t$, $N^F_t$, and $N^R_t$ are the abundances of juvenile, first-spawning, and repeat-spawning fish at time $t$, $s^J_{t}$, $s^F_{t}$, $s^{FR}_{t}$, and $s^{RR}_{t}$ are the survival probabilities for the transitions $J \rightarrow J$, $J \rightarrow F$, $F \rightarrow R$, $R \rightarrow R$, respectively, and $m_t$ is the probability of maturation during the next time step.

Here we have assumed that, at any time $t$, the survival probability for transitions $R \rightarrow R$ is independent of the number of preceding spawning events.
The maturity ogive can always be expressed in terms of stage-specific abundances:

\[ o_t = \frac{N_t^F + N_t^R}{N_t^F + N_t^R + N_t^R} = \frac{1}{1 + \frac{N_t^F}{N_t^F + N_t^R}}. \]  

(3)

With expressions derived from Equations 2a–2c, the terms \( N_t^I \) and \( N_t^F + N_t^R \) can be expressed in terms of the cohort composition at time \( t + 1 \). First, rearranging Equation 2b gives \( N_t^I = \frac{N_t^F}{s_t^F} / m_t \). The maturation probability \( m_t \) can be solved from Equations 2a and 2b as

\[ m_t = 1 + \frac{s_t^F N_t^I}{s_t^F N_t^I + 1}. \]  

(4a)

Substituting Equation 4a into the expression for \( N_t^I \) gives

\[ N_t^I = \frac{N_t^F (1 + \frac{s_t^F N_t^I}{s_t^F N_t^I + 1})}{s_t^F}. \]  

(4b)

Second, dividing Equation 2c with \( N_t^F + N_t^R \), using the definition \( r_t = N_t^R / (N_t^F + N_t^R) \), and rearranging gives

\[ N_t^F + N_t^R = \frac{N_t^R}{s_t^F (1 - r_t + 1) + s_t^R r_t}. \]  

(4c)

Inserting Equations 4b and 4c into Equation 3 gives

\[ o_t = \frac{1}{1 + \frac{N_{t+1}^F}{N_{t+1}^R + \frac{s_t^F}{s_t^F} N_{t+1}^I},} \] 

(5a)

This equation still contains two unknown ratios of abundances. As ratios, they are independent of total abundance and can instead be expressed solely in terms of parameters \( o_{t+1} \) and \( r_{t+1} \).

Specifically,

\[ N_{t+1}^I / N_{t+1}^R = o_{t+1} (1 - r_{t+1}) / o_{t+1} r_{t+1} \]  

and

\[ N_{t+1}^I / N_{t+1}^F = (1 - o_{t+1}) / o_{t+1} (1 - r_{t+1}) \]  

Using these relationships, rearranging, and shifting the time index back by one time step gives
This iterative equation allows determining the value $o_{t-1}$ of the maturity ogive at time $t - 1$ from three sources of information: (i) the ratio $r_t$ of repeat spawners among all mature individuals, known from (representative) sampling, (ii) three ratios of survival probabilities, possibly known from independent observations, and (iii) the value $o_t$ of the maturity ogive at time $t$, known from the equation’s previous iteration or because the cohort is known to be fully mature at time $t$. Equation 5b is similar to Equation 1a, but includes a correction in form of the denominator, which accounts for differences in survival between the life stages. It is readily seen that Equation 5b reduces to Equation 1a as a special case when all survival probabilities are equal.

Equation 5b contains three ratios of survival probabilities that all include $s_{t-1}^{RF}$, which therefore naturally serves as the reference against which the other survival probabilities can be compared. Sometimes it is more convenient to use another survival probability as the reference: for instance, when we use $s_{t-1}^{RR}$ as the reference, Equation 5b becomes

$$o_{t-1} = \frac{o_t r_t}{o_t r_t + \left( o_t (1 - r_t) + (1 - o_t) \frac{s_{t-1}^{RF}}{s_{t-1}^{RF}} \right) \left( \frac{s_{t-1}^{FR}}{s_{t-1}^{RF}} (1 - r_t) + r_t \right)}.$$

Figure 2 illustrates the sensitivity of the estimated maturity ogive to departures from equal age-specific survival between maturity stages. Not surprisingly, the sensitivity is greater when the estimated maturity proportion is near the middle of the possible range (Fig. 2, left panels) compared to when the proportion is near the border of the possible range (Fig. 2, right panels). The general tendency is that assuming equal survival ratios between maturity stages leads to positively biased maturity estimates (red colors in Fig. 2) when juvenile survival is low relative to repeat-spawning survival ($s_{t-1}^{RF}/s_{t-1}^{RR} < 1$) and/or when juvenile-to-first-spawning survival is low relative to repeat-spawning survival ($s_{t-1}^{RF}/s_{t-1}^{RR} < 1$); the opposite is true when
these ratios are high.

4. Example: Northeast Arctic cod

We illustrate the generalized Gulland’s method for the 1928 cohort of Northeast Arctic cod, the first cohort for which suitable data are available. For this stock, historic samples are available from the spawning grounds, distinguishing first-time spawners and repeat spawners, but no representative data are available for juvenile individuals (e.g., Jørgensen, 1990; Heino et al., 2002). For the 1928 cohort, the proportions of repeat spawners among all mature individuals equals 0 for ages 6 years and younger, equals 0.03, 0.24, 0.47, 0.66, 0.70, 0.85, 0.96, and 0.95 for ages 7 to 14 years, respectively, and equals 1 for older individuals. Because only mature fish were subject to fishing in the spawning grounds, it is likely that juveniles experienced a higher age-specific survival \( s_t^{IJ} \) than fish that entered the spawning grounds \( s_t^{IF}, s_t^{FR}, \) and \( s_t^{RR} \). We therefore let the ratio \( s_t^{IJ} / s_t^{RR} \) vary. In addition to considering the case \( s_t^{IF} / s_t^{RR} = 1 \) and \( s_t^{FR} / s_t^{RR} = 1 \), we examine a scenario in which individuals lacking spawning experience suffer from additional mortality during their spawning migration, by considering the case \( s_t^{IF} / s_t^{RR} = 0.7 \) and \( s_t^{FR} / s_t^{RR} = 0.9 \); the particular numbers here are chosen for illustrative purposes only.

Applying our generalization of Gulland’s method reveals that the estimated maturity ogive is potentially sensitive to departures from equal age-specific survival between maturity stages (Fig. 2, 3). For instance, when spawning individuals suffer from higher mortality than those that do not spawn, assuming that no such survival difference exists results in an ogive that is downward biased. If the survival difference is large \( s_t^{IJ} / s_t^{RR} = 2 \), the true ogive is up to about 15 percent points higher than the estimated one (Fig. 3a). If we assume that lack of spawning experience reduces survival, the maximal bias when \( s_t^{IJ} / s_t^{RR} = 2 \) is slightly lower, at
about ten percent points (Fig. 3b).

A potential source of bias for estimating the maturity ogive of Northeast Arctic cod is skipped spawning (Jørgensen et al., 2006; Skjæraasen et al., 2012). The effect of skipped spawning on spawner demography is that the sampled proportions of repeat spawners among all mature individuals ($r_\gamma$) are less than their true proportions. The strength of this bias will vary with a cohort’s age, because skipped spawning depends on spawning experience. Figure 4a shows that if skipped spawning is very frequent and leads to a serious underrepresentation of repeat spawners, the estimated maturity ogive can be seriously biased downward. However, for the documented levels of skipped spawning (~24 % in 2006–2008, Skjæraasen et al., 2012), the bias is modest, at most seven percent points (Fig. 4a for $x = 0.25$).

Another possible source of uncertainty is the misidentification of first-time and repeat spawners. Figure 4b shows that misidentifying first-time spawners as second-time spawners or vice versa at a relatively high rate (20%) results in a modest downward bias in the estimated maturity ogive. The largest error is about seven percent points for ages 10–11 years.

5. Discussion

Here we have presented a derivation of the generalized Gulland’s method to estimate maturity ogives in the absence of data on juveniles. The information required instead are age-specific proportions of repeat spawners among spawning individuals, as well as ratios of age-specific survival among juveniles, maturing individuals, first-time spawners, and repeat spawners, all for a given cohort. These survival ratios can be based on independent observations or expert knowledge. This is more practical than the correction proposed by Jørgensen (1990), which requires adjusting the input data before applying the original Gulland’s method assuming stage-independent survival (his Equation 3 and our Equation 1a).

As underscored by our examples above, assuming the aforementioned survival ratios to
equal 1 can greatly bias the estimation of maturity ogives when these ratios in fact significantly
differ from 1. While estimating survival in wild populations is always difficult, two mitigating
considerations are worth emphasizing. First, it is only the aforementioned survival ratios that
enter the generalized Gulland’s method, not the absolute values of survival probabilities. Sec-
ond, these ratios will deviate from 1 only when maturation stages differentially impact age-
specific survival. When such effects of maturation stages within each age class are weak, as-
suming the ratios to equal 1 will not cause major biases in the estimated maturity ogives.

Because maturity ogives result from maturation dynamics of a cohort of individuals, the
most natural biological unit for estimating ogives is a cohort. For this reason, we have presented
the derivation here for cohorts, as did Gulland (1964) and Jørgensen (1990). However, Gul-
land’s method—and estimation of maturity ogives in general—can also be used with data from
a single year or with data averaged over a range of years. The implicit assumption is that age-
specific changes in maturity observed for concurrently recorded age groups is similar to what
would have been observed when following a cohort over time. The situation is analogous to
growth curves, which can be estimated either by cohort or by year (Beverton and Holt, 1957, p.
282; Gulland, 1969, p. 93; Ricker, 1975, p. 205). The disadvantage of any such estimations by
year is that factors that are specific to a cohort will confound the detection of age-specific
change, be it in maturity or in size. For example, strong year classes of Norwegian spring-
spawning herring show different maturation dynamics compared to weak ones (Engelhard and
Heino, 2004b; ICES, 2016). Whether cohort-to-cohort or year-to-year variability leads to prac-
tically significant differences between estimations by cohort and by year is probably case-spe-
cific.

Gulland’s method also applies to irreversible life-history transitions other than matura-
tion, such as metamorphosis, smolting, other ontogenetic niche shifts, and sex change. Each of
these transitions might pose specific challenges, for example, in regard to the identification of
newly transitioned individuals. Furthermore, some of these transitions might not be strictly ir-
reversible. For example, sex change can be bi-directional in some non-commercial reef fishes
(e.g., Sunobe and Nakazono, 1993; Nakashima et al., 1996; Munday et al., 1998).

Skipped spawning has been implicated in a number of fish stocks (Rideout et al., 2005),
including the stocks for which Gulland’s method has been used (Engelhard and Heino, 2005;
Skjæraasen et al., 2012). Skipped spawning has the potential to bias maturity ogives downwards,
if not accounted for. For the documented levels of skipped spawning, this bias is modest, but
may act in the same direction as other sources of bias. Furthermore, when good estimates of
skipped spawning are available, the estimation of maturity ogives can readily be adjusted to
account for it.

A major limitation of Gulland’s method is that it requires data that are only seldom
recorded: distinguishing first-time spawners from repeat spawners with routine observations is
rarely possible. Exceptions mainly come from stocks with long spawning migrations (such as
cod and herring) or an anadromous life cycle (such as shortnose sturgeon and steelhead trout).
These show a so-called spawning check, a visually detectable change in the zonation pattern of
otoliths or scales. Long migrations increase the energetic cost of spawning, making the slowing
down of growth upon maturation more marked than it would otherwise be (e.g., Folkvord et al.,
2014).

For Northeast Arctic cod, the recording of spawning checks is part of routine data col-
lection (Mjanger et al., 2010). However, a strict validation of the assumption that the formation
of the first spawning check is associated with the first spawning is as yet lacking. Experiments
support the notion that substantial energy investments in reproduction are reflected by reduced
otolith growth, but leave open the question whether such changes in the otolith growth of wild
cod are always associated with reproduction or can originate also from other sources of ener-
getic stress. Furthermore, it remains possible that some spawning cod do not develop a corre-
sponding spawning check (Irgens, 2018; Arild Folkvord, University of Bergen, pers. comm.).

Our numerical tests suggest that Gulland’s method is not overly sensitive to moderate error
rates in assessing whether a spawning fish is a first-time or second-time spawner.

There are a number of possibilities to identify first-time spawners in the absence of
visually marked changes in otoliths or scales. First, numerical methods might allow detecting
changes in growth that are not visually obvious as spawning checks (Rijnsdorp and Storbeck,
1995; Engelhard et al., 2003; Baulier and Heino, 2008; Brunel et al., 2013). This requires back-
calculations of growth, which can be based on both archived and fresh materials. The efficiency
of such estimates could potentially be improved using automated image analyses. Unfortunately,
detecting maturation from growth trajectories suffers from limited accuracy, especially for in-
dividuals captured soon after maturation (Baulier and Heino, 2008; Brunel et al., 2013).

Second, advances in sclerochronology offer new possibilities for extracting life-history
information from otoliths and scales that go far beyond traditional visual examinations. For
example, patterns of ontogenetic vertical migrations in deep-sea fish can be deduced from oto-
lith microstructures and stable-isotope composition (Lin et al., 2012; Chang et al., 2015). Like-
wise, migrations of eel between marine, brackish, and freshwater environments can be deduced
from the ratios of strontium and calcium in their otoliths (Jessop et al., 2008). An experimental
study with European plaice (Pleuronectes platessa) showed that reproduction alters the zinc-
to-calcium ratio in the blood plasma and otoliths of females, offering a potential tool for detect-
ing both age at first reproduction and skipped spawning seasons (Sturrock et al., 2015). Also
these methods apply to archived as well as fresh materials.

Third, histological methods offer what is potentially the most precise approach to sepa-
rating first-time and repeat-spawning female fish, at least for determinately spawning boreal
species: mature females with postovulatory follicles (POFs) are repeat-spawners, whereas those
lacking POFs are first-time spawners, provided that POFs persist long enough after spawning relative to the timing of the sample collection (Rideout et al., 2005). This condition is easily fulfilled in cod where POFs persist for more than a year (Witthames et al., 2010; Folkvord et al., 2014). Unfortunately, histological methods require samples that are specifically conserved for such analysis, which makes them unlikely to be applicable to historical materials. Moreover, obtaining age estimates still requires the reading of otoliths or scales.

Gulland’s method offers the prospect of estimating maturity ogives for species in which it is difficult to obtain representative data on the juvenile part of the population. This will often necessitate collecting new kinds of data, or using existing materials in novel ways, in order to differentiate between first-time and repeat spawners. At the same time, elucidating individual life cycles with such new data will probably be valuable in its own right. The prospect of obtaining information on a population’s demographic composition by applying Gulland’s method can add motivation for investing scarce resources in enhanced analyses of otoliths and scales, as well as into histology. Exciting options for future applications of the generalized Gulland’s method presented here include obtaining information on the oceanic phase of anadromous iteroparous salmonids and estimating the maturity ogives of enigmatic deep-sea fishes such as orange roughy.

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References


Figure captions

Fig. 1. Schematic illustration of Gulland’s method when survival is equal for all individuals at a given age. At any point in time, a cohort is composed of juvenile (J), first-spawning (F), and repeat-spawning (R) individuals. For all ages $t$, the proportion of repeat spawners among all spawners is known from sampling, $r_t = n_t^R / (n_t^F + n_t^R)$. The maturity ogive $o_t$ is known from sampling to equal 1 down to the latest age $T$ at which first-time spawners are still present in the samples. For earlier ages $t < T$, $o_t$ can be calculated iteratively using the equation $o_{t-1} = o_t r_t$.

For understanding Gulland’s method, it is important to recognize that the proportions $o_t$ of mature individuals among all individuals and the proportions $r_t$ of repeat spawners among all mature individuals are measured relative to different totals (all individuals vs. all mature individuals), as indicated by the gray extensions of the black curly braces.

Fig. 2. Sensitivity of the estimated proportion of mature individuals to variations in relative survival between maturity stages. The left and right columns correspond to situations that could be encountered when estimating maturity proportions for near median and relatively early ages, respectively, that is, relatively high and low proportions of mature and first-spawning individuals. On the left, assuming that all survival ratios are equal, the estimated maturity proportion is $o_{t-1} = o_t r_t \approx 0.56$, whereas on the right, it is much lower, at $o_{t-1} \approx 0.062$. The color bands indicate how much this estimate deviates from the true value (red: overestimation; blue: underestimation). Each color band has a width of 0.05. The white band is centered on the true value; hence, it covers an area in which the absolute error is smaller than 2.5%. In the top row, all survival ratios are varied, but $s_{t-1}^{JF} = s_{t-1}^{JF}$ are kept equal, whereas in the middle row, $s_{t-1}^{JF} = s_{t-1}^{FR}$ are kept equal. In the bottom row, $s_{t-1}^{JF}$ and $s_{t-1}^{JF}$ are varied independently, while $s_{t-1}^{FR} = 1$ is kept fixed. Notice that all axes are logarithmic.

Fig. 3. Application of the generalized Gulland’s method to the 1928 cohort of Northeast Arctic
cod, *Gadus morhua*. In (a), maturing fish and first-time spawners are assumed to have experienced the same survival probability as repeat spawners \( s_t^{I_F}/s_t^{RR} = s_t^{FR}/s_t^{RR} = 1 \), whereas in (b), they are assumed to suffer from reduced survival during the spawning migration \( s_t^{IF}/s_t^{RR} = 0.7 \) and \( s_t^{FR}/s_t^{RR} = 0.9 \). In both panels, the ratio of juvenile to repeat spawner survival probability is varied; the size of the circular markers increases with the survival ratios \( s_t^{IJ}/s_t^{RR} \), which apply to all ages \( t \). Filled circles correspond to the simpler case in which survival is independent of maturation stage, as is assumed when using the original Gulland’s method without our generalization. The results show how estimation errors as large as 100% can result when applying the original Gulland’s method to situations in which age-specific survival probabilities are affected by maturation stage.

**Fig. 4.** Application of the generalized Gulland’s method to the 1928 cohort of Northeast Arctic cod when accounting for (a) skipped spawning and (b) errors in assessing an individual’s spawning experience. When some mature fish skip the spawning migration, samples from the spawning grounds show too low proportions \( r^*_\gamma \) of repeat spawners among all mature individuals. In (a), \( r^*_\gamma \) is corrected for this underrepresentation as \( r'_\gamma = r^*_\gamma(1 + x)/[r^*_\gamma(1 + x) + 1 - r^*_\gamma] \), where \( x \) is the proportion of mature fish skipping spawning. In (b), it is assumed that there is a 20% probability of assigning a first-time spawner as a second-time spawner, and vice versa. The thick curve shows the true ogive when spawning experience is assumed to have been correctly estimated. The boxes show the median value together with the interquartile range of 1000 Monte-Carlo replicates in which erroneous assignments are present. Whiskers extend to the most extreme data point no more than 1.5 times the interquartile range away from the box, and dots show more extreme data points.
Fig. 1

\[ o_{T-1} - r_{T-1} \]

\[ o_T = 1 \]
Fig. 2

\( o_t = 0.75, r_t = 0.75 \)

\[ s_{JJ}^{RR} = s_{JJ}^{FR} = s_{JJ}^{JJ} = 0.562 \]

\( o_t = 0.25, r_t = 0.25 \)

\[ s_{JJ}^{RR} = s_{JJ}^{FR} = s_{JJ}^{JJ} = 0.062 \]
Fig. 3  

$s^{JJ}/s^{RR} = 0.5...2$, $s^{JF}/s^{RR} = 1$, $s^{FR}/s^{RR} = 1$

$s^{JJ}/s^{RR} = 0.5...2$, $s^{JF}/s^{RR} = 0.7$, $s^{FR}/s^{RR} = 0.9$
**Fig. 4**

**Skipped spawning**

- **Proportion mature** vs **Age (yr)**
- Correction factor $x$

- $0$
- $0.25$
- $0.5$
- $0.75$
- $1$

**Errors in spawning experience**

- **Proportion mature** vs **Age (yr)**