

**MATHEMATICAL &
INFORMATION SCIENCES**



MARINE RESEARCH

**ESTIMATING RELATIVE PER CAPITA SBT EGG
PRODUCTION AS A REPLACEMENT FOR SSB**

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Abstract

Histological and length-distribution-at-depth data on SBT in the spawning grounds have been collected from the Indonesian longline fishery since 1990. These data have been used to infer relative per capita egg production as a function of fish length, incorporating: (i) proportion mature, (ii) number of spawning events per mature fish, and (iii) eggs released per spawning event. Although results depend to some extent on choice of stock assessment and assumptions about depth distributions, it seems clear that larger fish must spawn much more often than smaller fish. In other words, larger fish contribute more eggs than their SSB would suggest. An example is given in which 50% of asymptotic spawning potential is only reached at age ~ 17 , compared with age ~ 11 for asymptotic SSB. Total egg production is known to be preferable to SSB as the "stock" variable for stock-recruit modelling; an example is included to show how the new estimates might change the time series of "stock".

1 Introduction

This document forms part of a FRDC report (FRDC 1999/106) on maturity, egg production, and recruitment of Southern Bluefin Tuna. The aim of this particular part is to estimate relative spawning contribution as a function of fish size. Spawning stock biomass (SSB) is widely recognized to be an imperfect proxy for total egg production of a population, and can yield misleading results when used as the "stock" axis in a stock-recruit relationship. Typically, SSB overstates the contribution of small fish, so that stock-recruit curves can show apparent hysteresis; the proportion of small fish is usually lower as a stock declines (at a given total SSB) than as the stock recovers, so recruitments in the recovery phase tend to be smaller than predicted using decline phase data. The way to avoid this, is to use estimates of total egg production in place of SSB. Total egg production can be estimated by taking a weighted sum of assessed numbers-at-length, the weights being relative average individual egg production of different length classes.

Neglecting the possibility of differential viability according to parental size, relative spawning contribution is proportional to expected per-capita egg production over a spawning season. In principle, this is simple to calculate for a mature fish:

individual egg production of mature fish = (number of spawning events) \times (eggs per spawning)

Eggs per spawning is also relatively easy to estimate, from histological data on ovary weights. However, the number of spawning events is harder to get at. One possible route is via

number of spawning events = (duration on spawning ground) \div (average spawning interval)

Average spawning interval can be estimated from histological data. However, there is no obvious way of estimating duration of spawning ground; direct estimation will probably be impossible until the advent of archival tag data that covers spawning seasons, and for large (i.e. old) fish this will be some years in coming. There is one possible indirect route, relying on the fact that fish are fat when they arrive at the spawning grounds, but thin when they

leave (Warashina & Hisada, 1970). By noting the date of first arrival of (say) 160cm fish, and the date at which thin 160cm fish are first found, it *might* be possible to form some estimate of the duration. A moment’s reflection, though, will indicate that this approach is fraught with difficulties.

There is an additional difficulty. Note that

$$\text{average egg production of any fish} = (\text{individual egg production}) \times (\text{proportion mature})$$

so that proportion mature also needs to be estimated. It is clearly impossible to do this from data collected on the spawning ground, since all the fish in the spawning grounds are mature. Unfortunately, there are also major and probably insuperable difficulties associated with collecting appropriate off-spawning-ground on pre- and non-spawners (Davis *et al.* , 2003).

A direct estimate of proportion-mature would require histological samples prior to the start of the spawning season, and away from the spawning ground. No such data are available.

To circumvent all these difficulties, we have adopted a quite different approach. Consider the aggregate contribution of all fish of given length:

$$\begin{aligned} \text{total egg production} &= (\text{total number of spawning events}) \times (\text{eggs per spawning}) \\ \text{average individual egg production} &= (\text{total egg production}) \div (\text{number of fish}) \end{aligned}$$

Again, eggs per spawning can be estimated from biological data. Estimated number of fish is available from the stock assessment, so the only missing quantity is total number of spawning events. In fact, since we are only interested in *relative* spawning contributions as a function of fish length, it is enough to estimate *relative* number of total spawning events across length classes. This is clearly going to be based somehow on the number of about-to-spawn fish in the samples. The calculation is not straightforward, though, because (i) the depth distribution varies with length and spawning status, and (ii) fishing mortality is distributed in an unknown and probably uneven pattern across depths. To deal with this, note that total number of spawning events for fish in a given length class can be calculated (in principle) via

$$\begin{aligned} &\text{total number of spawning events} \\ = &\sum_{\text{depths}} (\text{total “fishdays” at that depth}) \times (\text{spawning rate at that depth}) \end{aligned}$$

where spawning rate is implicitly in units of “events per day per fish while on the spawning grounds”. Precise depth data are unavailable, but we can use bigeye index (the ratio of bigeye catch to yellowfin catch, known to increase with setting depth; see Davis *et al.* , 2003) as a proxy. The aim of the exercise is really to correct as far as possible for an observable relationship (the observed effect of bigeye index on spawning rate) which would bias results if ignored; once this is corrected for, we assume there is no residual effect of “true depth” requiring correction.

Since we are only interested in relative average spawning contributions, both multiplicands can be considered in relative rather than absolute terms, i.e. compared to fish of some arbitrary

reference length. Relative spawning rate at depth and length can be estimated from histological data. Total fishdays at depth and length and year is proportional to number of fish sampled at depth and length and year; under a few additional assumptions, it is possible to estimate statistically the relative per capita fishdays at depth for fish of different lengths (see below).

The actual steps involved in producing a time series of total egg production, are as follows:

1. Use the histology data to estimate (relative) proportion that will spawn every day, by depth and length class.
2. Use (i) the length-depth data, (ii) a stock assessment, and (iii) some assumptions about sampling probability by depth, to establish (relative) average time spent by an individual fish on the spawning grounds, by depth and length.
3. Combine the two to predict RAISE (Relative Average Individual Spawning Events), by length.
4. Use the histology data to estimate relative batch fecundity, by length.
5. Multiply RAISE by relative batch fecundity to get REPC (Relative Eggs Per Capita), by length.
6. To generate a time series of total (relative) egg production, take a time series of total numbers-at-length from a stock assessment (the same as in step 2), multiply by REPC, and sum across length classes within each year.

There are a couple of general points to note:

- This approach does not and cannot separate between a proportion mature and time spent on grounds; the same number of daily spawnings could arise from a group of fish with high proportion mature and low residence time, or vice versa. This does not matter whatsoever from the viewpoint of total egg production, but is important to bear in mind when comparing results to other approaches.
- Because the results rely on a specific assessment, which itself uses (part of) the same data, there is some apparent risk of circularity. However, the assessment does not explicitly use depth data, while the whole focus of the next few stages is on dealing with depth-related issues. The results are consistent with, but not an inexorable consequence of, whichever assessment is chosen. Closer linking with assessment is desirable, through incorporation of depth modelling into the assessment itself; doing this carefully will eliminate any risk of circularity.
- There is an implicit assumption that, for all fish that happen to be on the spawning grounds and within the same depth band at a given time, vulnerability to fishing gear in that depth band is equal. This seems reasonable; all the fish are large active predators within a fairly narrow size band (160-200cm). Note that this assumption is *much* weaker than assuming “catchability is constant” or “catchability at depth is constant”; there is an allowance for different vulnerabilities at depth, different depth distributions depending on size, and different lengths of stay on the spawning grounds depending on size.

1.1 Estimating spawning rates by depth

Very few fish (about 2%) are caught during the daily act of spawning itself, i.e. with brand-new POFs. In any case, because there is no guarantee that each spawning event lasts for the same amount of time regardless of length class, it would be dangerous to base estimates on direct counts of spawning fish. The histological data provides a better measure: presence of oocytes with migratory nuclei. Once nuclei have migrated, the progression to a spawning event within the next 12 or so hours (at any rate, less than 24 hours) is inevitable. Assuming that the time taken for eggs to develop from migratory nucleus stage to actual spawning is independent of fish length— a reasonable assumption, since this is simply a function of metabolism— then the proportion of fish (at given size and given depth) with migratory nuclei is an indicator of the relative spawning rate at that size and depth.

[An equivalent approach is to use the presence of POFs as a *post hoc* indicator of whether a fish has spawned within the last 24 hours. The two approaches give very similar answers, although the proportion with POFs is about 2.5X higher than the proportion with stage 4 or stage 5 oocytes. This simply indicates that the time taken to pass from the migratory nucleus stage to spawning is correspondingly less than the time taken for POFs to be reabsorbed.]

Table 1 shows proportions at depth by length group, by spawning status. The general trend towards bigger fish spending more time at shallower depths is clear. There is also a strong tendency for about-to-spawn fish of given size to be found in shallower waters.

| Length (cm)→ Bigeye ratio↓ | About to spawn | | | | Not about to spawn | | | |
|-------------------------------|----------------|-----|-----|------|--------------------|-----|-----|------|
| | <165 | 170 | 180 | >184 | <165 | 170 | 180 | >184 |
| 0-0.2 | 4 | 10 | 9 | 18 | 18 | 19 | 24 | 35 |
| 0.2-0.4 | 24 | 20 | 27 | 24 | 16 | 29 | 27 | 20 |
| 0.4-0.6 | 23 | 23 | 22 | 18 | 24 | 18 | 15 | 18 |
| 0.6-0.8 | 34 | 24 | 24 | 21 | 29 | 15 | 25 | 11 |
| 0.8-1 | 16 | 23 | 20 | 19 | 13 | 19 | 9 | 17 |
| (N) | 102 | 172 | 199 | 146 | 38 | 62 | 79 | 66 |

Table 1: Percentage at “depth”, within length class and spawning status. Depth proxied by bigeye index). “About to spawn” means “with ovaries that have migratory-nucleus or hydrated eggs”.

Table 2 shows actual relative spawning rates by length and depth. The depth effect is obvious, with shallow depths (bigeye index < 0.2) containing a much higher proportion of about-to-spawn fish. However, there is no apparent length effect *after* accounting for depth.

| Length (cm)→ | <165 | 170 | 180 | >184 |
|---------------------|-------------------|-------------------|-------------------|-------------------|
| Shallow (BI<0.2) | 64 ₁₁ | 41 ₂₉ | 53 ₃₆ | 47 ₄₉ |
| Medium (0.2<BI<0.8) | 24 ₁₀₈ | 25 ₁₅₄ | 27 ₁₉₆ | 26 ₁₂₄ |
| Deep (BI>0.8) | 24 ₂₁ | 24 ₅₁ | 15 ₄₆ | 28 ₃₉ |

Table 2: Percentage of fish with migratory-nucleus or hydrated oocytes. Small numbers are sample sizes.

1.2 Estimating time spent on grounds

The underlying “length-depth” model for number of fish caught by length, depth, and year is quite simple:

$$\mathbb{E}[C_{\ell dy}] = N_{\ell y} \times \theta_{\ell} \times p_{d|\ell} \times f_{dy} \quad (1)$$

where

- $C_{\ell dy}$ is the number sampled at length, depth, year
- $N_{\ell y}$ is numbers at length, year (from the assessment)
- θ_{ℓ} is the “average availability” of length class ℓ on the spawning grounds, i.e. proportion mature \times average length of stay of mature fish
- $p_{d|\ell}$ is the (behavioural) distribution of depth for fish of length ℓ on the spawning grounds, incorporating both spawning and non-spawning phase, with $\sum_d p_{d|\ell} \equiv 1$;
- f_{dy} is the fishing mortality (or “sampling mortality”) at depth d in year y , i.e. the probability that a fish at depth d will be caught.

Unfortunately, equation (1) is not identifiable. Rewriting $\theta_{\ell} p_{d|\ell}$ as an unconstrained parameter $\phi_{d\ell}$, it is clear that it would be possible to (say) double all the $\phi_{1\ell}$ ’s while halving all the f_{1y} ’s, and still get the identical expected catches. To get unique parameter estimates, it is necessary to assume values for either (i) $p_{d|\ell}$ for all d and one particular length group ℓ' , or (ii) relative fishing mortality by depth in one year (i.e. $f_{dy'}/\sum_{d'} f_{d'y'}$ for all d and some particular y').

Because fishing mortality varies with depth, and depth distribution varies with length, equation (1) has an implicit length selectivity (year-specific). It might be possible to adjust $f_{dy'}$ to get a reasonable match to age-specific selectivities estimated during the stock assessment. However, there is a risk of circularity, and such possibilities would need to be carefully considered within an integrated assessment that included depth data.

The length-depth model (1) can be fitted using a Negative Binomial GLM with a log-link and $\theta = 7$, which gives acceptable residual plots. There is substantial over-dispersion relative to a Poisson model, indicating some systematic deviations from the underlying model structure. The overall fit is nevertheless good (Figure 1), although this is hardly surprising since the assessment incorporates Indonesian catch-at-age data (albeit without length, and without explicit consideration of depth).

There are some interesting implications for the stock assessment itself. For example, an examination of the estimated f_{dy} shows a clear shift towards deeper fishing over the 1990-2002 period. Since smaller fish tend to be deeper, there will have been a corresponding shift in the selectivity-at-age towards younger fish. Again, the way to address this is by integrating depth effects into the assessment itself.

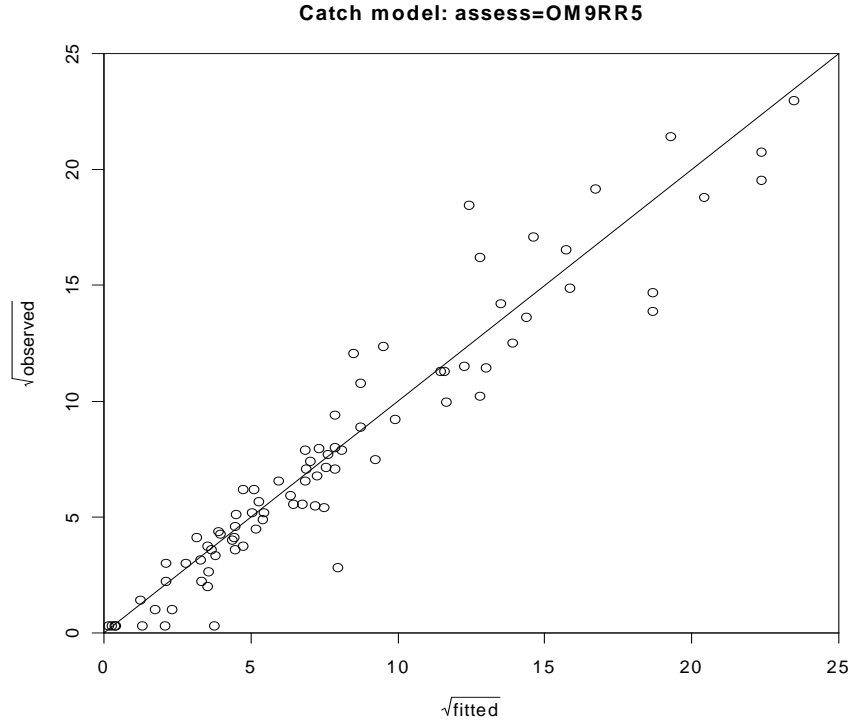


Figure 1: Overall fit of the length-depth model

1.3 Estimating relative average individual spawning events

Once estimates of $p_{d|\ell}$ and $p_{s|d,\ell}$ are available, the RAISE r_ℓ at length ℓ can be estimated by

$$r_\ell = \theta_\ell \sum_d p_{d|\ell} p_{s|d,\ell} = \theta_\ell \sum_d p_{d|\ell} p_{s|d}$$

In other words, RAISE is a weighted average of spawning rates by depth, the weights depending on how long an average fish spends in a particular depth band at the spawning grounds.

An important assumption is that the depth range fished really does span almost the whole depth range of SBT. If a substantial proportion of a tuna's time on the spawning grounds is spent beyond the depth range of the fishery but still ready to spawn that day, and if this proportion varies by length class, then the results will be biased.

1.3.1 Confidence intervals and effect of assessment choice on RAISE

Choice of assessment affects estimates of RAISE. The main reason for this is that if different assessments imply different length distributions, then the length-depth model has to adjust RAISE in order to predict the same number of about-to-spawn fish (which is the data being fitted to). Tables 3 and 4 show point estimates for different assessments (with f -at-depth assumed equal across depths; see below), together with 95% confidence intervals obtained by

bootstrapping. The assessments used are the most “optimistic” and “pessimistic” assessments in Kolody & Polacheck, 2001, known as OM9RR5 and PM2RR8 respectively. The uncertainty arising from $p_{s|d}$ is negligible compared to that arising from $p_{d|l}$.

| | Point estimate | LCL (95%) | UCL (95%) |
|-------|----------------|-----------|-----------|
| 160cm | 0.02 | 0.01 | 0.03 |
| 170cm | 0.09 | 0.03 | 0.15 |
| 180cm | 0.34 | 0.16 | 0.51 |
| 190cm | (1) | (1) | (1) |

Table 3: Estimated per capita number of spawning events, relative to 190cm fish. Assumes equal f across depths. Assessment OM9RR5

| | Point estimate | LCL (95%) | UCL (95%) |
|-------|----------------|-----------|-----------|
| 160cm | 0.05 | 0.02 | 0.08 |
| 170cm | 0.17 | 0.07 | 0.26 |
| 180cm | 0.42 | 0.09 | 0.77 |
| 190cm | (1) | (1) | (1) |

Table 4: Estimated per capita number of spawning events, relative to 190cm fish. Assumes equal f across depths. Assessment PM2RR8

It is clear that smaller fish have many fewer spawning events per capita than larger fish. Nevertheless, confidence intervals in both tables are reasonably wide, and even more striking is the difference between the two tables. (Note that it is not appropriate to assess “significance” of the between-table differences based on the confidence intervals— both tables use the same response variables.) The size of the confidence intervals reflects the large number of unknown parameters currently included in the model. A more restrictive model— e.g. one that imposes limits on the between-year variability in f by depth— is likely to give tighter prediction intervals, and this should be pursued as the results of this study are integrated with the stock assessment. Uncertainty arising from difference between assessments, though, will remain.

If two assessments differ only in their time trends of *total* numbers of fish, choice of assessment will not affect the goodness-of-fit of this model, because the estimated “fishing mortalities” can be changed to compensate perfectly. But if two assessments show differing time trends in abundance across different length groups, then the goodness-of-fit of the length-depth model will differ between the two models. This is the case for the two assessments considered here, where OM9RR5 shows a more drastic change in the length composition (towards smaller fish as time goes by) than PM2RR8 does. Interestingly, the length-depth model seems to fit OM9RR5 rather better than it does PM2RR8 (about 7 units of log-likelihood, and considerably narrower confidence intervals), though this depends on the assumption made about relative fishing mortalities at depth. No attempt should be made to assess the “significance” of this result outside of the context of the full assessment, since clearly numerous other components of the likelihood need to be considered. However, the length-depth model itself— regardless of the implications for spawning contribution— may be worth considering in the future development of SBT assessment methods.

Given the size of the confidence intervals, and the dominant rôle of assessment uncertainty, it is very unlikely that there is enough information to infer anything about age effects beyond what is implied by age-length relationships, and so we have not investigated this further.

1.4 Effects of assumptions about f -at-depth on RAISE

Figure 2 shows contours of RAISE, which varies as different assumptions are made about average f -at-depth. (Note that annual deviations around the average are fitted within the model, but the average must be set externally.) The $(0,0)$ $x - y$ position in each graph, has equal f in all three “depth” bands. Each unit of change corresponds to a factor of 2 change in the corresponding f , so that the top right-hand corner implies that both f_{deep} and f_{medium} are both 16 times higher than f_{shallow} . Increasing the range of the axes, even to ludicrous levels, does not change the maximum and minimum values much beyond what is seen here. The limiting cases are when one of the f 's is very low relative to the other two, i.e. the top right corner, the bottom right corner, and the top left corner. In these cases, the only way to explain the rather large number of observed catches in a depth stratum where f is very low, is to assume that fish spend almost all their time in that stratum. For purposes of estimating the number of spawnings, this amounts to disregarding the data from the other two strata. Although this can produce quite large proportional changes in RAISE, the absolute magnitude of the changes is not great, at least for plausible (4-fold, i.e. within ± 2 units) changes in f with depth.

1.5 Batch fecundity

Batch fecundity was only measured explicitly for a small number of fish (37, between 1996 to 2002; Davis *et al.*, 2003), and the very wide scatter makes it impossible to estimate the relationship with fish length to any precision; the point estimate of the slope of $\log(\text{fecundity})$ on $\log(\text{length})$ is 3.90 but with a standard error of 1.37. In this study, we have instead estimated batch fecundity indirectly, by the difference between ovary weights before and after spawning (for each size of fish). The working definitions of “before” and “after” are:

Before spawning: hydrated oocytes (stage 5) and no new POFs (to ensure that no partial spawning has occurred).

After spawning: oocytes advance-yolked (stage 3), and with POFs.

The point estimates of slopes on \log -length are very similar (about 2.45 before spawning, vs. 2.51 afterwards), although the confidence interval on before-spawners is wide because there are only 51 such fish. On this evidence and *a priori* grounds, it is reasonable (but not proven) to assume that ovary weight increases by a constant proportion just before spawning, independent of fish length. There is a suggestion that variances are slightly higher for “before” fish (estimated residual standard error of 0.41 vs. 0.31), but allowing for this would make only a minor effect on point estimates and we have ignored it. We fitted a Gamma GLM with \log -link to all the “before and after” fish, where intercept depends on before/after status but slope does not, i.e.:

$$\begin{aligned}\log \mathbb{E}[w_{\ell B}] &= \beta + \gamma \log \ell \\ \log \mathbb{E}[w_{\ell A}] &= \alpha + \gamma \log \ell\end{aligned}\tag{2}$$

for ovary weight w at length ℓ , before/after indicated by B/A , and parameters α , β and γ to be estimated (Figure 3). With this formulation, the *relative* batch fecundity of length ℓ_2

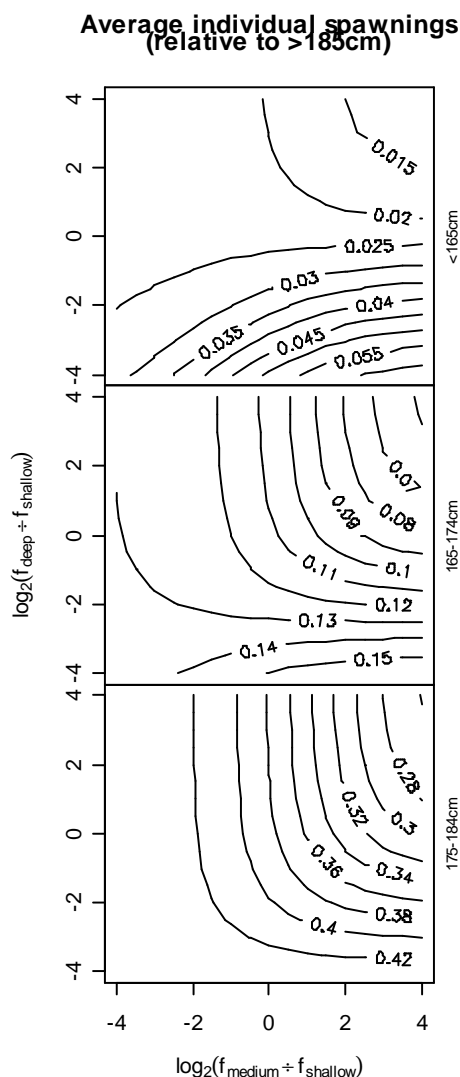


Figure 2: Contours of relative estimated per capita spawning events. Assessment OM9RR5.

compared to length ℓ_1 is given by

$$\frac{w_{\ell_1 B} - w_{\ell_1 A}}{w_{\ell_2 B} - w_{\ell_2 A}} = \left(\frac{\ell_1}{\ell_2}\right)^\gamma \quad (3)$$

which does not explicitly require estimates of β or α .

The point estimate of γ is 2.47 (SE=0.21); since body weight is roughly proportional to ℓ^3 (actually 2.91 according to Kolody & Polacheck, 2001) and $2.45 < 3$, this means that ovaries become lighter relative to body weight as (mature) fish continue to grow. Table 5 shows the corresponding relative batch fecundity across lengths, compared to a 190cm fish¹:

¹Strictly speaking, the table applies only to fish of the exact size indicated. In practice, the actual mean lengths within each length class (155-165, 165-174, 175-184, 185+cm) are very close to the sizes given. However, because the length-to-weight-loss relationship is nonlinear, the mean length within a length class won't correspond to the mean ovary weight loss. Nevertheless, the results will not be much affected by this—certainly less than the spread of standard errors.)

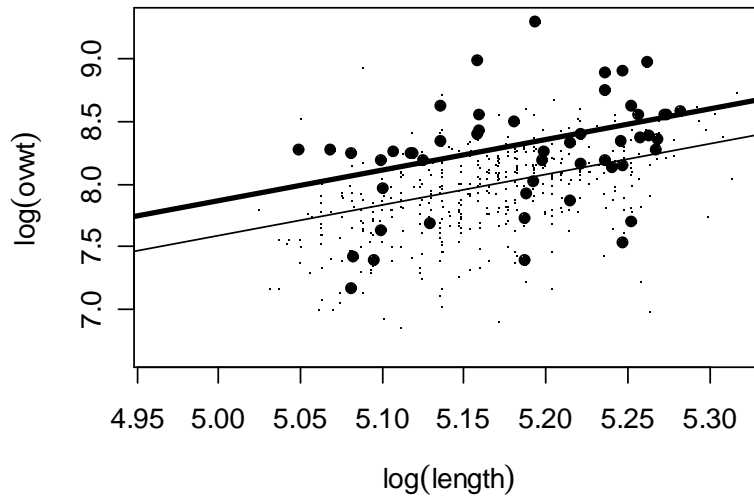


Figure 3: Ovary weights versus length. Small dots/thin line are ovaries at stage 3 with POFs; solid dots/thick line are ovaries at stage 5 without stage 1 POFs. Regression lines have different intercepts but identical slopes.

| | Median | LCL (95%) | UCL (95%) |
|-------|--------|-----------|-----------|
| 160cm | 0.65 | 0.61 | 0.70 |
| 170cm | 0.76 | 0.73 | 0.80 |
| 180cm | 0.88 | 0.86 | 0.89 |
| 190cm | (1) | (1) | (1) |

Table 5: Estimated batch fecundities, relative to 190cm fish

The point estimate of $\beta - \alpha$ is 0.28 (SE=0.05), indicating that about 33% of the hydrated ovary weight is lost during each spawning event. Although the confidence interval is fairly tight, this depends on an *assumption* (supported, but not proved by, the data) that the slopes of the regressions in Figure 3 really are equal, i.e. that hydration increases the weight of an ovary by a constant proportion ($\sim 33\%$), regardless of fish length. More support for this plausible assumption could be obtained either by getting more samples from hydrated-oocyte fish, or by looking at data for other tunas.

It is interesting to note that heavier fish have proportionally lighter gonads relative to body weight. This is based on a large sample size, and cannot be due to sampling noise. The point estimate based on direct batch fecundity measurements, however, would imply the opposite (i.e. proportionally heavier gonads relative to body weight). This is presumably an accident that reflects the very large variability associated with the direct measurements.

1.6 Forming a time series of relative egg production

Three choices have to be made to produce a time series of relative egg production:

- which assessment to use (i.e. which time series of numbers-at-length);
- which relative f 's at depth to use, in some reference year;
- batch fecundity at length: which relationship to use?

Once these choices have been made, model (1) can be fitted and used to predict RAISE. Multiplying RAISE by relative batch fecundity gives a table of relative eggs per capita (REPC) by length. For the equal- f -at-depth model (Tables 3 and 4) and the point estimates of relative batch fecundity (Table 5), the point estimates of REPC under assessments OM9RR5 and PM2R88 are:

| | OM9RR5 | PM2RR8 |
|-------|--------|--------|
| 160cm | 0.010 | 0.027 |
| 170cm | 0.052 | 0.093 |
| 180cm | 0.24 | 0.30 |
| 190cm | (1) | (1) |

Table 6: Relative egg production per capita by length, combining RAISE and batch fecundity

To estimate egg production in a given year, the numbers in one column of this table then simply need to be multiplied by numbers-at-length from the corresponding assessment, and summed across the four length classes.

Table 6 contains “egg production ogives” by length, which can be converted to an age ogive using length-at-age data (here taken from proportions in the recent assessment, and so applicable only to more recent cohorts). This can be compared with the age-specific SSB (i.e. average weight at age \times ppn. mature at age) estimated in the assessment itself (Figure 4; the picture for assessment PM2RR8 is similar). It must be emphasized that the conversion to age is very crude, because the 10cm length classes in the assessment are much too big to allow accurate back-conversions. Nevertheless, the general implication is clear; under the assumptions here, fish are not reaching 50% spawning potential until about age 17, compared with about age 11 that is estimated if relative fecundity is ignored.

1.6.1 Sensitivity to model assumptions

Choice of assessment has by far the most impact (Figure 5). The difference between the two lines is explained by the greater decline in large fish implied by PM2RR8. By way of compensation, the spawning model for the pessimistic effort has relatively higher Indonesian “fishing effort” in 2000 than the model for the optimistic effort (so that the expected catch in 2000 is similar in both cases).

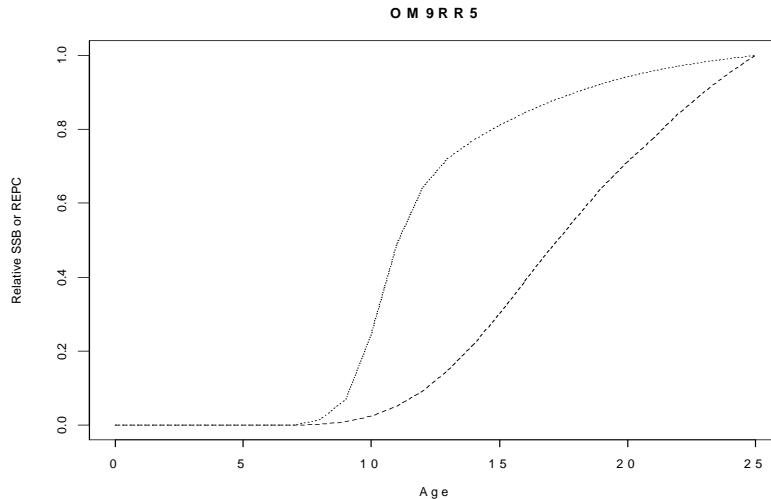


Figure 4: Relative individual SSB (dotted) and egg production (dashed) by age.

Assumptions about relative f 's have less impact. Figure 6, for the OM9RR5 assessment only, shows the effects of assuming low f in shallow water (i.e. very high proportion of time spent in shallow water, in order to explain catches there) *vs.* assuming low f in deep water (i.e. very high proportion of time spent in deep water). These are extreme assumptions, but produce only about a 10% difference at most. Differences are even less for assessment PM2RR8.

The relationship between batch fecundity and length is moderately well determined, but the exponent of the relationship is still subject to some uncertainty. In principle, bigger values for the exponent will increase the relative spawning contribution of bigger fish. However, as shown in Figure 7, the projected difference in *relative* egg production across this time period is imperceptible in practice. Taking a 190cm fish as the baseline, then changing from the upper to the lower 95% confidence limit of the exponent only produces about a 5% increase in the relative batch fecundity of a 180cm fish, rising to about a 15% increase for 160cm fish. Since smaller fish spawn much less often than larger fish, these changes are diluted even further when considering total egg production.

1.7 Comparison with SSB series

The stock assessments in Kolody & Polacheck, 2001 span the years 1951-2000, and include estimates of SSB. Figure 8 shows comparative time series of SSB and egg production, calculated as above. For the pessimistic assessment PM2RR8, the two series are quite similar, indicating about a 95% decline in SSB. For the optimistic assessment, though, the egg production series has an 86% decline in SSB whereas the SSB series has “only” a 71% decline. Also, the SSB series shows a strong rise over the last five years or so, which is not mirrored in egg production. The differences are amply large enough to mean that egg production needs to be properly incorporated into stock assessment and management work.

Given the major differences in Figure 4, it is perhaps surprising that the differences between

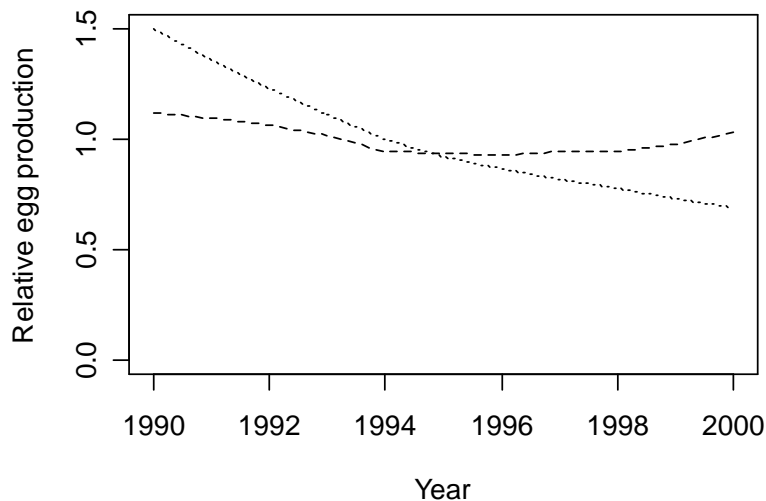


Figure 5: Time series of total egg production. Dashed line: “optimistic”. Dotted line: “pessimistic”. Both lines normalized to have mean 1. 1994 f_d set equal at all depths.

SSB and egg production time series are not bigger. It turns out that, for current stock age composition at least, total egg production is divided very evenly across all ages from 11 up, with 25% coming from the “plus-group” aged 25+; mortality and recruitment almost exactly balance the increasing *per capita* contribution with age. With such an even split of contributions, the scope for dramatic shifts is perhaps limited. However, further investigation of these issues awaits a closer integration of egg production results into the stock assessment process itself.

2 Conclusions

2.1 Further data requirements

2.1.1 Histology

There is now a large sample of histological data (941 fish), allowing a good understanding of the dynamics of spawning. For the purposes of estimating relative spawning potential by size, the histology data have successfully allowed identification soon-to-spawn fish (oocyte stages 4 and 5) and post-spawning-event fish (presence of post-ovulatory follicles). Although questions do remain about the biology of tuna spawning (resting periods, duration at spawning grounds, proportion mature), the existing data are largely sufficient for linking with assessment work.

The main exception concerns the relationship between batch fecundity and size, which is somewhat uncertain. The impact on time series of egg production appears to be small in

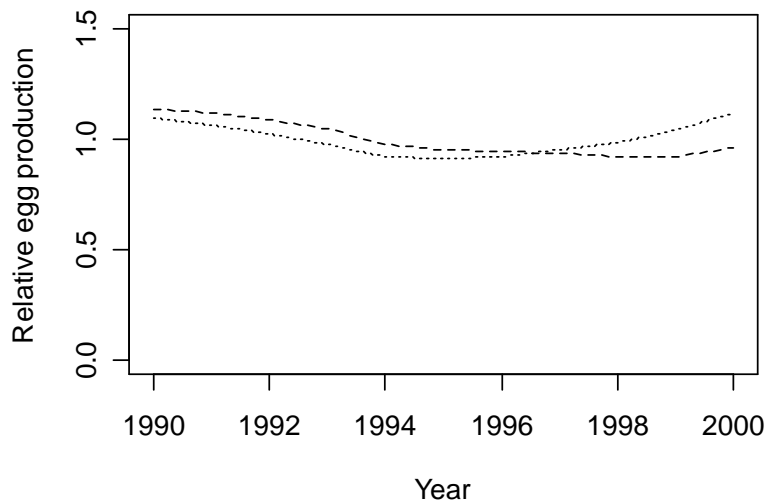


Figure 6: Total egg production relative to mean. Dotted line: low f on deep. Dashed line: low f on shallow.

comparison to other sources of uncertainty. However, this somewhat rests on a assumption which, though *a priori* plausible and certainly consistent with available data, is not yet proven: that the weight of hydrated ovaries (i.e. immediately pre-spawning-event) scales with length in the same way as the weight of post-spawning-event ovaries.

How could this situation be bettered? At the moment, the standard error of the exponent of $\log(\text{direct batch fecundity})$ on $\log(\text{length})$ is about 1.4. To reduce this to a reasonable level of around 0.25, a 25-fold increase in the number of samples would be required! The situation is slightly better for estimates of hydrated ovary weights, which have been measured more often and show less individual variation, but even so about a 12-fold increase in sample size would be needed to get standard errors down to the same level. Direct evidence via sampling along existing lines therefore seems unattainable in the near future. As a cheap preliminary step, studies from other species might provide enough circumstantial evidence to lend credence to this assumption.

2.1.2 Biological data on depth distribution

It is possible to fit the data equally well with different assumptions about average f -at-depth, by varying the estimated depth distribution (i.e. time-at-depth) in inverse proportion. Thus, there is no way to separate these two phenomena statistically, even though the depth distribution does affect the relative spawning contribution of different lengths. Although there are limits to the overall effect this can have on time series of egg production, there is still room for making a substantial improvement in precision if more data can be collected to pin down either relative f -at-depth (in any one year), or relative time at depth (in any one length

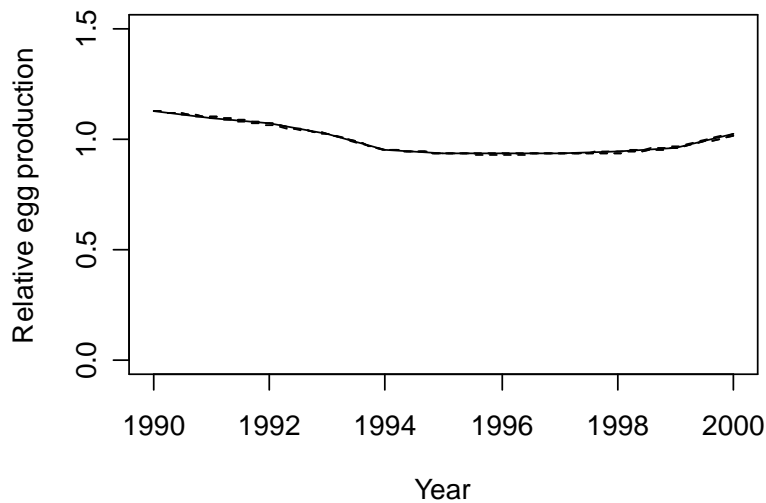


Figure 7: Total egg production relative to mean. Solid line uses point estimate of 2.47; dotted & dashed lines are lower and upper 95% confidence limits (~ 2.1 and ~ 2.9). Assessment OM9RR5, equal f across depths.

group). The former seems intractable, but time-at-depth could be assessed accurately from archival tag data.

Archival tag data would also allow direct estimation of duration on the spawning grounds. At a minimum, this would provide a useful consistency check on estimates of availability by age. More ambitiously, though, duration on grounds and proportion of spawning could be used to provide estimates of relative abundance by length that are effectively independent of the rest of the assessment. Assuming equal catchability for all sizes of fish present in the grounds at a particular depth, then the number of captures at that depth (relative across length classes) will be proportional to relative abundance of length classes, times mean duration of grounds. As well as helping to establish an unambiguous direct biological estimate of relative egg production, this would be of great value to the assessment itself.

2.2 Further integration with assessment

This report provides a template for incorporating improved “SSB” series in stock assessment and prediction. The main benefits are likely to be in better predictions. If a “stock-recruitment” relationship is genuinely based on spawning potential, it is more likely that the past will be a useful guide to the future. One example is North Sea herring (ICES? Daan, 1998?), where using SSB as a proxy for spawning potential gives quite a different S-R relationship during a period of stock decline, than during the subsequent recovery (which was slower than expected). However, this artefact disappears if a better proxy for spawning potential is used.

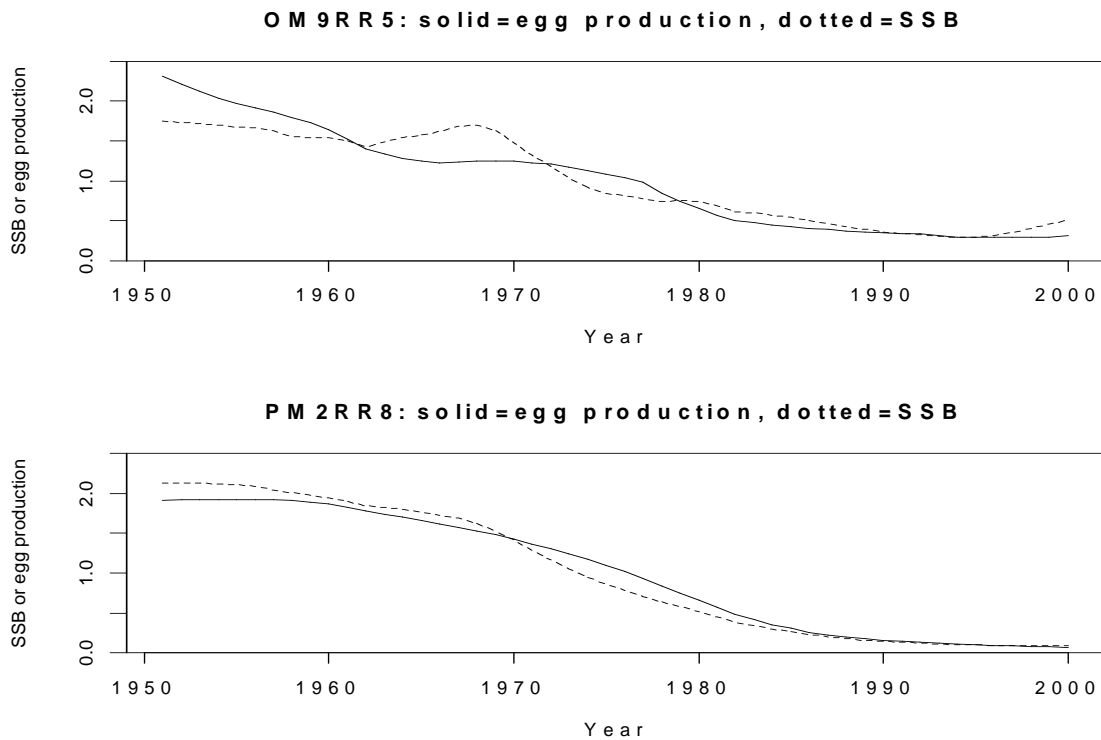


Figure 8: Comparison of SSB and egg production series for two different assessments; all lines normalized to have mean 1. Equal f -at-depth assumed.

To actually incorporate these results into assessment, further work will be required in the stock assessment itself. The recalculation of spawning potential and fitting of stock-recruit relationships is comparatively easy, but there are two related issues to be addressed:

1. Reducing circularity

The approach used here should be seen as consistent with, rather than a circular by-product of, any chosen stock assessment. The focus is on reducing depth-sampling biases in the length data, and in incorporating depth effects on spawning frequency, while the assessment itself does not use depth data. However, there is another area where circularity potentially does arise. The stock assessments in Kolody & Polacheck, 2001 have an internally-estimated stock-recruit relationship based on SSB, so the estimated stock sizes used here already incorporate some stock-recruit modelling. This is philosophically awkward. In practice, though, stock-recruit relationships are so ineffective at predicting individual cohort strengths (where CVs of 60% are typical) that very little predictive power is gained by including the stock-recruit relationship inside the assessment. This mitigates the risk of circularity. However, in further work, close attention should be paid to this point.

2. Including length-depth modelling

The results of this analysis depend to some extent on length-depth modelling of fishery selectivity in Indonesia. There is also a signal in the data, in that some assessment

series are easier to reconcile with the length-depth data than others. This suggests it might be worth considering whether a length-depth model of the form used here (even without the knock-on effects for stock and recruitment) might be incorporated into the assessment framework in its own right. Equally, some further consideration of plausible f -at-depth models from a stock assessment perspective could help in tightening up confidence intervals on spawning potential. In all this, it will again be particularly important to take good care to avoid any danger of circularity.

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