NORTHWEST ATLANTIC FISHERIES ORGANIZATION

Scientific Council Studies
Number 44

Report of the Workshop on Implementation of Stock Reproductive Potential into Assessment and Management Advice for Harvested Marine Species

2012
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ISSN-0250-6432
Report of the Workshop on Implementation of Stock Reproductive Potential into Assessment and Management Advice for Harvested Marine Species

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Abstract

A workshop on Implementation of Stock Reproductive Potential into Assessment and Management Advice for Harvested Marine Species that was held at the University of Aberdeen, Scotland on April 12–14, 2011. This Workshop was a key deliverable for the NAFO WG on Reproductive Potential. This workshop was held in conjunction with the EU COST Action Fish Reproduction and Fisheries (FRESH).

The workshop was organized by Tara Marshall (UK), Joanne Morgan (Canada), Loretta O’Brien (USA), Iago Mosqueira (UK) and Santiago Cervino (Spain). The objectives were to provide workshop participants with expert advice in implementing information on reproductive potential into the assessment of their stocks and to review and recommend best practices for incorporating information about growth, maturation, condition and fecundity into management of harvested marine species.

Invited presenters were Bridget Green (Australia), Adriaan Rijnsdorp (Netherlands), Peter Wright (UK), Coby Needle (UK), Paul Spencer (USA) and Liz Brooks (USA). Presentations were also made by Joanne Morgan and Santiago Cervino (Spain). The presentations were made under four themes: Estimating Stock Reproductive Potential; Implementing Estimates into Assessments; Are we doing it better, worse or just differently?; and Coding It Up.

The workshop concluded that it is clear that the incorporation of more complex indices of SRP can make a difference in the perception of stock status. Trends in biological parameters and the quality of the data on these parameters are both important components. Variation in weight at age and in maturity at age are both common and can have a large impact on perceived SRP. The collection of data on weight, maturity, sex ratio and fecundity is encouraged. Work on whether or not advice is improved by incorporating more biology into our estimates of SRP is only beginning. These studies should be continued and applied to more stocks and species with more varied reproductive strategies. One possible approach is likely to be within a management strategy evaluation context. This type of process would require the input of both modelling experts and experts in species biology.

Introduction

Scientific Council established the Working Group on Reproductive Potential followed a recommendation of the Symposium on “Variations in Maturation, Growth, Condition and Spawning Stock Biomass Production in Groundfish” hosted by NAFO Scientific Council from 9–11 September 1998, Lisbon, Portugal. Through the work of this group and the work of other investigators it has become clear that incorporating Stock Reproductive Potential (SRP) into assessments can lead to different perceptions about stock status and productivity. Given the potential importance of this work, in 2008 Scientific Council endorsed the development of a Workshop to help facilitate the transfer of techniques developed by WG members to stock assessment personnel that routinely conduct NAFO stock assessments.

In conjunction with the EU COST Action Fish Reproduction and Fisheries (FRESH) a workshop on ‘Implementation of stock reproductive potential into assessment and management advice for harvested marine species’ was held from 12–14 April 2011 at the University of Aberdeen.

The objectives of this workshop were to provide workshop participants with expert advice in implementing information on reproductive potential into the assessment of their stocks and to review and recommend best practices for incorporating information about growth, maturation, condition and fecundity into management of harvested marine species.

The workshop was organized by Tara Marshall (UK), Joanne Morgan (Canada), Loretta O’Brien (USA), Iago Mosqueira (UK) and Santiago Cervino (Spain). Invited presenters were Bridget Green (Australia), Adriaan Rijnsdorp (Netherlands), Peter Wright (UK), Coby Needle (UK), Paul Spencer (USA) and Liz Brooks (USA). Presentations were also made by Joanne Morgan and Santiago Cervino. The presentations were made under four themes: Estimating Stock Reproductive Potential; Implementing Estimates into Assessments; Are We Doing It Better, Worse or Just Differently?; and Coding It Up. Following the presentations in each theme, areas for further discussion were identified and groups formed to participate in these discussions and report back to plenary. In addition to the organizers and invited speakers, 16 others participated in the workshop. The presentations and discussions allowed people with diverse backgrounds to become familiar with the techniques used to compute SRP, the potential impact of SRP on our perception of stock status and some of the issues around incorporating SRP into scientific advice.
Theme 1: Estimating Stock Reproductive Potential

Bridget Green ‘What can maternal effects tell us about stock recruit relationships?’

The identification of a consistent source of recruitment variability has the potential to streamline the process of identifying stock recruitment relationships. In the past decade, maternal effects were lauded as a significant source of variation in offspring quality and subsequent recruitment variability. In particular, size and age of females in a stock, and their impact on offspring quality were assessed in laboratory correlative experiments. Of more than 140 papers examined on maternal effects in fishes, 10 studies (16 stocks or species) measured the effects of maternal age on offspring quality but only two identified age as key. Laboratory experiments offer a sometimes unique means of documenting relationships between life history features of adults and their offspring, but these relationships are not necessarily general or directly applicable to natural populations, and there is often scant support of a link between laboratory-derived metrics and recruitment in nature. Maternal effects can provide useful information about variation within a stock, and in some well studied stocks (e.g. cod, Gadus morhua) female quality can be used as a predictor for offspring quality. For well studied species like cod, within species diversity has been well documented and the maintenance of such diversity is considered to be important in stock productivity. Single traits of females such as size or age have been broadly accepted to be important to recruitment despite mixed evidence supporting this. However, to detect such effects, long time series of good quality data are required. So far evidence indicates that the key generalizations in maternal effects drawn from such well studied cases do not hold well between species or stocks, and have not yet provided the universal patterns that would be so useful in streamlining the identification of stock recruitment relationships. In the complex natural environment variables such as food availability and the physical environment have well-documented effects on offspring survival that swamp such relationships. Maternal effects interact with the environment in an often unpredictable way. Environmental effects on offspring quality can be equal or stronger than maternal effects alone. As environmentally explicit S-R relationships increase in use so should consideration of environmentally explicit maternal effects. If maternal effects are a source of phenotypic plasticity to deal with a variable environment and local adaptation of characters, this emphasizes the importance of maintaining diversity with a changing environment. The question is what are the important traits to maintain?

Adriaan Rijnsdorp ‘Factors affecting reproductive potential: application to North Sea plaice’

A key assumption in stock assessment and stock forecasts often is that spawning stock biomass and egg production are proportional and that the reproductive potential is independent of stock structure (age composition and sex ratio). On the basis of a 60-year time-series of total egg production (TEP) of North Sea plaice, we show that this assumption can lead to a biased perception of the temporal trend in reproductive potential. The time-series incorporates (i) annual observations on maturity, growth and condition, (ii) a predictive model for inter-annual variations in fecundity caused by variations in body condition and by the probability of being a recruit spawner, and (iii) a cohort analysis of sex-specific landings-at-age since 1948. Different from other studies, we took full account of the effect of age and size on the maturation probability, as well as on the probability to be a recruit spawner. Comparison of the reconstructed time series of stock reproductive potential showed that the assumptions on the weight at age of the spawning fish and the probability to spawn had the largest effect on the reconstructed time series of TEP. Taking account of variations in the size-specific fecundity only had a marginal effect. However, changes in fecundity have been limited over the time series. Following an increase in fishing mortality rate, total egg production declined by a factor of 7–8 from a peak in the 1970s to a minimum in 1999–2000. Concurrent with this decline, the contribution of recruit spawners decreased.

The observation that inter-annual variations in size-specific fecundity have little effect on the variations in the TEP of North Sea plaice is related to the reproductive biology of the species. Plaice is a capital spawner that supports its reproductive investment with the energy stored during the previous feeding season. Interannual variations in the conditions during the feeding season will mainly reflect in the variations in somatic growth but not in differences in the size-specific reproductive investment. Only if feeding conditions are insufficient to replenish the energy loss of the previous spawning period, will it negatively affect the size-specific reproduction in the current year. For income spawners we expect that the feeding conditions during the spawning period will have a direct effect on the reproductive investment. A framework on the inter-relationship of different characteristics (seasonal amplitude in body condition, maximum GSI, determinate or indeterminate fecundity type) of fish species is presented that is linked to the spawning time and the maximum body size of the species. This framework may help to infer whether annual variations in fecundity can be expected to have an influence on the TEP.
Peter Wright ‘Estimating Stock Reproductive Potential in North Sea haddock’

The use of spawning stock biomass as a proxy for stock reproductive potential has been criticised in recent years due to known size, age and condition effects on fecundity, maternal effects on egg size and the influence of spawning time. In addition, for many ICES stocks a constant maturity at age key is applied to estimate SSB. In this presentation options for estimating total egg production and the implications of spawning time are discussed in relation to the SRP of North Sea haddock (*Melanogrammus aeglefinus*). Using annual sex stratified maturity-length ogives mature female biomass was found to deviate from the ICES estimate by up to 67%. This was due to a declining trend in size at maturity, resulting in the proportion of age two mature varying from 0.11–0.86. However, inferences about SRP arising from these changes in maturity are somewhat misleading as age two haddock produce fewer eggs per body mass than older fish. Hence, increases in SSB associated with the entry of age two from a large year-class do not equate to a similar magnitude of increase in total egg production. Added to their lower relative fecundity, is the low survival probability of offspring from the age two spawning period. Hence, it is important to take account of age related differences in maturity, relative fecundity and survival probability in estimating changes in stock reproductive potential.

**Group Discussions Estimating Stock Reproductive Potential**

**Growth**

This group structured their discussions around a series of questions.

**Question 1. How growth can affect reproductive potential?**

The SSB and all components of the RP that are based on estimates of length and weight-at-age will be affected by bad estimates of age: it becomes the problem of ageing fishes, *i.e.* maturity-at-age, fecundity-at-age, and sex-ratio-at-age can be affected by poor or biased estimates of age. The relation between length and age is particularly important for converting numbers-at-length into numbers-at-age (catch and abundance indices) that are used as inputs into stock assessment models.

Some methods such as GADGET (www.hafro.is/gadget) model biological processes as length based and as such are not affected by ageing error.

**Question 2. Should we include the estimation of the growth into the stock assessment (parameter inference) or before?**

Theoretically, it should be better to integrate all sources of uncertainty to propagate the observation error throughout the stock assessment model results (*e.g.* integrated models such as Multifan-CL; Fournier *et al.* 1998). Some particular statistical tools (*e.g.* delta method implemented into the ADMB) are adapted to propagate the uncertainty.

On the other hand, it might be better (or/and simpler) to first fit a growth model and then include the results into the assessment model. In such cases, it remains possible to include the observation variance into the estimation process through the addition of the variance term into the likelihood components.

**Question 3. What kind of information is required for modelling growth?**

The way of approaching the growth will be dependent on the type of available data and stock assessment model used:

- Delay-difference model (two or more stages)
- Length-structured model
- Age-structured model

Modelling the growth can be based on different types of data:

- Hard part data (otoliths, scales, spines)
- Tagging data
- Length-frequency catch data (model progression)
- Experiments

And sex ratio to model growth separately in case of sexual dimorphic species.

**Question 4. How do we model growth?**

1. Mean length-at-age
2. Age-length keys (proportion of each age for a given length)
3. Growth curve

It is of major importance to include yearly variations into length-at-age and weight-at-age data. Age-length keys might be more appropriate than fixed growth curves for accounting for yearly variations but different age-length keys should be considered according to the data (gear-specific commercial catch data vs. scientific survey data). In addition, the growth model should account for spatial
variations in growth, sexual sexual dimorphism, and seasonal variations.

To go further in the growth modelling:

Mechanistic growth model as a function of gonado-somatic index (Roff 1984)

Linking growth data and bioenergetics (Walters and Essington, 2010)

Dynamic Energy Budget Theory (Kooijman 2010) Including ecosystem effects (predation, bottom-up processes favouring growth rates)


**Question 5. How do we compare growth models?**

Statistical techniques can be used to compare models and two good references are Burnham and Anderson (2001) and Haddon (2001).

**Condition**

*What is condition?*

Essentially condition comes down to the energetics/consumption formula:

\[
\text{Energy intake} = \text{energy lost to excretion} + \text{maintenance} + \text{somatic growth} + \text{reproductive growth}
\]

- So condition is nutritive condition which is simply the energy available for maturation
- If you are considering a capital spawner then they must store energy acquired during the feeding season for the time when maturation takes place. In this case you can measure condition (i.e. energy available for maturation) if you can measure stored energy. However, if you are considering an income spawner then energy for reproduction is not stored so it is not possible to measure condition.

**Condition and fecundity**

- Once fecundity is set increased condition cannot lead to increased fecundity in a determinate spawner
- However, decreased condition can lead to decreased fecundity (i.e. atresia) or even complete cessation of spawning (i.e. skipped spawning through mass atresia)

- Fecundity time series are lacking; however, if condition can be used to estimate fecundity then condition indices could be used where long-term data series are available
  - Length and weight data are readily available for many stocks so condition indices based on weight/length relationships are used most often
  - For some limited stocks more direct data may be available, *i.e.* liver weight data from Norway. In these cases the more direct indices are the better condition indices to use.
  - Could also use other methods such as fatmeter, mesenteric fat weight or visual estimation, BIA etc. to measure condition

**How to measure condition?**

- The means by which you measure condition depends on the fish type you are considering
  - Some fish (i.e. gadoids) store energy in their liver
  - Other fish (i.e. clupeids) store energy in their muscles and mesenteries
  - Some fish depend on fat, some on protein and some on both
- As fish store energy in different ways it does not seem useful or possible to have a universal answer to measuring condition – the best method will be species dependent.
- Length/weight relationships are used universally but there are issues
  - \( K \) (aka Fulton’s K) can be biased as it does not take into consideration variation in weight due to stomach contents and gonad size.
  - \( K \) also tends to increase with length and this must be taken into account
  - All length/weight condition indices suffer from the issue that water and fat can be inversely related in fish muscle so that when lipid decreases it is replaced by water. Therefore there may be a reduction in nutritive condition with no or little discernable change in mass
- However, as length and weight data are so readily available it seems that these are the indices that will most often be used
  - The von Bertalanffy growth equation can be used for weight rather than length and as such can reflect condition

**What next?**

- Measures of condition (further than simply weight and length) need to be taken systematically in
order to create condition time series that can be used in the future

- Liver weights
- Fat meter values
- Mesenteric fat weights/estimations
- Etc.

- How would you incorporate condition into the assessment?
  - In New England weight-at-age is currently used to predict fecundity in the assessment. Therefore, a crude measure of condition is already in the assessment.

**Maturity**

The source of information and quality of data are important aspects to understand in the calculation of maturity ogives. Need to know what the shortfalls are for each data source. For example, for species that migrate to a spawning area any surveys during spawning time that cover only the spawning area will have a bias. One can assume a constant bias, or combine data sets to produce a single data set which covers the whole population and use single maturity ogive. Selectivity issues would need to be addressed. Need to be aware of such aspects of selectivity, growth differences. The timing of the collection of the data is also important. Generally it is best practice to collect data close to spawning. Histological calibration of maturity scale to verify macroscopic classification is important.

If variability is observed in the proportion mature, then one should investigate other parameters that might explain the changes (e.g. temperature).

Maturities should be estimated by cohort if possible and of course by sex. However, estimation by cohort requires a lot of data over many years so that sometimes annual ogives are all that can be produced.

Should skipped spawners be included in SSB? They do not contribute to the SRP and can be a substantial proportion of adults (Barents Sea cod, age group dependant… 70–80% in older age female). However, it is difficult to subtract skippers since SSB is often used as management measure (fishable or harvestable biomass). If TEP is being estimated then skip spawners should definitely be removed. When removing skip spawners it is probably better to calculate maturity ogives as usual (including all adult fish) and then remove the estimated proportion of skip spawners at each age in each year.

**Sexual dimorphism and sex ratio**

Much of the group discussion focussed on Greenland halibut which has strong sexual dimorphism. This can create a practical problem for mesh size regulation. If mesh size is too large then only females will be caught which impacts SRP.

Greenland halibut sex ratios at length present a pattern with 50:50 for small length classes (before maturity); after males mature (males mature before females) the proportion of males increases for a short range of lengths; and afterwards males progressively disappear until only females contribute to the population (females have larger asymptotic length than males). A similar pattern was also observed in other species like hake, were male matures at lengths shorter than females and males also have a Lmax shorter than females. Probable explanation for that is the change in growth and/or natural mortality after maturity.

Another topic that got discussed in relation to Greenland halibut was the need to adjust maturity ogives for non-annual spawning. From the perspective of estimating SSB it would be interesting to estimate spawning ogives rather than maturity ogives as that would correct for skipped spawners and non-annual spawning. Oocyte size distribution could be useful in establishing spawning ogives for Greenland halibut. This could create practical problems for management when non-annual spawning, i.e. SSB is not SSB in the usual sense, however, the SSB would be more reflective of the species biology.

Other topics discussed by the group were whether females are necessarily the critical sex for reproduction. This is the normal assumption but there are species where this is not the case, e.g. species that reverse their sex.

In some cases data are available that could be used to do sex-specific stock assessment. The growth and mortalities could be treated separately for the sexes. This used to be done for North Sea flatfish with the output being combined to develop advice. YPR by sex could be explored, if differences in the sexes are large. The increase of biological realism is an important issue in modelling that should be considered with caution. The sex ratio at age is one of the easiest and cheapest information to get for assessment purposes. Their inclusion in assessment models should be considered under criteria of improving advice thorough a balance between increased model realism vs. decreased model parsimony.

One alternative which could provide some insight into stock status would be to include this type of information about sex ratios and dimorphism in a stock synthesis report, similar to how environmental issues are handled.
The specific case of pelagic stocks in the Adriatic Sea

In this working group we discuss about particular stocks in the Adriatic Sea (GSA 17 and GSA 18). Namely, small pelagic fish stocks of sardine and anchovy which are the most important commercial stocks of the whole Adriatic Sea. Both stocks are shared between Italy, Croatia, Slovenia, Montenegro and Albania. Till now, assessments of both pelagic stocks have been carried out in the ambit of the AdriaMed-SP research programme and done by Virtual Population Analysis (VPA). Only for the last three years DEPM (Daily Egg Production Method) was applied in the area of GSA 18 and only for anchovy. VPA is tuned with acoustic survey data.

There are some good data time series concerning the reproduction of those two pelagic fish species, like monthly variation of GSI and maturity stages throughout 12 years. However, the main question addressed by the group was how to improve the collection of data for maturity ogives and fecundity. With respect to maturity it was suggested that to determine the L50 it will probably be best to collect the samples over the whole stock area and to collect it just before or during the spawning season with the emphasis on collection of the specimens from age 0 and 1 as both species are fast growing, and appear to reach maturity during the first year of life. Concerning fecundity, it will be more useful to determine spawning frequency by tracking the post-ovulatory follicles (POFs). As anchovy and sardine are batch spawners the batch fecundity will need to be determined and for faster processing the best method for fecundity estimates will be the autodiametric method. It may be possible to extend the fecundity time series if there is a relationship between GSI and fecundity. The availability of monthly GSI samples may make this possible. With the data on maturity and fecundity also DEPM could be used and compared with the SSB obtained with VPA.

Theme 2: Implementing Estimates Into Assessments

Paul Spencer ‘Methods for incorporating reproductive biology into stock assessments’

Marine fish populations exhibit a number of complexities in their reproductive dynamics, including skipped spawning (not all mature fish spawn in each year), weight-specific relative fecundity, and variation in larval quality and/or spawning time due to maternal age/size. However, many stock assessments do not incorporate these complexities and make simplifying assumptions to generate estimates of spawning stock biomass. Abortive maturation from mass atresia (a form of skipped spawning) and decreased larval survival have been found in rockfish species off the U.S. west coast (Berkeley et al. 2004, Hannah and Parker 2007). Additionally, a recent meta-analysis of fecundity for U.S. west coast rockfish indicates that relative fecundity increases with fish size (Dick 2009); thus, spawning stock biomass is not proportional to egg production. These complexities are often not included into stock assessments, although several assessments of U.S. west coast rockfish have defined stock biomass reference points in terms of eggs rather than spawning stock biomass to reflect weight-specific relative fecundity.

The utility of incorporating more realistic measures of reproductive biology in stock assessments can be examined with respect to the effect on three critical tasks in stock assessment: 1) the estimation of abundance and biomass; 2) the estimation of target and limit fishing rates; and 3) estimation of a benchmark population size at which a stock is “overfished”. Data sets from the Gulf of Alaska walleye pollock and Bering Sea/Aleutian Islands (BSAI) Pacific ocean perch (POP) are used as example cases to illustrate potential effects. The Gulf of Alaska pollock are one of the few Alaska examples with a time-series of maturity data, and the size at age has also been increasing in recent years. The BSAI POP case was examined with respect to a potential maternal effect on larval survival. For each case, various measures of reproductive potential (reflecting the maturity data and choice of units of SSB, eggs, or viable larvae) did not have a substantial effect upon estimated recruitment, which were largely determined by fishery and survey age and length composition data. In data-poor situations with a reduced level of age and size composition data, it is conceivable that the units of reproductive potential and/or the form of the stock-recruitment curve could have a more significant affect upon recruitment estimates.

For the GOA walleye pollock case, the estimation level of “depletion” (the level of reproductive potential relative to the reproductive potential for an unfished stock) and the estimated fishing rate reference point Fmsy were influenced by the b exponent in the allometric relationship between eggs and body weight, E = aWb. Large values of b amplify increases in estimated egg production in recent years caused by the increasing weight at age, thus changing the perception of stock status. In addition, increased levels of b also result in increased levels of Fmsy. For the BSAI POP case, a maternal effect in larval survival results in a reduction in Fmsy relative to no maternal effect in larval survival. Taken together, these two cases suggest that relative to using SSB as reproductive potential (where b = 1), values of b greater that one indicate an increased level of reproductive potential and stock productivity,
and maternal effects in larval survival indicate a reduced level of reproductive potential and stock productivity. This range of results emphasizes the importance of determining the potential degree of these effects for any given stock.

The results above indicate the potential importance of reproductive processes on fishing rate reference points. To more fully incorporate reproductive information into the estimation process of stock assessments, a necessary requirement is the use of data that more directly reflects reproductive processes relative to standard trawl surveys which typically begin to observe fish several years after they are spawned. A larval survey is an example of this type of data, and is used in some U.S. west coast assessments. Within the assessment model, information on fecundity and other aspects of reproductive biology is then used to obtain a statistical fit to the index of larval abundance. Of course, any survey requires a significant investment of money and labor, but the observation that reproductive biology can affect both the estimated level of depletion and fishing rate reference points suggests that more data on population-level reproductive output may be warranted.

### Coby Needle ‘Implementing SRP estimates in management advice: the case of North Sea haddock’

This was a case study arising from the benchmark assessment for North Sea haddock. This is a stock with very strong recruitment signals, so the assessment has always been relatively well-behaved. However, the underlying biological data had not been closely examined within the assessment context. During the benchmark, estimates of natural mortality from a multispecies VPA and maturity at age were examined. Maturity at age was simply smoothed across year. The smoothed maturity estimates showed clear trends to an increase in proportion mature at age over time. Both natural mortality and maturity estimates differed from the constants used in the assessment. Incorporating these varying estimates resulted in a change in the SSB and recruitment estimates but did not really improve the S-R relationship. Including this variability did, however, result in a large increase in the reference point B(pa) and suggested that the stock, which previously had been perceived to be above B(pa), was now well below it. However, at the same time as the maturation rate increase, TEP has declined because the realized fecundity of younger fish (which make up a larger proportion of the current SSB) is much less than that of older fish, so the implications for reproductive potential are complicated. The report of the benchmark meeting included these estimates, but concluded finally that it would be best to consider the generation of management advice and reference points based on reproductive potential rather than SSB.

### Theme 3: Are we doing it better, worse or just differently?

**Joanne Morgan and Hilario Murua ‘Can we improve our advice by incorporating SRP into assessments?’**

**Introduction**

It has become clear that incorporating SRP into assessments can lead to different perceptions about stock status and productivity. However, it is not yet clear whether doing so leads to an improvement in these perceptions. Since biological factors incorporated into more complex indices of RP are themselves estimated with error, their use may simply add more error to the estimate of RP. Whether the incorporation of RP into fisheries advice results in an improvement in that advice is a major area that needs to be addressed.

There has been some work done on this area. Much of it relates to whether or not using more complex indices of RP will result in an improved S-R relationship or ability to predict recruitment. This is because of the importance of the S-R relationship to our understanding of population productivity and because of the often poor fit of S/R models to the available data. The rationale being that SSB is not a good estimate of RP and that, by incorporating variables which move us closer to viable egg and larval production, we will improve these estimates. Another aspect of “performing better” is how robust is the advice generated using different indices of RP and how sensitive is it to the different assumptions that are incorporated. Is the risk of the stock being outside safe limits lower using a particular index of RP?

These two aspects were reviewed. The results of the studies as well as the methods used in the various studies were highlighted. An attempt was made to identify factors which may be important in determining whether or not incorporating more reproductive biology into our assessments improves our advice.

### Improved S/R relationships affecting limit reference points

Alternative indices of SRP have been found to improve the S-R relationship in some studies but not in others.
Murawski et al. (2001) found that for Georges Bank cod, the fit of the Beverton-Holt S-R relationship was slightly better for viable larvae than for SSB, using residual sums of squares as the measure of model fit. The incorporation of fecundity estimates, and time series of sex ratio and maturity improved the S-R relationship for Baltic cod (Kraus et al. 2002). Improved model fit was evaluated using $r^2$. SSB, FSB and TEP were produced for Northeast Arctic cod to look at the impact of different indices of RP on estimates S/R parameters and perceptions of stock status (Marshall et al. 2006). Fecundity for TEP came from a relationship with length and condition. As part of this study, model fit statistics were reported as residual sums of squares and $r^2$. They found that SSB gave better model fit than FSB or TEP using a Sailing-Lord S-R model. Murua et al. (2010) produced indices of RP including variable maturity (SSB), sex ratio (FSB) and fecundity (TEP) for European hake and compared these to an RP which did not include any variation in reproductive biology. They fit three S-R models (Beverton-Holt, segmented and Ricker) for each index of RP and found that in all cases the Ricker model fit the best. The Akaike information criteria for the fits demonstrated that the best fit was achieved with an SSB including no variation in reproductive biology followed closely by the TEP-recruitment model.

Morgan et al. (2011) determined if including increased information on reproductive biology in indices of RP results in better predictions of recruitment for four populations in the Northwest Atlantic: Southern Grand Bank (NAFO Div 3NO) cod, Flemish Cap (NAFO Div. 3M) cod, Newfoundland (NAFO Div. 3LNO) American plaice (Hippoglossoides platessoides) and Greenland halibut (Reinhardtius hippoglossoides) (in NAFO Subarea 2 + Div. 3KLMNO). Four indices of RP were constructed for each: no change in reproductive biology, SSB where maturity at age is estimated by cohort, FSB where sex ratio is also estimated by cohort and TEP where fecundity is also included. Two methods were used to examine whether or not more complex indices of RP gave better predictions of recruitment. The first was the ability to predict 10% of the data which were selected at random and removed and the model then fit without these data. This first procedure was repeated 100 times for each S-R model for index of RP for each population. The second test was the ability to predict the most recent 10% of the data when these data were not used in the model fitting. Three S-R models were fit to each index of RP. These were both parametric (Beverton-Holt and Ricker) and nonparametric (generalized additive models). The measure of model fit was mean absolute error. For each S-R model the RP that gave the best predictor of recruitment was determined to see if predictability was improved for a given S-R model by using more complex indices of RP. Different indices of RP may not just alter the fit of a particular S-R model but may actually change the shape of the S-R relationship from one best described by one model to one best described by a different model. Poor ability to predict recruitment could be due to inappropriate model choice rather than a real change in predictive ability. The issue of potential bias of using a single S-R model was accounted for by examining three different S-R models. The combination of S-R model and RP index giving the best prediction of recruitment was determined. Stock recruit models paired with complex indices of RP gave a better estimate of recruitment in slightly more than half of the tests conducted (always for 3M cod and never for Greenland halibut). When there were larger trends in the reproductive biology (maturity at age, sex ratio and egg production) more complex indices of RP were more likely to provide a better estimate of recruitment, although the improvement was generally small.

A number of studies that have looked at the prediction of recruitment have examined the impact of the age structure of the spawning population, and again results have been mixed. Marteinsdottir and Thorarinsson (1998) were among the first to propose an impact of age diversity on reproductive success. Working with Icelandic cod, they produced a Shannon diversity index for the age composition of the SSB. They found that a linear model including log (SSB) and age diversity (and an interaction between these two) had a much better fit to the data based on $r^2$. Wigley (1999) examined S-R data for Georges Bank haddock and Gulf of Maine witch flounder (Glyptocephalus cynoglossus). She compared the $r^2$ from Ricker S-R fits to total SSB with fits to SSB with varying percentages of first time spawners removed. She found an improvement in the S-R relationship for haddock, but a deterioration for witch flounder, as the contribution of first time spawners was discounted. However, for both species, since data were limited, the calculation of first time spawners was based on maturity ogives fit annually or over blocks of time rather than by cohort. O’Brien et al. (2003) used egg and larval data from ichthyoplankton surveys in an examination of whether or not accounting for first time spawners improved the model fit for S-R data from Georges Bank cod. They used step wise multiple linear regression to choose the factors to include in a model to explain egg survival. The best model included the age diversity of repeat spawners. Data on maturity were limited and spawning history of a cohort was determined from maturity ogives fit over blocks of time. The effect of age structure on recruitment was examined for three species of cod and one of American plaice around Newfoundland by Morgan et al. (2007). A smoother was fit to the S-R data and the residuals were examined for a relationship with the proportion of first time spawners and age diversity of the SSB. There was little evidence that the age composition of the SSB played a role in
recruitment in these populations. Oskarsson and Taggart (2010) divided egg production by Icelandic summer spawning herring (*Clupea harengus*) into production by repeat and recruit spawners. Using a combination of generalized additive models and generalized linear models they found that the model with the best fit to the data included only egg production by repeat spawners. Brunel (2010) examined the effect of spawner mean age, age diversity, and proportion of recruit spawners for 39 stocks. Three S-R models were fit to each data set of SSB and R. The model with the best fit in each case formed the basis of the analyses. The residuals from this model were examined for correlations with the age diversity metrics. These metrics were also included as covariates in the S-R models in another test. Although significant effects were found for some species and metrics, the overall conclusion was that there was not strong evidence for an effect of age structure on recruitment.

**Improving the advice generated**

Simulation studies using a management strategy evaluation approach have provided the best avenue to date for examining whether or not advice may be improved by incorporating alternative indices of SRP. (DeOliveira *et al.* 2006) examined whether proxies for fecundity could improve the management of western horse mackerel (*Trachurus trachurus*). They constructed a known population and a relationship between this population and observed egg abundance. A proxy for fecundity was then used to calculate perceived SSB from the observed egg abundance. They then projected the true and perceived population to evaluate performance against Bpa. They found that if the proxy does not have a strong relationship with real fecundity and/or is based on only a short time series of data, then the population is kept above Bpa more frequently by assuming that fecundity does not change. DeOliveira *et al.* (2010) extended this simulation work on western horse mackerel. This study included an improved model of fecundity and examined the impact of trends in fecundity. In this case they compared the estimates from their population model against the ‘true’ rather than against a limit reference point. They found that estimates of SSB and F were biased if there were a trend in fecundity as this was not accounted for in the model of realized fecundity. Murua *et al.* (2010) also used a Management Strategy Evaluation approach to examine if the management strategy (MS) for European hake was robust to excluding biological data. Their results indicated that when including more information about reproductive biology in the simulation, the number of years below the reference points is higher in the “perceived” population than in the “true” population (i.e. the probability of a wrong perception increased). For the historic period, the probability of a disagreement between ‘true’ and ‘perceived’ is diminished when alternative reproductive indices are included.

**Conclusions on improvement in advice**

There is evidence that we can do better at predicting recruitment and in providing advice for fisheries management if we include reproductive biology into our stock assessments. However, it is also clear that whether or not this is the case depends on the stock being examined. There are two main reasons why this is so. Populations differ both in the amount of change that there has been in reproductive parameters and in the quality of the data available to estimate these reproductive parameters.

When there are real trends over time in reproductive biology, indices of RP that do not take variation in reproductive biology into account are less reflective of the true RP of the population. In essence, it increases the error with which these simple indices of RP measure true RP. This will lead to a reduced ability to predict recruitment and to erroneous perceptions of stock productivity. Reference points and perceptions of stock status relative to these reference points will be affected. If there is little or no trend in reproductive biology then, since these factors are all estimated with some error, the addition of these to our estimates of population size will likely just increase the error with which these estimates are made and we will not ‘do better’. However, there are many examples of trends in reproductive biology, particularly as population size decreases under exploitation. In addition, a population which has had relatively stable reproductive characteristics may not continue to do so in the future. Efforts to incorporate this information into our scientific advice are likely to be beneficial in many cases.

The quality and amount of the data that are available to estimate reproductive parameters varies greatly. Fecundity data are particularly lacking (Tomkiewicz *et al.* 2003). Without adequate data, trends can not be detected or incorporated into our population estimates. Factors that are estimated with large error or bias because of inadequate data will not improve the situation. Improvement in data collection should be pursued where possible.

There has been a wide range of approaches taken when using alternative indices of RP or investigating their utility. Some appear to be more appropriate than others. First, the biomass or abundance of spawners likely matters. S-R models should incorporate spawner abundance as a factor even if additional factors are included. This can take the form of SSB, FSB, or TEP, depending on what data are available. When comparing among indices of RP the choice of the S-R model matters. The best S-R model for
each index of RP should be determined. Different indices of RP may change the shape of the S-R relationship from one best described by one model to one best described by a different model. Poor performance of an index of RP in a comparison among indices could be due to inappropriate model choice rather than a real change in predictive ability. Similarly, if one is evaluating the status of a stock relative to reference points using different indices of RP, the reference points should be derived from the relevant index of RP, rather than using a single set of reference points that are applicable to only one index.

**Group Discussion Implementing Estimates into Assessments and Are We Doing it Better, Worse, or Just Differently**

**Relative fecundity and links to reference points**

The discussion was stimulated by the presentation given by Paul Spencer showing results from PhD research by E. J. Dicks that for the Fecundity = a Weight^b relationship the exponent b is systematically larger than 1. Note that this violates the assumption that b = 1, which is required for the assumption Fecundity/Weight (i.e., relative fecundity at the individual level) is a constant. If this assumption does not hold, then relative fecundity at the stock level (i.e., TEP/SSB) cannot be regarded as constant. This has already been shown to be true empirically (e.g., Marshall et al. 2006, Mehault et al. 2010). It is therefore of interest to follow the impact of b > 1 on biological reference points, similar to the analysis done by Spencer et al. 2007.

The discussion began with a technical point made that measurement error could be impacting estimates of b. If fish are sampled for fecundity at a single time point and the sample includes a range of sizes then larger fish will presumably be closer to spawning than smaller fish. Larger fish will have undergone a higher degree of down regulation and thus have more precise estimates of fecundity compared to smaller fish that will not have undergone full amounts of down regulation. Thus the fecundity of small fish will be overestimated relative to large fish causing b to potentially be underestimated compared to if all fish had been estimated at a fixed maturity stage rather than a fixed time point. This means that the modelling done with values of b might need to be corrected for a possible systematic bias.

Accepting that the value of b is likely to be greater than one and also potentially under estimated, the discussion then moved to recent work of Mehault et al. (2010). A time series of values of TEP divided by female-only SSB (TEP/FSSB), which is an expression of relative fecundity estimated on a population scale, for the southern hake stock was examined. The time series shows a downward trend (1982–2007) due to the change in size composition of the stock to a higher proportion of younger aged females over time.

Given that there is a size-dependent systematic bias in the estimation of reproductive potential, the question became what is the effect of this bias on reference point estimation. To understand this, an approach used by Spencer et al. (2007) of constructing both the stock/recruit curve and the replacement line was discussed. There was some discussion as to the exact impact of b > 1 on the stock/recruit curve compared to the b = 1 curve. Some felt that b > 1 curve would be lower than the b = 1 curve when SSB was low (because of the dominance of smaller sized individuals in the SSB) and then become higher than the b = 1 curve when SSB was high (because of increased representation of larger sized individuals). This would have some impact on the replacement line. The study by Spencer et al. (2007) showed that if b > 1 (in weight fecundity relationship) there are two opposite impacts on biological reference points. (1) reduced depletion per recruit for the same F level and (2) increased steepness in the stock recruitment relationship. Both effects counteract each and F reference points may change in one or another direction depending on the weight of these two effects.

**Uncertainty**

There is uncertainty in inputs and also in model outputs and how to incorporate that uncertainty into advice for management. Discussions in this group focused on the uncertainty in inputs.

- Sampling error/Data uncertainty
  - Spawning frequency
    - spatial distribution of stock, and inability to adequately sample all spawning aggregations
  - Batch spawners
    - inability to determine how much spawning has occurred (what is left in the fish when you catch it) and how many times it will spawn; this differs between determinate and indeterminate most likely to underestimate this (for potential rather than realized fecundity);
  - Relative inference on batch fecundity may be a way to deal with this
  - Larger fish produce more batches and more eggs per batch (hake, e.g.); however, number of batches can be
influenced by external factors, and not just length; also the seasonal pattern to batch spawning varies; in general, larger fish spawn for longer time periods

- Maturity
  - Observation error between macro/micro examination; need histology to confirm it, but also requires consistency in slide readers; somewhat dependent on the number of stages considered (four or seven) and how you interpret some of the finer scale categories
  - Uncertainty between immature and resting (or skipped spawning); takes experience to determine resting/spent from skipped spawning. The bias could go either way (over or under) as you confuse immature with resting, or vice-versa

- Length
  - Estimation error is introduced depending on how you model total egg production (whether you use population mean length and apply the estimated fecundity relationship, or if you estimate fecundity at the individual fish level and then scale that up to the population)

- Sex ratio
  - Proportion of each sex at length or age, difficult to determine especially for very small fish (hard to identify sex for immature); however, this point may not be important because unsexed immature fish would not contribute to SSB; it may impact estimation of the maturity ogive; sampling error may impact stocks that segregate spatially or vertically by sex (even on spawning grounds)

- Model error
  - Fecundity
    - How variable should the fecundity exponent be – you expect it should vary by year, but you may not be able to estimate it so you may assume it is constant (misspecification error)
  - Abundance at age
    - Need a method to quantify this (bootstrapping of VPA or internal accounting of variance in SCAA)

- This propagates directly into your TEP calculation

Uncertainty in outputs was not discussed here but links with a previous section (Improving the advice). Management Strategy Evaluation is a tool to evaluate the impact of biological uncertainty on assessment and advice (Murua et al., 2010 and De Oliveira et al., 2006)

Alternative reference points

The goal of this discussion group was to brainstorm alternative reference points that account for changes in reproductive potential (TEP or component: age diversity, size diversity, sexual composition) of a stock.

Initial discussions focussed on current reference points, particularly those pertaining to the spawning stock biomass. Ad-hoc or explicit fitting algorithms such as a hockey stick model can be used to define SSB thresholds (e.g. B_{lim}), beyond which recruitment is impaired. Where suitable data are available, SSB can be converted to total egg production (TEP) such that alternative reference points may be defined, e.g. TEP_{lim}. These could be estimated in a similar way to those based on SSB.

Where it is not possible to estimate TEP, proxies such as age or size diversity were discussed. In effect, the relationship between SSB and recruitment is extended in these additional dimensions, which are thought to impact upon recruitment success. For example, where the diversity of ages that comprise the spawning component of a population is thought to impact egg production, a measure of age diversity can be incorporated into the stock recruitment relationship. Which features captured the distribution of ages, e.g. variance, skewness, kurtosis or some combination thereof, was discussed. Whether the formulation of the extended SR relationship is achieved in a heuristic or derived fashion was discussed. The point was made that the derivation of most stock recruitment relationships includes egg production in their derivation. These are ultimately combined into slope at the origin or maximum productivity, which combines egg production and density-independent mortality. A focus on these earlier steps may assist in the derivation of defensible reference points.

Once a functional form or suite of functional forms for the extended recruitment relationship is decided upon, this can be fit to the data using maximum likelihood or other method. What is then achieved is a surface over SSB, R, and age diversity. To maintain a given recruitment level over the additional dimension, the reference point
becomes isoclines in SSB and age diversity space. Data may not be sufficient to precisely estimate these isoclines and they should therefore be associated with an estimate of uncertainty based on the maximum likelihood fitted parameters. In addition, the uncertainty associated with TEP should be propagated where available.

The issue of changes other than those in reproductive biology was raised. For example, predation could be more proximally important to recruitment than reproductive output given the very high rates of natural mortality occurring at young ages. It is important to note however that the converse argument could also be made that if we are interested in estimating predation effects, changes in reproductive potential should be isolated from interaction coefficients.

The difficulty of communicating additional dimensions to managers was raised.

Projecting SRP

How best to do this is likely very dependent on species biology and life span.

It is important to have a basic data set including:

- Stock composition – that is number at age or length,
- Length-weight relationship (to estimate weight at age or length)
- Growth models
- Sex composition/sex ratios
- Some knowledge on the reproductive biology, maturation, egg production, who is contributing to spawning, sexual dimorphism etc
- Maturity ogives (including standardization/validation)
- Estimate stock reproductive potential size in numbers (at age or length)
- Stock-recruitment model

When time series of these factors are available then one may have a basis for proceeding into SRP projections.

**Criteria needed to include SRP into management**

A couple of opinions arose out of the presentations from Theme two and three. Do we need to show we are making improvements? But why should stock reproductive potential be held to any higher standard to other measures. Do not want to add any further noise and can do whole process on SSB. It was concluded that the answer is yes because since we are providing advice we do not want to introduce deterioration in the quality of that advice. We
want to be able to have the best predictor of recruitment possible.

Current practice may not be giving you the best possible time series.

The challenge is in determining if alternative indices of SRP lead to an improvement in advice.

It is only after you have actually calculated alternative indices of SRP that you can judge whether you should use these alternative indices. So researchers should continue to compile time series of fecundity, maturity, and sex ratio. If you have data you should start to investigate the quality and whether the alternate indices you are producing are improving things. If stock assessment working groups also calculate TEP as well as SSB (even if not used in the formulation of advice) this would provide a data set for others to explore if advice could be improved by using TEP.

Criteria

1. Examine the uncertainty in the estimates themselves: can you detect the trend through the noise.

2. Does it improve subsequent management advice

A couple of avenues were discussed with respect to this item two. First it is possible to evaluate whether or not the S/R relationship is improved by removing a percentage (10%) of the data and refit SR curve (reproductive potential) and see if model now predicts well the missing data. Model quality could also be examined through use of indices such as AIC, r², DIC etc.

It is also possible to look retrospectively at whether or not stock performance would have been improved by using alternative indices of RP. Does management perform better with TEP or SSB approach? Models can be run many times to see what percentage of time biomass falls below B_{hm}, however, the retrospective analysis would have to go back far enough in time so that recruitment would be having an influence. This would be easier to test on stocks with young recruitment, i.e. 1–2 year olds.

A good approach is likely to be within a management strategy evaluation context. In this approach an operating model (OM) representing “true world” would be constructed where the population has similar characteristics to the population being studied and recruitment is generated from TEP (in case of uncertainty in fecundity, alternative b parameter may be tested). There would be two ‘perceived’ worlds. In one the assessment uses TEP and the reference points are based on TEP. In the second the assessment advice is based on SSB and the reference points come from SSB. In both “perceived worlds” the sampling errors should be considered, particularly those in the biological sampling (maturity, sex ratios, egg production or “b” parameter, etc). A number of years would be simulated in each case and the corresponding management decision based on the perceived world is applied in each year to the OM. This would be done numerous (1 000) times and the risk of the population being outside of safe “real” biological limits is calculated. One approach would be to evaluate the risk of population collapse using different indices of RP. For example if the risk is lower for the ‘TEP perception’ of the world then this is what should be used. This could occur if less complex indices of RP poorly represent the actual RP of the population (see DeOliveira et al. 2010).

Another approach would be to find harvest control rules that are robust to different assumptions about RP. It might be possible that it would be sufficient to build a series of these simulations which span several different types of populations (e.g. gadoid like, hake like) rather than having to apply this approach to every stock.

This type of process would require the input of both modeling experts and experts in species biology. The number of people with the required expertise in modeling is limited. In addition the management framework needs to be considered (if the management approach is one based on SSB then SSB still needs to form the basis of the advice so one would need to demonstrate that the approach needed to be changed and convince managers to do so).

The discussion above relates to assessments with age disaggregated models. Stock recruit relationships are not used in every assessment however, measures such as fecundity estimates, etc. may be indicators of changes in stock productivity and may help explain other trends in the stock.

Theme 4: Coding it up

Liz Brooks ‘Relationship between biological parameters and biological reference points.’

Analytical solutions for biological reference points are derived in terms of maximum lifetime reproductive rate. This rate can be calculated directly from biological parameters of maturity, fecundity, and natural mortality or a distribution for this rate can be derived from appropriate metadata. Minimal data needs and assumptions for determining stock status were discussed. The derivation of a re-parameterization of the common stock–recruit relationships, Beverton–Holt and Ricker, in terms of spawning potential ratio was shown. Often, parameters
in stock–recruit relationships are restricted by tight prior distributions or are fixed based on a hypothesized level of stock resilience. Fixing those parameters is equivalent to specifying the biological reference points. An ability to directly calculate reference points from biological data, or a meta-analysis, without need of a full assessment model or fisheries data, makes the method an attractive option for data-poor fisheries.

A detailed example of the impact of variation in maturity, fecundity and mortality on reference points was given. This was done to illustrate how one could explore this issue and was accompanied by R code that was distributed to participants to allow them to explore this on their own (Appendix SS).

Santiago Cervino ‘An introduction to FLR’

An introduction and overview of the software FLR which is platform for quantitative fisheries science based on the R statistical language. FLR aims to facilitate and promote research about: stock assessment and provision of management advice; data and model validation through simulation; risk analysis; capacity development and education; promote collaboration and openness in quantitative fisheries science; support the development of new models and methods; promote the distribution of new models and methods to a wide public. The FLR library is a collection of tools in the R statistical language that facilitates the construction of bio-economic simulation models of fisheries and ecological systems. It is a generic toolbox, but is specifically suited for the construction of simulation models for evaluations of fisheries management strategies.

Development is managed through R-Forge (http://r-forge.r-project.org/projects/flr/), source code and the packages can be downloaded from here. Alternatively, current stable release may be installed directly from R (> 2.13.0) using > install.packages (repos="http://flr-project.org/R"). Documentation for the software (courses, tutorials, code, data, etc) can be found at (http://www.flr-project.org).

The software provides a potentially powerful platform for research into the impact of incorporating reproductive potential into fisheries science. Stochastic simulations and the constructions on Management Strategy Evaluation frameworks are among the main FLR contribution to the research involving reproductive issues into assessment and management.

Future Directions – Plenary Discussion

In order to make further progress in this area there are a number of interlinked areas which should be explored.

Many of the causes of change in growth, reproduction and condition are known in general but the effect of a change in a particular biotic or abiotic factor can not be quantitatively predicted. Further, although we know that growth, reproduction and condition are all related through tradeoffs in energy allocation, we rarely have a quantitative model of these tradeoffs. A better understanding of the driving forces behind trends in changes in these biological parameters and the tradeoffs among them would enhance our ability to predict changes in SRP under varying conditions such as climate change. They would also greatly aid in our ability to do projections of stock size and determine rebuilding potential and stock resilience. Use of bioenergetic modelling may help in this area.

Comparative analyses of changes in the components of productivity and in the impact of these on SRP would greatly improve our understanding of the importance of these factors. These should be done on a variety of types of species. The accessibility of the data through a single portal would greatly aid in conducting meta-analyses.

Larval survival is generally ignored in our estimate of SRP (for some exceptions see Murawski et al. 2001 and Spencer et al. 2007). More study on this aspect could lead to improvements in our understanding of the factors affecting recruitment and in our estimation of S-R relationships.

The compilation of a list of stock assessments that use or could potentially use more complex indices of SRP would likely encourage the introduction of more biological parameters into advice.

Conclusions of the workshop

It is clear that the incorporation of more complex indices of SRP can make a difference in the perception of stock status. The past trajectory of the stock can be affected as can the estimated limit and target reference points and current stock status relative to those reference points. In addition, perceptions of projected stock status can vary depending on the information that is incorporated into estimates of SRP. It is also clear that there are no real technical impediments to incorporating this information.
Trends in biological parameters and the quality of the data on these parameters are both important components. There will be a greater difference in perception of stock status if there are large trends in reproductive parameters and advice is more likely to be improved by the incorporation of these data into estimates of SRP. The ability to detect trends in biological parameters will be affected by the quality of the data that are collected (one must be able to detect the signal in the noise). The quality of the data will also affect the ability to detect any difference in various estimates of SRP and will have an impact on the likelihood of improving advice.

Variation in weight at age and in maturity at age are both common and can have a large impact on perceived SRP. Often weight at age is from commercial catch at age and is calculated using an invariant length weight relationship. It is likely that variation in weight at age is greater than currently thought as a result of variation in condition. Consideration should be given to updating length weight relationships on an ongoing basis. Maturity at age should be estimated where possible by cohort and macroscopic classification scales verified with histology.

In general it has been found that changes in fecundity are small and have not had a great impact in variation in SRP. However, data on fecundity tend to be limited and more data should be collected to determine if this is indeed the case.

The collection of data on weight, maturity, sex ratio and fecundity is encouraged. Only through the collection of good quality data on these factors can we begin to fully determine how much of an influence there is of not incorporating them into our advice.

Work on whether or not advice is improved by incorporating more biology into our estimates of SRP is only beginning. These studies should be continued and applied to more stocks and species with more varied reproductive strategies. Errors in the reproductive variables incorporated into new estimates of SRP should be considered when determining whether estimates of SRP are improved. In some cases it is not yet clear how to do this. A management strategy evaluation approach is likely to be a useful way to examine whether or not the incorporation of more biology into estimates of SRP improves advice. This type of process would require the input of both modeling experts and experts in species biology.

References


## Appendix 1: Timetable

### Implementation of Stock Reproductive Potential Into Assessment and Management Advice for Harvested Marine Species

April 12–14 2011, University of Aberdeen, UK

<table>
<thead>
<tr>
<th>Time</th>
<th>Tuesday April 12</th>
<th>Wednesday April 13</th>
<th>Thursday April 12</th>
</tr>
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<tbody>
<tr>
<td>9‒10:30</td>
<td>Welcome (10 min)</td>
<td>Theme Session 2</td>
<td>Theme Session 4</td>
</tr>
<tr>
<td></td>
<td>Workshop format (10 min)</td>
<td>Paul Spencer (USA), Coby Needle (UK)</td>
<td>Liz Brooks (USA), Santiago Cervino (Spain)</td>
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<tr>
<td></td>
<td>Introductions (1 hour)</td>
<td>Discussion (led by LO’B)</td>
<td>Discussion (led by SC)</td>
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<tr>
<td>10:30‒11:00</td>
<td>Coffee</td>
<td>Coffee</td>
<td>Coffee</td>
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<tr>
<td>11:00‒13:00</td>
<td>Theme Session 1 Bridget Green (Australia), Adriaan Rijnsdorp (the Netherlands), Peter Wright (UK) (30 minutes each) Discussion (led by CTM)</td>
<td>Theme Session 3 Joanne Morgan (Canada) and Hilario Murua (Spain) Discussion (led by JM)</td>
<td>Tutorial Stock/recruit relationships and other fun stuff (led by Liz Brooks as described in description of Session topics)</td>
</tr>
<tr>
<td>13:00‒14:00</td>
<td>Lunch</td>
<td>Group discussions</td>
<td>Group discussion</td>
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<tr>
<td></td>
<td></td>
<td>Estimating alternative indices of Stock Reproductive Potential</td>
<td>Where do we go from here? Recommendations for best practice will be summarised with a view to preparing a publication describing state of the art including needs for future research.</td>
</tr>
<tr>
<td>14:00‒15:30</td>
<td>Coffee</td>
<td>Group discussions</td>
<td>Group discussion</td>
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<tr>
<td></td>
<td></td>
<td>Fitting biological reference points for the alternative indices of Stock Reproductive potential</td>
<td>(Cont’d)</td>
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<tr>
<td>15:30‒16:00</td>
<td>Coffee</td>
<td>Group discussions</td>
<td>Group discussion</td>
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<tr>
<td></td>
<td></td>
<td>(Cont’d) about Best Practice – what was learned?</td>
<td>(Cont’d)</td>
</tr>
<tr>
<td>16:00‒?</td>
<td>Group discussions (Cont’d) Short discussion (15 minutes) about Best Practice – what was learned?</td>
<td>Group discussions (Cont’d) Short discussion (15 minutes) about Best Practice – what was learned?</td>
<td>Group discussion (Cont’d) Workshop wrap-up (30 minutes) Participants will discuss best practice in relation to their own stocks</td>
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### Appendix II: List of Participants

<table>
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<tr>
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</table>
What can maternal effects tell us about stock-recruitment relationships?

Bridget S. Green

Institute of Marine and Antarctic Studies, University of Tasmania, Tasmania, Australia

Goal of fisheries science

- sources of variation in recruitment

- What makes the survivors survive?

‘survival of fry hatched from large eggs may be better than from small ones’, (Beverton and Holt, 1957)

Goal of fisheries science

- sources of variation in recruitment

Effects of fishing on a stock

- High fishing mortality depletes SSB

- Reduce intraspecific diversity
  - Fisheries are selective
  - Effects age and size structure, genetic composition
**Effects of fishing on a stock**

**Declines in max size since harvest**


**Effects of fishing on a stock**

**Declines in max size since harvest**


**Importance of within species biodiversity**

**Example Atlantic cod, Gadus morhua**


**Importance of within species biodiversity**

Importance consequences of maintaining within species diversity identified in well studied stocks

- high levels of information
- lots of research
- long-term data
- high biomass

Not feasible in all fisheries

**Maternal effects**

Non-genetic contribution of the female to offspring (Reznick 1991)

Maternal effect can explain 5-10% of variation in benign conditions – more under heavy fishing mortality

Nb: The non-genetic variation in offspring can be from either parent, but as the female that provisions the egg with nutrients, hormones and cytoplasm and generally chooses where to deposit them, she is a more likely source

**Fisheries science looked towards generalisations that can be applied across species**

**Maternal effects**

Examples:
- Female traits: size, condition, endocrine and hormonal systems
- Female behaviour: nest site selection, mate choice, timing of spawning
- Female environment: contaminants, temperature, oxygen levels, prey abundance

**SIZE**
Pending selective mortality

**Size and recruitment generalisations**

Bigger or older females believed to produce:
- more offspring
- bigger/better offspring
resulting in higher recruitment

**Evidence of female size-egg number**

Larger females do produce more eggs: basic body size scaling: \( \text{vol} = \text{length}^3 \)

Atlantic cod *Gadus morhua*

- smallest fish (~300 eggs/g)
- c.f. large cod (~500 eggs/g)

(Marshall et al. 1998)

**Female size**

Size is
genetic environmental
dynamic

Size as a maternal effect can be as a result of an interaction of genes and the environment, or a byproduct of stage-specific growth

Size is the most obvious trait of an organism, and the easiest to measure and so is the most commonly measured trait in the field of maternal effects

**Evidence of female size-egg number**

Exceptions ... ...

Coho salmon (*O. kisutch*)

- individual egg mass increased significantly with female length in 20 of 30 population brood years,
- total clutch biomass and number increased with female length in 19 of 21 populations (Fleming and Gross, 1990),

suggesting that this is not a standard relationship but is contingent on other unmeasured factors
Maternal age as a maternal effect

Few studies find age is a source of maternal effects.

Of > 140 maternal effects papers, 11 studies (17 stocks or species) measured the effects of maternal age on offspring quality, 3 identified age as key (Johnston, 1997; Berkeley et al., 2004a; Wright and Gibb, 2005).

Age was not the sole predictor, rather age and size covaried. When effects of maternal age and length examined separately, length was a better predictor of offspring condition than age.

Adding maternal age to a model containing population, maternal length and their interaction explained only a further 0.3% variation in egg size (Johnston and Leggett, 2002).

Maternal effects through life cycle

Very few studies have actually tracked offspring from female to recruitment in the wild.

When single parts of life cycle considered: Contradictory evidence of generalisations.

Summary: generalities

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<td>3</td>
<td>L</td>
<td>16</td>
<td>0</td>
<td>1</td>
<td>2</td>
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</table>

Few/no studies look at all parts and link maternal quality through the life cycle directly to recruitment.

Maternal age as a maternal effect

BUT including age in a SR model, 31% of recruitment was accounted for with stock size, age diversity, and the interaction between the two, compared with less than 15% by single factor models of either age diversity or stock size. MARTEINSDOTTIR, G. & THORARINSSON, K. (1998) Improving the stock-recruitment relationship in Icelandic cod (Gadus morhua) by including age diversity of spawners. Canadian Journal of Fisheries and Aquatic Sciences, 55, 1372-1377.

Maternal effects through life cycle

Very few studies have actually tracked offspring from female to recruitment in the wild.

When single parts of life cycle considered: Contradictory evidence of generalisations.
Rethinking single trait approach to ME

A lack of universality in trends does not mean that maternal effects are not important or not worth managing to protect.

Female and offspring traits are under constant modification from the environment, and so do not operate alone.

Maternal effects are not just simple correlations between a female trait and a trait of her offspring

They are the summation of lots of effects throughout a complex lifecycle, with constant external influences.

Female traits interacts with environment

The environment can influence the expression of variation in ELH traits arising from maternal variation in a number of ways:

99.9% of larvae do not survive to recruit.

Starvation, predation, advection………..

maternally mediated offspring traits interact with the offspring’s environment

the environment influences female condition or physiology during oogenesis

females may allocate resources to their offspring according to environmental conditions

Female size is interactive

Size interacts with:

Spawning site selection/availability of oxygen for egg:
The number of ideal egg incubating environments is limited, so female size can increase access to best spawning habitat.

Conversely when oxygen is limited, big eggs are at a disadvantage.

In Atlantic salmon size and age at first spawning increase with the distance to spawning grounds and river harshness.

Timing of spawning:

Where a seasonal migration to spawning grounds, larger, older females arrive first and spawn first (e.g., brooktrout Blanchfield and Ridgway, 2005.

Early spawning within a season can provide an extended growing season to the offspring, and greater access to seasonal food production.

Growth advantages at hatching may be transient or even negative in a harsh environment.

In salamanders, larvae from large eggs had a survival advantage in ponds with constant water level, but were at a disadvantage in seasonally drying ponds.
**ME x PE X environment**

When mated with different males, females produced clutches that differed in:
- egg length
- length at hatch
- length at metamorphosis
M x f x t influenced
- Time to metamorphosis
- Larval growth rate
- mortality

Maternal and paternal effects determine size, growth and performance in larvae of a tropical reef fish, Marine Ecology Progress Series, 289, 263-272.

**Demersal egg laying...**

3 sources of variation from embryo:

Environment:
- heat
- gas exchange (O2)
- nest design

Parental maintenance:
- modify the embryonic environment

Maternal:
- genetic
- egg allocation
- nest design
- development
Eggs from periphery of clutch
- smaller,
- used less oxygen,
- hatched into smaller larvae,
- which were smaller at metamorphosis

Size variation in fish at hatching is partly generated during early embryogenesis, either from maternal endowment or maternal nest design, and was amplified throughout development.

Propagule size is a result of maternal allocation, modified by environment

Environment:
- gas exchange (O2)
- nest design

Maternal:
- egg allocation
- nest design

Genetic
- maternal condition
- maternal age
- environment

Environmental
- Local scale variation
  - physical factors
  - temperature
  - Oxygen
  - food
  - predators
  - advection
- Broad scale variation
  - latitudinal
  - ecosystem
- Unexplained variation

Multiple sources of variation in ELH traits

Producing variation in offspring increases chance of some offspring surviving in a variable environment: a bet-hedging strategy, maximise fitness
Maternal effects and environment

Tomcod: *Microgadus tomcod*

Environment effects greater than maternal effects for:
- time to hatch,
- size of yolk at hatch,
- post-fertilisation time to starvation without food.

Maternal effects accounted for more variance in:
- egg diameter,
- egg number and survival,
- size at hatching and post-hatching survival without food.

Maternal effects on offspring traits, while significant, were less important than those attributable to the geographic source population.


Maternal effects and environment


I have discussed mainly the relationships between individual fish and their offspring……..
Theme Session 1: Bridget Green

Conclusions: where to?

• Many gaps in our understanding of how ME operate in fishes: generalities do not hold across species.

Conclusions: where to?

• Employ other tools to understand how stages are linked (e.g., natural or introduced tags (otolith marking, genetics, Jones et al. 2005))
• Include meta-analysis to see if ME trends across populations (e.g., age structure) increase in use, e.g., age structure.
• If disproportionate contribution of BOFFFF’s to a fishery should be apparent in lots of fisheries with moderate fishing levels as BOFFFF severely reduced even at moderate fishing levels. Should see lower steepness and possible S-shaped SR curve.

Conclusions: where to?

• ME: inherited environmental effects, but the environment is so often left out of the assessment.
• More complex approach required: environment interacts with female and offspring (e.g., Atlantic cod, Marshall et al., Marteinsdottir).

Conclusions

Conclusions


If maternal effects are a source of phenotypic plasticity to deal with a variable environment and local adaptation of characters (Mousseau and Fox, 1998), this emphasizes the importance of maintaining diversity with a changing environment. The question is what are the important traits to maintain?

Acknowledgements

Many thanks to Chris Chambers who was instrumental in the conception and planning of these ideas. This work was conducted while BSG was supported by an National Academies NRC fellowship.

Factors affecting reproductive potential: application to North Sea plaice

Adriaan D. Rijnsdorp
Collaborators Cindy van Damme (IMARES) & Peter Whithames (CEFAS)
IMARES, IJmuiden, The Netherlands
Wageningen University, Wageningen, The Netherlands

Objectives
- Study parameters affecting Total Egg Production (TEP)
  - Model species: North Sea Plaice
  - Rijnsdorp et al 2010 ICES JMS 67: 1931-1938
- Infer generic framework
  - See also upcoming presentation of Cindy van Damme at the Fresh Symposium, Vigo (May 2011)

Factors affecting relationship TEP - SSB
- Total Egg Production (TEP)
  \[ TEP = \sum_{r=1}^{2} \sum_{i} \sum_{j} n_{ij} m_{ij} w_{ij} o_{ij} \]
- Recruit - repeat spawners \((r = 1, 2)\)
- Allow for allometric and age relationships (age \(i\) length \(j\))
  - \(n\) - population numbers (stock structure)
  - \(m\) - maturation (proportion of recruit and repeat spawners)
  - \(w\) - weight
  - \(o\) - fecundity

Approach: estimate length distribution, weight and %maturity by age group for each cohort
Step 1. Fit VBG-relation by cohort through length-at-age of pre-recruits (age 1-5) and recruited age groups (>5).

Step 2. Fit maturity ogives by age group by cohort → maturity proportions at age 2 – 7.

Step 3. Fecundity: analyse effects of month (atresia) recruit spawner probability & condition

\[ \text{Fec} = a L^b \quad \text{with} \quad b = 3.2 \]

Figure 2. Lowest variability is provided here for three size classes (80, 10, and 10 cm) by geographical area from parameter estimates. Table 2. * = significant. Treatment names: A = IJML, B = BS, C = CIG, D = BR, E = FLAM.

Rijnsdorp 1991 IJMS 48: 253-280
Step 3. Effect condition & recruit spawning probability on fecundity

\[
\begin{align*}
\ln\text{Length} &\quad \ln\text{Fecundity} \\
K_n=1.2 &\quad K_n=0.8
\end{align*}
\]

Step 4. Estimate probability to be a recruit or repeat spawner from maturity ogives by age per cohort

\[
\begin{align*}
\%\text{mature} &\quad \text{Length (cm)} \\
\text{Cohort X} &\quad \text{Age 4} \quad \text{Age 3} \\
\text{Repeat spawners at age 4}
\end{align*}
\]

Step 4. Estimate probability to be a recruit or repeat spawner from maturity ogives by age per cohort

\[
\begin{align*}
\%\text{mature} &\quad \text{Length (cm)} \\
\text{Cohort X} &\quad \text{Age 4} \quad \text{Age 3} \\
\text{Recruit spawners} \quad \text{Repeat spawners}
\end{align*}
\]

Step 4. Estimate probability to be a recruit or repeat spawner from maturity ogives by age per cohort

\[
\begin{align*}
\%\text{mature} &\quad \text{Length (cm)} \\
\text{Cohort X} &\quad \text{Age 4} \quad \text{Age 3} \\
\text{Correct for growth of repeat spawners}
\end{align*}
\]
Result: contribution recruit spawners to SSB and TEP and changes in stock structure (H = age-composition diversity)

![Graph showing SSB and TEP recruit contributions]

Implications for recruitment?

![Graph showing recruitment variability]

Changes in size structure and sex ratio

![Graph showing size and sex ratio changes]

Maximum size of males is decreasing
**Conclusions plaice case study**

- Dominant parameters affecting TEP
  - Variability in growth (length at age)
  - Variability in maturation (maturation ogives at age)
  - Distinguish between variations and time trends
- Fecundity relatively stable
  - Recruit spawners < repeat spawners
- Body condition relatively stable
- Changes in size structure and sex ratio

**Part 2. Develop a generic framework**

- Ecological - evolutionary perspective on growth and reproduction

**Environment constrain feeding and reproduction → capital and income spawners**

**Energy allocation somatic growth and reproduction**
theme Session 1: Adriann Rijnsdorp

Income spawners (expectations)
- Realised fecundity variable due to conditions during spawning
  - Food and temperature

Correlated traits with capital & income spawner continuum

Expectations capital spawners
- Size-specific fecundity buffered against variable conditions during feeding period through variations in somatic growth
- Buffer effect decrease with fish size
- Effect decrease with productivity of ecosystem
- Jellied condition large flatfish off eastern Canada

Conclusions on parameters affecting TEP

- Variations / changes in growth and maturation
- Fecundity
  - Differences between species along capital - income continuum
  - Level and inter-annual variations in surplus production
  - Proportion of surplus energy invested in reproduction
- Stock structure
  - Sex dimorphism
  - Effects on reproductive success??
SRP

Many ICES stocks use a fixed maturity – age key to estimate SSB
e.g. North Sea haddock:

<table>
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<tr>
<th>Age</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7+</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proportion mature</td>
<td>0.01</td>
<td>0.32</td>
<td>0.71</td>
<td>0.87</td>
<td>0.95</td>
<td>1.00</td>
<td>1.00</td>
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</table>

Age 2:
Raitt (1933) 0.11
Hislop & Shanks (1981) 0.14

But maturity at size is changing!

Size at maturity has changed since the 1970s, particularly in the West North Sea

Wright et al. in press, MEPS
Implications of varying maturity to SSB

\[ m = \text{length} + f(\text{age}) + f(\text{cohort}) \] applied to predicted mean length from ICES

\[ \text{FSSB} = \text{numbers}_{\text{length}} \times \text{mean weight}_{\text{length}} \times m_{\text{length}} \times \text{proportion female}_{\text{length}} \]

Underestimation of SSB due to increasing proportion of age 2 and 3 maturing - 1980 - 2009

FRESH workshop, University of Aberdeen
April 2011

However

The increase in eggs SSB will not have been proportional because:

Relative fecundity of age 2 is significantly lower than 3+ (Hislop, 1988)

Hence: \( \text{SSB}_{\text{age}2} \neq \text{SSB}_{\text{age}3+} \)

Relative fecundity

Age 2 relative fecundity was around half that of age 3+ but it has generally increased over time

FRESH workshop, University of Aberdeen
April 2011

Fecundity – size relationship changes

Predicted potential fecundity (Fp) at length for condition = 1.0 and age = 3. Stippled lines = 95% CI

FRESH workshop, University of Aberdeen
April 2011
**Theme Session 1: Peter Wright**

**TEP and SSB**

![Graph showing TEP and SSB](image)

**Demographic influence on SPR**

Older females may be a pre-requisite to high recruitment.

- Older females produce more eggs, larger eggs, and spawn earlier.

![Graph showing demographic influence on SPR](image)

**Effect of age composition on eggs per SSB**

![Graph showing effect of age composition on eggs per SSB](image)

**Time of spawning and SPR**

![Graph showing time of spawning and SPR](image)

Figure 5 Temporal changes in age-stratified egg production of North Sea haddock and relative fitness (bold curve) based on the difference in proportions of eggs produced (by ages 2 to 5+ years haddock) and demersal juveniles for a given date from the years 1994, 1996 and 1999. Redraw from Wright and Gibb (2005).

Wright & Gibb (2005) JAE
Time of spawning and SPR

| Year | High | Medium | Low | Pre-spawn | Spawning | Post-spawn | Total
|------|------|-------|-----|-----------|----------|-----------|------
| 2000 | 23.1 | 31.2  | 47.7| 1.3       | 11.4     | 1.9       | 15.8 |
| 2001 | 21.8 | 35.8  | 42.4| 1.5       | 11.9     | 1.7       | 15.1 |
| 2002 | 22.3 | 33.5  | 44.2| 1.4       | 12.1     | 1.8       | 15.3 |
| 2003 | 21.9 | 36.6  | 41.5| 1.4       | 11.7     | 1.6       | 15.5 |
| 2004 | 21.7 | 35.9  | 42.4| 1.4       | 11.8     | 1.6       | 15.6 |

Summary

- Maturity at size in ages 2 and 3 has increased substantially
- Fecundity differs in relation to age and has increased
- Eggs per SSB
- Survival from ages 2 and 3+ may differ due to spawning time
- SSB changed due to increase in proportion age 2 mature
- But lower relative fecundity and survival potential of age 2 may have limited the increase in SRP

For replacement a good climate year needs to coincide with peak SSB cohort when F is high. For replacement a good climate year needs to coincide with peak SSB cohort when F is high.
Methods for incorporating reproductive biology into stock assessments

Paul Spencer
(also help from E.J. Dick and Martin Dorn)
National Marine Fisheries Service
Alaska Fisheries Science Center
Seattle, WA

Outline
1) Complexities of fish reproduction
2) How reproductive output (RO) is simplified in assessments
3) How assumptions of RO can affect management reference points
4) The mechanics of incorporating RO into assessments
5) Examples of incorporating reproductive output into assessments
6) Recommendations for future improvements
7) Conclusions

Complexities of fish reproduction
The proportion of fish that spawn
Skipped spawning
Maturity ogives
The quality of reproductive output
Maternal effects (plus changes in spawning season)
Changes in spawning season by age class
The quantity of reproductive output
Weight-specific fecundity

The proportion of fish that spawn
"Abortive maturation" may be an issue
Types of "skipped spawning"
(from Rideout et al. 2005)
1) Retention of eggs
2) Resorption of eggs (mass atresia)
3) Resting
(Hannah and Parker 2007)
The quality of reproductive output
(i.e., "maternal effects")

(from Berkeley et al. 2004)

The quantity of reproductive output

Work by EJ Dick (NOAA Santa Cruz Laboratory, USA) suggests that fecundity may not be proportional to weight

- Small sample sizes
- Extreme estimates $W^{2.5} \approx L^{7.5}$

Rockfish
Fecundity
Meta-Analysis

- 24 studies
- 41 species
- 2048 observations

Sub-generic groups per Hyde and Vetter (2007)

Hierarchical Linear Model

\[ F = a W^b \epsilon^e \]

\[ \epsilon \sim N(0, \sigma^2) \]

\[ \log(F_{ij}) = \log(a_j) + b_j \log(W_{ij}) + \epsilon_{ij} \]
MORGAN et al: Stock Reproductive Potential for Harvested Marine Species

Theme Session 2: Paul Spencer

Posterior exponent distribution by species

\[ \Phi = aW^{b_\varepsilon} \]

Advice for data-poor rockfish species

- Posterior predictive distribution for unobserved rockfish species

How reproductive output (RO) is simplified in assessments

**Measures of reproductive output**

1) Viable eggs or larvae

\[ VL_y = N_{a,y} \times prop_{a,y} \times mat_{a,y} \times fec_{a,y} \times surv_{a,y} \]

2) Total eggs or larvae

\[ Eggs_y = N_{a,y} \times prop_{a,y} \times mat_{a,y} \times fec_{a,y} \]

3) Female spawning biomass

\[ FSB_y = N_{a,y} \times prop_{a,y} \times mat_{a,y} \]

4) Total spawning biomass

\[ TSB_y = N_{a,y} \times mat_{a,y} \]

How has reproductive output been modeled in stock assessments?

**Alaska assessments**

SSB is used. Typically, there are limited data on fecundity

**West coast assessments for rockfish**

Of 16 west coast rockfish cited in Dick (2009), the units of reproductive output are:

SSB - 9 stocks
Eggs - 7 stocks
How can assumptions of reproductive output affect management reference points?

There are two types of reference points:

1) The stock status relative to an "overfished" limit (direct function of the reproductive output – often SSB)

2) The fishing rate relative to an "overfishing" limit (often, a function of the stock-recruitment parameters governing productivity)

The mechanics of incorporating reproductive output into assessments

Stock assessments consist of three tasks:

1) Estimate the abundance of fish by age class

2) Estimate a recommended rate of fishing, and a benchmark overfishing rate

3) Estimate a benchmark population size at which a stock is "overfished"

Harvest control rule for Alaska groundfish

Most Alaska groundfish are based on SPR proxies and avoid using the stock-recruitment parameters

The influence of maternal effects on fishing reference points for Bering Sea/Aleutian Islands (BSAI) POP

- $F_{\text{min}}$ decreased 3%
- $F_{\text{crash}}$ decreased 17%

- $F_{\text{min}}$ decreased 9%
- $F_{\text{crash}}$ decreased 22%

(from Spencer et al. 2007)
How can assumptions of reproductive output affect perception of stock status

(from Spencer et al. 2007)

The mechanics of incorporating reproductive output into assessments

Many formulations of the Beverton-Holt curve have non-intuitive parameters, or parameters that are not comparable between species.

\[
R = \frac{aS}{b + S}
\]

The units and scale of \( b \) can differ between stocks

\[
R = \frac{S}{\alpha + \beta S}
\]

\( \alpha \) = The inverse of the maximum per capita rate of production

Examples of incorporating reproductive output into assessments

Gulf of Alaska Walleye pollock

1) Statistical catch at age model
2) Several data types (acoustic, acoustic age 1 index, several trawl surveys, egg production scaled to biomass)
3) Annual maturity estimates, 1983-present
4) Variable size at age
5) Historical fecundity data
   (the fecundity - weight exponent \( b \) is 1.0785)
GOA walleye pollock maturity ogives

GOA pollock age and length at 50% maturity

GOA walleye pollock spawning weight

GOA walleye pollock pollock assessment model runs

1) 8 choices of reproductive output
   a) Eggs or SSB
   b) Four options for maturity curves
      (Avg, min (1983), max (1991), time-varying)

2) Sensitivity to fecundity-weight exponent

3) Outputs
   Depletion, Fmsy, SR plots, yield curves, fit to data components
Estimates of recruitment are not affected by choice of reproductive output.

GOA walleye pollock relative depletion

GOA walleye pollock example SR graphs

GOA walleye pollock example equilibrium yield graphs
GOA walleye pollock sensitivity to fecundity-weight exponent ($b$)

Increases in weight in recent years get amplified with large values of $b$.
This can affect our perception of depletion.

Effect of weight-specific fecundity on steepness and $F_{msy}$ for GOA walleye pollock

Using time-varying maturity results in a worse fit to the egg production index.
Examples of incorporating reproductive output into assessments

_Bering Sea/Aleutian Islands Pacific ocean perch_

1) Statistical catch at age model
2) One abundance index
3) No area specific information on maturity and fecundity

_BSAI POP assessment model runs_

3 choices of reproductive output
(Eggs, SSB, viable larvae)
How can assumptions of reproductive output affect the fishing rate reference points (i.e., \(F_{msy}\))?

Consider a case where the true population has density-independent maternal effects, and we estimate SR parameters and equilibrium recruitment both with and without maternal effects.

**Summary of effect of reproductive output upon fishing rate reference point**

<table>
<thead>
<tr>
<th>Species</th>
<th>RO units</th>
<th>steepness</th>
<th>Fmsy</th>
</tr>
</thead>
<tbody>
<tr>
<td>pollock</td>
<td>SSB</td>
<td>low</td>
<td>low</td>
</tr>
<tr>
<td></td>
<td>eggs (b&gt;1)</td>
<td>high</td>
<td>high</td>
</tr>
<tr>
<td>POP</td>
<td>VL</td>
<td>high</td>
<td>low</td>
</tr>
<tr>
<td>SSB</td>
<td>low</td>
<td>mid</td>
<td></td>
</tr>
<tr>
<td>eggs (b&gt;1)</td>
<td>mid</td>
<td>high</td>
<td></td>
</tr>
</tbody>
</table>

Eggs (b>1) relative to SSB: Higher steepness, higher Fmsy
Viable larvae relative to SSB: Higher steepness, lower Fmsy
The mechanics of incorporating reproductive output into assessments

Stock assessments consist of three tasks:

1) Estimate the abundance of fish by age class
   
   No impact

2) Estimate a recommended rate of fishing, and a benchmark overfishing rate
   
   Impact (if SR curve is used)

3) Estimate a benchmark population size at which a stock is "overfished"
   
   Impact (if SR curve is used)

How does choice of RO affect these three tasks?

Advantages of the egg/larval indices (from archived early 1990s GOA pollock assessment)

1) Eggs are often easier to sample than fish

Disadvantages

1) Requires a lot of knowledge of the reproductive biology

Perhaps additional advantage:
   If reproductive biology is highly complex and can affect the reference points, then egg and larval surveys would give the model some information on these processes.

Recommendations for future improvements

The things that are incorporated into assessment models correspond to the types of data we have available.

One obvious way to incorporate reproductive biology into assessments is to fit to indices that are more closely tied to reproductive output.

Example: CalCOFI larval abundance index. Used as an index of population spawning output in many US "west coast" assessments, including bocaccio.

Selectivity is set to fecundity

Conclusions

1) The mechanics of incorporating reproductive biology into assessments is straightforward. The difficulty lies on the data side, not the modeling side.

2) For many models for which I am familiar, the data do not provide information on reproductive biology.

3) Maturity data at increased temporal resolution did not help for GOA walleye pollock (signal to noise issue).

4) Measures of reproductive output that are not linear to SSB can affect management reference points, sometimes in different directions (assumption of $b > 1$ may increase target F rates, maternal effects may decrease F rates).

5) The first step in incorporating reproductive biology into assessments may be to get population-level data that more directly reflects the reproductive biology.
Future steps

How do we find out how well we are doing when we incorporate alternative measures of reproductive output into assessment and management? We need to compare our estimates to the "truth".

Simulate populations, estimate quantities, and compare our estimates to the "truth".
Implementing SRP estimates in management advice: the case of North Sea haddock
Coby Needle
Marine Laboratory, Aberdeen, Scotland

Background

- Marine Laboratory, Aberdeen
  - 1996 to present
- Mostly stock assessment and population modelling
  - Co-chair SGGROMAT 2002 & 2004
  - Chair WGNSSK 2004-06
  - Chair WGMG 2007-09
- Currently leader of Fishery Systems Group
  - Fleet dynamics and decision making

WKBENCH

- ICES Workshop on benchmark assessments
  - Lisbon, January 2011
- Paraphrased ToRs:
  - “Evaluate the appropriateness of data and methods to determine stock status, including consideration of fishery-dependent, fishery independent, environmental, multi-species and life history data."
  - “Evaluate the possible implications for biological reference points.”
Theme Session 2: Coby Needle

Smoothed and unsmoothed maturity estimates. Source: IBTS Q1

Reference points: original

Stock-recruit data from WGNSSK (2000)

Blim = "Smoothed Bloss" = third lowest B (101 kt, 1992) rounded to nearest 5 kt tonnes = 100 kt
Bpa = 1.4 * Blim = 140 kt

Blim = "Smoothed Bloss" = third lowest B (101 kt, 1992) rounded to nearest 5 kt tonnes = 100 kt
**Reference points: WKBENCH**

Blim = “Smoothed B loss” = third lowest B (186 kt, 1992) rounded to nearest 5 kt tonnes = 185 kt

Bpa = 1.4 * Blim = 260 kt

**EU-Norway management plan**

- Target F between 0.1 and 0.3
- TAC constraint ±15%

**Reference points in relation to current estimates**

<table>
<thead>
<tr>
<th>XSA fixed M</th>
<th>XSA varying M and Mat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bpa = 140 kt</td>
<td>Bpa = 260 kt</td>
</tr>
<tr>
<td>B(09) = 178 kt</td>
<td>B(09) = 232 kt</td>
</tr>
</tbody>
</table>

**Reproductive potential**

- But increasing M not the whole story…
- Per capita egg production changing
- Hence: management should perhaps be based on TEP, not SSB
- To be discussed at WGNSSK next month…
Theme Session 2: Coby Needle

Questions...

- How to generate reference points based on TEP?
- Is it worthwhile? Will management improve? How to convince ICES?
ARE WE DOING IT BETTER, WORSE OR JUST DIFFERENTLY?
Joanne Morgan and Hilario Murua

- Predicting recruitment
- Stock performance relative to reference points
- Highlight results and methods used

Can we improve our advice by incorporating SRP into assessments?
**Theme Session 3: Joanne Morgan and Hilario Murua**

**Murawski et al 2001**
- Georges Bank cod
- SSB TEP, viable eggs, viable larvae
- Proportion first time spawners
- Relationships from other areas
- Viable larvae slightly better fit of B-H based on RSS

**Kraus et al 2002**
- Baltic cod
- TEP (PEP)
- Fecundity estimates based on relationship with food availability
- Sex ratio, maturity
- Rsq increased from 0.32 to 0.43 using TEP instead of SSB

**Marshall et al 2006**
- Northeast Arctic cod
- SSB, FSB, TEP
- Fecundity from relationship with length and condition
- SSB gave best model fit of Salla-Lorda based on RSS and Rsq

**Morgan et al In Press**
- Looked at improvement in prediction of recruitment using 4 populations
  - 3NO cod, 3M cod, 3LNO American plaice, 2+3 Greenland halibut
  - RPconstant, SSB, FSB, TEP
- Fecundity usually based on only one or a few years
- 3 S/R curves and best fit for RP index used as the S/R for that index
MORGAN et al: Stock Reproductive Potential for Harvested Marine Species

Theme Session 3: Joanne Morgan and Hilario Murua

Morgan et al 2011

- 3M cod had the biggest trends in reproductive parameters (maturity, sex ratio, fecundity)
- More complex indices of RP always predicted recruitment better (overall and for a given S-R)

Better S/R by incorporating age structure?

- Idea that more (older) ages in SSB will lead to better recruitment than equivalent SSB with only small number of (young) ages
- Difference in success of recruit spawners
- Difference in time and duration of spawning season

Morgan et al 2011

- Greenland halibut had little trend in reproductive biology
- 10+ biomass (assuming no change in reproductive parameters) was overall the best predictor of recruitment

Marteinsdottir and Thorarinsson 1998

- Icelandic cod
- Shannon diversity index (H) of age composition (more ages in SSB bigger index)
- Linear model including both SSB and H better fit (rsq of 0.3 vs 0.15 or less)
O'Brien et al. 2003
- Georges Bank cod
- Fit stepwise multiple linear regressions to egg survival data
- Including age diversity of repeat spawners
  increased rsq from 0.44 to 0.54 over model including all spawners
- SSB not included
- Ogives over blocks of time

Oskarsson and Taggart 2010
- Icelandic summer spawning herring
- Fecundity based on length and condition
- Recruit and repeat egg production
- Used GAM and GLM to choose model
- Repeat egg production explained ~40% of the deviance
- SSB, TEP, recruit egg production, K not important

Brunel 2010
- 39 stocks
- Metrics - mean age spawners, H, proportion recruit spawners
- Each stock examined separately
  - Residuals correlated with metrics after removing effect SSB (best model fit of 3)
  - Metric added as covariate to S-R model
- Also combined in meta-analyses
- Little evidence of effect of age structure

Performance against reference points
Simulation (MSE) western horse mackerel
True population
Observed egg abundance
Proxy for fecundity to relate egg abundance to perceived SSB (constant, known exactly, or estimated with error)

Apply HCR to percSSB to produce TAC
How often is the true population below Blim
Unless the relationship estimating fecundity very good and/or based on many years data do better assuming constant fecundity

Extended the earlier work
Better model to estimate fecundity based on improved information about biology
Model worked well except if there were a trend in fecundity that was not accounted for.

MSE approach European hake
SSBwg, SSB, FSB, TEP
Found best S-R for each (was Ricker)
Calculated reference points for each
Looked at history of stock
Projected 30 years, assessment each year, applied MS and compared to ‘true’ (OM for each index of RP)
Murua et al 2010

- SSBwg was perceived
- Found differences mainly in the historic part of the results
- When include reproductive biology number of years below Blim higher in perceived
- Probability of disagreement b/w real and perceived is diminished when alternative reproductive indices are included

Conclusions

- Whether we do better or not is stock dependent
  - Trends in biological parameters
    - Not much trend may just add noise
  - Data quality and amount
    - Poor quality or limited data may just add noise
  - Lots of evidence of trends in reproductive characteristics

- When evaluating whether or not we do better
  - SSB matters
    - Should include some parameter for abundance of spawners (could be TEP) in S-R
  - S-R model matters
    - Choose the best one for each index of RP
  - Use reference points derived from each index of RP
Coding it up: Effects on Reference Points of Variable Reproductive Potential (RP)

Liz Brooks
Northeast Fisheries Science Center
Woods Hole, MA USA

Variability in Reproductive Potential

• What are the biological factors (parameters)?

  • Maturity at age (year)
  • Fecundity at age (year)
  • Mortality at age (year)

• How do we calculate Reproductive Potential (RP)?

  ➢ Probability based on age/size (macro/micro determination)
  ➢ May incorporate estimated fraction that skip spawning/yr (microscopic determination)
**Variability in Reproductive Potential**

- What are the biological factors (parameters)?

  - Maturity at age (year) ➢ May vary based on experience (age) of spawner
  - Fecundity at age (year) ➢ May vary based on condition of spawner (environmental?)
  - Mortality at age (year) ➢ May use weight (age/yr) as a proxy for egg production

- May vary based on experience (age) of spawner
- May vary based on condition of spawner (environmental?)
- May use weight (age/yr) as a proxy for egg production

**Variability in Reproductive Potential**

- What are the biological factors (parameters)?

  - Maturity at age (year) ➢ May vary based on age/size/density
  - Fecundity at age (year) ➢ May vary by year, depending on environment, predators, etc.
  - Mortality at age (year) ➢ May include F, depending on selectivity

**Variability in Reproductive Potential**

- What are the biological factors (parameters)?

  - Maturity at age (year)
  - Fecundity at age (year)
  - Mortality at age (year)

**Example of calculating maturity from vectors of individual components**

- Consider maturity, \( P(a,y,\text{skip}) \), for a given \textit{year}:

\[
P(a,y,\text{skip},...) = P(\text{age})_{\text{year}} \times (1 - P(\text{skip})_{\text{year}})
\]

\[
P(\text{age})_{\text{year}} = [0 \ 0.25 \ 0.5 \ 0.68 \ 0.82 \ 0.95 \ 1.0]_{\text{year}}
\]
Example of calculating maturity from vectors of individual components

• Consider maturity, \( P(a,y,\text{skip}) \), for a given \textit{year}:
  \[
  P(a,y,\text{skip},\ldots) = P(\text{age})_\text{year} \times (1 - P(\text{skip})_\text{year})
  \]
  \[
  P(\text{age})_\text{year} = [0.0 \ 0.25 \ 0.5 \ 0.68 \ 0.82 \ 0.95 \ 1.0]_\text{year}
  \]
  \[
  P(\text{skip})_\text{year} = [0 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0 \ 0]_\text{year} \quad \text{(null)}
  \]
  \[
  P(\text{skip})_\text{year} = [0 \ 0 \ 0.7 \ 0.4 \ 0.15 \ 0.1 \ 0.01 \ 0]_\text{year} \quad \text{(skip)}
  \]

\textbf{NOTE:} Skipped spawning is being treated as a scalar that reduces maturity at age.

Example of calculating fecundity from vectors of individual components

• Consider fecundity, \( E(a,y,\text{condition},\text{experience},\ldots) \), for a given \textit{year}:
  \[
  E(a,y,\text{condition},\text{experience},\ldots) = E(\text{age})_\text{year} \times E(\text{condition})_\text{year} \times E(\text{experience})_\text{year}
  \]
  \[
  E(\text{age})_\text{year} = [0.0 \ 0.0 \ 0.16 \ 0.29 \ 0.45 \ 0.63 \ 0.82 \ 1.0]_\text{year}
  \]
  \[
  E(\text{condition})_\text{year} = [1 \ 1 \ 1 \ 1 \ 1 \ 1 \ 1 \ 1]_\text{year} \quad \text{(null.cond)}
  \]
  \[
  E(\text{condition})_\text{year} = [1 \ 1 \ 1.05 \ 1.08 \ 1.1 \ 1.13 \ 1.2]_\text{year} \quad \text{(good.cond)}
  \]
  \[
  E(\text{condition})_\text{year} = [1 \ 1 \ 0.6 \ 0.67 \ 0.72 \ 0.75 \ 0.85 \ 0.95]_\text{year} \quad \text{(bad.cond)}
  \]

\textbf{NOTE:} Condition (perhaps due to environment) and experience (probably age effect) are scalars that modify fecundity.
Example of calculating fecundity from vectors of individual components

- Consider fecundity, $E(a,y,\text{condition},\text{experience}...)$, for a given year:
  - $E(a,y,\text{cond}, \text{exper}...) = E(\text{age})_{\text{year}} \times E(\text{cond})_{\text{year}} \times E(\text{exper})_{\text{year}}$
  - $E(\text{age})_{\text{year}} = [0.0 \ 0.0 \ 0.16 \ 0.29 \ 0.45 \ 0.63 \ 0.82 \ 1.0]_{\text{year}}$
  - $E(\text{cond})_{\text{year}} = [1 \ 1 \ 1 \ 1 \ 1 \ 1 \ 1 \ 1]_{\text{year}}$ (null.cond)
  - $E(\text{cond})_{\text{year}} = [1 \ 1 \ 1.05 \ 1.08 \ 1.1 \ 1.13 \ 1.2]_{\text{year}}$ (good.cond)
  - $E(\text{cond})_{\text{year}} = [1 \ 1 \ 0.6 \ 0.67 \ 0.72 \ 0.75 \ 0.85 \ 0.95]_{\text{year}}$ (bad.cond)
  - $E(\text{exper})_{\text{year}} = [1 \ 1 \ 1 \ 1 \ 1 \ 1 \ 1 \ 1]_{\text{year}}$ (null.exper)
  - $E(\text{exper})_{\text{year}} = [1 \ 1 \ 0.7 \ 0.75 \ 0.8 \ 0.85 \ 0.9 \ 1]_{\text{year}}$ (exper)

Example of calculating Mortality from vectors of individual components

- Consider mortality, $Z(a,y,\text{density}, \text{environ}, \text{Fishing}...)$, for a given year:
  - $Z(a,y,\text{dens}, \text{env}, \text{F}...) = Z(\text{age})_{\text{year}} \times Z(\text{dens})_{\text{year}} \times Z(\text{env})_{\text{year}} \times Z(\text{F})_{\text{year}}$
  - For this example, we’ll assume that $F=0$, and that $M$ is constant for all years and all ages, with no density-dependence and no environmental effects.
  - $Z(\text{age}) = [0.2 \ 0.2 \ 0.2 \ 0.2 \ 0.2 \ 0.2 \ 0.2]_{null}$

A simple evaluation

- Calculate reference points corresponding to SPR30% for the null vectors and all permutations of maturity/fecundity scalars
  - How does $\phi_0$ vary with each permutation?
  - How does this impact $F_{30\%SPR}$?
  - What is the impact on YPR?
Solutions are simple math

- Recall the relationship:

\[
SPR_{MER} = \frac{1}{\sqrt{\alpha}} = \frac{1}{v(\alpha \varphi_0)}
\]

- Given any two quantities, you can solve for the third
  - I set \( SPR_{MER} = 0.3 \)
  - I can calculate \( \varphi_0 \) given each of the biological vectors (and assuming selectivity for this illustration)
  - Easy to solve for \( a \) (slope at origin)

Calculated values for \( \varphi_0 \)

Calculated values for \( F_{30\%SPR} \)

Calculated values for \( YPR(F_{30\%SPR}) \)
Another example

- We just explored variable reproductive potential on reference points given an SPR=30%
- This SPR corresponds to $\dot{\alpha}=11.1$
- Recall that $\dot{\alpha} = a\varphi_0$
- In our present example, $\varphi_0=1.215$ (null values)
- This implies that $a=11.1/1.215 = 9.15$
- Repeat this for each value of $\varphi_0$
Reference point uncertainty

- Each of these histogram bars represents a reference point for a given fixed input vector
- You can conceive of this serving as the basis for characterizing uncertainty in reference points

Distribution of $F_{\text{SPR30\%}}$

Distribution of $\alpha$

Distribution of $\text{YPR}(F_{\text{SPR30\%}})$
Distribution of steepness

Conclusions

- These are very simple illustrations to demonstrate how the biological components contribute to reference points (and I made up the vectors—no idea how realistic they are)
- The “uncertainty” histograms give equal weight to each combination of biological inputs
- In reality, you would need some estimate of how frequently each of these processes occurred to weight each outcome

Conclusions (cont.)

- These calculations would normally be part of a stock assessment
- Overall model uncertainty could potentially swamp the uncertainty due to reproductive potential
- Future projections for catch advice and rebuilding would be dependent on ability to forecast probability of each reproductive potential outcome
An introduction to FLR presented by Santiago Cerviño is available [http://www.flr-project.org/doku.php?id=presentations](http://www.flr-project.org/doku.php?id=presentations)
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The Journal is for the primary publication of original practical and theoretical research that is unpublished and is not being submitted for publication elsewhere. While it is intended to be regional in scope, papers of general applicability and methodology may be considered. Space is also provided for notes, letters to the editor and notices. Each paper is assigned to an Associate Editor of the Journal’s Editorial Board, and is normally reviewed by two referees regarding suitability as a primary publication.

NAFO Scientific Council Studies
The Studies publishes papers which are of topical interest and importance to the current and future activities of the Scientific Council, but which do not meet the high standards or general applicability required by the Journal. Such papers have usually been presented as research documents at Scientific Council meetings and nominated for publication by the Standing Committee on Publications. Studies papers are not peer reviewed.

Content of Paper
The paper should be in English. The sequence should be: Title, Abstract, Text, References, Tables and Figures.

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The paper should start with the title, followed by the name(s), address(es) and emails of the author(s) including professional affiliation, and any related footnotes.

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An informative concise abstract should be provided along with key words listed alphabetically.

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In general, the text should be organized into Introduction, Materials and Methods, Results, Discussion, and Acknowledgements. Authors should be guided by the organization of papers that have been published in the NAFO Journal or Studies.

Introduction should be limited to the purpose and rationale of the study.

Materials and Methods should describe in sufficient detail the materials and methods used, so as to enable other scientists to evaluate or replicate the work.

Results should answer the questions evolving from the purpose of the study in a comprehensive manner and in an orderly and coherent sequence, with supporting tables and figures.

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Acknowledgements should be limited to the names of individuals who provided significant scientific and technical support, including reviewers, during the preparation of the paper, and the names of agencies which provided financial support.

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All Tables and Figures must be cited in the text. Tables and Figures must be numbered consecutively and correspond with the order of presentation in the text. Figure captions should be included as a separate page. Each table and figure should have a complete concise descriptive caption. Figures should always be submitted in black and white. Colour plots and photographs are acceptable only if colour is essential to the content. Preferably, all figures should be submitted as separate files in .eps or .ps format. Photographs, maps and contour plots can also be submitted in high quality .jpg format.

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