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Considerations for defining reference points for Atlantic Salmon that conform to the Precautionary Approach

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

This paper addresses four of the terms of reference in support of a science review of reference points for Atlantic salmon that conform to the Precautionary Approach (PA) framework. The fixed escapement strategy and single reference point approach presently used for the management of Atlantic salmon does not conform to the PA as it does not set a maximum removal rate for the stock nor does it define an Upper Stock Reference (USR) at which the maximum removal rate would apply. The stock dynamics of Atlantic salmon are most often presented as spawner and recruit relationships which differs from the PA framework for which stock status is presented relative to the removal rate of the stock. It is straightforward to reconcile these two views by treating the recruitment on the stock and recruitment framework as the stock status axis in the PA framework. Three candidate limit reference points can be derived from exclusively freshwater dynamic models which respect population conservation considerations, are determined by the environment where the stock and recruitment density dependent dynamic is expressed, and are robust to variations in productivity associated with density independent dynamics (marine survival). The choice of the USR will depend upon the objectives of the fishery and the risk profile of the management strategy. The removal rate reference could be determined once the upper stock reference point is defined. The modelling of stock and recruitment relationships and the development of reference points are challenged by two conflicting considerations; the need for a long time series of contrasting abundance with which to adequately estimate life history parameters versus the risk that there will be systematic and sustained changes in the life history parameters being estimated. The consequences of reduced productivity, manifest in either freshwater or marine environments, are to reduce the adult recruitment per spawning stock which lowers the values of most reference points derived from full life cycle models. Provided the productivity in freshwater is stationary, then the few limit reference points defined on the basis of maintaining freshwater production levels would be robust to variations in marine productivity. The objective should be to maintain freshwater production to take advantage of better marine productivity periods when they occur. Since it is not possible to obtain stock and recruitment data from the over 1,000 rivers with Atlantic Salmon populations in eastern Canada, consideration must be made to transferring reference values from monitored rivers to rivers which lack such information. Hierarchical Bayesian methods are most appropriate in situations where reference points from data rich situations are transported to populations with limited to no information because the uncertainties associated with intra-population stock and recruitment dynamics and inter-population variation of this dynamic within a set of exchangeable units can be quantified. Quantifying uncertainty in the development and use of reference points consists of three components: uncertainty associated with the derivation of the reference point, the choice of the value of the reference point posterior distribution used in management, and uncertainty in the current status of the stock relative to the reference point. Bayesian approaches provide a means of considering these uncertainties in reference point development and application.

Considérations pour la définition de points de référence pour le saumon de l'Atlantique conformes à l'approche de précaution

RÉSUMÉ

Le présent document aborde quatre éléments du cadre de référence à l'appui d'un examen scientifique des points de référence pour le saumon de l'Atlantique qui sont conformes à l'approche de précaution (AP). La stratégie d'échappée fixe et l'approche de point de référence unique actuellement utilisées pour la gestion du saumon de l'Atlantique ne sont pas conformes à l'approche de précaution, car elles n'établissent pas de taux d'exploitation maximal pour le stock et ne définissent pas de point de référence supérieur (PRS) auquel le taux d'exploitation maximal puisse s'appliquer. La dynamique des stocks de saumon de l'Atlantique est le plus souvent présentée sous forme de relation recrues-reproducteurs, ce qui diffère du cadre de l'AP dans lequel l'état du stock est présenté par opposition au taux d'exploitation du stock. Il est simple de concilier ces deux notions en traitant le recrutement dans le stock et le cadre de recrutement comme axe de l'état du stock dans le cadre de l'AP. Trois points de référence limites possibles peuvent être tirés des modèles de dynamique exclusivement dulcicole qui respectent les considérations de conservation de la population, sont déterminés par l'environnement dans lequel la dynamique des stocks et du recrutement qui dépendent de la densité est exprimée, et qui résistent aux variations de productivité associées à la dynamique indépendante de la densité (survie en milieu marin). Les choix du point de référence supérieur du stock dépendent des objectifs de la pêche et du profil de risque de la stratégie de gestion. Le taux d'exploitation de référence peut être calculé une fois que le point de référence supérieur du stock est défini. La modélisation de la relation stock-recrutement et l'élaboration de points de référence sont remises en question par deux considérations contradictoires : la nécessité d'une longue série chronologique d'abondance contrastée pour estimer les paramètres du cycle biologique par opposition au risque qu'il y ait des changements systématiques et durables dans les paramètres estimés du cycle biologique. Les conséquences d'une diminution de la productivité, en eau douce ou en milieu marin, sont la réduction du recrutement d'adultes par stock reproducteur, qui fait baisser les valeurs de la plupart des points de référence découlant des modèles de cycle vital complet. Puisque la productivité en eau douce est stationnaire, les quelques points de référence limites déterminés en fonction du maintien des niveaux de production en eau douce seraient suffisamment solides pour résister aux variations de la productivité marine. L'objectif devrait être de maintenir la production en eau douce afin de tirer avantage des périodes de meilleure productivité marine lorsqu'elles surviennent. Étant donné qu'il est impossible d'obtenir des données sur les stocks et le recrutement pour les 1 000 rivières et plus de l'est du Canada comprenant des populations de saumons de l'Atlantique, il faut tenir compte des transferts de valeurs de référence des rivières surveillées aux rivières pour lesquelles il manque de tels renseignements. Les méthodes bayésiennes hiérarchiques sont les mieux adaptées lorsque les points de référence provenant de situations bien documentées sont transférés à des populations pour lesquelles les données sont limitées, voire inexistantes, puisque les incertitudes en rapport avec la dynamique des stocks et du recrutement intrapopulation, et les variations entre les populations pour ces dynamiques pour un groupe d'unités échangeables peuvent être quantifiées. La quantification de l'incertitude pour l'élaboration et l'utilisation des points de référence se compose de trois éléments : l'incertitude associée au calcul du point de référence, le choix de la valeur de la distribution a posteriori du point de référence pour la gestion et l'incertitude concernant l'état actuel des stocks relativement au point de référence. Les méthodes bayésiennes sont des moyens de tenir compte de ces incertitudes dans l'élaboration et l'application des points de référence.

INTRODUCTION

In 2009, Fisheries and Oceans Canada published the Sustainable Fisheries Framework that provides the basis for ensuring Canadian fisheries are conducted in a manner which support conservation and sustainable use (DFO 2009a). The framework provides the foundation of an ecosystem-based and precautionary approach to fisheries management in Canada. The framework is comprised of a number of policies for the conservation and sustainable use of fisheries resources including "A Fishery Decision-Making Framework Incorporating the Precautionary Approach" (DFO 2009a; hereafter referred to as the PA).

The Fishery Decision-making framework (the PA) applies where decisions on harvest strategies or harvest rates for a stock must be taken on an annual basis or other time frame to determine Total Allowable Catch (TAC) or other measures to control harvests. This is the case for many Atlantic salmon fisheries (recreational, Food Social and Ceremonial (FSC) fisheries for aboriginal peoples) in eastern Canada and internationally.

Recently, the Wild Atlantic Salmon Conservation Policy (WASCP) identified the concept of lower and upper benchmarks against which to assess stocks status (DFO 2009b). The translation of the presently used conservation limit for Atlantic salmon within this benchmark framework has yet to be done and will need to be considered in the context of other departmental policies including the Precautionary Approach.

In a recent review of development of reference points for semelparous and anadromous salmonid species, Chaput et al. (2013) provided an overview of the history of the development of reference points for Pacific salmon and Atlantic salmon and provided a list of candidate reference points, analysis methods, and examples for transferring reference points among stocks. Although most of the principles for developing reference points for other species apply equally to Atlantic salmon, life history features of semelparous species and for Atlantic salmon that differ from a large number of other species groups lead to differences in the management strategy for exploitation and the development of harvest decision rules.

This manuscript was prepared in support of a peer review meeting (DFO 2015) to review reference points for Atlantic salmon that conform to the Precautionary Approach (PA) framework (DFO 2009a). The manuscript is structured along the following objectives of the peer review meeting:

- Describe and propose candidates for limit reference points, upper stock reference points, and maximum removal rate reference points which could be defined for Atlantic salmon
- Advise on the appropriateness of using reference points that are specific to variations in productivity, particularly sea survival, which have occurred for Atlantic salmon.
- Review methods to transfer reference points to rivers which do not have river-specific values defined.
- Review and advise on methods to develop age-specific or size-specific (if appropriate) reference point values.
- Uncertainties in the development and use of reference points in fisheries management.

LIFE HISTORY FEATURES

Semelparous species such as Pacific salmon undertake a single reproductive event in their life cycle and die after spawning. Because of semelparity, spawning stock abundance is determined exclusively by the abundance of first time spawning individuals and variations in spawning stock abundance on year is entirely determined by recruitment as there is no accumulation of spawners over years. In most species, there are generally few age groups in the spawning population originating from a few year classes and fisheries on semelparous species occur on immature and/or first time spawning and maturing animals (Chaput et al. 2013).

In contrast to Pacific salmon, anadromous Atlantic salmon (*Salmo salar*) are iteroparous. Despite this propensity for multiple reproduction, the dominant component of the annual spawning stock is comprised of first time spawners and there are few year classes in the annual spawning run, even in stocks with a high degree of iteroparity (Chaput and Jones 2006). For these reasons, fisheries on Atlantic salmon occur predominantly on first time spawning and maturing animals, with limited marine fisheries on immature animals. The management of semelparous and anadromous salmonid species has been extensively focused on achieving escapement goals to ensure a level of spawning that would provide fishing and species benefits in the subsequent generation (Chadwick 1985).

Anadromous salmonid species utilize two distinct environments to complete their life cycle and population structuring at the scale of an individual river is highly evolved. Recruits return with high fidelity to the natal spawning locations (Keefer and Caudill 2014). In salmonid species that spend an extended period of time in freshwater as juveniles, density-dependent population regulation is well established, occurring in the first year or two of freshwater residency (Jonson et al. 1998; Elliott 2001; Gibson 2006) whereas there is no strong evidence of density-dependent survival at sea (Hansen and Quinn 1998). Due to the generally low abundance of Atlantic salmon in the North Atlantic (Chaput 2012), survival at sea is presumed to be density independent.

Atlantic salmon spawning and rearing habitat is highly spatially structured and anadromous salmonid females deposit a few (single digit) batches of hundreds to thousands of eggs in excavated gravel redds. As a result, the total progeny from a given year’s spawning can be subjected to highly heterogeneous survival and growth conditions within a large watershed while a batch of 100s to 1000s of individuals sharing a redd from a single female would be subjected to locally highly homogenous survival conditions.

In many stocks of Atlantic salmon, there is a strong sex bias in the sea age at maturity (O’Connell et al. 2006; Fig. 1). In Atlantic salmon populations that are dominated by one-sea-winter (1SW) age at maturity, there is a high proportion female in the returns and in the smolt migrants, with a high propensity for precocious male parr maturation. In salmon populations with multiple sea ages at maturity, males are more abundant in the returns of 1SW salmon and females are more abundant in the returns of multi-sea-winter (two-sea-winter, three-sea-winter) salmon (Chaput et al. 2006; O’Connell et al. 2006). There can also be important differences in the relative abundances of the sea age group in the annual returns to a river (Chaput et al. 2006). For this reason, stock status in Atlantic salmon is generally assessed relative to the estimated total number of eggs, with adjustments for increasing fecundity with body size and proportion female by size or age group.

The variations in environmental conditions in freshwater can be as important as those in the marine environment (Klemetsen et al. 2003). Early life stage survival in freshwater to migration to the ocean can be quite high for Atlantic salmon with estimated egg to smolt survivals as high as 7% in some stocks at low abundance (O’Connell et al. 2006), although it is usually much less than this. In contrast to many other fish species, survival at sea of larger animals remains quite low, and as a result of the high early stage survival rates in freshwater, populations can replace themselves at very low levels (<5%) of marine survival (Chaput 2003).

CANDIDATE REFERENCE POINTS AND THE PRECAUTIONARY APPROACH

BACKGROUND TO PRECAUTIONARY APPROACH

The chronology of the development of the PA framework is provided in DFO (2009a). In general, the PA is "about being cautious when scientific information is uncertain, unreliable or inadequate and not using the absence of adequate scientific information as a reason to postpone or fail to take action to avoid serious harm to the resource" (DFO 2009a).

There are three components to the general decision framework for the PA:

1. Reference points and stock status zones (Healthy, Cautious and Critical) (Fig. 2),
2. Harvest strategy and harvest decision rules, and
3. The need to take into account uncertainty and risk when developing reference points and developing and implementing decision rules.

The PA framework is generally presented as a two-dimensional plot with three status zones (Critical, Cautious, Healthy) with stock status on the x-axis and removal rate on the y-axis (Fig. 2). Along the stock status axis, the Limit Reference Point (LRP) corresponds to the boundary between the Critical and the Cautious stock status zones. The Upper Stock Reference (USR) point corresponds to the boundary between the Cautious and the Healthy stock status zones. A removal reference is defined along the removal rate axis.

In the context of fisheries management, the limit reference point is defined as the stock level below which productivity is sufficiently impaired to cause serious harm (DFO 2009a). There are two challenges associated with defining the LRP: the first is the choice of the indicator of potential productivity of the stock and the second is to consider what constitutes serious harm to productive potential.

The USR is the stock status level below which removals must be progressively reduced in order to avoid reaching the LRP. Under the PA framework, the USR, at minimum, must be set at an appropriate distance above the LRP to provide sufficient opportunity for the management system to recognize a declining stock status and for management actions to have effect. The USR can also be interpreted as a target reference point (TRP) determined by productivity objectives for the stock, broader biological considerations, and social and economic objectives for the fishery (DFO 2009a). While socio-economic factors may influence the location of the USR, these factors must not diminish its minimum function in guiding management of the risk of approaching the LRP.

The LRP is based on biological criteria and established by Science through a peer reviewed process (DFO 2009a). The USR would be developed by fishery managers informed by consultations with the fishery and other interests, with advice and input from Science (DFO 2009a).

The Removal reference is the maximum acceptable removal rate for the stock which would apply when the stock is in the healthy zone and includes all anthropogenic mortality. To comply with the United Nations Fisheries Agreement (UNFA), the Removal reference must be less than or equal to the removal rate associated with maximum sustainable yield (DFO 2009a). The removal rate through the cautious zone is expected to decline from the maximum removal rate allowed in the healthy zone to the lowest level possible when the stock reaches the critical zone.

The actual values of the removal rates in the cautious zone would be determined based on uncertainties in the stock status before exploitation such that after exploitation, the spawning stock has a high probability of being above the LRP.

When a stock is in the critical zone, management actions must promote stock growth and removals by all human sources must be kept to the lowest possible level. When the stock is in the Cautious or Healthy zone, management actions could be differentially considered on the basis of both stock status (e.g. abundance) and trajectory or rate of change in status, within the bounds of the removal rate strategy appropriate for the status zone (DFO 2009a).

The key point of the PA status zone diagram is that the stock status axis represents abundance before anthropogenic losses and reference points that conform to the PA must be defined accordingly.

REFERENCE POINTS PRESENTLY DEFINED FOR ATLANTIC SALMON

The history of the definition and use of reference points in management of Atlantic salmon in Canada, Europe and in the international forum has been previously described by Potter (2001), Chaput (2006), and Chaput et al. (2013).

In summary, reference points have been informally used in Canada to provide advice for the management of Atlantic salmon fisheries since the 1970s. The formal definition of conservation for Atlantic salmon and the establishment of spawner requirements were motivated by the 1990 Supreme Court of Canada decision in the case of *Regina vs Sparrow* (CAFSAC 1991a). Conservation requirements were defined on the basis of an egg deposition rate in fluvial habitat with for insular Newfoundland an additional value for the lacustrine habitat used by salmon juveniles (CAFSAC 1991b). More recently, an interim conservation requirement was proposed for salmon rivers of Labrador (Reddin et al. 2006). An alternative reference point was established for the salmon rivers of the province of Québec. The egg deposition rate was defined from a stock and recruitment analysis based on the Ricker model with the optimum spawning escapement (S_{opt}) defined as the level of egg deposition which produced the maximum gain in eggs (Caron et al. 1999; Prévost et al. 2001) (Table 1).

In 1991, CAFSAC (1991a) formally defined conservation for Atlantic salmon as a level of egg deposition that would be applied to individual rivers and in a subsequent advisory document provided values of the conservation requirements for a number of rivers in eastern Canada and provided advice on the surplus to conservation requirements which may be available (CAFSAC 1991b). These two documents established the regional reference points for subsequent fisheries management based on a fixed escapement strategy with all fish in excess of this requirement considered surplus and available for harvest.

The priority of conservation over resource use enunciated in the Sparrow decision is consistent with the concept of a limit reference point as defined in the PA policy; i.e. conservation has priority over resource use, or when the spawning stock is less than the LRP (in the critical zone), removals by all human sources must be kept to the lowest possible level. Recently, ICES has moved to management advice based on MSY. Under this paradigm, ICES has identified a group of species for which only one reference point value is defined, termed $B_{escapement}$. This point is considered for “short-lived” species and the use of a single reference value is justified as follows:

> The future size of a short-lived fish stock is sensitive to recruitment because there are only a few age groups in the natural population. Incoming recruitment is often therefore the main component of the fishable stock. In addition, care must be given to ensure a sufficient spawning-stock size as the future of the stock is

> highly dependent on annual recruitment. For short-lived species, estimates or predictions of incoming recruitment are typically very imprecise, as are any catch forecasts. For short-lived stocks, the ICES MSY approach is aimed at achieving a target escapement ($B_{msy\text{-}escapement}$, the amount of biomass left to spawn), which is more robust against low SSB and recruitment failure than a fishing mortality approach. The catch corresponds to the stock biomass in excess of the target escapement. No catch should be allowed unless this escapement can be achieved. (ICES 2013a).

The management of Atlantic salmon in Canada, Europe and internationally is based on a fixed escapement strategy, with all fish in excess of the conservation requirement considered surplus and available for harvest (Crozier et al. 2004). All the reference points for Atlantic salmon are interpreted as limit reference points and in some cases fisheries management has responded by restricting fishing on certain life stages of salmon (for Quebec, mandatory catch and release of multi-sea-winter salmon when expected escapements are below spawner requirements) to closures of all fisheries (Chaput 1997; Crozier et al. 2004).

In the Maritime provinces, large areas are closed to exploitation by all users because of low abundance, other rivers are open to modest Aboriginal fisheries and catch and release fishing, while most of the rivers of the Gulf Region are open to retention of small salmon in recreational fisheries, small and large salmon harvests in Aboriginal fisheries. In the province of Québec, there is a broad range of management in place, from closures to all fisheries of small rivers with returns of less than 100 salmon, retention of small salmon only, to retention of small and large salmon supported by inseason assessments. In Newfoundland and Labrador, river-specific management plans have been developed with exploitation based on the size and status of rivers relative to achieving conservation. Hence, some rivers are open for various levels of removals while others are open for catch-and-release only.

A fixed escapement strategy and single reference point does not conform to the PA as it does not set a maximum removal rate for the stock nor does it define an USR at which the maximum removal rate would apply (Fig. 3). Although the removal rate does indeed fall to zero when the stock status declines to the conservation point, the removal rate rises continually whereas spawning stock becomes constant after abundance exceeds the conservation objective (Fig. 3).

CANDIDATE REFERENCE POINTS FOR THE PA

Stock dynamics of Pacific salmon and Atlantic salmon are universally presented as spawner – recruit relationships with spawners on the x-axis and recruits on the y-axis (Holt et al. 2009; Potter 2001). As the spawner component in Atlantic salmon is dominated by new recruitment to the spawning stock, managing for escapement entails managing the recruitment in the subsequent generation. Under this framework, potential reference points (LRP, USR) and benchmarks (lower and upper) have been proposed in terms of spawners (Holt et al. 2009; Chaput et al. 2013).

This is different from the PA framework for which stock status or an index of total abundance is presented on the x-axis and the removal rate on the y-axis (Fig. 3). In the PA context, the stock status refers to stock abundance or an index prior to anthropogenic losses.

Reconciling these two views requires a translation of spawner and recruitment values from the stock and recruitment frame to the PA frame (Fig. 4). The translation involves treating the recruitment on the stock and recruitment framework as the stock status axis in the PA framework. When stock abundance before exploitation is at or below the LRP, the removals must be at the lowest level possible, i.e. recruitment essentially equals spawners. On the other hand, when recruitment before exploitation is in the healthy zone of the PA, then removals can occur but at a rate that does not result in the abundance after exploitation, i.e. spawners, falling to or below the LRP.

Candidate Limit Reference Points (LRPs)

Under the PA, the stock status axis corresponds to abundance before exploitation. The LRP is intended to define a threshold or minimum size for the stock that should it fall below, could result in serious and irreversible harm to the stock. Under the guidance of the PA policy, when abundance is at or below the LRP, anthropogenic losses must be at the lowest level possible, i.e. abundance equates to spawners. In that sense, the LRP could be defined as a level of spawning escapement which when realized would not put at risk population viability. As stated by CAFSAC (1991a) and reiterated in a number of exercises, the stock abundance below which serious irreversible harm will occur is very difficult to define.

With this in mind, the following discussion on candidate LRPs is phrased in the context of defining the LRP as a spawner abundance along the spawner axis of the stock and recruitment function. Several candidate LRP values have been proposed (Table 2; Figs. 5 and 6). The ones which have gained favour include: $0.4B_{MSY}$, $S_{0.5Rmax}$, N*, and $S_{0.2B0}$.

The $0.4B_{MSY}$ LRP is the default value in DFO (2009a) and corresponds to an abundance of 40% of the recruitment at S_{msy} (i.e. 40%R_{msy}). This reference point can be calculated if the recruitment and spawners are in identical units, such as eggs or fish. As such, the derivation of this point requires a full life cycle model.

In an analysis of properties of biological reference points relative to different forms of stock and recruitment dynamics, and in particular the degree of compensation, Mace (1994) indicated that it would be more appropriate to use a reference point that increases as the degree of resilience of the population declines. The degree of resilience refers specifically to the extent of the increased recruitment rate as spawner abundance declines. Populations with high resilience have a high recruitment rate at low spawning stock size compared to those with low resilience. A reference point that considers resilience is one based on a percentage of maximum recruitment and the spawner abundance that produces 50% of maximum recruitment is referred to as the half saturation constant (Mace 1994; Myers et al. 1994; Gibson and Claytor 2013). Myers et al. (1995) concluded that thresholds based on 50% Rmax are appropriate because the estimation is reasonably robust and they generally produce values above which recruitment is substantially higher than below the threshold. This value can be calculated from a stock recruitment data corresponding to the full life cycle model or from freshwater phase only provided density dependence is expressed within the phase examined. Maximum recruitment from a population is defined at the density dependent stage which for Atlantic salmon is expressed during the freshwater portion of the life cycle.

Chaput et al. (2015) proposed an alternate LRP, S_{LRP}, defined as the spawning stock size that results in a greater than 75% chance of the recruitment being greater than 50% Rmax. This reference point estimation incorporates the additional uncertainty of the realized recruitment at a given stock size.

The minimum spawners that resulted in the maximum constant recruitment under a hockey stick fitting model (N*) was proposed by Bradford et al. (2000). This is a simplified stock and recruitment dynamic model in which the survival of recruits is independent of density (recruitment rate is constant) up to a threshold value at which point the habitat becomes fully seeded and recruitment becomes constant (survival declines with density) for increasing spawner abundance (Figure 5).

$S_{0.2B0}$ is the spawner abundance that equals 20% of the virgin abundance (replacement point on the stock and recruitment curve) has also been proposed. Gibson and Claytor (2013) indicate that in some conditions, $S_{0.2B0}$ is approximately equivalent to $0.4B_{MSY}$. Myers et al. (1995) did not recommend $20\%B_0$ as a reference level because in addition to estimation uncertainty due to limited observations, this point is not responsive to differences in resilience.

In simulation work conducted by Holt (2009) and Holt and Bradford (2011), the performance of a suite of lower benchmarks was evaluated based on Pacific salmon life history dynamics (i.e. semelparity). In particular, the risk of extirpation and probability of recovery were evaluated for lower reference points over a variety of assumptions including patterns of intrinsic productivity, and underlying modeled population dynamics. The two reference points that were the most robust and indistinguishable in terms of extirpation risk and recovery potential for Pacific salmon type population dynamics were $S_{0.5Rmax}$ and S_{gen} (Table 2; Holt and Bradford 2011). S_{gen} represents the spawner abundance that will result in recovery (recruitment) to S_{MSY} in one generation in the absence of fishing under equilibrium conditions (Holt and Bradford 2011). The properties of S_{gen} as a LRP are interesting. As productivity declines, the value of S_{gen} increases which could be considered to impart an additional level of protection for stocks of lower productivity.

Examples of the candidate limit reference points derived from a freshwater only stock and recruitment dynamic are shown in Figure 5 and reference points from a full life cycle stock and recruitment dynamic are shown in Figure 6.

Only three of the candidate limit reference points can be derived from exclusively freshwater dynamic models: $S_{0.5Rmax}$, S_{LRP}, and N* (Tables 2 and 3; Fig. 5). As discussed under the section "Considerations for productivity", the LRP should be based on population conservation considerations, be determined by the environment where the stock and recruitment density dependent dynamic is expressed, and therefore robust to variations in productivity associated with density independent dynamics. Most reference points that therefore require a full life cycle dynamic and subjected to these productivity variations would not be good candidates for LRPs, the exception being S_{gen} as discussed above.

Candidate Upper Stock Reference Points (USR)

The USR candidates correspond to values along the recruitment axis of the stock and recruitment function (Table 4; Fig. 7). The choice of upper stock reference points must in large part be determined by the chosen limit reference point. The DFO (2009a) policy on the PA states that "the USR, at minimum, must be set at an appropriate distance above the LRP to provide sufficient opportunity for the management system to recognize a declining stock status and sufficient time for management actions to have effect…while socio-economic factors may influence the location of the USR, these factors must not diminish its minimum function in guiding management of the risk of approaching the LRP".

The USR choice will also depend upon the management objective for the resource, as for example such as maximizing harvests (yield) or maximizing fishing opportunities. Recruitment corresponding to the abundance that provides long term average maximum sustainable yield (R_{msy}) is a common candidate upper stock reference point that provides maximum sustainable harvest. The USR point of $80\%R_{msy}$ is consistent with DFO's PA Framework (DFO 2009a). Candidates for target reference points which would be above the USR include proportions of R_{msy}, R_{max}, and R_{rep}. R_{rep} is the long-term replacement value under equilibrium conditions. R_{max} is particularly interesting for recreational fisheries, particularly for catch and release fisheries, where catch opportunities will be maximized at maximum recruitment, (Table 3). In the case of the Beverton-Holt and hockey stick asymptotic stock and recruitment models, proportions of R_{max} could be considered, such as 90% of R_{max} ($S_{0.9Rmax}$) (Chaput et al. 1998).

Examples of the candidate upper stock reference points derived from an example full life cycle stock and recruitment dynamic model are shown in Figure 7.

There is no upper stock reference point to be recommended at this time. The specific USR will depend upon the objectives of the fishery and the risk profile of the management strategy. Upper stock reference points are determined using full life cycle considerations. At a minimum, the USR must be greater than the LRP and there should be a very low probability (<5%) of the recruitment from the spawning stock after exploitation falling below the LRP.

Candidate Removal Rate Reference

The UN Agreement of Straddling Fish Stocks and Highly Migratory Fish Stocks (FAO 1995) recommends that F_{MSY} (fishing mortality at maximum sustainable yield) be used as a maximum removal rate and DFO (2009) indicates that the maximum removal rate in the healthy zone should not exceed the value corresponding to F_{MSY}.

The fishing mortality reference point recommended by Holt et al. (2009) was F_{msy}. This benchmark was associated with a <25% probability of extinction over 100 years for populations with equilibrium abundances greater than 30,000 and a >75% probability of recovery to S_{MSY} within three generations. This removal rate was also more robust to variability in stock productivity than other benchmarks explored. Other candidate removal rate values have been discussed (Table 5) but their performances have not been assessed. Alternative removal reate references include the slope at the origin of the stock-recruitment relationship (F_{max}), the median log-transformed recruits-per-spawner (F_{med}), and the slope at the origin of the smolt-recruitment relationship (Table 5). Without additional information to constrain the latter three alternative lower benchmarks, such as independent estimates of habitat capacity, their use as removal rate references may result in unsustainable rates of fishing compared to F_{msy}.

The removal rate reference could be determined once the upper stock reference point is defined. The maximum removal rate would then simply be: $h_{max} = R_{usr} – S_{usr} / R_{usr}$. Examples of removal rate reference values for candidate USR points are shown in Figure 8.

The actual removal rate reference (h_{max}) would also need to be determined on the basis of a defined risk tolerance (for examples < 5% chance) of the spawning stock after exploitation falling below the LRP.

CONSIDERATIONS FOR ESTIMATING REFERENCE POINTS

Converting freshwater population dynamics models to full life cycle models

All the reference points listed in Tables 2 to 4 can be derived from full life cycle models of eggs to eggs (or adults to adults) but only a few can be defined from stock and recruitment models of spawners to juvenile life stages. Density independent eggs per recruit (from smolts for example) estimates can be derived based on assumptions of marine survivals and phenotype of the returning adults to convert out-migrating smolts to eggs at the adult recruiting stage (Table 6). Combining these with the egg to smolt population dynamics results in an equivalent egg to egg relationship (conditional on the adult characteristics used), termed an equilibrium model (Gibson et al. 2009a, 2009b). These equilibrium models have been used to define reference points for some stocks with only freshwater dynamics observations, for population viability analyses, and for recovery potential assessment (Prévost and Porcher 1996; Wyatt and Barnard 1997; Chaput et al. 1998; Gibson et al. 2009a, 2009b; Gibson and Claytor 2013). The assumptions on marine survival are the most uncertain and difficult to obtain.

It has been reported that sea-age at maturity, proportion female, size, fecundity, and propensity for repeat spawning is highly variable (e.g. Hutchings and Jones 1998) but regionally predictable among salmon populations of eastern Canada (O'Connell et al. 2006; Chaput et al 2006). This predictable variation in adult characteristics can be used to develop regionally specific reference points based on generalized freshwater dynamics models (Chaput et al. 1998).

Example calculations to translate an egg to smolt freshwater dynamic relationship to an adult relationship are shown in Table 7 for two contrasting salmon populations in eastern Canada, the Miramichi River, New Brunswick and Conne River, Newfoundland. The Miramichi River is a multi-sea-winter salmon stock whereas Conne River is a one-sea-winter (grilse) salmon stock. Return rates to 1SW salmon at Conne River have declined over the past two decades; highest estimated values were in the order of 7% to >15% accounting for exploitation in marine fisheries, at the beginning of the time series but have declined to generally less than 5% since 1996 averaging 4.56% to 1SW maiden salmon for the 1988 to 2003 return years (Dempson et al. 2004), but falling to less than 3% in recent years (DFO Unpublished data). Return rates to the Miramichi River summed over 1SW and 2SW maiden salmon for the smolt cohorts of 2001 to 2006 (excluding 2005) ranged from 1.89% to 10.19% (Douglas et al. 2013). Both populations have repeat spawners present, more so in the Miramichi River. The smolts were converted to eggs in returning adults over their lifetime based on the average biological characteristics of each river (Table 7).

Converting smolts to recruiting eggs using average biological characteristics ignores a large portion of the uncertainty associated with the marine phase of Atlantic salmon.

Accounting for iteroparity of Atlantic salmon

Although maiden salmon comprise the majority of the annual returns of adult salmon in studied Atlantic salmon populations, repeat spawners in some populations can make up important proportions of the spawning stock, especially when maiden salmon recruitment is low (Moore et al. 1995; Chaput and Jones 2006; Chaput et al. 2006; O'Connell et al. 2006).

Returns rates to a second spawning vary among stocks with relatively high returns rates (15% to 25% to a second spawning) reported in the Miramichi River (Chaput and Benoît 2012) and lower return rates in the Saint John River (Chaput and Jones 2006), in the LaHave River (Hubley and Gibson 2011) and Conne River (Newfoundland) (Klemetsen et al. 2003). Repeat spawners grow at each spawning event and since fecundity has been shown to be related to size of the fish, they contribute more eggs per fish than their maiden counterparts although egg size and presumably quality may not increase, particularly for consecutive repeat spawners (Reid and Chaput 2012). In some Atlantic salmon populations such as the Miramichi River, egg contributions from repeat spawners have comprised as much as 25% of the lifetime egg production of a year class (Chaput and Jones 2006). The examples shown in Table 6 show the accounting of life stages among spawning life histories and the lifetime contributions to eggs attributable to repeat spawners in some stocks.

In some instances, the lifetime contribution was approximated using a plus group for the adult returns. Chaput and Jones (1992) modelled adult to adult stock and recruitment data for large salmon, a size group which contained maiden 2SW salmon and repeat spawners, based on annual returns of large salmon unadjusted for smolt cohort year. Similarly, Caron et al. (1999) modelled egg to egg stock and recruitment data for six rivers of Quebec using adult returns data by age group, including a plus group representing repeat spawners within the assessment year.

Alternatively, Gibson et al. (2009b) presented an example in which repeat spawning events of adults were modelled using average return rates to subsequent spawnings estimated over several cohorts.

If only recruitment of adults at the maiden spawner stage is considered, this will underestimate the lifetime reproductive contribution of recruits and consequently bias downward the estimation of a number of reference points (S_{msy}, S_{rep}, h_{max}). Excluding egg contributions from repeat spawners is equivalent to estimating the dynamics of a population at lower marine productivity (see next section).

Accounting for removals of adult returns

This section considers accounting for all recruitment, in particular recruitment which is harvested at sea prior to returns to rivers where assessments are usually conducted. Where possible, removals of adult salmon in marine fisheries should be accounted for. Failing to account for removals of adult salmon in marine fisheries biases the lifetime contribution of eggs from the recruits (same as lower productivity).

Caron et al. (1999) and Prévost et al. (2001) analysed adult stock and recruitment time series that included an adjustment for the local and coastal commercial fisheries but did not account for catches of these monitored populations in the commercial fisheries of Newfoundland and Labrador, the West Greenland fishery, nor the fishery at Saint-Pierre and Miquelon.

Dempson et al. (2001) estimated exploitation rates on Newfoundland stocks attributed to marine fisheries during the 1984 to 1991 period which averaged 45% (30–57%) on small salmon and 74% (58–84%) on large salmon. Adjusting for these marine fishery catches for individual rivers is generally not possible other than by adjusting the returns to rivers by an assumed exploitation rate of the interceptor marine fisheries.

Estimates of the exploitation rates on the North American 2SW salmon at West Greenland (corrected for natural mortality from the time of the fishery to the returns to homewaters) exceeded 30% in many years until 1991 and in the past decade, the fishery was estimated to have harvested 5% to 14% of the potential returns of 2SW salmon to the rivers of eastern North America (ICES 2013b). The attribution of catches in these mixed stock marine fisheries to individual rivers is not yet possible.

Accounting for hatchery contributions

The contributions of hatchery origin salmon must be considered in the context of both recruitment and spawners.

In some rivers of eastern Canada, numerous juvenile salmon have been reared in hatcheries and then stocked to rivers. The contributions of hatchery origin salmon in some rivers can make up important proportions of the total returns, especially in stocks in which abundance of wild salmon is declining (Chaput and Jones 2006; Gibson et al. 2009b; Jones et al. 2014). In some cases, stocked fish can be identified or are estimated among the returns whereas in many other cases not all the hatchery progeny are marked or identifiable. If the contributions of hatchery fish are not excluded from the returns, the effect is to bias the productivity upwards, resulting in generally higher reference points, including the removal rate and the anticipated yield.

There is some debate as to the value of hatchery fish as spawners in the natural system, with some suggestions that hatchery origin salmon may have reduced reproductive fitness compared to wild salmon (see Clarke et al. 2014; O'Reilly et al. 2014). If hatchery fish have inherently lower reproductive fitness compared to wild con-specifics but are treated as equal to wild fish spawners, the net effect is to lower the productivity in the wild because the spawning stock variable is estimated to be higher than realized for the estimated smolt production of the cohort.

APPROPRIATENESS OF USING REFERENCE POINTS THAT ARE SPECIFIC TO VARIATIONS IN PRODUCTIVITY

Anadromous Atlantic Salmon utilize two distinct environments to complete their life cycle; the freshwater environment for spawning and juvenile growth, and a marine component that results in rapid growth, and maturation. Density-dependent population regulation is well documented in the freshwater stage of the life cycle (Jonson et al. 1998; Elliott 2001; Gibson 2006). Marine mortality is generally considered to be density-independent because salmon abundance is not thought to be constrained by competition for food or space in the North Atlantic (Jonsson et al. 1998).

The modelling of stock and recruitment relationships and the development of reference points are challenged by two conflicting considerations; the need for a long time series of contrasting abundance with which to adequately estimate life history parameters versus the risk that there will be systematic and sustained changes in the life history parameters being estimated. A directional and sustained change in life history parameters over time is referred to as non-stationarity, which is different from expected short term stochastic variations in life history features (Hilborn and Walters 1992).

EVIDENCE OF CHANGES IN PRODUCTIVITY IN THE MARINE ENVIRONMENT

There is substantial evidence of sustained changes in some life history parameters of Atlantic salmon, particularly in survival at sea, over the past 40 years (Chaput 2012; ICES 2013b). In many monitored rivers in eastern Canada, return rates of smolts to a first spawning have declined over the past two decades, with the most important declines occurring in the late 1980s and early 1990s (Fig. 9). This pattern is particularly strong for the hatchery smolt return rates time series from the southern stocks of Canada and for the multi-sea-winter stock (de la Trinité) in Quebec and a few rivers in Newfoundland (Fig. 9). Returns rates in some of these rivers show a slight upturn in the past decade. Survival to repeat spawning has decreased in some populations (Hubley and Gibson 2011) or increased in others (Chaput and Benoît 2012) with both attributed to changes in the marine ecosystem. These changes in survival have occurred and persisted through periods when many of the marine fisheries for salmon in the Northwest Atlantic have been closed, or greatly reduced by comparison with earlier decades.

Temporal changes in biological characteristics (other than sea survival) have also been noted, with increases in fork length at age over periods of decades noted in a number of salmon populations in eastern Canada (Moore et al. 1995; O’Connell et al. 2006) but these changes were explained by reductions in size selective marine fisheries.

Productivity, expressed as the ratio of abundance at the first winter at sea stage per spawning stock size of the smolt cohort, of stock complexes in the North Atlantic shows a sharp decline in the late 1980s which was attributed to changes in the marine environment (Chaput et al. 2005; Chaput 2012; Mills et al. 2013) (Fig. 10). The productivity parameter is an integration of the survival rates from modelled eggs through the freshwater phase and in the first year at sea (to January 1 of the first winter). Since estimated egg depositions in the North American stock complex have actually increased over the same time period, suggesting that freshwater output of smolts has increased or remained stable, the decline in the productivity parameter is attributed to a decrease in marine survival (Chaput 2012). The analysis at the stock complex level indicates that an increasing proportion of the total smolt production from eastern Canada is returning as 1SW salmon (maturing component). Some authors have characterized this as a change in the probability of maturing but the pattern can be just as easily explained by an increase in the mortality rate in the second year at sea that affect 2SW salmon (Massiot-Granier et al. 2014). In the multi-sea-winter salmon stocks of eastern Canada where smolt to adult returns are monitored, the proportion of the smolts returning as 1SW salmon has not changed over time, with the possible exception of a slight increase in1SW salmon proportions in de la Trinite River (Fig. 9). There is less evidence of temporal trends in the proportions female in the sea age groups (O'Connell et al. 2006) which would be consistent with a change in the probability of maturing.

Variations in biological characteristics (other than survival) of the stocks may affect the lifetime contribution of eggs of a smolt cohort. For example, if 5% of the smolts survive and return as adults but in one instance half the adults return as 1SW (with 1SW fish contributing 2000 eggs and 2SW fish contributing 5,000 eggs) whereas in the other instance, 75% of the adults return as 1SW (different maturation rate) but with similar adult characteristics (proportion female, size), then the egg contributions from a surviving smolt in the first instance is 175 eggs whereas in the second situation, each surviving smolt contributes 138 eggs.

EVIDENCE OF PRODUCTIVITY CHANGES IN FRESHWATER

Evidence of productivity changes in freshwater corresponding to regime shifts as reported for marine environments has not been reported. Changes in the freshwater dynamics, corrected for density dependence, have been documented for some Atlantic salmon populations subjected to anthropogenic stress (Gibson et al. 2009a) and variations in smolt characteristics (age and size at migration, date of migration) have been reported and attributed to factors such as climate change (Russell et al. 2012). With the exception of situations where freshwater habitat has been degraded , for example through acid precipitation, installation of barriers, degradation of habitat by siltation, or in the case of climate change, there is limited evidence of abrupt and sustained changes noted for the marine environment. Gradual changes in dynamics are noted in some cases.

The residuals of model fits (Beverton-Holt) of egg to smolt monitoring data from fourteen rivers were analyzed and examined for temporal trends (Fig. 9; Chaput et al. 2015). There are two rivers (Saint-Jean, de la Trinite) with a statistically significant ($p < 0.05$) temporal trend in the residuals suggesting a systematic change over time in egg to smolt dynamics, after accounting for spawner abundance (Chaput et al. 2015) (Fig. 11).

Another example of potential changes in freshwater productivity is shown in Figure 12 based on indices of juvenile abundances from the Kedgwick River (Restigouche River, NB) for the years 1972 to 2012. Indices of abundance (number of fish per 100 m^2) of fry, small parr (age-1) and large parr (age-2+) are used as proxies of interstage survival rates. There are statistically significant ($p < 0.05$) trends in the residuals, with both suggesting improved interstage survival rates after adjusting for abundance of the size group in the previous year over the 40+ years of monitoring (Fig. 12).

CONSEQUENCES OF CHANGES IN PRODUCTIVITY ON DERIVATION OF REFERENCE POINTS

Changes in productivity in either phase will have consequences on derived reference points (Fig. 13). The effects of lower productivity, manifest in either rearing environment, is to reduce the adult recruitment per spawning stock. This reduced recruitment rate per spawner lowers the values of most reference points derived from full life cycle models. In some stocks with small population sizes to begin with (a few hundred to a few thousand fish), the impacts of reduced productivity are to reduce the abundance and drive the populations to even lower population sizes with the inherently increased stochastic and demographic pressures. The reference points are lower and the catches and the exploitation rates are also lower.

If reduced productivity is restricted to the marine environment during the density-independent stage but the freshwater environment remains productive, decreasing adult recruitment will push the smolt production towards the steeper portion of the slope of the density dependent freshwater recruitment relationship, with reduced density dependent effects and anticipated gains in relative production expected but with overall declines in total production of smolts (Fig. 13). The net effect of lower smolt production associated with lower egg depositions is reduced adult abundance, already constrained by reduced sea survival. The additional risks to stocks at small population sizes associated with demographic and stochastic environmental effects become more important.

Provided the productivity in freshwater is stationary, then the few limit reference points defined on the basis of maintaining freshwater production levels would be robust to variations in marine productivity (Fig. 13). Reference points that result in a fixed proportion of the recruitment derived during the density dependent portion of the life cycle are appropriate reference points for salmon ($S_{0.5Rmax}$, N*). The S_{gen} reference value increases as productivity declines, as reported by Holt and Braford (2011) and is considered precautionary for conservation objectives.

Some reference points are not robust to variations in the density independent dynamics; $S_{0.2B0}$, $0.4B_{MSY}$, and are not good candidates for LRPs (Fig. 13).

The objective should be to maintain freshwater production to take advantage of better marine productivity periods when they occur. In doing so, there will be reduced harvest opportunities with more frequent and larger reductions in fisheries exploitation but the population will be at reduced risk.

TRANSPORT OF REFERENCE POINTS TO OTHER STOCKS

Since it is not possible to obtain stock and recruitment data from the over 1,000 rivers with Atlantic Salmon populations in eastern Canada, consideration must be made to transferring reference values from monitored rivers to rivers which lack such information. In the case of unstudied populations but for which information exists from other populations, reference points are frequently transported based on a spawner requirement from studied populations which is standardized to an exchangeable metric representing the size of the population (rate).

There is a general and positive relationship between the number of smolts produced in a river and the size of the fluvial rearing area for salmon juveniles (Fig. 14). Within individual rivers, there can be large variability in the quantity of smolts produced, attributed in part to annual variations in spawning stock realized in individual rivers.

Scaling production and spawning stock on the basis of the amount of habitat area is the first scale of consideration for salmon. If reference points are defined in terms of rates, such as eggs per area or spawners per km^2 of wetted fluvial area, these reference points can be transferred across a set of exchangeable rivers. The issue of exchangeability is a key consideration in the transfer of rates among rivers. Gelman et al. (2004; p. 121) states: "Generally, the less we know about a problem, the more confidently we can make claims of exchangeability. (This is not, we hasten to add, a good reason to limit our knowledge of a problem before embarking on statistical analyses)."

Exchangeability is presented as follows:

> If no information other than the data *y* is available for a set of experiments *j* to distinguish among the parameters specific to each experiment (θ_j), and no

> ordering or grouping of the parameters can be made, one must assume symmetry among the parameters in their prior distribution, this symmetry is represented probabilistically by exchangeability (extracted with modification from Gelman et al. 2004, p. 121).

As an example in Figure 14, given that we have information on the total smolt production and the size of rivers, we can write a model to predict smolt production conditional on the size of the river. In that sense, the smolt production data are considered to be exchangeable conditional on river size. The data in Figure 14 also hint at a possible difference in the smolt production for a given river if there is lacustrine habitat present and used by salmon juveniles. In that case, given this additional information, the smolt production from a given river could be considered exchangeable conditional on the river size and presence of lacustrine habitat.

Prévost et al (2001) provide an overview of methods used to transport reference points among rivers, beginning with approaches to standardize the habitats of the rivers to common scales. This standardization of habitat quantity that takes into account quality and value is an exercise to reduce variations in productivity among rivers due to differences which could be measured and modelled, and therefore increase the extent of exchangeability among rivers.

CAFSAC (1991b) initially assumed that the egg deposition rate for conservation was exchangeable among salmon rivers in eastern Canada conditional on the presence / absence of lacustrine habitat. The conservation egg deposition rate of 240 eggs per 100 m^2 of fluvial wetted area was considered transferrable across all salmon rivers, with an additional requirement of 368 eggs per hectare of lacustrine habitat for rivers in Newfoundland. Lacustrine habitat is extensively used for rearing by juvenile salmon in many areas of Newfoundland (Dempson et al. 1996; O'Connell and Dempson 1996). An adjustment to the eggs per lacustrine area was later added that distinguished rivers from the northern portion of Newfoundland (150 eggs per ha of lacustrine habitat area) from the rest of the island (O'Connell and Dempson 1995). Using these default egg deposition rates, conservation requirements could be defined for other rivers if fluvial habitat areas were known and based on the presence of lacustrine habitat used by salmon juveniles in Newfoundland.

Symons (1979) constructed a juvenile life history model for Atlantic salmon and concluded that the freshwater dynamics of salmon rivers were exchangeable conditionally on the average age of smolts produced; knowing the average river age of the stock, different egg deposition rates could be applied. Chaput et al (1998) modelled egg to smolt stock recruitment data from eastern Canada and concluded that the presence / absence of lacustrine habitat was a more important covariate than mean smolt age to explain the variation in smolt production adjusted for egg depositions.

Caron et al. (1999) transported a fixed egg deposition rate derived from a joint analysis of adult to adult stock and recruitment data from six rivers by calculating for each of the 110 salmon rivers in Quebec a measure of habitat capacity termed a unit of production. Habitat type (such as riffle, rapid, run, pool), substrate type, and width of the river were used to downweight the total wetted area according to its quality to produce juveniles. They included an additional variable, degree days, to further scale the productive potential of the rivers across the province, with the degree days included in the calculation of the total units of production for each river. Prévost et al. (2001) conducted the same analysis but in a hierarchical Bayesian framework with the unit of production as a covariate to establish the transferrable egg deposition rate.

In the past decade, hierarchical Bayesian modelling of monitored rivers has been used to define reference points and to transfer them among rivers conditionally on measured covariates that were found to be important explanatory variables of productivity. Habitat area, in terms of wetted fluvial area and latitude of the rivers were found to be important conditioning variables for the transport of reference points across rivers in Europe (Prévost et al. 2003) and in Ireland (Ó Maoiléidigh et al. 2004). Chaput et al. (2015) analyze a set of 14 rivers with egg to smolt monitoring data and examine factors which can be used to explain variations in carrying capacity of smolts (smolts per area of habitat) and density independent survival.

Bayesian modelling approaches are now widely used in stock assessments and for the provision of management advice and these allow for a more complete quantification of these uncertainties. Hierarchical Bayesian methods are most appropriate in situations where reference points from data rich situations are transported to populations with limited to no information (Prévost et al. 2003; Michielsens and McAllister 2004). The uncertainties associated with intra-population stock and recruitment dynamics and inter-population variation of this dynamic within a set of exchangeable units can be quantified using these approaches.

The use hierarchical models in a Bayesian framework is an excellent approach for addressing exchangeability and transfer of points across populations. When used in this way, it assumes that the monitored rivers are conditionally (on the covariates) exchangeable. It also assumes that the rivers which were monitored are representative of the dynamics of Atlantic salmon within their respective regions. In absence of the latter assumption, we are left with no information for developing reference points for salmon populations.

TRANSLATING EGG REQUIREMENTS INTO FISH

Most reference points for Atlantic salmon have been defined on the basis of eggs in the spawning stock and in cases of full life cycle models with eggs in the recruitment. In most cases, eggs from all phenotypes of salmon are included in both the stock and recruitment variables (Chaput et al. 1998; Prévost et al. 2003, Ó Maoiléidigh et al. 2004; Gibson 2006; ICES 2013b). This assumes that eggs regardless of parent characteristics have an identical value to future recruitment, i.e. similar value in terms of survival, growth with minimal heritability of sea age at maturity. This is a common assumption made for many species ranging from freshwater, marine fish and invertebrates when spawning stock is often expressed as spawning stock biomass combined over all sizes and age structure of spawners.

In salmon and other species, there are reported maternal effects associated with egg size, including survival rate, time of hatching, and possibly heritability of phenotype (Thorpe et al. 1984; Fleming 1996; Reid and Chaput 2012). Phenotype is definitely heritable in Atlantic salmon as evidence in the development of broodlines in the aquaculture industry, so the assumption that an egg is an egg may not be accurate. But there is more to population fitness than egg production and even though the egg contribution (in terms of number of eggs) by small salmon may be minor in some stocks, the genetic composition and biological characteristics of all age and size groups are evolutionary characteristics of the populations and all phenotypes should be assumed to contribute to fitness of the population.

Reference points have been translated into fish equivalents based on estimated fecundities of adult fish (CAFSAC 1991b; O'Connell et al. 1997). These values have been provided to fisheries managers as the units of measurement in fisheries are fish not eggs. CAFSAC (1991b) and others afterwards incorporated fisheries strategies/objectives considerations in translating eggs requirements to fish. In the Maritime Provinces in which multi-sea-winter salmon were historically abundant, predominantly female, and the life stage which was the most valued in the fishery, the choice was made to convert the egg requirement to MSW salmon equivalents, ignoring the egg contributions, however minimal in some cases, from 1SW salmon (CAFSAC 1991b).

The choice of translating egg requirements into MSW salmon equivalents in the Maritimes reflects a mix of fisheries objectives and an assumption of heritability of age at maturity. Management placed priority on the MSW age group in the Maritimes and provided fisheries access to small salmon (CAFSAC 1991b). In a sense, conserving the age group that provides the majority of the eggs is a reasonable approach and could provide opportunities for fisheries to other components of the stock. Similarly for many Newfoundland populations dominated by 1SW salmon, the egg requirements were translated into 1SW salmon equivalents, treating the large salmon (>63 cm fork length) which were comprised of repeat spawning 1SW salmon as a buffer or a bonus.

As the sex ratio of MSW salmon was biased to females, a small salmon or 1SW salmon requirement was defined with the objective of achieving a 1:1 male to female ratio for the spawner requirement (CAFSAC 1991b). No biological reason was provided for the 1:1 sex ratio derivation.

The calculation of the 1SW requirement used by CAFSAC (1991b) is as follows:

$$MSW_{cons} = \frac{Eggs_{cons}}{Eggs\ per\ MSW\ fish}$$

$$1SW_{cons} = \frac{MSW_{cons} * MSW_{prop.fem} - MSW_{cons} * \left(1 - MSW_{prop.fem}\right)}{1SW_{Prop.male}}$$

with

$$MSW_{cons} = number\ of\ MSW\ salmon\ to\ provide\ Eggs_{cons}$$

$$Eggs_{cons} = conservation\ requirement\ in\ number\ of\ eggs$$

$$Eggs\ per\ MSW\ fish = number\ of\ eggs\ per\ MSW\ spawner\ (sexes\ combined)$$

$$1SW_{cons} = number\ of\ 1SW\ salmon\ (sexes\ combined) to\ provide\ 1{:}1\ sex\ ratio$$

$$MSW_{prop.fem} = proportion\ female\ in\ the\ MSW\ component$$

$$1SW_{prop.male} = proportion\ male\ in\ the\ 1SW\ component$$

This was not the case for Newfoundland stocks for which this was not biologically realistic; the majority of salmon in many of these stocks are 1SW salmon which are predominantly female. In these stocks, precocious male parr undoubtedly play an important role (Dalley et al. 1983).

In some multi-sea-winter salmon stocks, a larger yield (kg of fish) for the same egg contribution can be extracted by harvesting grilse rather than MSW salmon; for example 147 kg of 1SW salmon contributes the same number of eggs as a single 4.73 kg MSW salmon for the Saint-Jean River (Table 8).

In some jurisdictions, age specific reference points have been defined and fisheries advice is provided on the basis of attainment of the age specific conservation objectives (ICES 2013b). In a recent Recovery Potential Assessment for Atlantic salmon, the recovery objectives were defined on the basis of the conservation egg requirement and translated into fish based on life history features and expected relative abundance of the age groups (DFO 2014). Conserving all the phenotypes or exploiting all the phenotypes equally may well be the soundest conservation measure.

The biological data and the approach summarized in Tables 6 and 7 are examples of how egg requirements could be converted to fish equivalents that would respect all the phenotype and age structure expected in a population.

QUANTIFYING UNCERTAINTY IN THE DEVELOPMENT AND USE OF REFERENCE POINTS

Quantifying uncertainty in the development and use of reference points consists of three components: uncertainty associated with the derivation of the reference point, the choice of the value of the reference point posterior distribution used in management, and uncertainty in the current status of the stock relative to the reference point.

From Bayesian models described above, posterior distribution summaries of parameters of interest, including reference points, provide a quantification of the uncertainty associated with the stock dynamic and the derivation of parameters of interest. In many examples, a single value from the posterior distribution is chosen to define the conservation requirement or the reference point for management, as for example, the mean or the median value. In some applications, a value other than the median of the posterior distribution was selected; Caron et al. (1999) chose the 75th percentile rather than the median estimate of S_{opt} as the point value for the reference point for management of Atlantic salmon fisheries in Quebec. A similar approach was used for the development of the conservation limits for salmon stocks in Ireland (Ó Maoiléidigh et al. 2004). The use of a single value for the reference point rather than the whole distribution is a compromise that facilitates the adoption and use of reference points in management. The choice of the percentile for the point value of the reference point is a statement of risk aversion.

Alternatively, the full posterior distribution of the reference point could be retained and applied jointly to the posterior distribution of the population assessment metric. The marginal probability distribution of having met or exceeded the objective could then be derived and this would indeed be a full integration of uncertainties in the assessment and uncertainties of the reference points. Prager et al. (2003) and subsequently Prager and Shertzer (2010) describe the theoretical framework for such a procedure and show a few examples of its application.

CONSIDERATIONS FOR SPATIAL STRUCTURING AND MIXED STOCK FISHERIES

Anadromous salmonids are characterized by population structuring at the scale of individual rivers and in some Pacific salmon species down to a subwatershed scale. Recruits return with high fidelity to their natal spawning locations. Fisheries on these species have historically occurred at times and locations where mature animals are returning to the coast and rivers to spawn and when they are concentrated at higher density than at other times of their life cycle. Populations are frequently mixed during their spawning migrations and although some fisheries can target specific populations due to differences in run timing, for a number of marine, coastal and frequently inriver fisheries, multiple stocks are prosecuted at the same time. The fishery on Atlantic salmon at West Greenland which takes place in August to December annually catches salmon from most salmon producing rivers in eastern Canada and the USA as well as salmon originating from rivers in Europe (ICES 2013b). These mixed-stock fisheries pose particular challenges to management of individual populations.

Sustained yield from mixed-stock fishery situations will always be less than yield when each stock is harvested separately due to differences in productivity among stocks, and due to environmental variation (the more uncorrelated and larger the random variability among stocks, the more yield is foregone) (Hilborn and Walters 1992).

Ideally, management of fisheries would occur such that “optimal” production takes place in all the populations subjected to exploitation. As such, the formulation of fisheries management advice should take account of the complexity of the mixed-stock fishery being managed, and the number of distinct production areas that are being exploited. Chaput (2004) illustrated that as the number of populations or areas being prosecuted in mixed-stock fisheries increases, the total escapement objective for the complex being exploited must be increased to ensure a given probability of simultaneously achieving the individual population reference levels (Fig. 15).

Alternatively, when evaluating management options based on forecasts, the catch options are presented on the basis of the probability of each stock unit achieving its reference point simultaneously relative to assumptions on exploitation rates of each stock in the mixed-stock fisheries (Chaput et al. 2005). Increasing the reference levels as described above in an attempt to account for the number of stocks being exploited in a fishery or in an attempt to compensate for lower productivity will result in reduced catch options. The trade-off between reduced catch and protecting smaller or less productive populations must be recognized (Hilborn and Walters 1992).

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TABLES

Table 1. Summary of presently defined reference points for Atlantic salmon by region in eastern Canada.

Region	Objective	Reference Point	Reference
Maritime provinces	Maximum freshwater production	240 eggs per 100 m^2 of fluvial habitat	CAFSAC (1991a, 1991b) O'Connell et al. (1997)
Insular Newfoundland	Maximum freshwater production	240 eggs per 100 m^2 fluvial habitat + 368 eggs per ha of lacustrine habitat (150 eggs per ha of lacustrine habitat for the northern peninsula)	CAFSAC (1991a, 1991b) O'Connell and Dempson (1995)
Labrador	50% of adult equilibrium point	190 eggs per 100 m^2 of fluvial habitat	Reddin et al. (2006)
Québec	Maximum gain of eggs (S_{msy})	167 eggs per 100 m^2 of units of production	Caron et al. (1999) Prévost et al. (2001)

Table 2. List of candidate limit reference points. Relative abundance levels for these candidate points are shown in Figures 5 and 6. Equations for estimating these reference points for three stock and recruitment models are provided in Table 3

Acronym	Description	Requirement	Reference
$0.4R_{MSY}$	Spawner abundance equivalent to 40% of recruitment at maximum sustainable yield	Full life cycle	DFO (2009) Holt et al. (2009)
$S_{0.5Rmax}$	Spawner abundance that gives 50% of maximum recruitment	Juvenile production; Full life cycle	Myers et al. (1994) Gibson and Claytor (2012) Holt et al. (2009)
S_{LRP}	Spawner abundance that provides greater than 75% chance of realized recruitment being at or above 50%Rmax	Juvenile production; Full life cycle	Chaput et al. (2015)
S_{gen}	Spawner abundance that will result in recovery to S_{msy} in one generation in the absence of fishing under equilibrium conditions	Full life cycle	Holt and Bradford (2011)
S_{msy}	Spawners that result in maximum sustainable yield	Full life cycle	Various
$S_{0.2B0}$	Abundance equal to 20% of B_0 (20% of virgin biomass or replacement value)	Full life cycle	Myers et al. (1995); Gibson and Claytor (2012)
N*	From the hockey stick model, the minimum spawners that will maximize production	Juvenile production Full life cycle	Bradford et al. (2000)

Table 3. Equations for calculating reference values and other features from Beverton-Holt and Ricker stock and recruitment functions. Reference values preceded by "@" can only be estimated from a full life cycle model.

Acronym	Hockey stick	Beverton-Holt	Ricker
SR model	$R = \begin{matrix} \alpha\, S \mid (S < Smax) \\ Rmax \mid (S \geq Smax) \end{matrix}$	$R = \frac{\alpha S}{\left(1 + \frac{\alpha}{\beta}\, S\right)}$	$R = \alpha\, S\, e^{-\beta S}$
S_{max}	*Smax*	∞	$\frac{1}{\beta}$
R_{max}	*Rmax*	β	$\frac{\alpha}{\beta} e^{-1}$
@ R_{msy}	*Rmax*	$\frac{\alpha Smsy}{\left(1 + \frac{\alpha}{\beta}\, Smsy\right)}$	$\alpha\, Smsy\, e^{-\beta Smsy}$
@ R_{rep}	*Rmax*	$(\alpha - 1)\, \frac{\beta}{\alpha}$	$\frac{log(\alpha) - \log(1)}{\beta}$
@ $0.4R_{MSY}$	*0.4 Rmsy*	*0.4 Rmsy*	*0.4 Rmsy*
$S_{0.5Rmax}$	$\frac{0.5\, Rmax}{\alpha}$	$\frac{Rmax}{\alpha}$	$0.5\, Rmax = \alpha\, S'\, e^{-\beta S\prime}$ solve numerically for S'
S_{LRP}	*solve by simulation*	*solve by simulation*	*solve by simulation*
@ S_{gen}	$\frac{Smsy}{\alpha}$	$\frac{Smsy}{\left(\alpha - \frac{\alpha}{\beta}\, Smsy\right)}$	$Smsy = \alpha\, S'\, e^{-\beta S\prime}$ solve numerically for S'
@ S_{msy}	*Smax*	$\frac{\beta}{\sqrt{\alpha}} - \frac{\beta}{\alpha}$	$\frac{log(\alpha)}{\beta}\left(0.5 - 0.07\, log(\alpha)\right)$
@ $S_{0.2B0}$	*0.2 Rmax*	$0.2\, (\alpha - 1)\, \frac{\beta}{\alpha}$	$0.2\, \frac{log(\alpha) - \log(1)}{\beta}$
N*	*Smax*	na	na

Table 4. List of candidate upper stock reference points (Figure 7).

Acronym	Description	Application	Reference
$0.8R_{msy}$	Abundance corresponding to 80% of R_{msy} (80% of R_{msy})	Full life cycle	DFO (2009); Holt et al. (2009)
R_{msy}	Recruitment at maximum sustainable yield (R_{msy}). This average recruitment occurs when spawners = S_{msy}	Full life cycle	Various
R_{max}	Maximum recruitment	Full life cycle	Various
$X\%R_{max}$	X% of maximum recruitment. Useful for non-dome shaped stock recruit relationships. Candidate values include 90% of R_{max}.	Full life cycle	Chaput et al. (1998)
$X\%R_{msy}$	X% of recruitment at MSY	Full life cycle	na
R_{rep}	Recruitment, or spawners (S_{rep}), corresponding to the replacement point	Full life cycle	na

Table 5. List of candidate removal rate reference points.

Acronym	Description	Reference
F_{msy}	Fishing mortality rate that provides equilibrium maximum sustainable yield (h_{opt})	DFO 2009
F_{max}	Slope at the origin of the spawner-recruitment relationship (maximum log transformed recruits per spawner at low spawner abundance)	Mace (1994)
F_{sm}	Slope at the origin of the smolt-recruitment relationship (independent of freshwater productivity)	Bradford et al. (2000)
h_{usr}	Removal rate corresponding to the surplus production of spawners at the USR: $(R_{usr} – S_{usr}) / R_{usr}$	this manuscript

Table 6. Conversion equations to go from smolts to eggs based on adult biological characteristics and estimated or assumed marine survival rates.

Number	Equation
1	$Smolts_y \sim f(Eggs_y, \theta)$
2	$Eggs_y \sim Smolts_y * Recruit\ eggs_y$
3	$Recruit.eggs_y$ = lifetime eggs per recruiting $smolt_y$ = lifetime marine $survival_y$ * eggs per fish $= \widetilde{A_y}/S_y * \widetilde{Eggs}$ with $\tilde{A}_y = \sum^a N_y^a$ = lifetime return of adults from smolt cohort *y* S_y = *number of smolts going to sea for cohort y, and* $\widetilde{Eggs} = Eggs\ per\ adult\ return$
4	Eggs per adult return $= \widetilde{A_y}^{-1} * \sum^a N_y^a * p.fem^a * Eggs\ per\ female^a$ *a* = spawning history type (maiden sea age, number of spawning events) $p.fem^a$ = proportion female in adult salmon of spawning history type *a* $Eggs\ per\ female^a$ = fecundity of female salmon of spawning history type *a*

Table 7a. Example of the biological characteristics required and the estimation of eggs per recruit for converting egg to smolt relationships to egg to egg stock and recruitment data based on data from the Miramichi from the 1994 to 2000 yearclasses and the average sum of the return rate of smolts to maiden 1SW and 2SW (a = 1.0, 2.0) for monitored years 2004 to 2008.

Spawning history type (a) (maiden sea age . number of previous spawning events)	Proportion female	Mean length (cm)	Fecundity (eggs per female)	Abundance estimate (returns) at age (a)
1.0	0.17	60.1	4,574	31,410
1.1	0.16	70.9	6,490	1,580
1.2	0.44	81.7	7,930	170
1.3	0.79	87.3	8,709	30
1.4				0
2.0	0.83	76.7	7,253	7,780
2.1	0.96	86.1	8,540	1,100
2.2	0.97	93.3	9,566	360
2.3	0.97	92.6	9,465	90
2.4	1	96.1	9,975	20
Maiden salmon (sum of 1.0, 2.0) / total adults			0.92	
Eggs per adult			2,047	
Average return rates to maiden salmon (2001 to 2006 smolt cohorts)			5.31%	
Adjusted lifetime return rate of smolt cohort			5.80%	
Eggs per recruiting smolt			118	

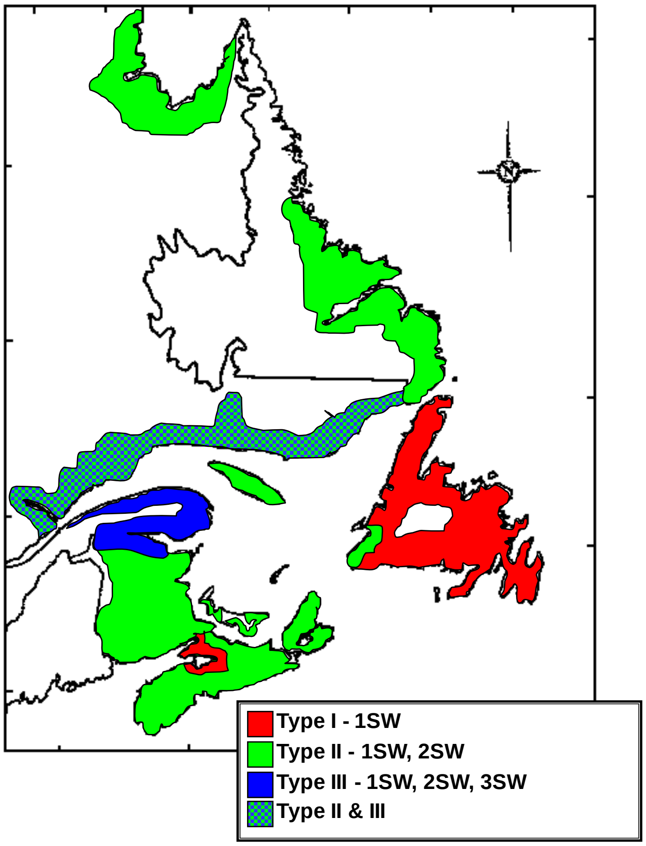
Table 7b. Example of the biological characteristics required and the estimation of eggs per recruit for converting egg to smolt relationships to egg to egg stock and recruitment data based on data for Conne River (Dempson et al. 2004).

Spawning history type (a) (maiden sea age . number of previous spawning events)	Proportion female	Mean length (cm)	Fecundity (eggs per female)	Abundance estimate (returns) at age (a)
1.0	0.77	51.1	3,122	3,806
1.1	0.75	62.5	3,819	383
1.2	0.75	62.4	3,813	69
1.3	0.75	67.1	4,100	14
1.4	0.75	66.5	4,063	2
2.0	0.75	67.1	4,100	21
2.1	na	na	na	na
2.2	na	na	na	na
2.3	na	na	na	na
2.4	na	na	na	na
1SW (1.0) / total adults			0.886	
Eggs per adult			2,458	
Average return rates to 1SW maiden salmon (1988 to 2003 smolt cohorts)			4.56%	
Adjusted lifetime return rate of smolt cohort			5.10%	
Eggs per recruiting smolt			126	

Table 8. Example calculation of yield in kg of 1SW salmon which corresponds to the egg equivalent of a multi-sea-winter (MSW) salmon from three MSW stocks of eastern Canada.

Characteristic	Miramichi (mean 2006-2010)	Saint-Jean	De la Trinite
MSW salmon			
% female	79.7%	70.5%	93.8%
Mean weight (kg) or mean length (cm)	3.78 (78.1 cm)	4.73	4.65
Fecundity per kg or per cm		1,535 per kg	1,535 per kg
Eggs per MSW salmon (mean weight or length)	5,862	5,119	6,697
Small salmon			
% female	8.9%	1.4%	11.5%
Mean weight (kg) or mean length (cm)	1.38 (55.6 cm)	1.63	1.88
Fecundity		2,430 per kg	2,430 per kg
Eggs per 1SW salmon (mean weight or length)	318	57	524
Weight of small salmon to produce one MSW egg equivalent	26 kg	147 kg	24 kg

FIGURES



Type I
- Mostly grilse (1SW)
- Grilse : >70% female

Type II
- Grilse and two-sea-winter salmon
- Grilse : 10-40% female
- Salmon : > 60% female

Type III
- Grilse, 2SW, 3SW salmon
- Grilse : 0%-10% female
- Salmon : > 60% female

Type I
- Surtout grilse (1SW)
- Grilse : >70% femelle

Type II
- Grilse et saumon dibermarin
- Grilse : 10-40% femelle
- Saumon : > 60% femelle

Type III
- Grilse, saumon diber, tribermarin
- Grilse : 0%-10% femelle
- Saumon : > 60% femelle

Figure 1. Distribution of generalized groupings of stock types of self-sustaining populations of Atlantic salmon in eastern Canada. Stock Type I consists mainly of 1SW spawners, Type II has 1SW and 2SW spawners, and Type III is comprised of 1SW, 2SW, and 3SW spawners. Within each stock type area there may be a few stocks which belong to another stock type. Adapted from Porter et al. (1986) and O'Connell et al. (2006).

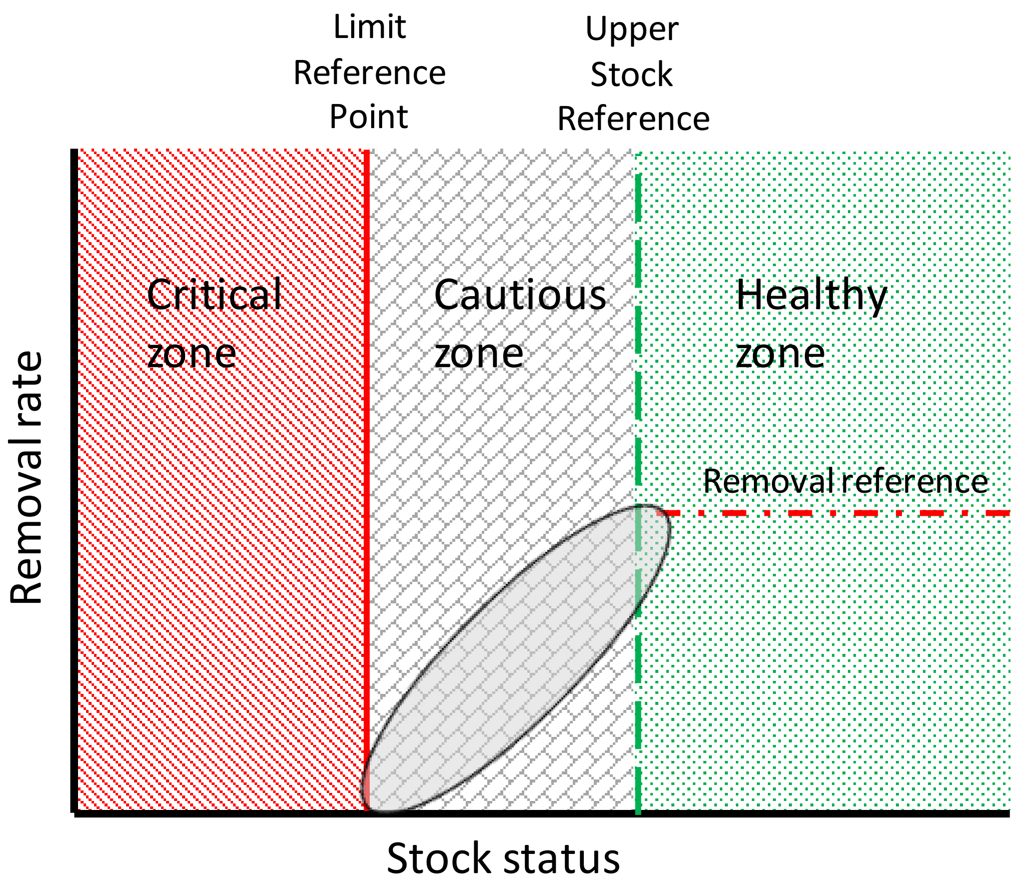


Figure 2. Standard Precautionary Approach diagram, based on a horizontal stock status axis and a vertical removal rate axis, showing the three status zones (critical as diagonal red line shading; cautious zone as grey brick fill; healthy zone as green dotted fill) and the reference points (limit reference point as solid red vertical line; upper stock reference as green long dash vertical line; removal reference as the dashed dotted red horizontal line in the healthy zone). The exploitation rate in the cautious zone (grey shaded diagonal oval) would be defined on the basis of a risk analysis of the chance that abundance after exploitation would be less than the limit reference point.

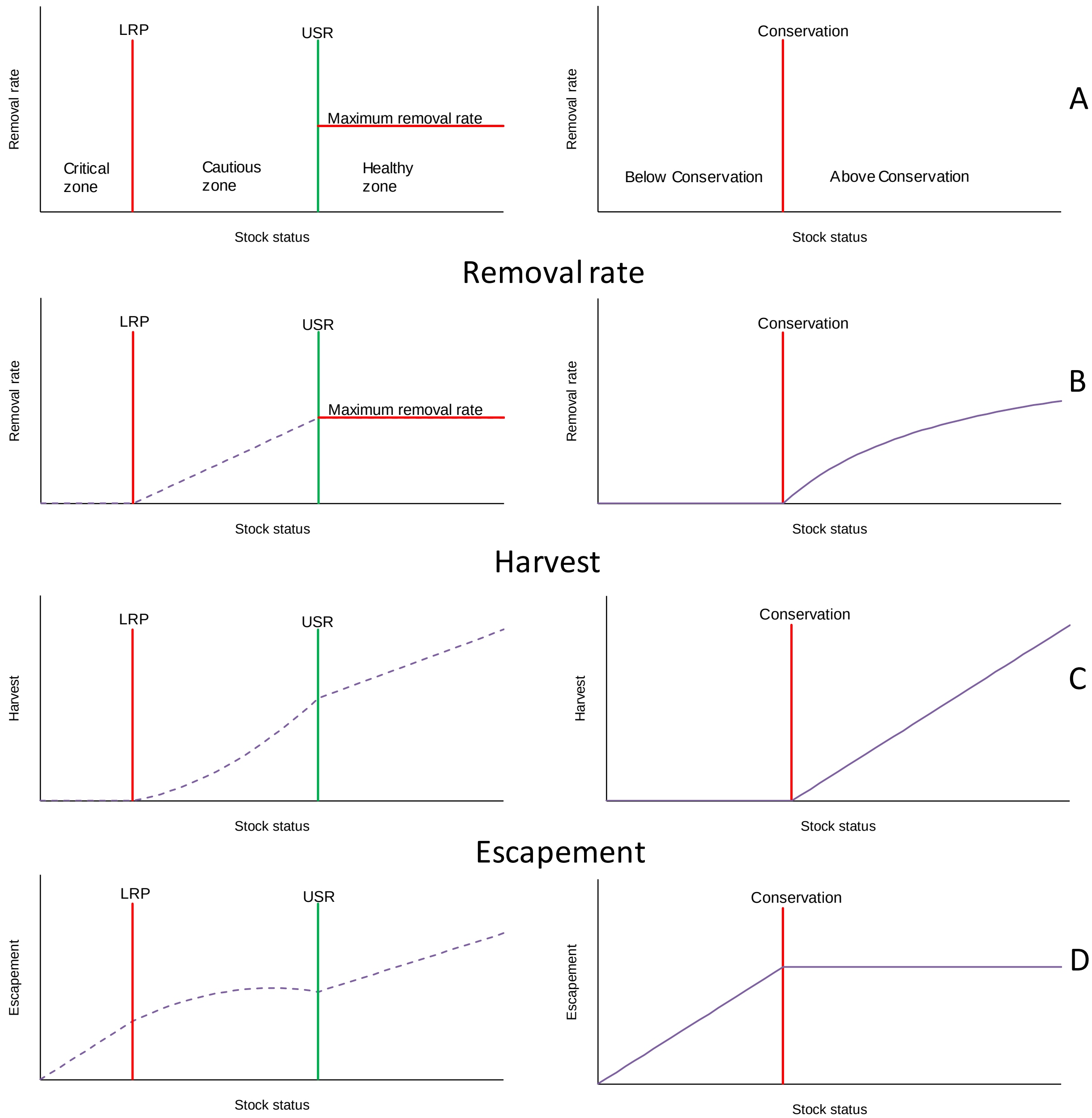


Figure 3. Contrasts of stock status and removal rate zones (upper row A) of a PA framework (left column) and the fixed escapement strategy and a single reference point framework (conservation, right column) as presently used for Atlantic salmon. The other rows show the corresponding removal rate (B), harvests (C), and escapement (D) for each management approach. A linear removal rate line in the cautious zone of the PA framework is shown as an example only. Reference values on the stock status and removal rate axes are arbitrary and for illustration only.

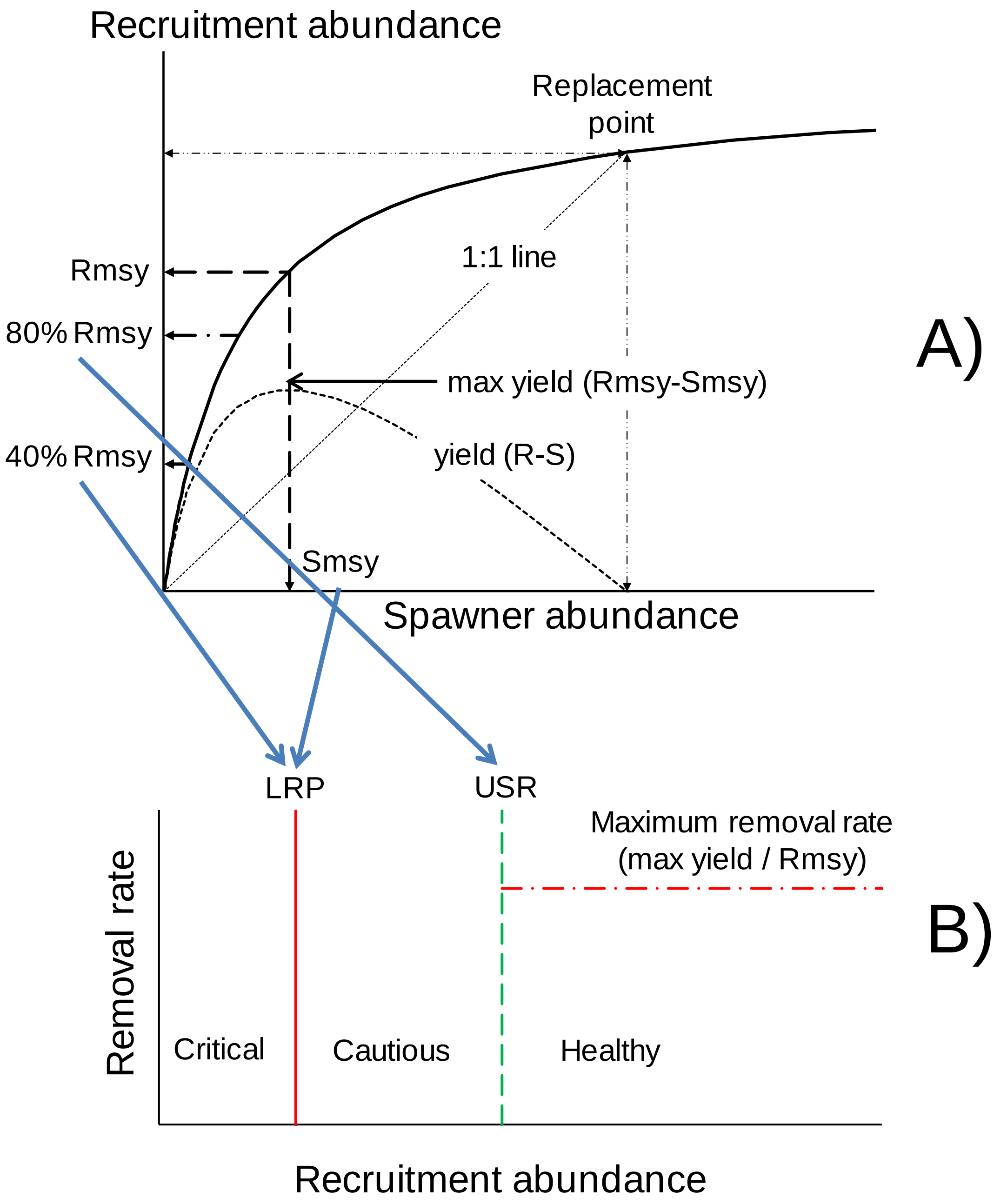


Figure 4. A) Features of an example mean stock and recruitment relationship (example Beverton-Holt relationship) with spawner abundance on the x-axis and recruitment abundance on the y-axis (in similar units) with candidate reference values for the PA framework. B) PA framework showing examples of reference values for the Limit Reference Point (LRP, solid red line), Upper Stock Reference (USR, dashed green line), and the Maximum Removal Rate reference (dashed dotted red line) translated from the stock and recruitment framework.

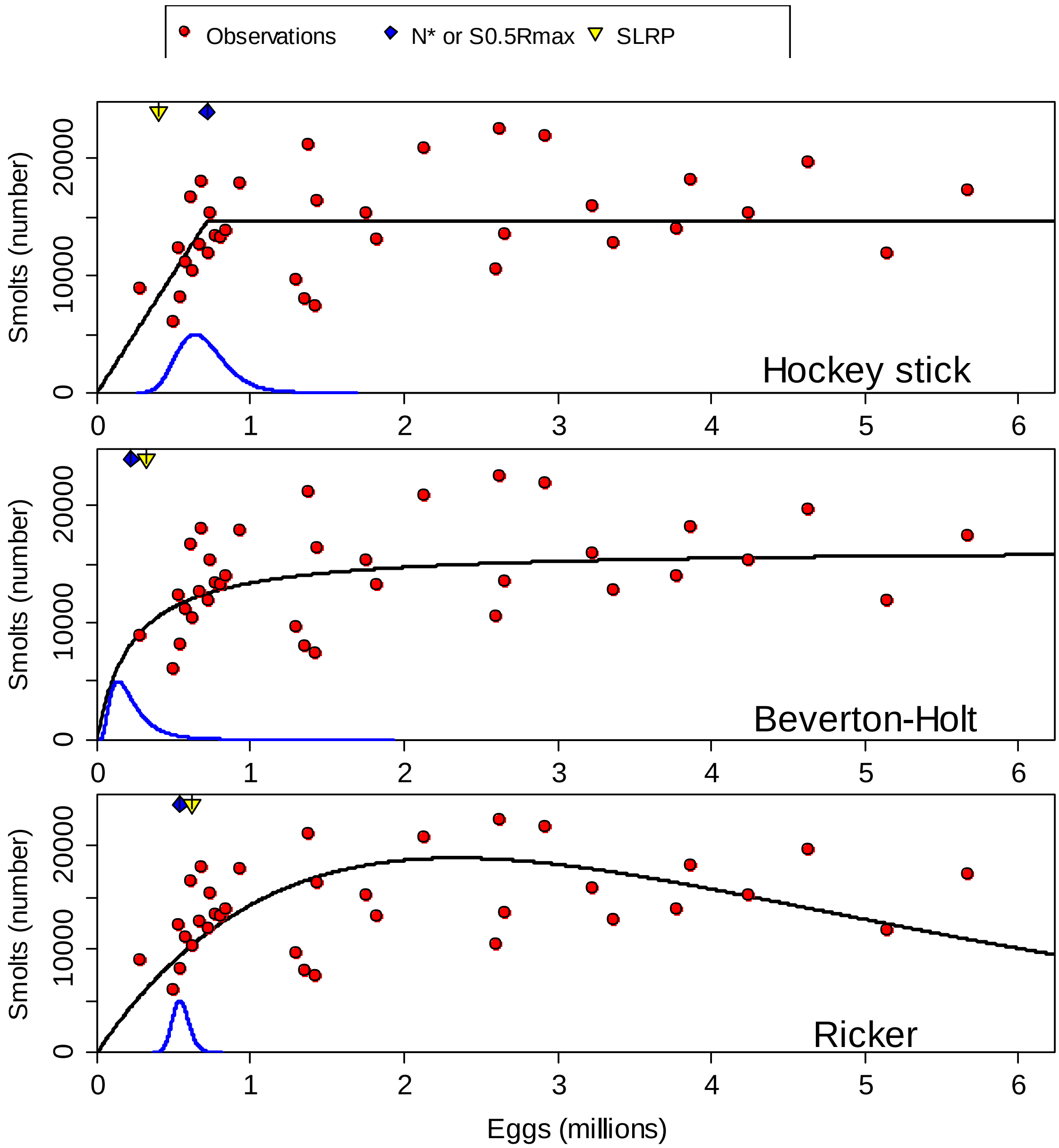


Figure 5. Examples of candidate limit reference points (N or S0.5Rmax, Slim) derived from analyses of a freshwater dynamic egg to smolt stock recruitment data series from Western Arm Brook (see Chaput et al. 2015 for details of data). The reference point N* is the minimum spawning stock that results in Rmax based on the hockey stick model (upper panel) and the reference point S0.5Rmax is shown for the Beverton-Holt (middle panel) and Ricker (lower panel) stock and recruitment assumptions. The stock and recruitment curves shown are the median curves based on the medians of the marginal distributions of the respective model parameters. The symbols along the egg axis (upper) correspond to the median values of the reference points (N*, S0.5Rmax) derived from the posterior distributions for each model and the curves are the density profiles for each reference point. The SLRP value is shown as a symbol.*

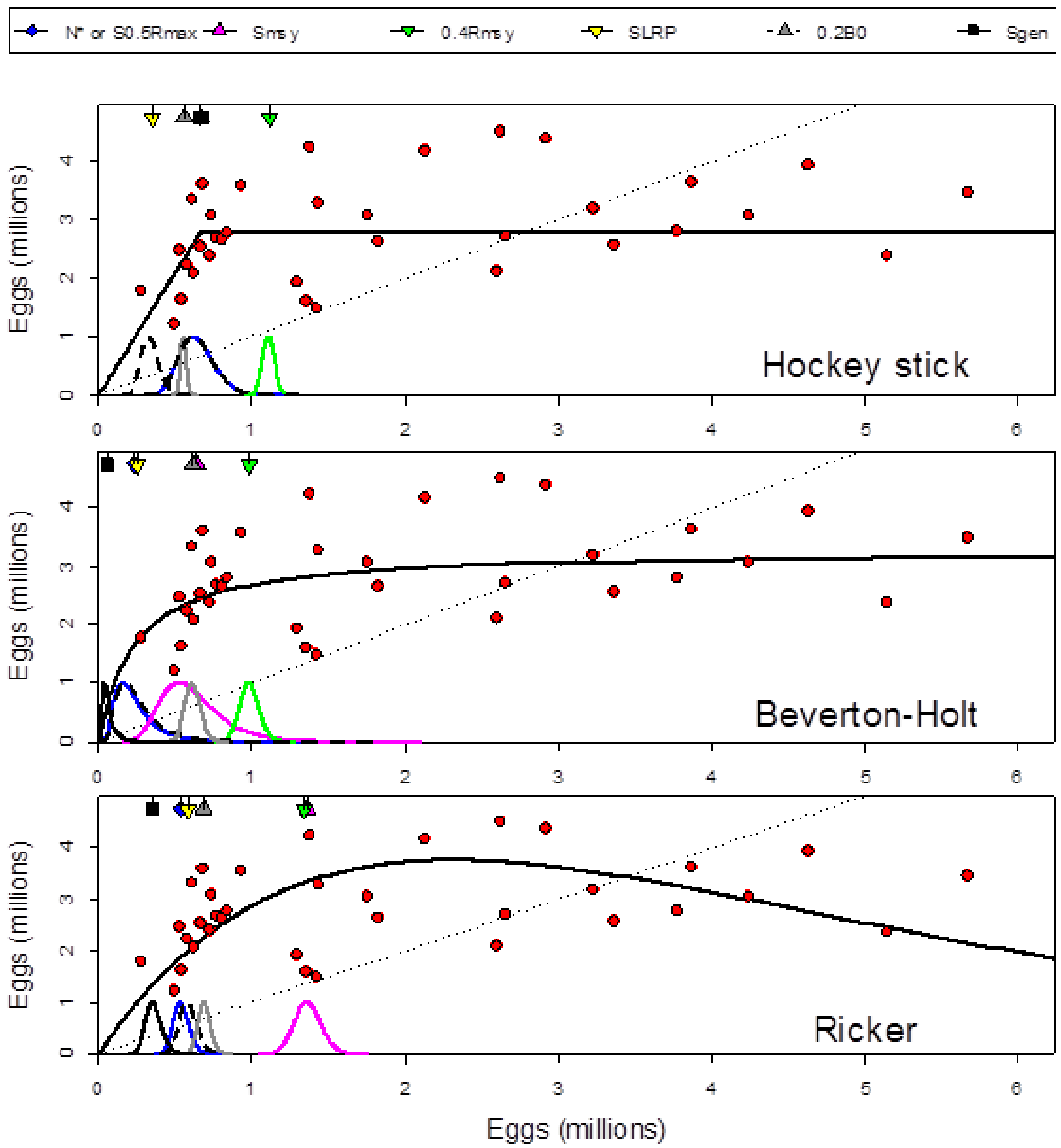


Figure 6. Examples of candidate limit reference points (N or S0.5Rmax, Smsy, 0.4Rmsy, SLRP, 0.2B0, Sgen) derived from three full life cycle models (upper panel - hockey stick; middle panel - Beverton-Holt; lower panel - Ricker) applied to the stock recruitment egg to smolt data series from Western Arm Brook (see Chaput et al. 2015 for details of data). The full life cycle model is based on egg to smolt data for the freshwater portion of the life cycle and an assumed average eggs per smolt (product of survival rate and eggs per adult return) of 200 to convert smolts to recruitment eggs. The reference point N* is the minimum spawning stock that results in Rmax based on the hockey stick model. The stock and recruitment curves shown are the median curves for each model based on the medians of the marginal distributions of the respective model parameters. The symbols along the egg axis at the top correspond to the median values of the reference points derived from the posterior marginal distributions and the curves are the density profiles for each reference point.*

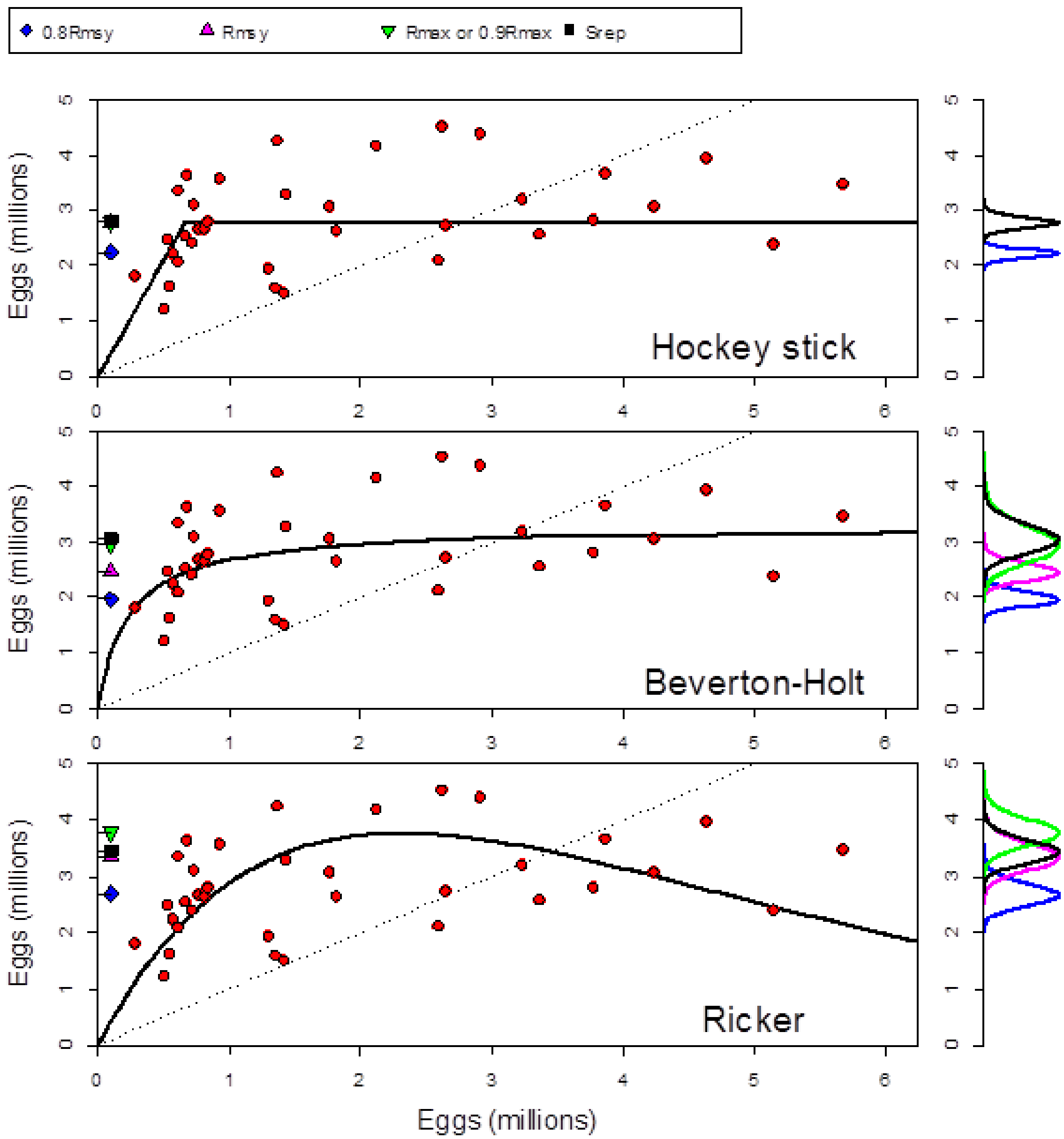


Figure 7. Example of candidate upper stock reference points (0.8Rmsy, Rmsy, Rmax or 0.9Rmax for Beverton-Holt, Srep) derived from three full life cycle models (upper panel - hockey stick; middle panel - Beverton-Holt; lower panel - Ricker) based on the stock recruitment egg to smolt data series from Western Arm Brook (see Chaput et al. 2015 for details of data). The full life cycle model is based on egg to smolt data for the freshwater portion of the life cycle and an assumed average eggs per smolt (product of survival rate and eggs per adult return) of 200 to convert smolts to recruitment eggs. The stock and recruitment curves shown are the median curves for each model based on the medians of the marginal distributions of the respective model parameters. The symbols along the y-axis correspond to the median values of the reference points derived from the posterior marginal distributions and the curves in the right panels are the density profiles for each reference point. For the hockey stick model, Rmax = Rmsy = Srep.

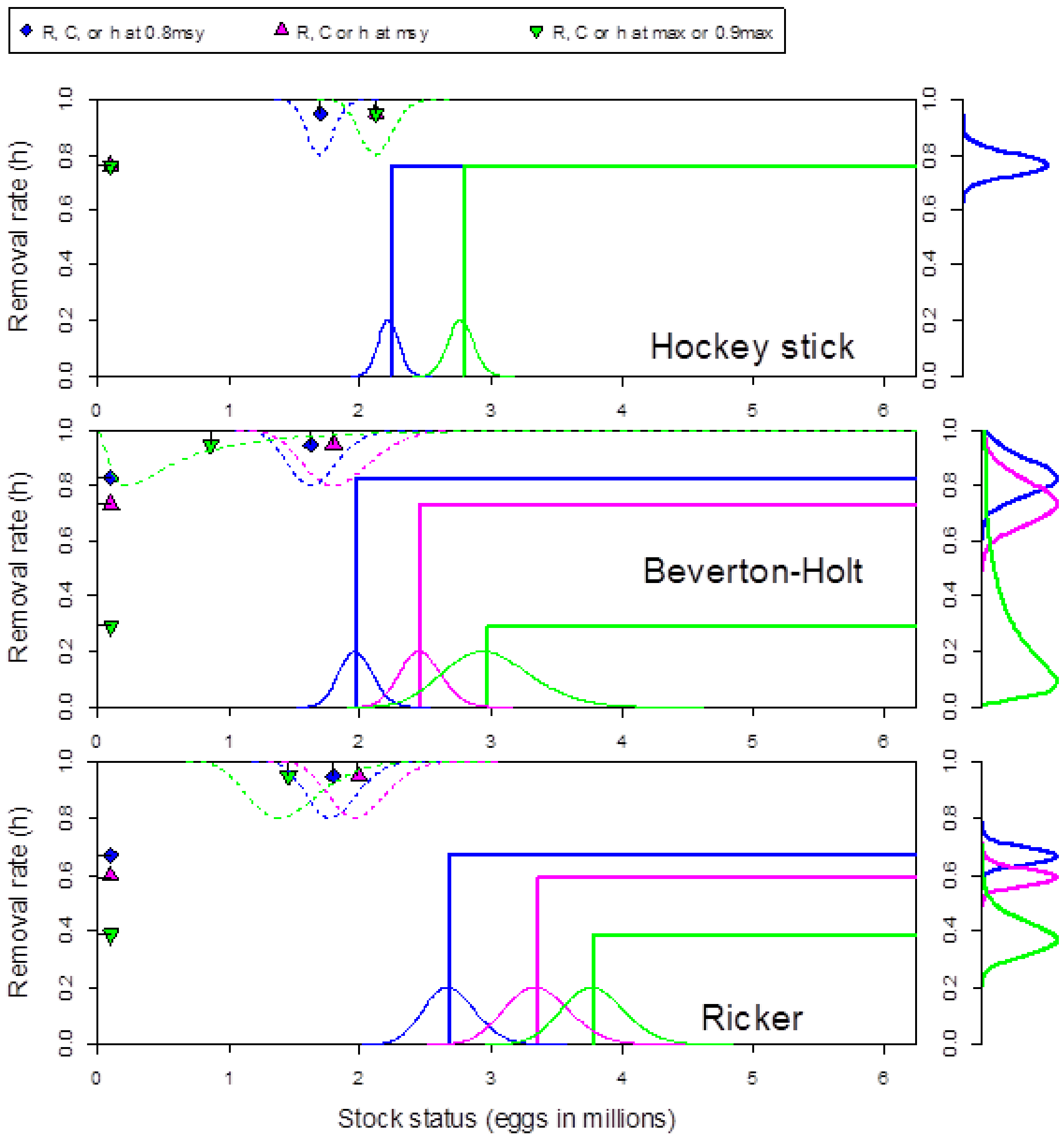


Figure 8. Examples of candidate upper stock reference points on the stock status axis (x-axis; 0.8Rmsy, Rmsy, Rmax or 0.9Rmax for Beverton-Holt) and corresponding removal rate reference points (y-axis: h0.8msy, hmsy, hmax or h0.9max) derived from three full life cycle models (upper panel - hockey stick; middle panel - Beverton-Holt; lower panel - Ricker) based on the stock recruitment egg to smolt data series from Western Arm Brook (see Chaput et al. 2015 for details of data). The full life cycle model is based on egg to smolt data for the freshwater portion of the life cycle and an assumed average eggs per smolt (product of survival rate and eggs per adult return) of 200 to convert smolts to recruitment eggs. The rectangular zones correspond to the respective upper stock reference points (median value) and their corresponding removal rate reference values (median). The distributions of the upper stock reference points are shown along the bottom stock status axis. The distributions of the removal rate references are shown on the right panels and their respective median values are shown as symbols along the removal rate axis of the left panels. The catches (in similar units to the stock status axis) corresponding to each of the reference values are shown as inverted distributions (dashed lines) and the medians as symbols along the top axis of each panel. For the hockey stick model, Rmax = Rmsy, Cmax = Cmsy, and hmax = hmsy = h0.8msy.

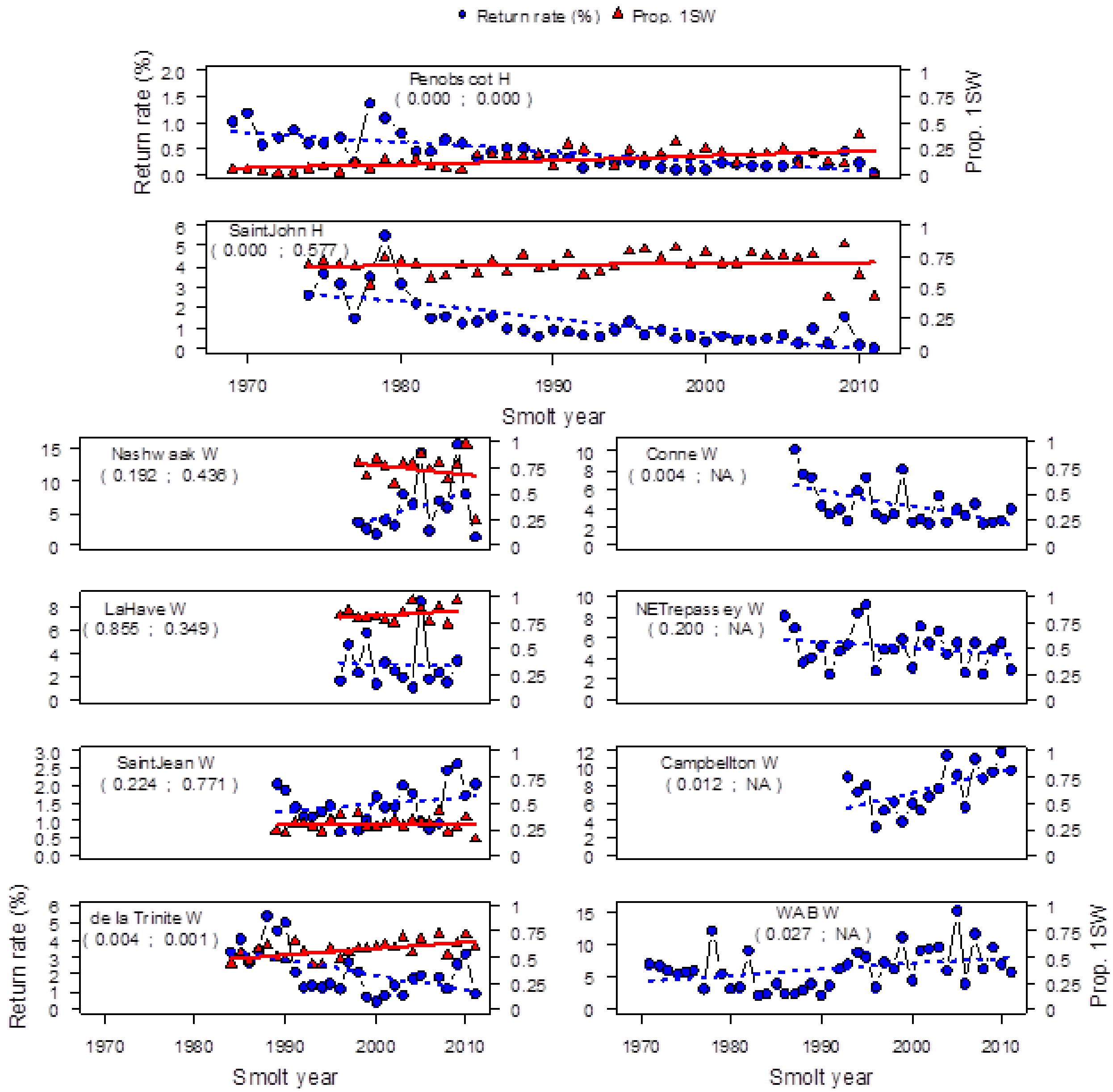


Figure 9. Examples of temporal trends in return rates (sum of maiden adult returns / smolts; blue circles and dashed line) and temporal trends in proportion of adult returns that are 1SW maiden salmon (red triangles, solid line) from monitored stocks of Atlantic salmon in eastern North America, by year of smolt migration. The two upper rows are hatchery origin smolt returns and the four bottom rows are wild origin smolt returns. The right panels in the four bottom rows are stocks from Newfoundland for which the proportion of the maiden returns are essentially all 1SW salmon. The first row of labeling in the figure describes the river name followed by the origin of the smolts (H = hatchery origin, W = wild origin). The second row of the labeling in the figure presents first the p-value of the linear trend in return rate followed by the p-value of the linear trend in proportion of the returns that are 1SW salmon.

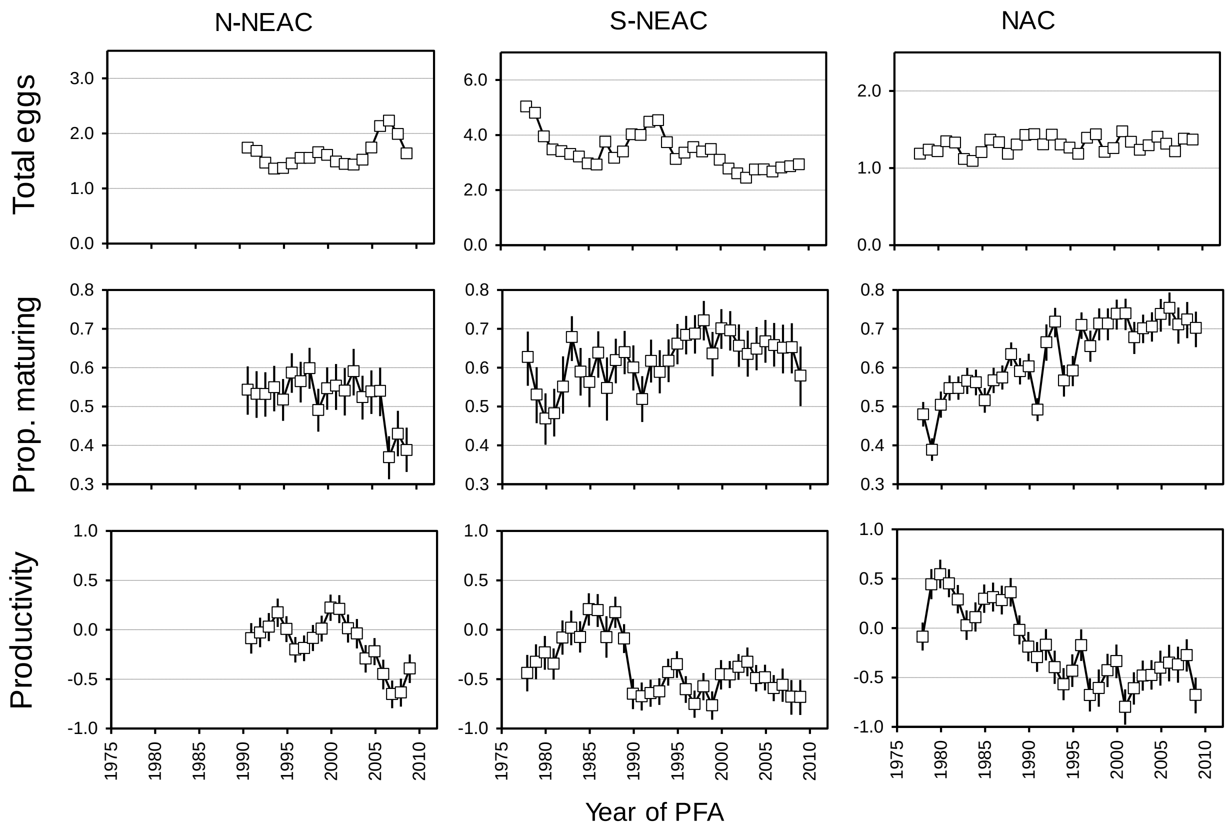


Figure 10. The estimated total eggs (billions) deposited (upper row), the proportions of the smolt cohorts (year of PFA – 1) returning as 1SW salmon (middle row) and the productivity (abundance at the PFA stage / eggs corresponding to the salmon at sea in the year of PFA) (lower row) of Atlantic salmon from the Northern Northeast Atlantic (NEAC) stock complex (left column), the southern NEAC stock complex (middle column), and the North American stock complex (right column) (Figures from Chaput 2012). The productivity variable is an integration of the freshwater dynamics and the marine mortality in the first year at sea (to Jan. 1 of the first winter at sea).

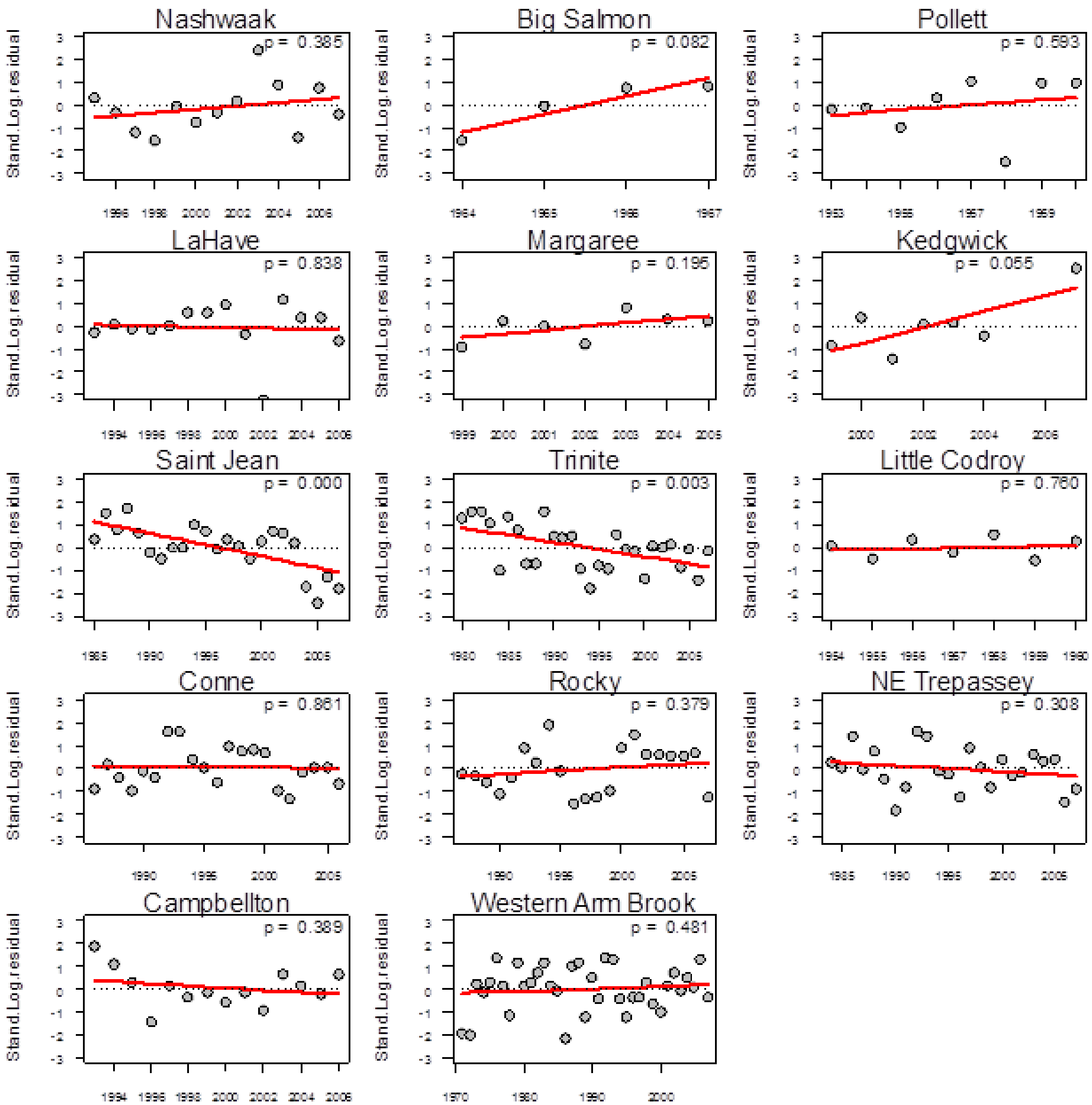


Figure 11. Trend analyses of the residuals (log-scale) from the Beverton-Holt stock and recruitment hierarchical Bayesian fits of egg to smolts by yearclass for 14 monitored rivers of eastern Canada. The trends (solid red line) are estimated using the median values from the posterior distributions. The p-values for the trend are shown in each panel (see Chaput et al. 2015 for details).

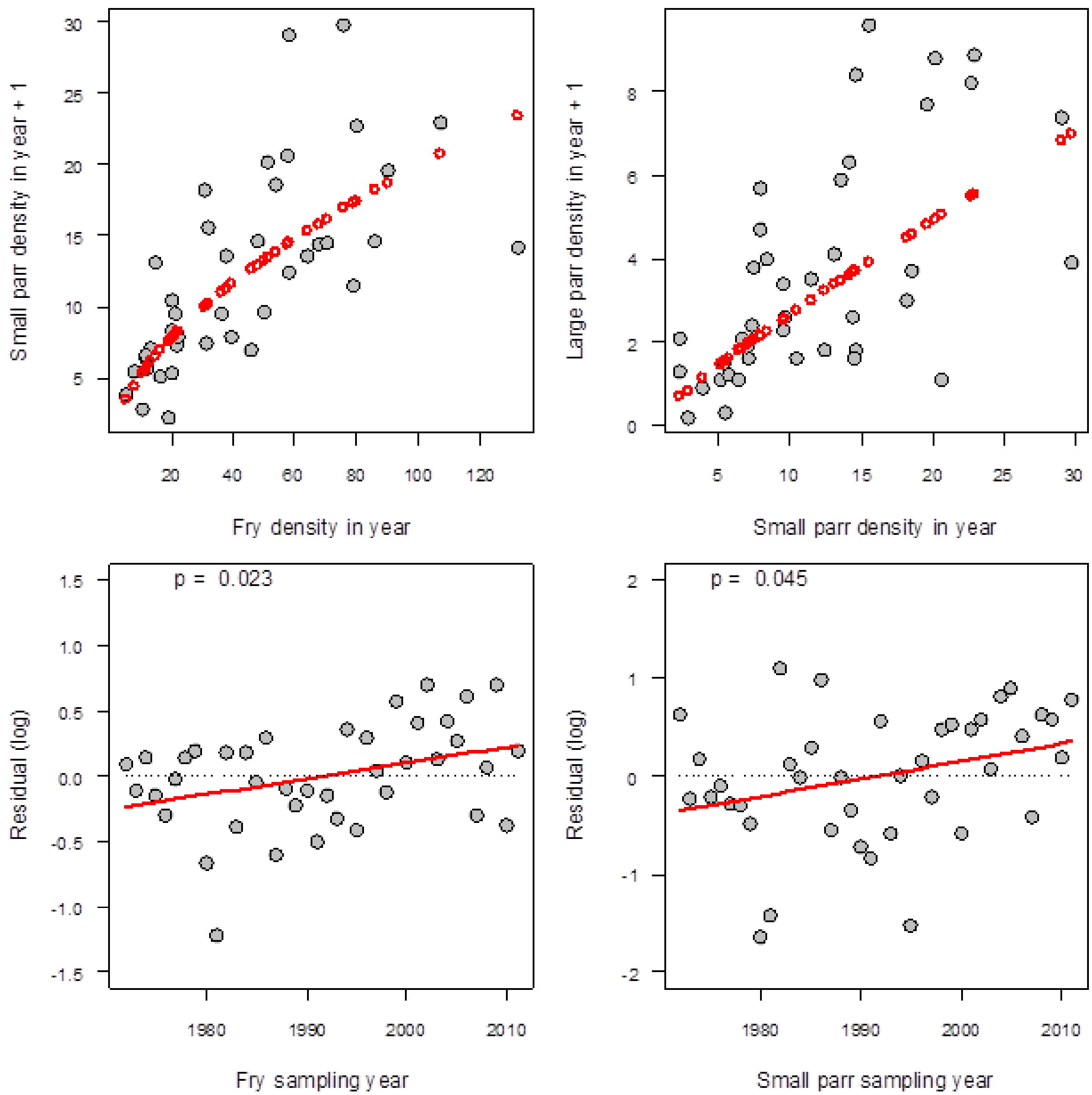


Figure 12. Relationship between the index of abundance of Atlantic salmon fry (age-0) in year y and index of abundance of parr (age-1) in year y + 1 is shown in the panels of the left column and the relationship between the index of abundance of parr (age-1) in year y and the index of abundance of parr (age-2+) in year y + 1 is shown in the panels of the right column. The pointed line in the upper panels is the median predicted density. The lower row shows the residuals (log) of the model fits by year of sampling. The data are from monitoring in the Kedgwick River (Restigouche, NB) as described by Cameron et al. (2009). The p-value of trend in log residuals are shown as insets in the bottom row panels.

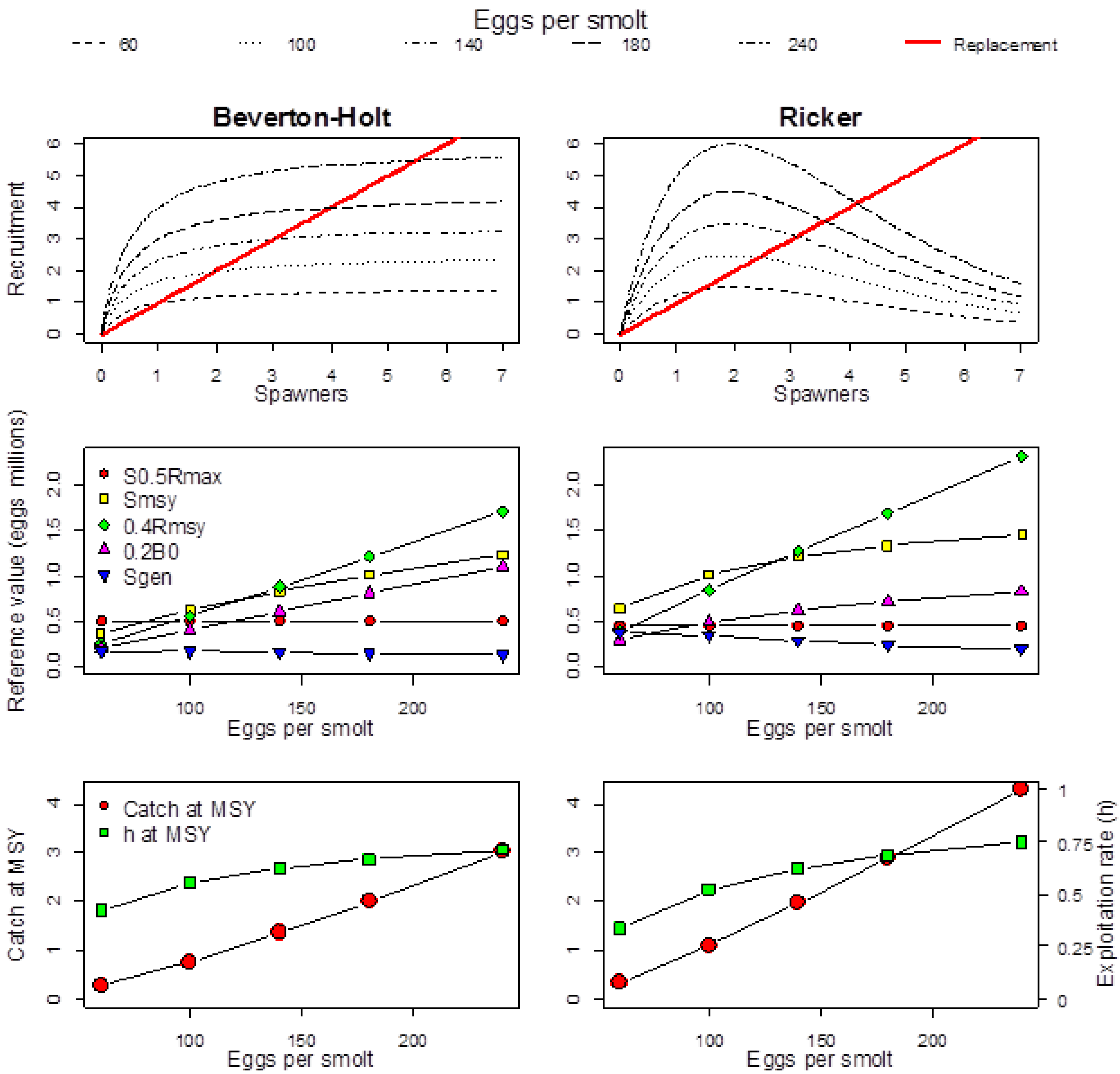


Figure 13. Example of effects of variations in density independent marine productivity for fixed density dependent freshwater dynamic on reference levels for the Beverton-Holt (left column) and Ricker (right column) stock and recruitment models. The upper row shows the mean deterministic stock and recruitment curves for five levels of marine productivity, the latter expressed in terms of eggs per smolt (product of return rate and eggs per returning adult; 60 to 240 eggs). The middle row shows the deterministic solution for the candidate limit reference points for each level of marine productivity. The bottom row shows the catches at MSY and the exploitation rates (h) at MSY for the five marine productivity levels. Alpha (survival at the origin in freshwater) was modelled as 0.05 for the Beverton Holt dynamic and 0.035 for the Ricker dynamic. For both models, freshwater carrying capacity (Rmax) was modelled as 25,000 smolts.

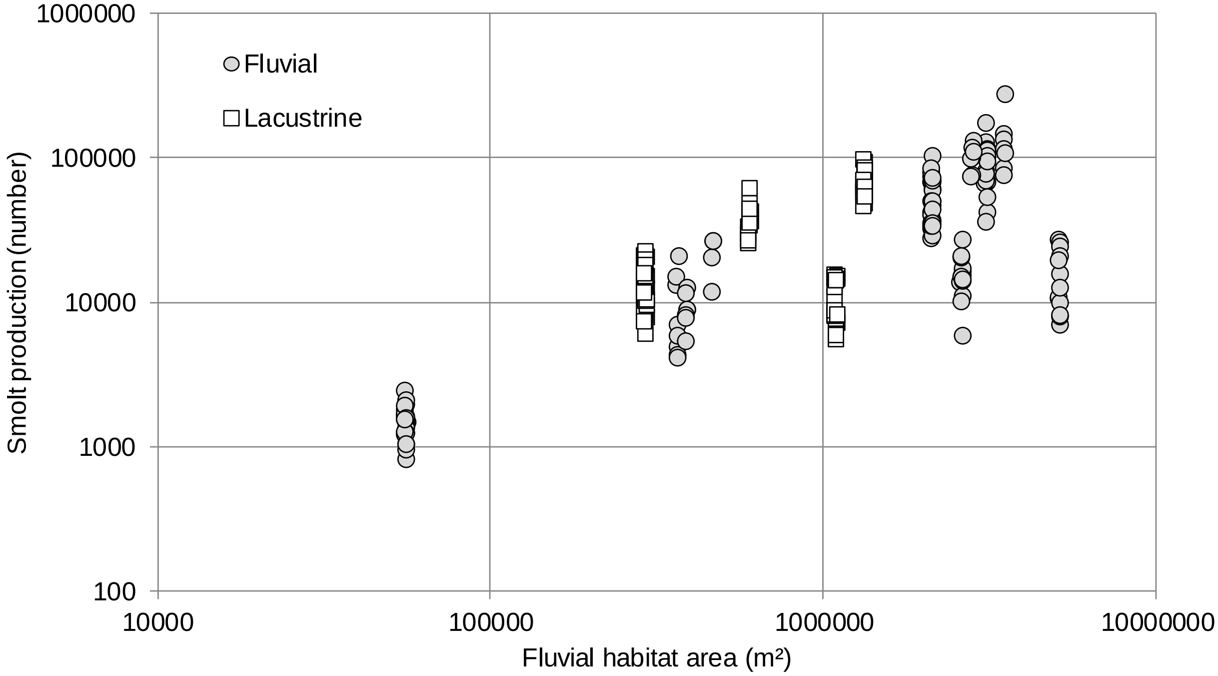


Figure 14. Relationship between smolt production from a river and the corresponding estimate of the area (m²) of fluvial habitat for rivers in which juveniles are known to rear in lacustrine habitat (with lacustrine) and rivers for which lacustrine habitat is not considered important for rearing juveniles (Fluvial only). The data plotted are from the 14 monitored rivers used in the analysis of Chaput et al. (2015).

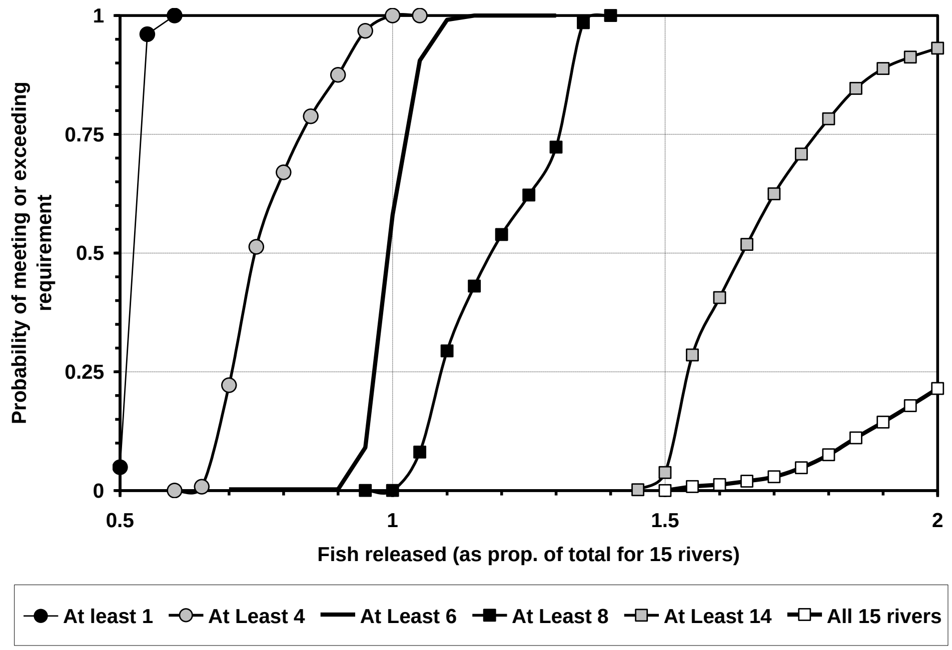


Figure 15. Example probability profiles of meeting or exceeding individual river spawner requirement (LRP) simultaneously in at least one river up to all 15 monitored rivers in an area, relative to the total fish escapement to the area's rivers (expressed as the proportion of the sum of the spawner requirements for all 15 rivers of the area). The sum of the spawner requirements for the 15 rivers equals 30,464 fish. Figure taken from Chaput (2004).