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Review

Depletion Estimation, Stock–Recruitment Relationships, and Interpretation of Biomass Reference Points

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Abstract: Stock depletion level is an important concept in the assessment and management of exploited fish stocks because it is often used in conjunction with reference points to infer stock status. Both the depletion level and reference points can be highly dependent on the stock–recruitment relationship. Here, we show how depletion level is estimated in stock assessment models, what data inform the depletion level, and how the stock–recruitment relationship influences the depletion level. There are a variety of data that provide information on abundance. In addition, to estimate the depletion level, unexploited absolute abundance needs to be determined. This often means extrapolating the abundance back in time to the start of the fishery, accounting for the removals and the productivity. Uncertainty in the depletion level arises because the model can account for the same removals by either estimating low productivity (e.g., low natural mortality) and high carrying capacity or high productivity and a low carrying capacity, and by estimating different relationships between productivity and depletion level, which are strongly controlled by the stock–recruitment relationship. Therefore, estimates of depletion are particularly sensitive to uncertainty in the biological processes related to natural mortality and the stock–recruitment relationship and to growth when length composition data are used. In addition, depletion-based reference points are highly dependent on the stock–recruitment relationship and need to account for recruitment variability, particularly autocorrelation, trends, and regime shifts. Future research needs to focus on estimating natural mortality, the stock–recruitment relationship, asymptotic length, shape of the selectivity curve, or management strategies that are robust to uncertainty in these parameters. Tagging studies, including close-kin mark-recapture, can address some of these issues. However, the stock–recruitment relationship will remain uncertain.

Keywords: depletion; fisheries management; reference point; stock assessment; stock–recruitment

Key Contribution: The stock–recruitment relationship, which is usually poorly determined, impacts both the depletion level estimate and the reference point it is compared against. Estimates of depletion (and reference points) are also dependent on growth, particularly when fitting to length composition data, and natural mortality, which can also be uncertain.

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Citation: Maunder, M.N.; Piner, K.R. Depletion Estimation, Stock–Recruitment Relationships, and Interpretation of Biomass Reference Points. *Fishes* **2024**, *9*, 447. https://doi.org/10.3390/fishes9110447

Academic Editors: Yuan Li, Chongliang Zhang, Xuefeng Wang, Kui Zhang and Zengguang Li

Received: 30 September 2024
Revised: 28 October 2024
Accepted: 29 October 2024
Published: 1 November 2024

1. Introduction

Stock depletion level is an important concept in fishery stock assessment because of its common use in the management of exploited fish stocks [1]. Depletion is usually defined as stock abundance (often spawning biomass) relative to some estimate of the unexploited level. Depletion level in stock assessment and fishery management is perhaps most important in its relationship to the expected recruitment. The prevailing assumption is that stocks depleted to low levels substantially reduce recruitment, based on stock–recruitment theory. A substantial loss of recruitment is undesirable as it reduces yield and may lead to stock collapse (at least in economic terms). The management implications of reduced recruitment at low relative biomass levels have been formalized through the development of biomass reference points [2]. Target reference points are often associated with maximizing yield, which is calculated from a cohort's total biomass as a tradeoff between increases due to growth and recruitment and decreases due to natural mortality (Figure 1). Limit reference points are intended to avoid stock abundance associated with recruitment levels that imperil the stock or its role in the ecosystem. They have been developed based on information on abundance and recruitment, simple assumptions about the stock–recruitment relationship, or subjectively defined (e.g., 20% of the unexploited level).

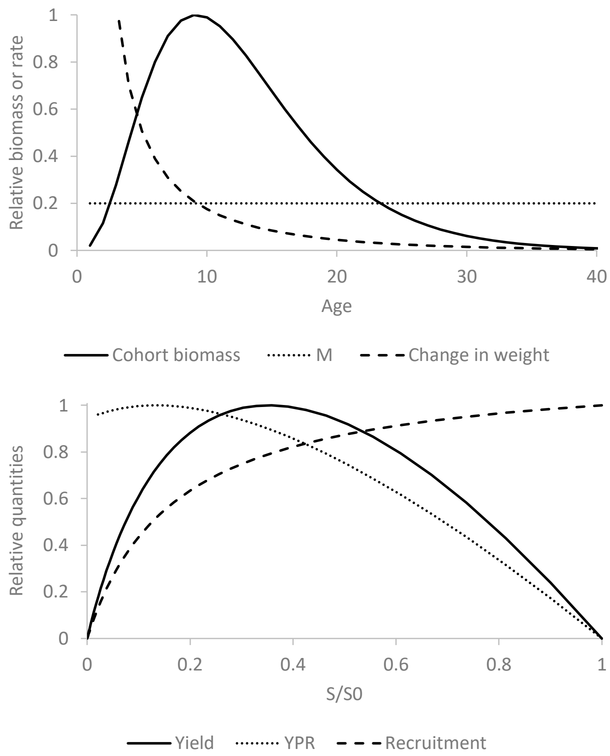

Figure 1. Illustration of the calculation of the depletion level corresponding to MSY. The upper figure shows that the biomass of a cohort changes as it ages due to a tradeoff between increases from individual growth and reductions from natural mortality. The maximum yield-per-recruit (YPR) is obtained when all the individuals are caught at the age that maximizes the biomass of the cohort, which occurs when the growth rate equals natural mortality. For illustrative purposes, natural mortality is assumed to be constant across age, while individual growth rates reduce as they age, forming a peak in population biomass growth. The lower figure shows how MSY is calculated by combing the YPR curve with the stock–recruitment relationship, which also gives the shape of the production function. For a given selectivity that catches multiple ages of fish, fish are caught at a younger age as the fishing mortality increases and the population becomes more depleted. The YPR initial increases with fishing mortality because fewer fish are left in the population and lost due to natural mortality, then decreases as more fish are caught at an age younger than the age that maximizes the biomass of the cohort. Yield is a tradeoff between increases in yield-per-recruit as the stock becomes more depleted and individuals are caught before the loss due to natural mortality is greater than the gain due to growth and losses in recruitment due to reduced spawning stock size through the stock–recruitment relationship.

Despite the importance of depletion in modern fisheries management, limited attention has been paid to how depletion estimates are derived and potentially what data types provide the most reliable information on depletion level [3,4]. In the simplest cases of estimating depletion, if an index of relative abundance (e.g., surveys or catch-per-unit-effort (CPUE)) is available from the start of the fishery, depletion estimation could be as simple as dividing the current estimate of relative abundance by the estimate from the start of the fishery. In practice, an index is seldom available from the start of the fishery, and a stock assessment model, based on the total catch history, must be used to estimate depletion levels. However, many possible issues must be addressed to provide a reliable estimate of depletion. Variability, trends, and cycles in recruitment that are independent of fishing make characterizing unexploited abundance difficult [5,6], and there are several factors affecting the relationship between abundance and the index that need to be addressed [7].

In the absence of a complete catch history, a short-term model that estimates the initial depletion level must be used. In this case, assumptions need to be made to determine the abundance in the absence of fishing. In particular, recruitment in the unexploited state needs to be determined, and its relationship with the current estimates of recruitment will rely on the stock–recruitment relationship, which is generally uncertain if not unknown. The stock–recruitment relationship is also an influential factor in determining reference points. Therefore, the assumptions about the stock–recruitment relationship can be important in determining depletion. Some limit reference points are based on the decline in recruitment due to fishing, which is a direct consequence of the stock–recruitment relationship (e.g., [8]). Reference points can also be highly dependent on the assumptions about natural mortality, which can be highly uncertain.

In this paper, we describe the main issues that must be considered when estimating depletion levels and the role that the stock–recruitment relationship plays in both the depletion estimates and the reference points they are compared against. We provide an overview of commonly available data types that inform estimation of depletion and how prevailing model assumptions can affect their contribution. A simple numbers-based age-aggregated population dynamics model that incorporates a Beverton–Holt stock–recruitment relationship is used to illustrate the concepts using total catch history and short-term modeling approaches. We show that the importance of the concept of depletion versus absolute measures as a management quantity results from the prevailing assumption of strong stock–recruitment relationships. It is our argument that the role of the stock–recruitment relationship in depletion as a management quantity is compounded because both the level of depletion estimated and the reference point it is compared against are often directly influenced by poorly understood assumptions about the stock–recruitment relationship.

2. Depletion Estimation

There are a variety of data that provide information on depletion, and they can all be integrated into a single analysis [9]. Here, we focus on the most commonly available data: indices of relative abundance and catch composition data, both in age and length. We do not discuss other less common data types like mark-recapture, census counts, etc. We also discuss how the system processes (recruitment, natural morality, growth, and selectivity) and temporal variation of the key system process recruitment impact the estimates of depletion.

2.1. Index of Relative Abundance

Magnusson and Hilborn [3] and Maunder and Piner [4] described how absolute abundance is calculated from an index of abundance. The change in the index of abundance caused by catch and adjusted appropriately for productivity (recruitment plus growth minus natural mortality) can be used to scale the catch to absolute abundance.

$$B_t = \frac{C_{\Delta t}}{1 + P_{\Delta t} - \frac{I_{t+\Delta t}}{I_t}} \tag{1}$$

where

B_t is the absolute biomass in time t.

$C_{\Delta t}$ is the catch in weight during time interval Δt.

$P_{\Delta t}$ is the production rate (growth plus recruitment minus natural mortality per unit biomass) during time interval Δt.

I_t is the index of relative abundance (related to B, i.e., in biomass) in time t.

The depletion estimator of biomass (Equation (1)) only provides information on abundance over the range of the index and only if the index is proportional to abundance. (Equation (1)) is formulated to illustrate estimation of depletion over a single given length of time Δt (i.e., from t to $t + \Delta t$), but typical application in a stock assessment information comes on an annual basis over many years). To estimate the depletion level, unexploited absolute abundance also needs to be determined. This often means extrapolating the abundance back in time to the start of the fishery, accounting for the removals and the productivity [10] (Figure 2). The simplest approach is to use a surplus production model to project the abundance from the start of the fishery, removing the catch, and fitting to the index of abundance (for example, see the observation error estimation approach in [11]). The formulation of the surplus production model accounts for the production at different depletion levels (Figure 1) and implicitly combines recruitment, growth, and natural mortality into the functional form and the model parameters [12]. The index of abundance does not only have to provide information about the absolute abundance (i.e., the catchability coefficient), but also about the parameters of the production function. In the simplest case (e.g., a Schaefer [13] or a Fox [14] model), the parameters of the production function are a parameter representing the carrying capacity and a parameter representing the production rate of the stock. The production model parameters and the functional form of the production function determine at what levels and how quickly the production rate decreases as a function of absolute biomass. In general, unless the index covers a period of substantial fishery-induced changes in abundance (often referred to as informative contrast), all the parameters of the model cannot be reliably estimated, resulting in uncertainty about the depletion level.

Uncertainty in the depletion level arises because the model can account for the same removals by estimating low productivity with a large carrying capacity or high productivity and a low carrying capacity (i.e., is the catch mainly removing standing biomass or mainly removing the production). For example, catch causing only a small amount of depletion could be due to a large unproductive stock for which the catch is only a small fraction of the total biomass or from a highly productive small stock for which the total production is close to the catch. The form of the production function (i.e., the depletion level where maximum production occurs, and thus maximum sustainable yield (MSY), occurs) can influence the estimated depletion level, but the form of the production function tends to be less important for estimating depletion than it is for estimating the depletion level corresponding to MSY (e.g., [15]), particularly as the length of the index of abundance increases. This estimation procedure is further complicated when estimating an additional parameter controlling the shape of the production function, as in the Pella–Tomlinson model [16].

In the ideal situation, the estimation of carrying capacity, productivity, and depletion is achieved when the catch history is known back to the start of the fishery so that the model begins without consideration of initial depletion. Reliable information from the start of fishing is rare, and, in some cases, analysts have resorted to reconstructing these historical catch histories (e.g., [17,18]). It is worth reminding analysts that these reconstructed historical catch histories often come with estimation bias and uncertainty that should be considered in the assessment model.

An alternative to using the entire catch history is to start the assessment model at an exploited state (a short-term model) and estimate the depletion level as a model parameter(s). Often the model is started when the index of abundance becomes available or when the catch data become reliable. As with estimating the shape parameter of the production function, estimating the initial depletion level further complicates the analysis and is likely only possible when there is informative contrast in the data. In a short-term model, similar catch-caused depletion over the period of the index can be obtained from the same stock due to low productivity when a stock is lightly exploited and close to its carrying capacity with large biomass or higher productivity when the stock is heavily exploited (e.g., close to the level that produces maximum sustainable yield) and at low biomass. This decouples carrying capacity from the depletion level. In addition, a low biomass level, for example, can be either a high carrying capacity stock depleted to low levels or a low carrying capacity stock less depleted. The decision about how to start the model may be a tradeoff between bias caused by high levels of error in the historic catch and regime shifts or long-term trends in recruitment in a total catch history model versus variance by estimating the depletion level in a short-term model [19] (Figure 3).

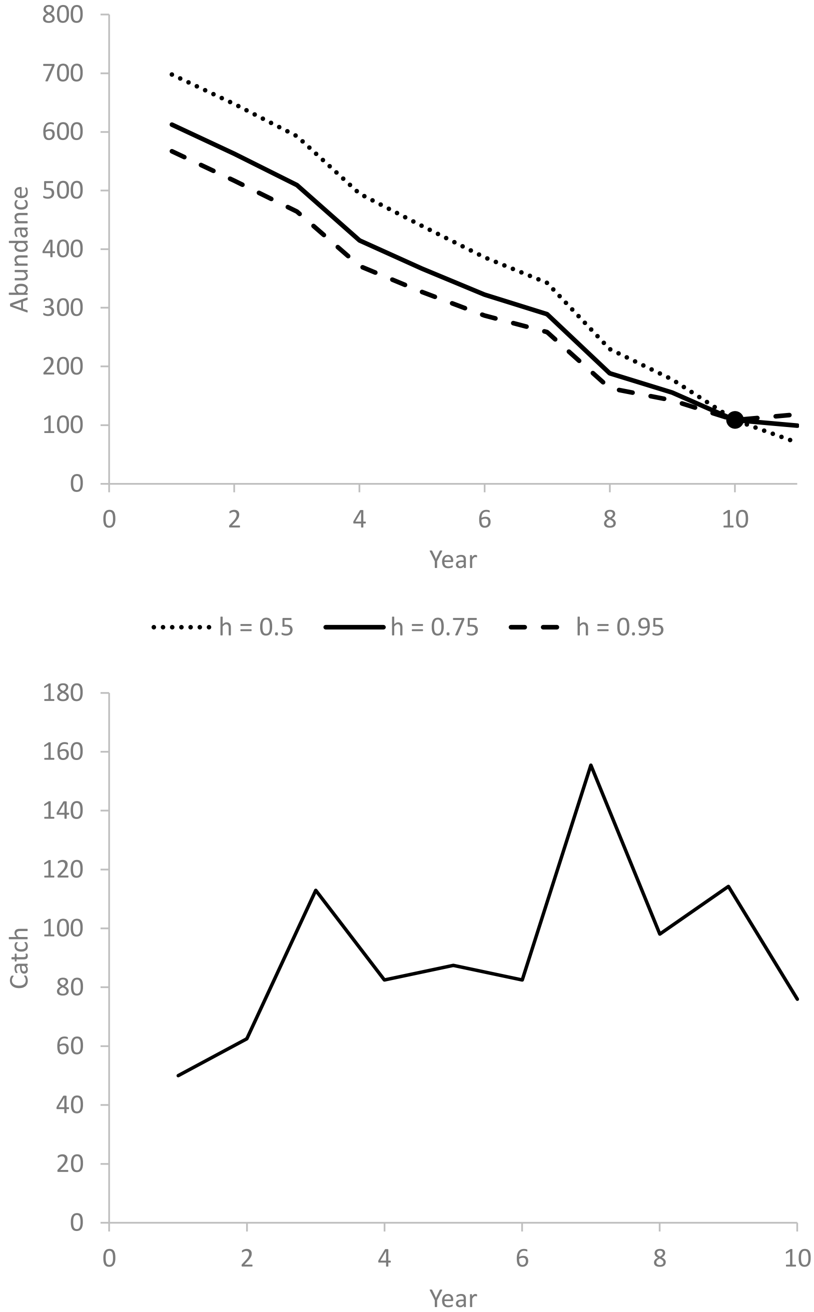

Figure 2. Estimates of historic abundance reconstructed with different steepness values of the stock–recruitment relationship from a given absolute abundance level in year 10 (**top**) under a given catch trajectory (**bottom**). Units in number of individuals. The simple population dynamics model is described in Appendix A and is fit to an absolute biomass estimate in year 10.

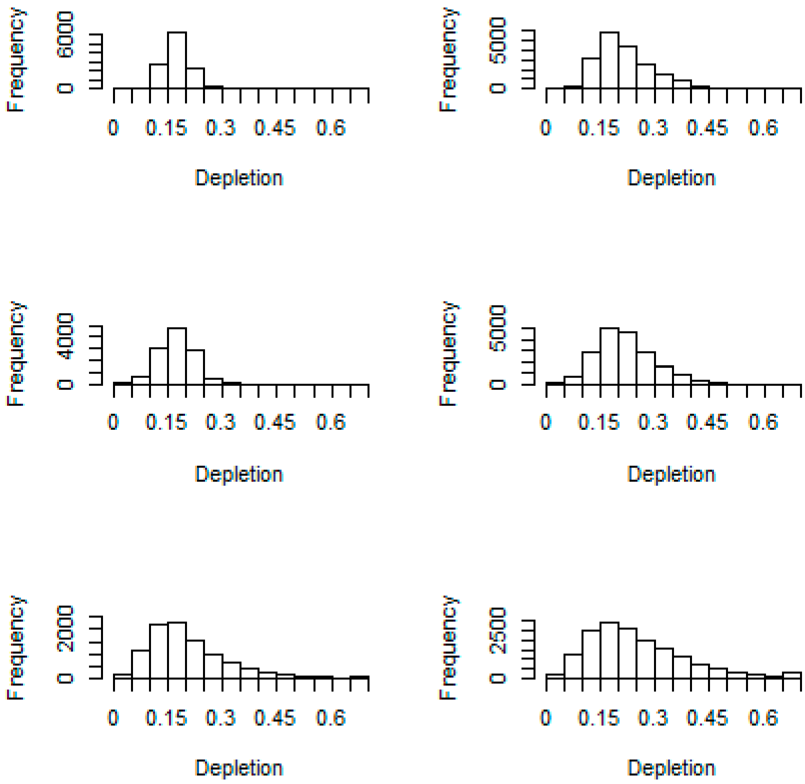

Figure 3. Uncertainty in depletion level represented by the posterior distribution for a total catch history model (R_0 estimated) (**left**) with known h = 0.75 and no recruitment variation (**top**), uniform prior on h = U(0.5, 1.0) and no recruitment variation (**middle**), uniform prior on h = U(0.5, 1.0) and recruitment variation sd = 0.6 (**bottom**) versus short-term model (R_0, initial recruitment, and initial fishing mortality estimated) (**right**) using the simple model described in Appendix A fit to an absolute biomass estimate in year 10. The prior on R_0 is U(0, 200).

Using the index of abundance to inform depletion, particularly when not starting the model in an unexploited state, requires a good understanding of the production function. Thus, using all available information about the production function should be considered. The production function combines growth, natural mortality, and recruitment, which are separate biological processes [12], and selectivity to some extent [20]. Therefore, it may be more appropriate to consider using a fully age-structured population dynamics model and account for each of these biological processes explicitly rather than as an aggregate in a biomass dynamic model [21]. Regarding how well we know these biological processes, we believe there is a general consensus that growth is reasonably well known for the common sizes of fish caught for many stocks and are the ages that most influence the production function [22]. Natural mortality is not as well known for most species and is almost always far more variable (age, sex, and temporally) than typically treated. Recruitment is perhaps the most variable, as it is impacted by unknown environmental drivers and is also where most of the density dependence is assumed to occur. The density dependence is described by the shape of the stock–recruitment relationship, and the relationship is often parameterized with a parameter that scales the absolute abundance and determines carrying capacity [23]. The steepness parameter (defined as the proportion of recruitment from an unexploited population realized when the stock is depleted to 20% of its virgin spawning biomass [24,25]), which determines how expected recruitment changes with spawning stock biomass, can greatly affect the shape of the production function (via the current recruitment relative to that of an unexploited population) and therefore the depletion level (Figure 4). Magnusson and Hilborn [3] and Lee et al. [26] show, using simulation analysis, that estimates of natural mortality are much more uncertain than estimates of the steepness of the stock–recruitment relationship even when both an index of abundance and composition data are available. However, estimates of the steepness of the stock–recruitment relationship can be biased. Estimates of natural mortality are more reliable when composition data are available from the start of the catch history (i.e., low fishing mortality), since composition data provide information on total mortality [3], but this is not commonly available.

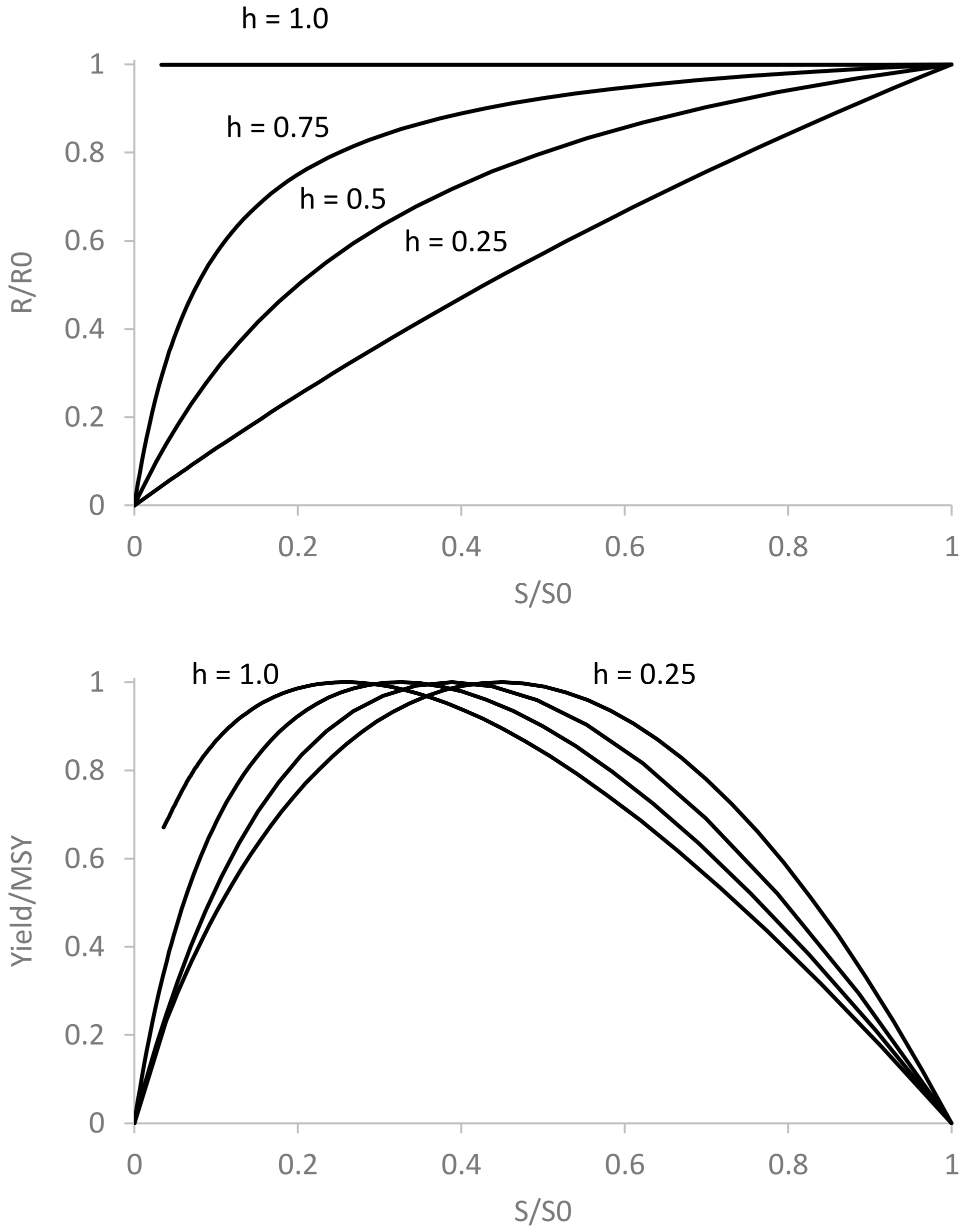

Figure 4. Recruitment as a fraction of virgin recruitment (**top**) and yield and a fraction of maximum sustainable yield (MSY, **bottom**) for different levels of depletion (spawning biomass divided by virgin spawning biomass, S/S_0) and different steepness values of the stock–recruitment relationship. The latter represents the production function.

In an age-structured model, the unexploited biomass is typically calculated as an equilibrium quantity by taking the average recruitment in an unexploited condition (R_0) and adjusting it for natural mortality as a cohort ages, then taking the product of the numbers at age with weight at age (or some other measure of reproductive output). To illustrate the process of calculating unexploited recruitment and its impact on the estimates of current depletion level, take an example where the absolute abundance and recruitment can be estimated well for the current state. The unexploited recruitment, and thus the unexploited biomass and depletion level, will simply be a function of how much the recruitment increases (or decreases in case of a dome-shaped stock–recruitment curve such as the Ricker) in an unexploited state, which is simply a function of the stock–recruitment relationship (like the concept illustrated in Figure 2). Therefore, to estimate the depletion level, it is important to use the correct stock–recruitment relationship.

Starting the model from a depleted state is more complicated when using an age-structured model because the abundance at each age in the initial population must be estimated [27]. The initial age structure could be constrained to reduce the number of parameters, but generally requires at least a parameter for the recruitment and a parameter for the equilibrium fishing mortality (Figure 5). In cases where the recruitment is assumed to be independent of stock size, the recruitment used to create the initial conditions could be set equal to the average recruitment. Annual variation in recruitment for cohorts compromising the initial conditions may need to be estimated.

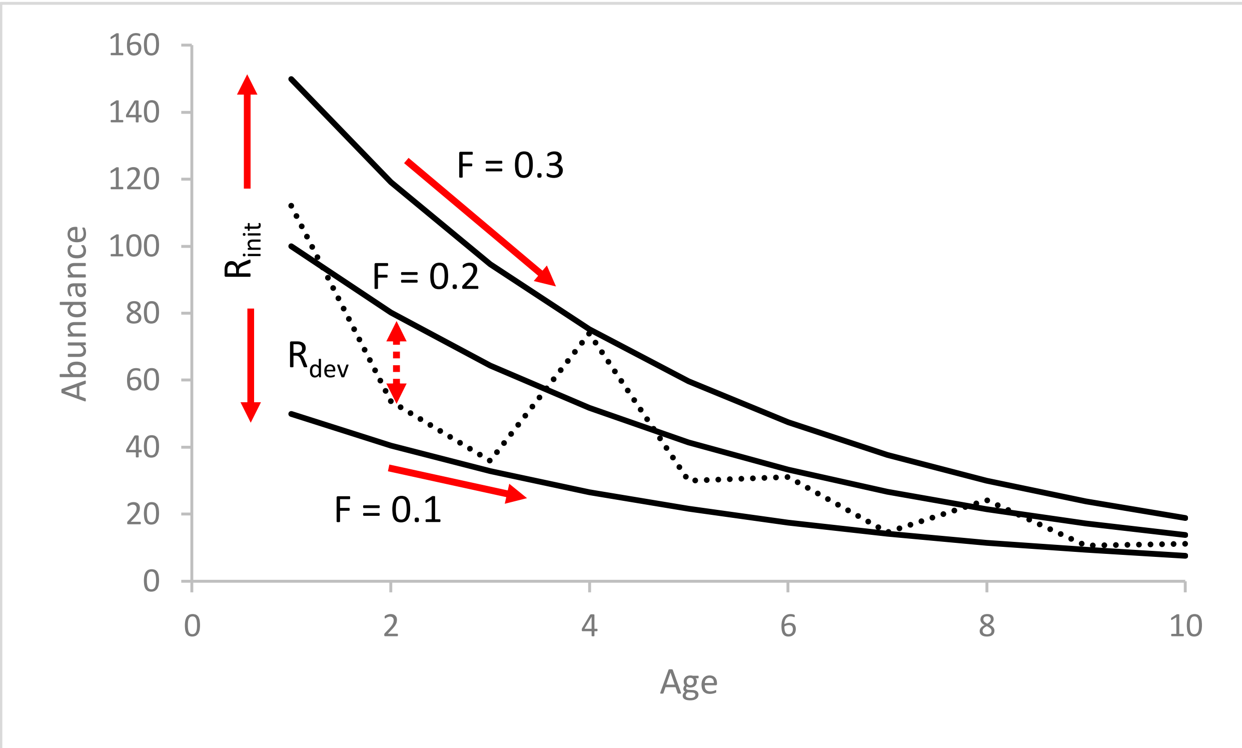

Figure 5. The age-structure of an exploited population at the start of the modeling time period in a short-term model is represented by R_{init} that scales the recruitment and compensates for the stock–recruitment relationship and any other trends or regime shifts in recruitment that occurred before the start of the modeling time period, F_{init} that represents the historic fishing, and R_{dev} that represents individual variation in recruitment (and fishing mortality or other process variation) related to that cohort [27].

2.2. Composition Data

Maunder and Piner [4] also described how absolute abundance is calculated from composition data. Catch-curve type information from measuring the decline in abundance of a cohort as it ages over time can be used to estimate the total mortality, and, after adjusting for natural mortality, the fishing mortality and catch can be used to estimate abundance. The depletion level can be determined by calculating the biomass under total mortality for any arbitrary recruitment level and under natural mortality and taking the ratio. This approach is independent of the absolute abundance or the average recruitment. However, it does assume that recruitment is the same with fishing and without fishing. Therefore, recruitment in an unexploited population relative to the exploited population needs to be known (i.e., derived from the stock–recruitment relationship) and the unexploited biomass adjusted accordingly. This has the same issues with the stock–recruitment relationship as mentioned when using an index of relative abundance. There are many complications when using composition data to estimate abundance or depletion due to factors like aging error, converting length compositions into age composition, recruitment variation, etc., which are more thoroughly described in [4].

Absolute abundance can also be calculated from catch at age, if the total catch-at-age is known, using cohort analysis [28], virtual population analysis (VPA) [29], or similar approaches (e.g., [30,31]). These approaches essentially sum up the catch-at-age adjusted by natural mortality for a cohort to estimate the absolute numbers at age, which can then be used to calculate absolute abundance. There is the complication that the fishing mortality for the oldest age of each cohort needs to be assumed or estimated, and there have been several approaches developed to deal with this (e.g., [32]). Cohorts that have been recently recruited are not represented by all ages, and therefore the terminal fishing mortality for each cohort (i.e., that in the most recent year) must be determined for younger ages. The resulting estimates of recruitment and the assumed value for natural mortality can then be used to calculate the unexploited abundance to determine the depletion level. Like the catch-curve approach, it also assumes that recruitment in the unexploited population is the same as the exploited and has the same issues with needing to know the stock–recruitment relationship and adjusted appropriately. The estimates are also clearly dependent on the value of natural mortality, as is also the case for the catch-curve approach described above since fishing mortality is the total mortality less the natural mortality.

2.3. Integrated Analysis

Integrated analysis allows the use of all available information to estimate the parameters of the stock assessment model and therefore extracts information on depletion level both from indices of abundance and from composition data [9,33]. Because all data are linked via the estimated dynamics, if any data contain the appropriate information, the parameters of unobserved processes can be theoretically estimated. For example, if the index of relative abundance provides strong information on absolute abundance and therefore on fishing mortality through the relationship between absolute abundance, known catch, and fishing mortality, then the information on total mortality from the composition data can be used to estimate natural mortality [34]. Magnusson and Hilborn [3] show how estimates of depletion are improved if both indices of abundance and composition data are used compared to only one of the data types by themselves, particularly if natural mortality and steepness of the stock–recruitment relationship are estimated.

The information on absolute abundance from the index of relative abundance requires the catch-caused depletion to be adjusted by production. As mentioned above, this production is recruitment plus growth minus natural mortality. If growth for the most abundant ages is known and natural mortality can be estimated from the composition data, then the remaining component of the production is recruitment. Cohort analysis also estimates recruitment from the catch-at-age data. This suggests that information may be available from an index of relative abundance and composition data on the stock–recruitment relationship, but the data would need to be available over a wide range of stock sizes to be informative, as has been illustrated by simulation analysis (e.g., [3]).

Information content of combining composition data and an index of relative abundance (i.e., integrated analysis) can be illustrated by applying a depletion estimator to each age and year. Using age composition data corresponding to the index, age-specific indices of abundance can be generated and, in combination with total catch-at-age data from the fishery, can be used in an age-specific depletion estimator. For illustrative purposes, assume that the catchability is the same for each age so that a consistent index of relative abundance is available for consecutive ages of the same cohort. Natural mortality is assumed to be independent of age. The catch-at-age and age-specific indices of abundance can then be used to determine the abundance for that cohort at that age (Equation (2)). Clearly, composition data and an index of abundance provide substantial information about a cohort (i.e., the abundance as the cohort ages), which, intuitively, should provide information on the initial abundance of the cohort (i.e., recruitment) and natural mortality (i.e., natural mortality is related to the change in abundance of a cohort from one age to another less the associated catch).

$$N_{t,a} = \frac{C_{t,a}}{e^{-M} - \frac{I_{t+1,a+1}}{I_{t,a}}} \tag{2}$$

Both recruitment and spawning biomass (summing the product of maturity, fecundity, and abundance for each cohort present in a particular year) are estimable, and these can be used to determine the stock–recruitment relationship if there is contrast in the spawning biomass and not excessive estimation error or recruitment variability. Arguably, in most cases (i.e., where the observation error for the index of abundance is moderate to high), the exploitation rate must be high and must change over the history of the fishery to be able to estimate age-specific natural mortality [35], unless composition data are available from the start of the fishery (i.e., low fishing mortality since composition data provide information on total mortality).

2.4. Temporal Variation in Recruitment's Influence on the Depletion Estimator

Recruitment is usually variable and does not simply follow the stock–recruitment relationship [35,36]. Both integrated models and cohort analysis estimate temporal variation in recruitment (as annual estimates of absolute recruitment or deviations from the expectation of the stock–recruitment relationship). Surplus production models traditionally ignored the process variation in the production function caused by recruitment variation or, alternatively, assumed no observation error [11]. However, more contemporary versions of production models (e.g., state space models; [20,37]) allow for process variation (often called process error) in addition to observation error. However, since they do not fit to composition data, the information on recruitment is combined over multiple cohorts in the index of relative abundance. In some stocks, recruitment makes up a large proportion of the stock biomass and therefore accounts for variation in recruitment in the estimates of current biomass, and thus depletion levels become important. Using surplus production models for these types of species and using age- or size-structured models that do not have information to estimate process variation (e.g., composition data or indices of recruitment) may not provide good estimates of depletion.

Research shows that extraction of information on absolute abundance from indices of relative abundance often requires information about recruitment variation [38]. This is particularly true for stocks for which recruitment makes up a large component of the biomass (i.e., short-lived species), have large fluctuations in recruitment, or exhibit regime shifts or trends in recruitment. Composition data are the main source of information on recruitment variation, but composition data also include information on absolute abundance through the catch-curve process (see above), and this type of information is particularly sensitive to uncertainty in population processes, including growth, when length composition data are used [39]. Good age data or other information on recruitment (e.g., recruitment surveys) improve the estimates of absolute abundance and therefore depletion levels.

3. Depletion-Based Reference Points

3.1. Double Jeopardy of the Stock–Recruitment Relationship

There are a variety of ways to determine biomass-based reference points. Often, they are set in terms of either absolute abundance or depletion level. Using depletion levels may be more common because the reference points often correspond to relative abundance levels, based on stock–recruitment theory, where recruitment is impaired. Furthermore, depletion-based (relative) reference points automatically adjust with each new iteration of the stock assessment. Absolute reference points based on historic biomass (e.g., the lowest observed biomass or median biomass) do not require estimating the depletion level accurately, only requiring estimation of the current biomass relative to the historic biomass. The logic is generally based around the fact that the stock did not collapse in the past, so the historic biomass levels are safe. However, the age-structure, environment, and other factors may not be the same. Relative reference points such as the arbitrary 20%B_0 or the more intuitive, but still arbitrary, limit reference points of Maunder and Deriso [8] based on predicted decline in recruitment require the estimation of depletion. Reference points such as the biomass at maximum sustainable yield (B_{MSY}), which have been used both as a target and a limit reference point, rely on the stock–recruitment relationship as do its proxies (due to their selection based on simulations with alternative stock–recruitment relationships, e.g., SBR35%; [40]).

Misspecifying the stock recruitment relationship not only biases the reference point, but as described above, also biases the estimate of depletion level, causing the double jeopardy. Take, for example, assuming the steepness of the Beverton–Holt stock recruitment relationship is 0.7 when it is close to 1.0. The biomass level at the MSY-based reference point (B_{MSY}/B_0) is estimated to be less depleted than it should be since the lower steepness causes the recruitment in an unexploited population to be higher than in an exploited population, and therefore the unexploited biomass is estimated to be higher (Figure 6). The estimated current depletion is often also estimated to be lower (it may depend on the type of data and whether the model covers the whole catch history of the fishery, see Figure 6), both making it less likely that the stock is above the reference point.

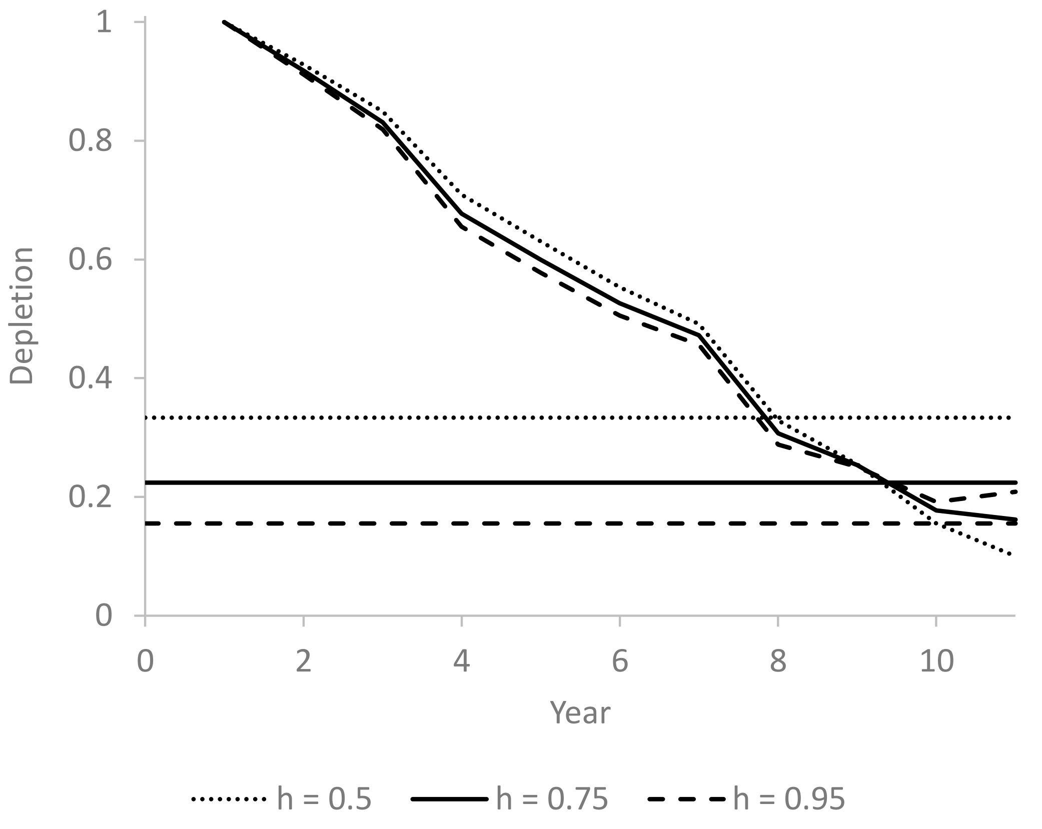

Figure 6. *Cont.*

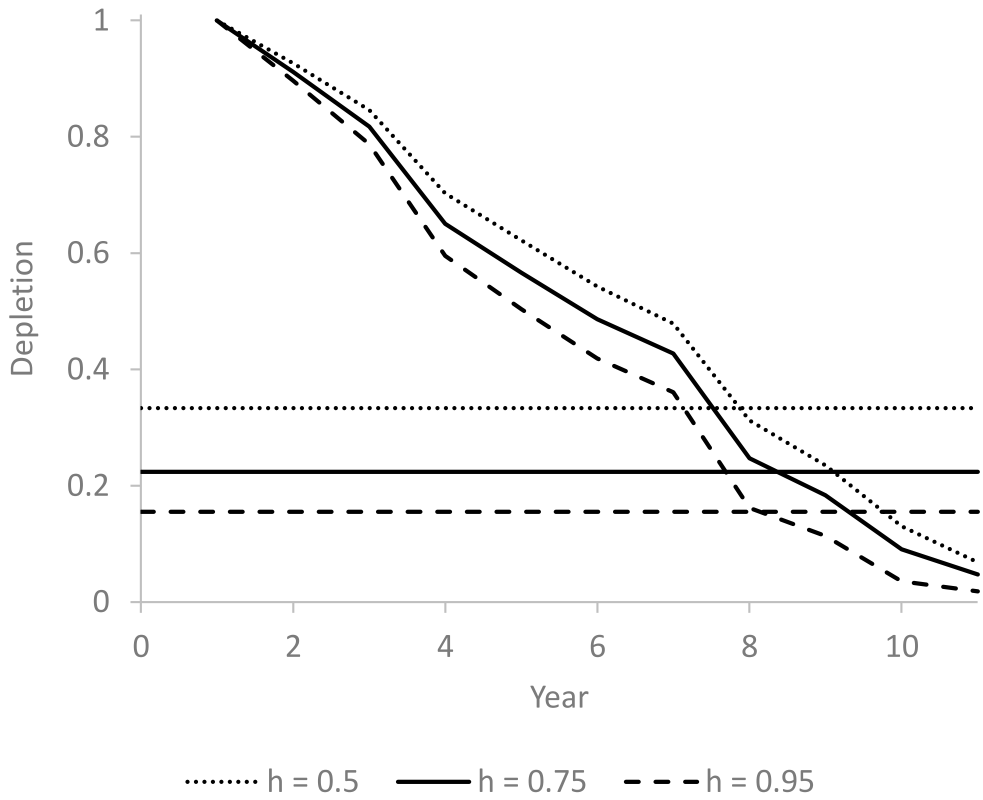

Figure 6. Estimates of depletion of a hypothetical application under different assumed values of h and the associated MSY-based biomass reference points when fit to an absolute abundance estimate in year 10 (**top**) and to the change in the index from year 10 to year 11 (**bottom**).

3.2. Temporal Variation in Recruitment's Influence on Reference Points

Accounting for variation in recruitment is not only important for estimating depletion level but also evaluating current status against biomass-based reference points [5]. An extreme example is a stock with highly variable recruitment that makes up a large component of the stock biomass. It is theoretically possible that the population could go below the reference point even in the absence of fishing just due to a run of low random recruitment. However, the more likely example is that a stock fished at the fishing mortality rate corresponding to MSY (F_{MSY}) will fluctuate around B_{MSY} due to random variation in recruitment. Therefore, having F_{MSY} as a target fishing mortality reference point and B_{MSY} as a limit biomass reference point would make little sense. The difference in strategy between target and limit reference points may be related to the question of whether the level of absolute or relative biomass causes the risk threshold. It is our contention that in situations where a strong stock–recruitment relationship is assumed to be the key component of risk, then a relative (depletion)-based reference point may be preferable. In situations where maternal stock size is not related to recruitment, perhaps absolute reference points may be applicable.

A more complicated component of temporal variability is when recruitment is highly autocorrelated or experiences regime shifts or trends over time that are dependent on the environment and unrelated to stock size. With environmentally driven non-stationary productivity, the analyst is forced to address the question of how to characterize the unfished state. Unexploited biomass can be calculated in multiple ways, which likely also relate to assumptions about the strength of the stock–recruitment relationship. Historically, the unexploited biomass was calculated using predictions of unexploited recruitment taken from the stock–recruitment relationship without depletion. This method produces what many refer to as an equilibrium unfished stock size (B_0). More recently, the alternative unexploited stock abundance has been calculated using only recent recruitments and projecting stock abundance over the historic period as if fishing had not occurred [41]. This method is often referred to as dynamic B_0, as it will fluctuate with changes in environmental productivity. Similarly, dynamic biomass corresponding to maximum sustainable yield (B_{MSY}) can be calculated by fishing at the fishing mortality corresponding to MSY. Clearly, the equilibrium B_0 assumes a strong maternal effect and stationarity of that effect, while the dynamic B_0 hypothesizes that environmental factors are the primary drivers of recruitment. An intermediate form of B_0 can also be calculated using the method of dynamic B_0 and adding in the estimated loss of expected recruitment based on the stock–recruitment relationship and estimated depletion levels. However, the logic of assuming stationarity in the stock–recruitment relationship and changing productivity regimes is not clear. In current practice, the dynamic B_0 appears more used for short- to moderately long-lived pelagic species such as tunas and the equilibrium B_0 for long-lived demersal fishes (although it is more complicated for long-lived species that are sustained by periodic large recruitment). The question of how to evaluate stock status against reference points in a non-stationary world is not yet settled, but it may be more appropriate to consider recruitment regimes in evaluating target reference points than limit reference points.

4. Discussion

Estimation of depletion and relative reference points are perhaps most crucial and applicable when a strong stock–recruitment relationship can be assumed. It therefore seems cruel that estimates of depletion are often uncertain precisely because they are dependent upon a poorly understood stock–recruitment relationship. The two most common conceptual approaches to overcome poorly understood stock–recruitment relationships are: (1) conduct research to improve stock–recruitment understanding (e.g., [23,35,42–45]), or (2) use management strategies (including defining reference points) that are independent of the stock–recruitment relationship (e.g., $F_{0.1}$; [46]), robust to uncertainty about the stock–recruitment relationship (e.g., [40]), or simply focus on management objectives that are independent of the stock–recruitment relationship (e.g., yield-per-recruit; [47]).

The success of the research aimed at better understanding stock-specific stock–recruitment relationships has been mixed at best. Even when a good time series of stock and recruitment is available, high variation in recruitment makes the relationship uncertain. To “smooth” out this variation, some authors have used meta-analysis to combine data from many stocks and estimate the parameter controlling density dependence (e.g., [48]). However, these methods may be misleading because phenomena like regime shifts or trends in the environment over time can bias the estimates [49–51]. Simulation studies aimed at evaluating the integration of its estimation within the stock assessment model have been equally underwhelming. Integrated model estimates are often biased towards recruitment being independent of stock size or with unrealistically low levels of density dependence [3,52].

Attempts to develop management strategies robust to uncertainty in the stock–recruitment relationship have not fared much better. Often strategies meant to overcome our lack of understanding of the stock–recruitment relationship are based on implicit assumptions about the stock–recruitment relationship (e.g., [37]). Other approaches dealing with the uncertainty in the stock–recruitment relationship are simply precautionary and do not optimize yield (e.g., keep biomass at the current level or increase it by 10%). What is clear is that estimation of depletion and development of good management strategies will be more easily accomplished for some stocks than others. For example, there is growing evidence that recruitment is not demonstrably reduced at low biomass for large mobile highly fecund pelagic spawners (e.g., tuna), and factors such as yield-per-recruit and profitability should become important limits on fishing before recruitment is reduced. In other cases where the species has low fecundity and complex spawner–recruit relationships (e.g., sharks), setting biomass reference points will only be as good as our understanding of that relationship. Clearly, a one-size-fits-all approach to developing and evaluating reference points will not work equally well for all species.

The issues associated with estimating depletion go well beyond the uncertainty in the stock–recruitment relationship. Although depletion level is a relative metric, all the issues associated with estimating absolute abundance outlined by [4] are still relevant. Estimates of depletion are dependent on the estimates of natural mortality, selectivity (degree of being dome-shaped), and the growth curve when fitting to length composition data. Of particular concern is the influence of the asymptotic length (L_∞) of the growth curve on the estimates of depletion level. The fewer individuals observed at the asymptotic length, the higher the model must make the fishing mortality to predict the length composition. Equally important, reliable estimates of depletion can only be derived from unbiased indices of abundance. Methodological improvements in the analysis of survey and CPUE data may aid in the development of indices (e.g., [7]), and improvements of genetic technology may provide some hope through close-kin mark-recapture to create alternative time series of absolute spawning biomass and estimates of natural mortality [53].

Clearly, natural mortality is important for estimating depletion from both indices of abundance and composition data [3,4]. However, natural mortality is often very uncertain because it is based on unreliable tagging studies, general relationships with other biological parameters (e.g., maximum age or growth rate), or borrowed from other stocks [54]. Also, estimates of natural mortality from within the stock assessment are uncertain [3,26] and generally require composition data from when the fishing mortality is low (i.e., at the start of the fishery [3]) or high contrast in the fishing mortality [55]. Given that obtaining composition data from periods of low fishing mortality is not practical for most commercial stocks, well-designed tagging programs, particularly close-kin mark-recapture [56], are likely the most promising approach to estimate natural mortality. In addition, tagging programs can provide estimates of absolute abundance, which would greatly improve the stock assessments and probably the estimates of depletion. However, they will not directly provide information on the stock–recruitment relationship.

Beyond the data used, questions regarding the modeling approaches will still need to be considered. Decisions need to be made on whether to use a total catch history model where much of the catch history is uncertain due to reconstruction [17,57] or a short-term model that starts at a depleted stock via estimating the initial conditions (see Figure 3). Proponents of the total catch history approach argue that the catch history provides information on depletion. Proponents of the short-term modeling approach argue that uncertain historical catch and regime shifts or long-term trends in recruitment or other processes caused by the environment can bias the results. In either case, we have shown how the assumed stock–recruitment relationship may impact the estimates of depletion. The short-term model may use the stock–recruitment relationship to reconstruct the recruitment from an unexploited population, which is used to calculate the unexploited biomass and thus the depletion level. More freedom to estimate the initial conditions (e.g., not fitting equilibrium catches, estimating recruitment prior to the start of the model) is often used, diminishing the influence of the stock–recruitment relationship. In contrast, the total catch history model relies on the stock–recruitment relationship to estimate the whole time series of recruitment back to the start of the catch history. In practice, total catch history models often estimate annual recruitment deviations over the entire period (including the period with only historical catches), which can disconnect the historical recruitment from the stock–recruitment relationship. When these early recruitments are given sufficient freedom, this approach becomes similar in function to a short-term model. This likely also reduces the early catch influence on depletion and allows the more recent data (composition and indices) to influence the estimation of depletion. Conceptually, it appears that when total catch history models are used, they should be somewhat influenced by the stock–recruitment relationship and that careful consideration should be given to allowing too much freedom in the early recruitment period. Otherwise, using the total catch history appears redundant, and the calculation of the unexploited biomass becomes more complicated. Conversely, short-term models may be more appropriate for short-lived species where a strong maternal effect is considered unlikely. In these cases, careful consideration should be given to allowing enough freedom in the initial conditions to reduce the effects of any assumed maternal influence on recruitment. It may be less clear what should be undertaken when a species is long-lived but exhibits periodic large recruitment events.

The tyranny of the stock–recruitment relationship does not stop with estimation of depletion but has also likely controlled our thinking regarding defining reference points. In general, limit reference points are designed to avoid substantial reduction in recruitment to avoid collapse of stock. Because the stock–recruitment relationship relates recruitment to stock size, it is important to know the stock–recruitment relationship to define the depletion level where expected recruitment is substantially reduced. This is the approach used to define limit reference points for tropical tunas in the eastern Pacific Ocean by [8]. However, even if the stock–recruitment relationship is well known, the level of recruitment reduction considered risky and used to define the reference point is still likely to be arbitrary. Reference points, harvest strategies, and management objectives that are robust to uncertainty about the stock–recruitment relationship may still be needed.

Author Contributions: Conceptualization, M.N.M. and K.R.P.; software, M.N.M.; formal analysis, M.N.M.; writing—original draft preparation, M.N.M. and K.R.P.; writing—review and editing, M.N.M. and K.R.P. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data underlying this article will be shared upon reasonable request to the corresponding author.

Acknowledgments: We would like to thank Andre Punt for providing comments on an early version of the manuscript.

Conflicts of Interest: There are no conflicts of interest.

Appendix A

A simple number-based age-aggregated population dynamics model, which assumes catch in numbers is removed at the start of the year and includes a Berton-Holt stock-recruitment relationship, with a hypothetical application.

Table A1. Parameter values used in the simulation.

Quantity	Value
Number of years	10
σ_R^2	0.6
σ_I^2	0.2
Q	1
R_0	100
M	0.2
H	0.75

$$N_1 = N_0 \tag{A1}$$

$$N_{y+1} = \left(N_y - C_y\right)(1 - M) + R_{y+1} \tag{A2}$$

$$R_y = \frac{\alpha N_{y-1}}{1 + \beta N_{y-1}} e^{\varepsilon_y - 0.5\sigma_R^2} \tag{A3}$$

$$\alpha = \frac{R_0(1 + \beta N_0)}{N_0} \tag{A4}$$

$$\beta = \frac{0.2 - h}{0.2N_0 h - 0.2N_0} \tag{A5}$$

$$N_0 = \frac{R_0}{M} \tag{A6}$$

$$\varepsilon_y \sim N\left(0, \sigma_R^2\right) \tag{A7}$$

For simulations:

$$C_y = u_y N_y \tag{A8}$$

u = (0.1, 0.1, 0.2, 0.2, 0.2, 0.2, 0.5, 0.5, 0.7, 0.7, 0.7)

$$I_y = qN_y e^{\omega_y - 0.5\sigma_I^2} \tag{A9}$$

$$\omega_y \sim N\left(0, \sigma_I^2\right) \tag{A10}$$

The realizations of the simulated data used in our analyses were as follows:

C = (50, 62, 113, 82, 87, 82, 155, 98, 114, 76)

B_{10} = 108.5

B_{11}/B_{10} = 0.52

Units are expressed as the number of individuals.

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