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ASSESSMENT OF THE MONKFISH *LOPHIUS VOMERINUS* RESOURCE OFF NAMIBIA

L. MAARTENS* and A. J. BOOTH†

The *Lophius vomerinus* component of the monkfish resource off Namibia was assessed by means of deterministic length- and age-based models. Steady state length cohort analyses illustrated that, although the model was sensitive to the rate of natural mortality, it was relatively insensitive to changes in terminal fishing mortality. These biases may, however, not be serious provided that estimates of abundance are used to reflect relative changes in the biomass dynamics of the population. The age-structured production model, tuned to trends in General-Linear-Modelling-standardized catch-per-unit-effort data and relative abundance indices calculated from hake (*Merluccius* spp.) biomass surveys, together with observed commercial and survey catches-at-age, showed similar trends. Both models provided evidence that the monkfish resource was fully to overexploited, with current harvesting levels higher than those concomitant with sustainable yields.

Key words: age-structured production model, length-based cohort analysis, *Lophius vomerinus*, Namibia

Monkfish (*Lophius vomerinus* and *L. vaillanti*) constitute a commercially important resource off Namibia. During 1998, the *Lophius* resource was the fourth most important commercial resource in terms of landed mass (c. 17 000 tons) and the fifth most important commercial resource in terms of export value (US\$19.8 million) of the Namibian fishing sector (Ministry of Fisheries and Marine Resources, Namibia, unpublished data). Historically, monkfish constituted an important bycatch in the trawl fishery directed at hake (*Merluccius* spp.), but due to increasing market demand since the early 1990s, a fishery directed at monkfish and sole (*Austroglossus microlepis*) has developed.

The Namibian Ministry of Fisheries and Marine Resources has identified the need to develop a management plan to ensure the resource's medium and long-term sustainability (Maartens *et al.* 1999). Long-term resource management plans include the identification of an assessment model to represent reality so that the implications of managing the resource in future under a range of assumptions about its present status and its future dynamics (Cochrane *et al.* 1998) can be examined. The aim of this study was, therefore, to assess the status of at least part of the monkfish resource using a length-based cohort assessment (Jones 1979, 1984, Sparre and Venema 1998) and an age-structured production model (Punt 1994, Punt and Japp 1994, Booth and Punt 1998).

MATERIAL AND METHODS

Life history

Monkfish are demersal fish that grow relatively slowly and live comparatively long in areas from the tidal zone to depths of more than 600 m (Maartens *et al.* 1999). The distribution of *L. vomerinus* extends from northern Namibia (21°S) to Durban, South Africa (30°S, 31°E; Leslie and Grant 1990) and that of *L. vaillanti* from north of Walvis Bay (23°S) to the Gulf of Guinea. *L. vomerinus* is the more important of the two species in terms of abundance, landed mass and value to the Namibian commercial trawl fishery. Aspects of the age, growth and reproductive biology of *L. vomerinus* have been studied by Maartens *et al.* (1999) and Maartens (1999). Unfortunately, no data on the life history of *L. vaillanti* are available, so restricting the current assessment to the *L. vomerinus* component of the resource.

Data availability and model selection

Since the 1940s, fisheries science has developed quantitative methods for assessing and managing fish stocks (Smith 1986). The type and source of data available for incorporation into the analysis therefore dictates

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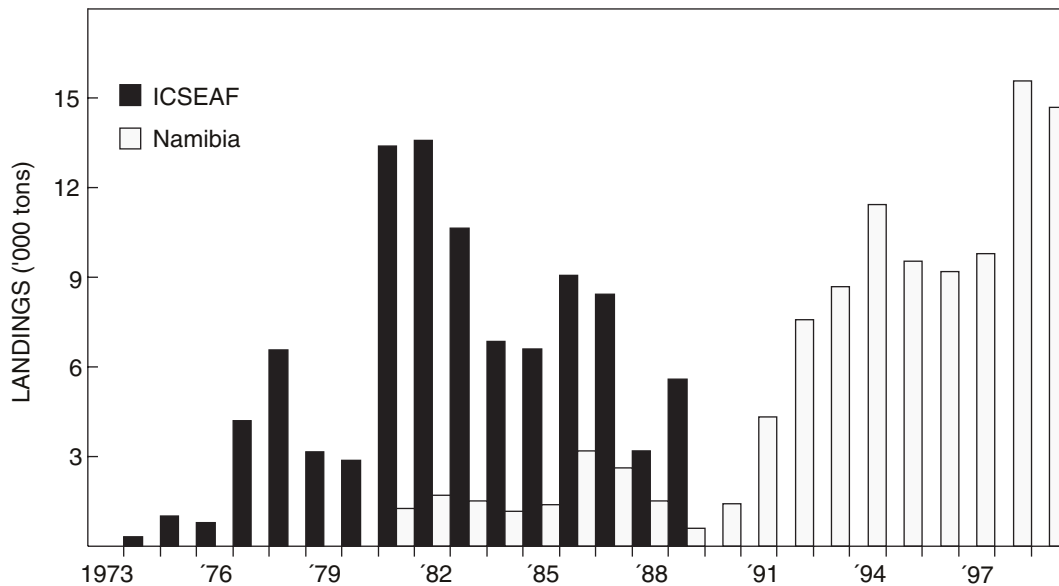


Fig. 1: Annual monkfish landings as recorded by ICSEAF, South Africa and the Namibian Ministry of Fisheries and Marine Resources between 1974 and 1999. For the period 1981–1989, it is not known whether Namibian landings were incorporated into ICSEAF records

the stock assessment technique deemed most appropriate (Hilborn 1992).

The data available for assessing *L. vomerinus* are a time-series of annual catches from 1974 to 1999

Table I: Adjusted annual catch-per-unit-effort (*cpue*) data, calculated using Generalized Linear Modelling, for *Lophius vomerinus* from the commercial fleet directed at monkfish and sole between 1991 and 1999 (after Maartens and Booth 2001), and biomass indices obtained from data collected by the R.V. *Dr Fridtjof Nansen* between 1994 and 1999 (after Maartens 1999)

| Year (month) | <i>Cpue</i> (kg day ⁻¹) | Biomass index (tons) | Biomass index CV |
|-----------------|--|-------------------------|---------------------|
| 1991 | 1 229.33 | – | – |
| 1992 | 1 485.81 | – | – |
| 1993 | 1 663.30 | – | – |
| 1994 (February) | 1 700.64 | 34 851.10 | 0.13 |
| 1994 (May) | – | 22 341.80 | 0.12 |
| 1994 (November) | – | 25 440.30 | 0.11 |
| 1995 (May) | 1 630.97 | 13 132.20 | 0.13 |
| 1996 (February) | 1 485.78 | 21 750.00 | 0.12 |
| 1996 (October) | – | 11 371.10 | 0.13 |
| 1997 (February) | 1 674.41 | 11 374.90 | 0.11 |
| 1998 (February) | 2 036.14 | 11 158.9 | 0.13 |
| 1999 (February) | 1 917.67 | 25 826.5 | 0.18 |

(Fig. 1; from the database of the Ministry of Fisheries and Marine Resources), General-Linear-Modelling-standardized catch per unit effort (*cpue*) data from the commercial fleet directed at monkfish and sole between 1991 and 1999 (Table I; Maartens and Booth 2001), biomass indices obtained from data collected by the R.V. *Dr Fridtjof Nansen* between 1994 and 1999 (Table I), commercial and research catch-at-age data (Tables II and III), and landing size category data from the industry between 1994 and 1999 (Table IV; Maartens 1999). As the monk resource consists of two species, annual catches and commercial catch-at-age data were reduced by 6% to reflect the average proportion of *L. vomerinus* in the monkfish catches made during the nine surveys of biomass between 1994 and 1999. GLM-standardized *cpue* was not, however, amended because the proportion was considered constant and, therefore, would not influence the *cpue* trend.

The short-term series of annual catch-at-age data makes it impractical to apply standard stock assessment techniques such as Virtual Population Analysis (Butterworth and Andrew 1984, Pope and Shepherd 1985, Butterworth *et al.* 1990), Integrated Catch Analysis (Deriso *et al.* 1985) or Adaptive Frameworks (Gavaris 1988). Assessment techniques that do not

Table II: Numbers caught at age aggregated for the fisheries directed at hake, monkfish and sole, 1994–1999. Values reflect the specific *Lophius vomerinus* component of the total catch, calculated by multiplying the total monkfish catch by a factor of 0.94

| Year | Numbers caught at age ($\times 10^6$) | | | | | | | |
|------|---|--------|-------|-------|-------|-------|-------|-------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| 1994 | 3.403 | 4.155 | 3.031 | 2.407 | 1.820 | 1.517 | 0.691 | 0.517 |
| 1995 | 3.096 | 5.010 | 3.449 | 2.598 | 1.350 | 1.125 | 0.477 | 0.336 |
| 1996 | 1.424 | 1.325 | 1.779 | 1.762 | 1.519 | 1.266 | 0.565 | 0.416 |
| 1997 | 5.447 | 5.850 | 3.435 | 2.428 | 1.366 | 1.138 | 0.486 | 0.345 |
| 1998 | 9.883 | 11.009 | 7.491 | 5.779 | 1.696 | 1.413 | 0.545 | 0.350 |
| 1999 | 6.530 | 5.695 | 4.642 | 3.991 | 1.895 | 1.580 | 0.662 | 0.462 |

require annual estimates of age composition are the biomass dynamic (surplus production) models (Schaefer 1954, 1957, Fox 1970). Despite their simplicity in only requiring a time-series of catch and abundance indices and their ability to estimate Total Allowable Catch (TAC) and effort controls, these models are insufficiently flexible to evaluate alternative harvesting strategies that have an age or size component (Punt *et al.* 1995).

Another analytical method, used predominantly in tropical fish and crustacean assessments (Gallucci *et al.* 1996, Sparre and Venema 1998), that could be applied is length cohort analysis (LCA; Jones 1979, 1984). This method, similar to age-based cohort analysis yet with less stringent age-based requirements, requires estimates of the total numbers caught by the commercial fishery and estimates of growth and mortality. These data are then used to construct a virtual (or synthetic) cohort (Lai and Gallucci 1988). The outputs are estimates of absolute stock size and fishing mortality per size-class. The latter can be used as input for predicting stock biomass and yield (Lai and Gallucci 1988) using, for instance, the Thompson and Bell prediction method (Sparre and Venema 1998),

resulting in an equilibrium estimate of maximum sustainable yield.

Age-structured production modelling was also considered because it encapsulates the dynamics of standard biomass dynamic models while taking the age-structured nature of the fish population into consideration, but without requiring estimates of the precise annual age composition of the catches (Hilborn 1990, Butterworth and Punt 1992, Punt *et al.* 1992, 1995, Punt 1994, Punt and Japp 1994, Geromont and Butterworth 1997, Booth and Punt 1998).

Model parameter estimates, together with alternative values for sensitivity tests used in both length- and age-based models, are summarized in Table V. Both age-at-maturity (a_{50}^m) and age-at-(50%) selection (a_{50}^{com} and a_{50}^{surv}) were estimated using a logistic ogive of the form $P_a = [1 + \exp(-(a - a_{50})/\delta)]^{-1}$, where P_a is the proportion of fish that are either mature or selected at age a , with a_{50} the inflection point and δ the width of the ogive. Age-specific selectivity was estimated by fitting the logistic to the ascending limb of the percentage commercial or research survey catch-at-age data. In commercial catches, *L. vomerinus* is fully selected in the XXS size category (10 and 16 cm total

Table III: Relative proportion of *Lophius vomerinus* caught at age during research surveys on the R.V. *Dr Fridtjof Nansen*, 1994–1999

| Month | Proportion of fish at age in survey catch | | | | | | | |
|-----------|---|-------|-------|-------|-------|-------|-------|-------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| Feb. 1994 | 0.046 | 0.161 | 0.244 | 0.128 | 0.157 | 0.126 | 0.095 | 0.031 |
| May 1994 | 0.022 | 0.109 | 0.175 | 0.123 | 0.181 | 0.176 | 0.151 | 0.042 |
| Nov. 1994 | 0.036 | 0.135 | 0.169 | 0.127 | 0.185 | 0.157 | 0.129 | 0.042 |
| May 1995 | 0.024 | 0.086 | 0.220 | 0.135 | 0.182 | 0.163 | 0.136 | 0.036 |
| Feb. 1996 | 0.121 | 0.123 | 0.173 | 0.162 | 0.163 | 0.115 | 0.098 | 0.030 |
| Oct. 1996 | 0.060 | 0.279 | 0.199 | 0.086 | 0.129 | 0.114 | 0.095 | 0.026 |
| Feb. 1997 | 0.097 | 0.249 | 0.274 | 0.095 | 0.088 | 0.085 | 0.077 | 0.023 |
| Feb. 1998 | 0.083 | 0.351 | 0.239 | 0.109 | 0.079 | 0.057 | 0.061 | 0.013 |
| Feb. 1999 | 0.036 | 0.188 | 0.273 | 0.158 | 0.155 | 0.096 | 0.068 | 0.019 |

Table IV: Total length and tail weight range of monkfish in six different size categories. Length data were collected on board M.F.V. *Lorraine* during April 1996 (after Maartens 1999)

| Category | Tail weight range (g) | Total length range (cm) |
|--------------------------|-----------------------|-------------------------|
| Extra, extra small (XXS) | 0–50 | 10–16 |
| Extra small (XS) | 50–100 | 17–25 |
| Small (S) | 100–250 | 26–36 |
| Medium (M) | 250–500 | 37–48 |
| Large (L) | 500–1 000 | 49–59 |
| Extra large (XL) | 1 000+ | 60+ |

length TL ; Tables IV, V), corresponding to approximately one year of age. This selection pattern is attributable to the high harvesting levels of juvenile fish by the fleet directed at hake and that directed at monkfish and sole and, either directly or indirectly, by the clogging effect of the nets caused by the heavy gear and tickler chains deployed.

Length-based modelling

Length cohort analysis (LCA) requires a length composition, representative of the catch under steady-state conditions (Jones 1984). These data were obtained from two different sources covering three time periods, 1994–1996, 1997–1999 and 1994–1999. The time periods were chosen on the basis of exploitation (11 000 and 14 000 tons on average annually for the periods 1994–1996 and 1997–1999 respectively) and the availability of data (size category data between 1994 and 1999 and length frequency data collected by observers between 1997 and 1999). Data used were size category data (mean number of monkfish per size category), as well as mean number of monkfish per 1 cm size-class collected by observers on board commercial vessels between 1997 and 1999. The results obtained by the LCA using observer data were compared with those from the LCA applied to size category data for the same period. The models make the assumption that the population was in equilibrium during these time periods.

Management quantities obtained from the LCA were estimates of absolute equilibrium stock size and fishing mortality per size-class. The latter vectors were used as input for the prediction of stock biomass and yield using a Thompson and Bell prediction approach (Lai and Gallucci 1988, Sparre and Venema 1998), resulting in an estimate of maximum sustainable yield (MSY).

Table V: Values of the fixed parameters of the population dynamics models used in the analyses. Values used in the sensitivity tests are in parenthesis

| Parameter | Estimate | Source |
|--|-----------|-------------------------------|
| L_{∞} (cm) | 95.04 | Maartens <i>et al.</i> (1999) |
| K (year ⁻¹) | 0.10 | Maartens <i>et al.</i> (1999) |
| t_0 (years) | -0.31 | Maartens <i>et al.</i> (1999) |
| α (g) | 0.011 | Maartens <i>et al.</i> (1999) |
| β (g cm ⁻¹) | 3.06 | Maartens <i>et al.</i> (1999) |
| M (year ⁻¹) | 0.3 (0.2) | This study |
| Maximum age (years) | 10 | This study |
| a_{50}^m (years) | 4 (3, 5) | Maartens (1999) |
| δ_{50}^m (year ⁻¹) | 1 | Maartens (1999) |
| a_{50}^{cm} (years) | 1 | This study |
| δ_{50}^{cm} (year ⁻¹) | 0.08 | This study |
| a_{50}^{surv} (years) | 1.92 | This study |
| δ_{50}^{surv} (year ⁻¹) | 0.39 | This study |
| Stock-recruitment relationship | | Beverton-Holt (Ricker) |

Age-based modelling

The age-structured production modelling approach involves constructing a deterministic age-structured model to simulate the population dynamics of the stock and tuning it to available abundance indices (Tables I–III) by maximizing a likelihood function. The underlying age-structured population dynamics model and likelihood function are described in the Appendix.

In the age-structured production model approach, values for only two parameters of the population dynamics model were estimated by maximizing the likelihood function, using a non-linear downhill simplex minimization algorithm (Press *et al.* 1997). These parameters were pristine biomass EB_0 and the “steepness” parameter h of the reparameterized Beverton and Holt or Ricker stock-recruitment relationships (see Appendix, Equations App.6 and App.7).

Management-related quantities used to assess the status and productivity of the monkfish stock from the age-structured production model were:

| | |
|----------------------|--|
| EB_0 , | the exploitable midyear biomass at unexploited equilibrium (EB_{1973}) in 1973 |
| h , | the fraction of equilibrium recruitment remaining if exploitable biomass is reduced to 20% of unexploited levels |
| $Depletion_{2000}$, | the current “depletion” in 2000 or the ratio of the exploitable biomass in 2000 to that in 1973 (i.e. EB_{2000}/EB_0) |

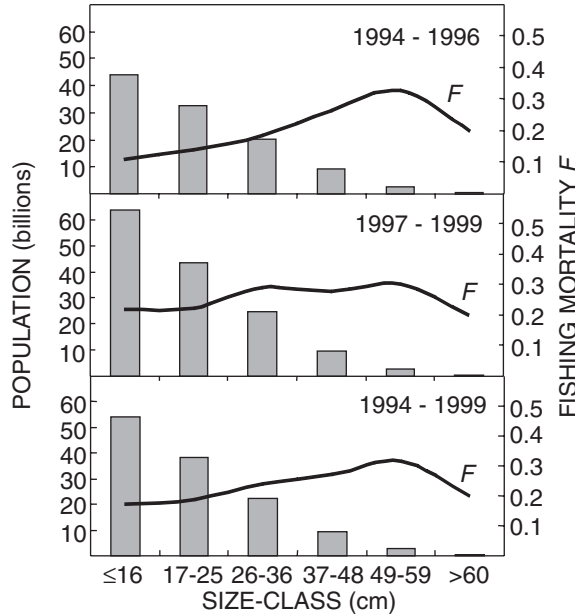


Fig. 2: Population numbers and fishing mortalities obtained through length cohort analyses using monkfish size category data for the periods 1994–1996, 1997–1999 and 1994–1999

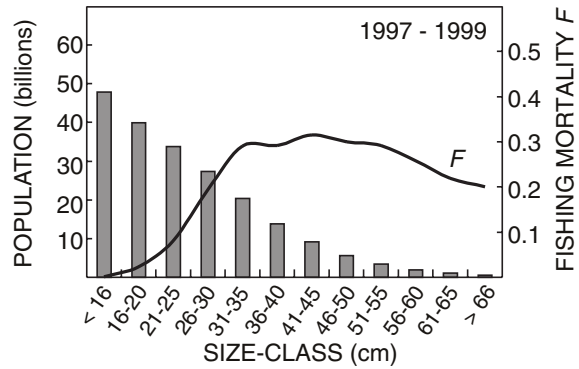


Fig. 3: Population numbers and fishing mortalities obtained through length cohort analysis using length frequency data collected by observers for the period 1997–1999

deviations and negative log-likelihood statistics describe how well the model fits the abundance indices and possible biases between the model and the abundance indices.

Coefficients of variation and percentile method 95% confidence intervals (Buckland 1984) for the management-related quantities were estimated using a condi-

- $MSYR$ (%), the ratio of TAC_{MSY} to the exploitable biomass at which it occurs (i.e. TAC_{MSY}/EB_{MSY})
- TAC_{MSY} , the equilibrium catch at F_{max} , the level of fishing mortality that maximizes the yield-per-recruit curve
- $TAC_{0.1}$, the equilibrium catch at $F_{0.1}$, the rate of fishing mortality at which the slope of the yield-per-recruit curve is 10% of its value near the origin
- σ^i , the standard deviation of the model fit to abundance index i
- q^i , the catchability coefficient (the effective bias) between the model and abundance index i and
- $-\ln L$, the negative of the natural logarithm of the likelihood function (Appendix, Equation App.16).

The quantities EB_0 , h and EB_{2000}/EB_0 are related to the current status of the monkfish resource relative to its pristine level, whereas $MSYR$, TAC_{MSY} and $TAC_{0.1}$ are related to the productivity and potential yield from the fishery. The catchability coefficients, standard

Table VI: Results from the length-based cohort analyses for size category data from 1994–1996, 1997–1999 and 1994–1999, and observer data for the period 1997–1999 for two choices of natural mortality

| Parameter | $M = 0.2 \text{ year}^{-1}$ | $M = 0.3 \text{ year}^{-1}$ |
|---------------------------------------|-----------------------------|-----------------------------|
| <i>Size category data (1994–1996)</i> | | |
| $\sum \bar{N}$ (millions) | 68.49 | 95.07 |
| $\sum \bar{B}$ (tons) | 34 589.45 | 42 943.18 |
| Mean F | 0.26 | 0.20 |
| <i>Size category data (1997–1999)</i> | | |
| $\sum \bar{N}$ (millions) | 88.23 | 117.14 |
| $\sum \bar{B}$ (tons) | 38 043.80 | 46 676.87 |
| Mean F | 0.32 | 0.25 |
| <i>Size category data (1994–1999)</i> | | |
| $\sum \bar{N}$ (millions) | 78.36 | 106.10 |
| $\sum \bar{B}$ (tons) | 35 991.60 | 44 244.17 |
| Mean F | 0.29 | 0.23 |
| <i>Observer data (1997–1999)</i> | | |
| $\sum \bar{N}$ (millions) | 79.47 | 111.07 |
| $\sum \bar{B}$ (tons) | 45 382.07 | 57 455.29 |
| Mean F | 0.27 | 0.21 |

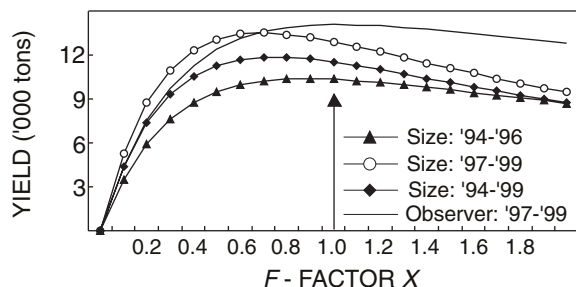


Fig. 4: Yield-per-recruit of monkfish as calculated by the length-based Thompson and Bell prediction model. The F -factor $X = 1$ indicates the current state

(Punt and Butterworth 1990, Francis 1992, Hilborn *et al.* 1993, Rosenberg and Restrepo 1994). The impact of future catches on the monkfish resource was assessed by projecting the estimated age structure at the start of 2000 ahead under a variety of possible future catch scenarios. Future annual catches of 4 000, 6 000, 8 000, 10 000 and 12 000 tons, as well as the estimated $TAC_{0.1}$ were considered. Parameter variability was incorporated into the risk analysis using the joint bootstrap parameter distributions of EB_0 and h . In all, 1 000 simulations of each future catch scenario were conducted.

RESULTS

tioned parametric bootstrapping procedure with 1 000 replicates (Efron 1981).

Risk analysis is a technique by which the effects of a future catch or fishing mortality trajectory on a resource, in terms of risk and reward, may be quantified

Length-based cohort analysis and Thompson and Bell prediction model

Results from the length cohort analyses using the size category data (1994–1996, 1997–1999, 1994–1999)

Table VII: Results from the Thompson and Bell prediction model for the “base case” assessment and when fishing mortality is reduced by either 40 or 50%. Values for the F -factor X are in parenthesis

| Parameter | “Base case” | 40% reduction | 50% reduction |
|---|-------------|---------------|---------------|
| <i>Size category data (1994–1996)</i> | | | |
| $Y_{current} (\times 10^3)$ | 10.35 (1.0) | 9.96 (1.0) | 9.48 (1.0) |
| $Y_{MSY} (\times 10^3)$ | 10.40 (0.9) | 10.40 (1.5) | 10.40 (1.8) |
| $\bar{B}_{current} \times \Delta t (\times 10^3)$ | 44.71 (1.0) | 70.83 (1.0) | 80.91 (1.0) |
| $\bar{B}_{MSY} \times \Delta t (\times 10^3)$ | 49.67 (0.9) | 49.67 (1.5) | 49.67 (1.8) |
| <i>Size category data (1997–1999)</i> | | | |
| $Y_{current} (\times 10^3)$ | 12.90 (1.0) | 13.42 (1.0) | 13.06 (1.0) |
| $Y_{MSY} (\times 10^3)$ | 13.51 (0.7) | 13.50 (1.2) | 13.51 (1.4) |
| $\bar{B}_{current} \times \Delta t (\times 10^3)$ | 49.11 (1.0) | 87.63 (1.0) | 103.30 (1.0) |
| $\bar{B}_{MSY} \times \Delta t (\times 10^3)$ | 74.95 (0.7) | 72.71 (1.2) | 74.95 (1.4) |
| <i>Size category data (1994–1999)</i> | | | |
| $Y_{current} (\times 10^3)$ | 11.52 (1.0) | 11.70 (1.0) | 11.31 (1.0) |
| $Y_{MSY} (\times 10^3)$ | 11.86 (0.7) | 11.87 (1.2) | 11.87 (1.5) |
| $\bar{B}_{current} \times \Delta t (\times 10^3)$ | 46.40 (1.0) | 79.46 (1.0) | 92.64 (1.0) |
| $\bar{B}_{MSY} \times \Delta t (\times 10^3)$ | 68.70 (0.7) | 66.79 (1.2) | 64.06 (1.5) |
| <i>Observer data (1997–1999)</i> | | | |
| $Y_{current} (\times 10^3)$ | 14.09 (1.0) | 13.12 (1.0) | 12.38 (1.0) |
| $Y_{MSY} (\times 10^3)$ | 14.09 (1.0) | 14.09 (1.7) | 14.09 (2.0) |
| $\bar{B}_{current} \times \Delta t (\times 10^3)$ | 57.85 (1.0) | 90.35 (1.0) | 102.81 (1.0) |
| $\bar{B}_{MSY} \times \Delta t (\times 10^3)$ | 57.85 (1.0) | 56.73 (1.7) | 57.85 (2.0) |

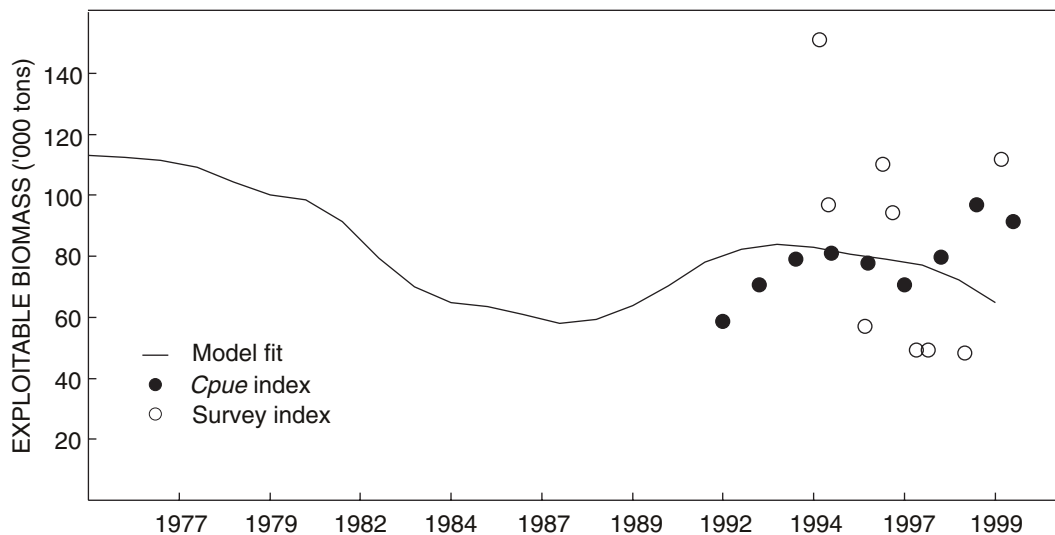


Fig. 5: Model fit to the survey and standardized *cpue* indices. Results are shown for the case in which $M = 0.3 \text{ year}^{-1}$ and recruitment is governed by the Ricker relationship. Initial biomass B_0 and the “steepness” parameter h were estimated using a non-linear search algorithm

and length frequency data collected by observers (1997–1999) for two choices of natural mortality are summarized in Table VI. Both mean population number and mean biomass increased as natural mortality increased, but the average fishing mortalities calculated for all size-classes decreased.

The sensitivity of the mean population number to different values of F_t ranging from 0.10 to 0.24 were considered. Low values of F_t have more effect on population numbers than higher values, as pointed out by Addison (1989).

Population numbers N and fishing mortalities F obtained through LCA for the four scenarios are shown in Figures 2 and 3.

The results of the length-based Thompson and Bell prediction model are shown in Figure 4. The yield-per-recruit curves show that, for three scenarios (size category data), the present level of fishing effort is well above that providing maximum sustainable yield, so a reduction in effort would yield bigger catches. A summary of the results for the “base case” analysis (Fig. 5) and when effort is reduced by 40 and 50% is summarized in Table VII.

Age-structured production model

Age-structured production model (ASPM) point esti-

mates, bootstrap CVs and 95% confidence intervals for 16 management-related quantities are presented in Table VIII. The range of the “steepness” parameter h was between 0.201 (as 0.2 is undefined) and 1.0 for the Beverton-Holt model, where $h = 1.0$ indicates no reduction in recruitment even if spawner biomass drops to very low levels, and between 0.201 and 2 for the Ricker model, where $h = 2.0$ doubles recruitment when spawner biomass drops to 20% of pristine.

The results of the sensitivity analysis for biological parameters, and for various combinations of abundance indices used in the log-likelihood, are summarized together with those of the “base case” analysis in

Table VIII: Estimates, bootstrap CVs and percentile method 95% confidence intervals (CI) for various management-related quantities, catchability coefficients and standard deviations of the various indices used for tuning, as estimated by the age-structured production model for the “base case”

| Quantity | Estimate | CV (%) | 95% CI |
|-----------------------------------|----------|--------|------------------|
| EB_0 ($\times 10^3$ tons) | 113.15 | 9.76 | [102.63; 149.92] |
| h | 0.91 | 8.07 | [0.70; 1.01] |
| $Depletion_{2000}$ | 0.58 | 8.72 | [0.48; 0.68] |
| $MSYR$ (%) | 17.16 | 7.28 | [13.51; 18.58] |
| TAC_{MSY} ($\times 10^3$ tons) | 9.59 | 7.27 | [8.45; 11.44] |
| $TAC_{0.1}$ ($\times 10^3$ tons) | 9.49 | 7.27 | [8.36; 11.33] |

Table IX: Estimates of 14 management-related quantities from the “base case” analyses and four sensitivity tests relating to the stock-recruitment relationship and estimates of natural mortality or age-at-maturity

| Quantity | “Base case” | Ricker | $M = 0.2 \text{ year}^{-1}$ | $a_{50}^m = 3 \text{ years}$ | $a_{50}^m = 5 \text{ years}$ |
|-----------------------------------|-------------|--------|-----------------------------|------------------------------|------------------------------|
| EB_0 ($\times 10^3$ tons) | 148.13 | 113.15 | 132.48 | 147.64 | 144.97 |
| h | 0.89 | 0.91 | 0.80 | 0.89 | 0.87 |
| $Depletion_{2000}$ | 0.48 | 0.58 | 0.16 | 0.48 | 0.46 |
| $MSYR$ (%) | 20.00 | 17.16 | 13.16 | 20.41 | 18.78 |
| TAC_{MSY} ($\times 10^3$ tons) | 9.40 | 9.59 | 5.86 | 9.42 | 8.93 |
| $TAC_{0.1}$ ($\times 10^3$ tons) | 9.03 | 9.49 | 5.66 | 9.04 | 8.61 |
| σ^{com} | 0.22 | 0.19 | 0.42 | 0.22 | 0.23 |
| σ^{surv} | 0.40 | 0.41 | 0.41 | 0.40 | 0.40 |
| $\sigma^{com \text{ age}}$ | 0.34 | 0.31 | 0.38 | 0.34 | 0.33 |
| $\sigma^{surv \text{ age}}$ | 0.45 | 0.45 | 0.44 | 0.45 | 0.45 |
| q^{surv} | 0.21 | 0.23 | 0.41 | 0.21 | 0.22 |
| $q^{com \text{ age}}$ | 1.27 | 1.22 | 1.49 | 1.28 | 1.27 |
| $q^{surv \text{ age}}$ | 1.07 | 1.06 | 1.09 | 1.07 | 1.07 |
| $-\ln L$ | -61.90 | -62.91 | -53.27 | -62.81 | -4.83 |

Tables IX and X.

Deterministic projections from the “base case” point estimates of exploitable biomass and “depletion” between 1999 and 2004 for five scenarios of future catches are presented in Table XI and Figure 6. The results, used to quantify catch scenario performance, represent the status of the resource after the five-year catch period by assessing “depletion”, the probability that the exploitable biomass in 2004 drops below current levels, and the probabilities that the exploitable biomass in 2004 drops below levels that achieve TAC_{MSY} and $TAC_{0.1}$.

DISCUSSION

Length-based methods can be satisfactory and useful for stock assessment, but they are usually less ambitious than catch-at-age methods (Hilborn 1992, Gallucci *et al.* 1996). One of the major limitations, however, is their restrictive assumption of a steady-state condition or constant parameter system (Sparre and Venema 1998). The model is, therefore, critically dependent on having length frequency distributions from a population in equilibrium state. It is further assumed that

Table X: Estimates of 14 management-related quantities from the model using a Ricker stock-recruitment relationship and the four sensitivity tests relating to choices in the abundance indices used for tuning the model. The four scenarios illustrate the use of all data (Scenario I), only commercial data (Scenario II), only research data (Scenario III), no catch-at-age data (Scenario IV) and no biomass data (Scenario V)

| Quantity | Scenario I | Scenario II | Scenario III | Scenario IV | Scenario V |
|-----------------------------------|------------|-------------|--------------|-------------|------------|
| $Cpue$ data | Yes | Yes | No | Yes | No |
| Survey abundance data | Yes | No | Yes | Yes | No |
| Commercial catch-at-age data | Yes | Yes | No | No | Yes |
| Survey catch-at-age data | Yes | No | Yes | No | Yes |
| EB_0 ($\times 10^3$ tons) | 113.15 | 133.02 | 149.98 | 431.59 | 137.58 |
| h | 0.91 | 0.69 | 0.72 | 0.77 | 0.61 |
| $Depletion_{2000}$ | 0.58 | 0.54 | 0.64 | 0.90 | 0.49 |
| $MSYR$ (%) | 17.16 | 13.30 | 13.81 | 14.72 | 11.58 |
| TAC_{MSY} ($\times 10^3$ tons) | 9.59 | 8.74 | 10.23 | 31.37 | 7.87 |
| $TAC_{0.1}$ ($\times 10^3$ tons) | 9.49 | 8.65 | 10.12 | 31.04 | 7.78 |
| σ^{com} | 0.19 | 0.20 | – | 0.15 | – |
| σ^{surv} | 0.41 | – | 0.40 | 0.41 | – |
| $\sigma^{com \text{ age}}$ | 0.31 | 0.34 | – | – | 0.33 |
| $\sigma^{surv \text{ age}}$ | 0.45 | – | 0.45 | – | 0.45 |
| q^{surv} | 0.23 | – | 0.17 | 0.04 | – |
| $q^{com \text{ age}}$ | 1.22 | 1.25 | – | – | 1.26 |
| $q^{surv \text{ age}}$ | 1.06 | – | 1.06 | – | 1.07 |
| $-\ln L$ | -62.91 | -37.75 | -25.15 | -16.23 | -4.83 |

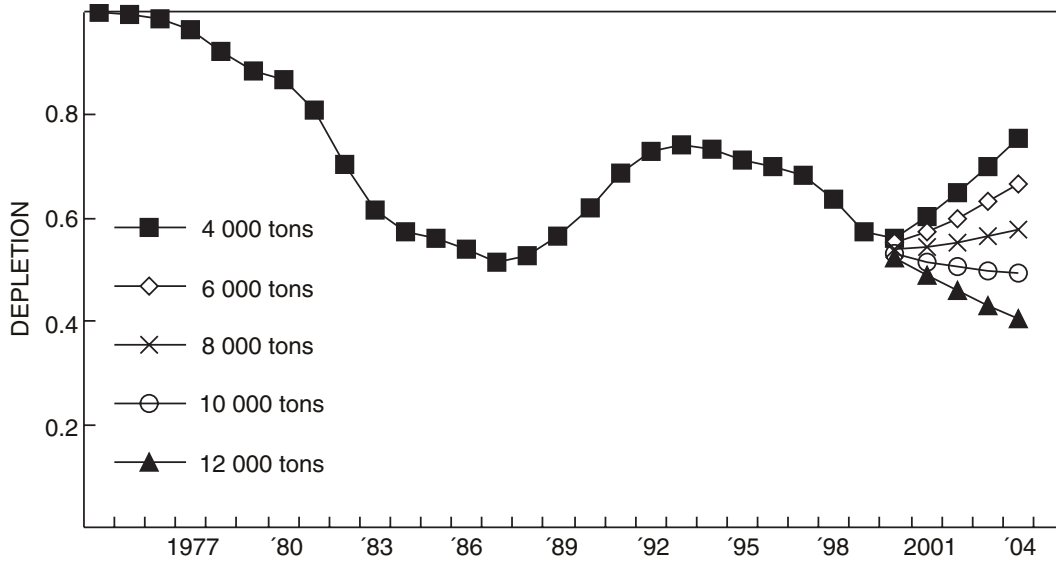


Fig. 6: Depletion projections for a scenario of possible future time sequences of catches from 1999 to 2004. Results are shown for the case in which $M = 0.3 \text{ year}^{-1}$ and recruitment is governed by the Ricker relationship. Initial biomass B_0 and the “steepness” parameter h were estimated using a non-linear search algorithm

the length frequency distribution of a catch is representative of the catch from one cohort over several years in the fishery, i.e. recruitment and exploitation rates have been stable with no significant trends in either (Lai and Gallucci 1988, Hilborn and Walters 1992).

Recruitment to the monkfish resource varied considerably between 1994 and 1999 (LM, unpublished data). Substantial variation can also be observed in the exploitation rates between 1990 and 1999 (Fig. 1, Table I) and a slightly declining, but insignificant ($p < 0.25$) trend was evident in the biomass estimates of monkfish obtained from data collected by the R.V. *Dr Fridtjof Nansen* between 1994 and 1998 (Table I).

If the data from 1999 were to be removed from the analysis, the trend would be highly significant ($p = 0.01$). A significantly increasing trend in abundance was, however, found in GLM-standardized *cpue* estimates over the years studied ($p = 0.01$). These indices are conflicting and should, therefore, be interpreted with caution.

The length-based cohort analyses were extremely sensitive to changes in natural mortality. As natural mortality increased, mean population number and biomass increased, whereas the mean fishing mortality F decreased. Hilborn and Walters (1992) state that, if the value for natural mortality M is chosen too high, the estimated cohort sizes will be larger than they

Table XI: Performance measures for a variety of possible future time sequences of catches from 2000 to 2004. Results are summarized for 1 000 simulations using the Ricker model with the parameters h and B_0 obtained from their joint bootstrap distribution

| Parameter | Performance measures at various levels of catch (tons) | | | | | |
|--|--|-------|-------|-------|--------|--------|
| | $TAC_{0.1} = 9.49$ | 4 000 | 6 000 | 8 000 | 10 000 | 12 000 |
| Average (SB_{2004}/SB_{1973}) | 0.52 | 0.79 | 0.69 | 0.59 | 0.49 | 0.39 |
| Average ($EB_{2004}/EB_{0.1}$) | 0.73 | 1.10 | 0.97 | 0.83 | 0.69 | 0.54 |
| $P(\text{Depletion}_{2004} < \text{Depletion}_{2000})$ | 0.96 | 0.00 | 0.00 | 0.01 | 0.99 | 1.00 |
| $P(EB_{2004} < EB_{MSY})$ | 0.88 | 0.05 | 0.34 | 0.73 | 0.91 | 0.97 |
| $P(EB_{2004} < EB_{0.1})$ | 0.94 | 0.21 | 0.70 | 0.88 | 0.96 | 0.98 |

should be. In contrast, if the estimated M is smaller than the true value, the cohorts will be too small. These biases may, however, not be serious provided that estimates of abundance are not regarded as absolute values, but rather as indices reflecting trends in abundance (Lai and Gallucci 1988, Addison 1989).

The LCA was insensitive to changes in terminal fishing mortality F_t , as indicated by Addison (1989). Low values of F_t (observer data between 1997 and 1999) had most effect on the population number, ranging between 125.0 and 112.6 million for values between 0.10 and 0.16 compared to population numbers of 112.6–108.7 million for values of F_t ranging between 0.18 and 0.24.

The mean population number was somewhat higher and the biomass somewhat lower for the size category data (1997–1999) than for the observer data over the same period (Table VI). This may possibly be explained by the undersampling of monkfish in the XXS and XS size-classes by observers, attributable to biased sampling techniques.

According to the LCA, the monkfish sizes most heavily exploited were 37–59 cm (size category data, 1994–1996), 26–59 cm (size category data, 1997–1999), 37–59 cm (size category data, 1994–1999) and 31–60 cm (observer data, 1997–1999).

Higher prediction estimates of current yield, MSY and $\bar{B}_{current} \times \Delta t$ were evident (observer data) when comparing the size category and observer datasets for the period 1997–1999. The estimate of $\bar{B}_{MSY} \times \Delta t$ was, however, somewhat higher when the analysis was carried out using the size category data for 1997–1999. Results from the Thompson and Bell prediction model for three scenarios (size category data) show that the monkfish population is exploited above MSY . However, using the observer data, exploitation is taking place at MSY levels. A reduction of approximately 40% in fishing effort yielded slightly higher catches (size category data 1997–1999, 1994–1999). The yield curves (Fig. 4, Table VII) show that, for the four analyses, yield ranged between 10 400 and 14 100 tons (at an F -factor of $X = 1$). A 50% reduction in effort would result in a very small, if any, increase in the current yield ($Y_{current}$). The current biomass $\bar{B}_{current}$ multiplied by Δt would, however, double if effort were reduced by 50% for all four scenarios (Table VII).

From the ASPM, estimates for the management-related quantities were quantitatively sensitive to the assumed rate of natural mortality. As expected, the results for $M = 0.3 \text{ year}^{-1}$ suggested a more productive stock owing to yield-per-recruit effects. The parameter h in the “base case” was estimated at 0.89, its bootstrap distribution corresponding to the prior distribution constructed using meta-analysis, as reported by Smith and Punt (1998). Higher estimates of the “steepness”

parameter h imply that the stock is more productive with little reduction in annual recruitment, even if the spawner biomass drops to very low levels. Previous assessments on other *Lophius* species have either noted a high h (Hilborn¹) or the lack of a discernible stock-recruitment relationship (Myers *et al.* 1995). These data point towards recruitment being dominated by density-independent processes, with density-dependent effects only dominating at low levels of spawner biomass. The best fit to the data was obtained using the Ricker stock-recruitment relationship. The Ricker “steepness” parameter ranged between 0.7 and 1.0 (CV 8.07%), so approximating the Beverton-Holt relationship, with the exception that there are slight density-dependent increases in recruitment when spawner biomass is reduced to between 50 and 70% of exploited levels.

The results in terms of productivity, resource status and projected catch levels were similar when age-at-50%-selectivity was either increased or decreased. In contrast, when natural mortality was decreased, the resource would be considered overexploited and unproductive, with low levels of TAC . When the Ricker model was tuned to various combinations of abundance indices it was evident that the incorporation of catch-at-age data from commercial and/or research surveys was necessary to offset the lack of signal in the biomass indices. This was because the additional scaling parameters reduced the risk of run-away estimates of pristine exploitable biomass. The incorporation of catch-at-age data provided lower TAC estimates and suggested that productivity of the resource, gauged from $MSYR$, was higher. Estimated CV s for the estimated management quantities (7.28–9.78%) were considered acceptable despite the conflicting trends in biomass between the $cpue$ and survey indices. The increasing trend in $cpue$ was offset by a decreasing trend in the survey estimates (Fig. 5) and the steadily decreasing trends in mean catch-at-age of both the research survey and commercial data.

Estimates of resource productivity ($MSYR = 13.51$ – 18.58%) for *L. vomerinus* were lower than the longer-lived kingklip *Genypterus capensis* (Punt and Japp 1994; about 10%, age 30 years) and similar to both panga *Pterogymnus laniarius* (Booth and Punt 1998; 17–19%, age 20 years) and hake *Merluccius* spp. (Punt 1994, Payne and Punt 1995; 15–20%, age 15 years) stocks. Results of the sensitivity analysis revealed that productivity of the monkfish resource increased or decreased slightly commensurate with an increase

¹ Hilborn, R. — An analysis of the status of the goosefish (*Lophius americanus*) stock in New England and the mid-Atlantic states. <http://fishingnj.org/hlbrnrpt.pdf>

or decrease in the assumed age at maturity, principally because of the increase in spawner biomass.

The “depletion” level of the monkfish resource is currently calculated to be 0.58% (CV 8.72%). Large numbers of juvenile monkfish are, however, currently harvested (Maartens 1999), which may lead to growth-overfishing in future. An important issue is the level of minimum spawning stock biomass required to prevent recruitment-overfishing (O’Boyle 1993). The use of a $TAC_{0.1}$ strategy should reduce the risk of reproductive failure because, under a range of stock-recruit relationships and biological parameters for groundfish species, such a harvesting strategy should maintain spawner biomass at acceptable levels of ~35–40% (Clark 1992).

Mean estimates of approximately 9 600 and 9 500 tons (CVs 7.27%) were obtained for TAC_{MSY} and $TAC_{0.1}$ respectively (Table VIII). These estimates were also incorporated into the catch projections, together with other future harvesting scenarios, to assess the risk to stock sustainability in 2004. Average “depletion” and the ratio of current exploitable biomass to the level at which $TAC_{0.1}$ levels are achieved ($EB_{0.1}$), decreased with increasing catches. Similarly, the risk that exploitable biomass would be less than $EB_{0.1}$ and EB_{MSY} in 2004 increased. Results also suggest that, under a scenario of future catches above the current estimates of sustainable yield, exploitable biomass would continue to decline. As a result, catches in excess of 12 000 tons for *L. vomerinus* would likely be unsustainable. If a future catch of c. 10 000 tons, the $TAC_{0.1}$ estimate, was considered, the risk of stock collapse would decrease and the exploitable biomass maintained at adequate levels. There is one complication, however: to estimate the proportion of *L. vaillanti* that can also be harvested considering that this is a two-species fishery and that no biological data are available for the latter species. It appears that current catches in excess of 15 000 tons are slowly eroding *L. vomerinus* exploitable biomass, and also possibly that of *L. vaillanti*. Therefore, to take a cautious approach, serious consideration should be given to reducing total catch levels of monkfish (both species) to between pre-1998 and 1999 levels of c. 12 000 tons per annum.

Reliable stock assessment results are usually obtained from long-term abundance series, even with a lack of knowledge of the age structure of the catch, that illustrate a defined change in biomass (i.e. when catches are constant or increasing, biomass decreases; when catches are constant or decreasing, biomass increases). Both survey and *cpue* indices are short, and their trends are conflicting. Considerable variability is also evident. Problems arise when abundance data are relatively uninformative about the dynamics of

the stock. The term “relatively” can be defined in this context as meaning when the abundance data series is too short (normally the data series are <5–10 years long) and/or the abundance indices do not reflect the response of the stock to harvesting pressures. Examples include a constantly declining trend in abundance data, also referred to as “one-way downhill trip” data by Polacheck *et al.* (1993). Such data can lead to negatively biased estimated levels of stock productivity or temporally invariant indices that do not increase or stabilize when harvesting levels are reduced, or they fail to illustrate a decreasing trend in abundance when harvesting levels are increased. As monkfish attain at least 10 years of age, a time-series longer than 10 years would be required to identify informative trends in both abundance and catch levels. This would be crucial to obtain meaningful results through the population modelling process.

As far as LCA is concerned, Hilborn and Walters (1992) stated that equilibrium length-based analysis has seldom led to useful management advice. Similarly, the ASPM has disadvantages. Limitations include, first, that recruitment is deterministically related to spawner biomass by the application of the stock-recruitment relationship via the “steepness” parameter *h*, and second, that the model assumes similar selectivity and exploitation patterns throughout the period under review. Finally, the ASPM estimates total mortality instead of fishing mortality in the calculation of annual catches. This is due to the correlation between fishing and natural mortality in the estimation framework (Appendix, Equation App.8).

A Bayesian statistical approach may be a possible option for future stock assessment work on *L. vomerinus*. Bayesian methods can appraise the full range of uncertainties related to the population dynamics model and parameter values used, so offering an elegant and theoretically consistent framework within which to provide policy advice (McAllister *et al.* 1994, Punt and Hilborn 1997). A Bayesian approach could also be the most suitable framework to assess the relative probability that either the Ricker or the Beverton-Holt model describes the “actual” stock-recruitment relationship, given that the model fits, despite being statistically similar to each other, predicted contrasting resource productivities and statuses.

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APPENDIX

The age-structured production model

Resource dynamics

Population abundance, in numbers, is governed by the following recursive equations

$$N_{y+1,a} = \begin{cases} R_{y+1}, & \text{if } a = 0 \\ N_{y,a-1} e^{-M-S_{a-1}^{com}} F_y, & \text{if } 0 < a < \max \\ N_{y,\max-1} e^{-M-S_{\max-1}^{com}} F_y + N_{y,\max} e^{-M-S_{\max}^{com}} F_y, & \text{if } a = \max \end{cases}, \text{ (App.1)}$$

where $N_{y,a}$ is the number of fish at age a at the start of year y , R_y the number of 0-year-olds at the start of year y , M the rate of natural mortality, S_a^{com} the age-specific commercial selectivity for age a , F_y the fully selected (asymptotic) fishing mortality in year y , and \max is a lumped plus-group.

The model is initiated in the year preceding fishing activity and the initial number of age-0 recruits, R_0 , is calculated as

$$R_0 = EB_0 / \left\{ \sum_{a=0}^{\max-1} W_{a+1/2} S_a^{com} \exp(-[a+1/2]M) + W_{\max+1/2} \frac{S_{\max}^{com}}{1-\exp(-M)} \exp(-[\max+1/2]M) \right\} \text{ (App.2)}$$

Annual recruitment

The number of recruits at the start of year y was considered to be deterministically related to the previous year's spawner stock biomass, using either the Beverton and Holt or Ricker stock-recruit relationships where

$$R_{y+1} = \frac{SB_y}{\alpha SB_y + \beta} \text{ (Beverton-Holt)}$$

$$R_{y+1} = \alpha SB_y e^{\beta SB_y} \text{ (Ricker)}, \text{ (App.3)}$$

and spawner biomass in year y is defined as

$$SB_y = \sum_{a=0}^{\max} N_{y,a} W_a \psi_a, \text{ (App.4)}$$

with ψ_a the proportion of fish at age a that are sexually mature and W_a the begin-year mass of a fish of age a , such that

$$W_a = \left[W_{\infty}^m \left(1 - e^{-K^m(a-t_0^m)} \right)^{\beta^m} + W_{\infty}^m \left(1 - e^{-K^f(a-t_0^f)} \right)^{\beta^f} \right] / 2, \text{ (App.5)}$$

and W_{∞}^i , K^i and t_0^i are the von Bertalanffy growth equation parameters for fish of sex i , and α^i and β^i are the mass-length relationship parameters.

The stock recruitment relationships were reparameterized to a single "steepness" parameter (Kimura 1988), such that

$$R_{y+1} = \frac{SB_y}{SB_0} \left[1 - A \left(1 - SB_y / SB_0 \right) \right]^{-1} \text{ (Beverton-Holt)}$$

$$R_{y+1} = \frac{SB_y}{SB_0} \exp \left(a \left(1 - SB_y / SB_0 \right) \right) \text{ (Ricker)}, \text{ (App.6)}$$

The constants A and a are calculated as that fraction of pristine recruit (f) when spawner biomass is reduced to a fraction of pristine levels (b ; in this study $b = 0.2$), such that

$$A = \frac{1-b/f}{(1-b)} \text{ (Beverton-Holt)}$$

$$a = \frac{\ln(f/b)}{(1-b)} \text{ (Ricker)}. \text{ (App.7)}$$

Catches and estimation of fishing mortality

Annual catches are described by the catch equation

$$C_y = \sum_{a=0}^{\max} W_{a+1/2} N_{y,a} \frac{S_a^{com} F_y}{M + S_a^{com} F_y} \left(1 - e^{-M - S_a^{com} F_y} \right), \text{ (App.8)}$$

where $W_{a+1/2}$ is the weight-at-age of a fish at the middle of the year.

The estimates of F_y are obtained by solving for C_y , which represents the observed annual catch. This is conducted by using an iterative linear bisection method (Press *et al.* 1997).

Yield projections

The estimate of projected catch at a specified fishing mortality $F_{0,n}$ for year $y+1$ is provided by

$$TAC_{0,n} = \hat{R}(F_{0,n}) \sum_{a=0}^{\max} W_{a+1/2} \tilde{N}_a \frac{S_a^{com} F_{0,n}}{M + S_a^{com} F_{0,n}} (1 - e^{-M - S_a^{com} F_{0,n}}) \quad (\text{App.9})$$

where $\hat{R}(F_{0,n})$ is the estimated equilibrium recruitment corresponding to a fishing mortality of $F_{0,n}$. The relative number of fish at age a , \tilde{N}_a , was calculated from

$$\tilde{N}_a = \begin{cases} 1, & \text{if } a = 0 \\ \tilde{N}_{a-1} e^{-M - S_{a-1}^{com} F_y}, & \text{if } 0 < a < \max \\ \tilde{N}_{a-1} e^{-M - S_{\max-1}^{com} F_y} / (1 - e^{-M - S_{\max}^{com} F_y}), & \text{if } a = \max \end{cases} \quad (\text{App.10})$$

Recruitment was estimated as a function of spawner biomass-per-recruit (opposed to spawner biomass) by reorganizing Equation App.6 such that

$$\hat{R}(F_{0,n}) = R_0 \frac{1 - SBR_0 - SBR_{F_{0,n}}}{SBR_0 A} / \left[1 - A \left(1 - \frac{1 - (SBR_0 - SBR_{F_{0,n}})}{SBR_0 A} \right) \right] \quad (\text{Beverton-Holt})$$

$$\hat{R}(F_{0,n}) = R_0 \frac{1 - \ln(SBR_0 / SBR_{F_{0,n}})}{A} \exp \left[a \left(1 - \frac{1 - \ln(SBR_0 / SBR_{F_{0,n}})}{A} \right) \right] \quad (\text{Ricker}) \quad (\text{App.10})$$

where spawner biomass-per-recruit as a function of F , $SBR(F)$, is calculated as

$$SBR(F) = \sum_{a=0}^{\max} W_a \tilde{N}_a \psi_a \quad (\text{App.12})$$

Two harvesting strategies for year $y+1$ were considered, TAC_{MSY} and $TAC_{0.1}$, each corresponding to those fishing mortalities that maximize yield ($F_{0,n} = F_{MSY}$) and where the slope of the yield curve is 10% of that at the origin ($F_{0,n} = F_{0.1}$). All estimates of $F_{0,n}$ were calculated numerically.

The likelihood function

The likelihood function was constructed assuming that

there is a proportional relationship between resource abundance in terms of mass between the research trawl survey and commercial catch-per-unit-effort indices, and in terms of numbers for the commercial catch-at-age and survey catch-at-age indices. All indices were assumed to be non-negative, log-normally distributed and consisting of observation-error only (no error is attributed to the deterministic resource abundance equations), such that in terms of biomass

$$O_y^i = \hat{q}^i \hat{E}_y e^{\epsilon_y^i} \quad \epsilon_y^i \sim N(0, (\hat{\sigma}^i)^2) \quad (\text{App.13})$$

and in terms of numbers at age

$$O_{y,a}^i = \hat{q}^i \hat{E}_{y,a} e^{\epsilon_{y,a}^i}$$

where O_y^i and $O_{y,a}^i$ are the observed indices of abundance (in terms of mass or number) in year y for index i , \hat{q}^i the proportionality coefficient of the abundance index i , $(\hat{\sigma}^i)^2$ the variance associated with the model fit to the observed abundance index i , and \hat{E}_y and $\hat{E}_{y,a}$ are the model estimates of resource abundance (in terms of mass or numbers) during y where midyear exploitable biomass from the commercial fishery is

$$E_y^i = \sum_{a=0}^{\max} W_{a+1/2} N_{y,a} e^{-(M - S_a^{com} F_y) / 2}$$

survey biomass in month m is

$$E_{y,m}^i = \sum_{a=0}^{\max} W_{a+m/12} S_a^{surv} N_{y,a} e^{-\frac{m}{12}(M - S_a^{surv} F_y)}$$

number of fish per age a landed by the commercial fishery is

$$E_{y,a}^i = N_{y,a} \frac{S_a^{com}}{M_a + S_a^{com} F_y} (1 - e^{-(M_a + S_a^{com} F_y)})$$

and the number of fish caught during each research survey is

$$E_{y,a}^i = N_{y,a} S_a^{surv} e^{-\frac{m}{12}(M + S_a^{surv} F_y)} \quad (\text{App.14})$$

where S_a^{surv} is the age-specific research survey selectivity.

Taking the natural logarithm of a log-normal likelihood, negating and dropping the terms independent of the model parameters gives the quantity $(-\ln L)$ which, when minimized, provides the maximum likelihood estimates for B_0 and h :

$$-\ln L = \sum_i (n^i \ln \hat{\sigma}^i + n^i / 2) \quad , \quad (\text{App.15})$$

where n^i is the number of data points in series i .

Maximum likelihood estimates of \hat{q}^i and $\hat{\sigma}^i$ were obtained by differentiating the log-likelihood with respect to the parameter of interest and solving the resulting equation, such that

$$\hat{q}^i = \exp \left(\frac{1}{n^i} \sum_y \ln \left(\frac{O_j^i}{E_j^i} \right) \right)$$

$$\hat{\sigma}^i = \sqrt{ \frac{1}{n^i} \sum_y \ln \left(\frac{O_j^i}{\hat{q}^i E_j^i} \right)^2 } \quad . \quad (\text{App.16})$$