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Methods for stock assessment of crustacean fisheries

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Abstract

Crustacean fisheries account for nearly 30% of all fish and shellfish landings by value world-wide. This paper reviews and evaluates the application of various stock assessment methods to crustacean fisheries. Methods covered include biomass dynamics models, delay-difference models, depletion methods, equilibrium yield and egg per recruit models and dynamic size-structured models. The development, underlying assumptions, data requirements, benefits and disadvantages of each model are briefly considered. The implications and treatment of uncertainty in data, parameter estimates and model structure are also considered. Finally, we speculate how crustacean stock assessment methodology may evolve in the future.
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1. Introduction

Fisheries for crustacean species are globally important, primarily due to their high unit value. Recent FAO statistics (1999) show that landings from wild marine crustacean fisheries totalled almost 6000 Mt with a value of just under $ 20 billion (FAO, 2001). With finfish stocks declining world-wide, crustacean fisheries are becoming increasingly important and now account for 7% of all fish and shellfish landings by weight and 28% by value. Many crustacean fisheries are artisanal, prosecuted by many small boats using static gears, and their socio-economic importance may therefore be even greater. This increasing importance requires that stock assessment and management programmes for crustacean fisheries should be effective.

Many crustacean assessments consist of descriptive summaries of catch statistics, population structure and abundance indices. These may provide sufficient information on the relative status of the fishery to be useful for management, but fall short of analytical assessments that attempt to provide an understanding of stock and fishery dynamics as well as estimates of population parameters in absolute and relative terms. The former tends to lead to reactive management, while the latter may provide a means for developing optimal management. Sampling and survey strategies fall outside the scope of this review, which describes and compares analytical stock assessment methods that model stock and/or fishery dynamics utilising commercial fisheries data, either independently, or in conjunction with additional fishery-independent information.

The models available to the stock assessment scientist range from relatively simple biomass dynamics models to more complex age- or size-structured analyses. This review is not intended as a manual, but aims to catalogue and clarify methods and point users to key references and examples where the methods have been applied to crustacea. It is not for assessment specialists, but rather for crustacean biologists who wish to carry out stock assessments. We briefly review the available methods, describe their underlying

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assumptions and data requirements, consider the advantages and disadvantages of the methods (Appendix A) and provide examples of their application to crustacean fisheries (Appendix B). We include a brief description of biological reference points provided by each method, but do not review the estimation or usage of reference points as this has been covered elsewhere (e.g. Caddy and Mahon, 1995). We do not consider spatial models for crustacean stock assessment in the form of either metapopulation modelling approaches, which describe a series of sub-populations linked by larval recruitment, or models that consider the spatial distribution of individuals within a sub-population. The categorisation of methods is not wholly discrete, with overlap from one category to another occurring as methods are developed and extended to account for features specific to particular fisheries or are generalised for wider application. The lack of clear divisions between methods prompted Xiao (2000) to suggest that each model be called after its originator, e.g. Schaefer (1954) production model. Throughout, we take into account specific biological aspects of crustacea, such as growth by moult and our inability to age individuals effectively, which may render standard finfish assessment methods unsuitable for the stock assessment of crustacean fisheries.

Following the description of stock assessment methods applied to crustacean fisheries, we consider the problem of uncertainty in stock assessment, which applies to all assessment methods, and describe ways in which uncertainty can be addressed by stock assessment biologists and managers. Finally, we suggest ways in which crustacean stock assessment methodology may advance in the future.

2. Biomass dynamics models

Biomass dynamics, or surplus production, models have a long tradition in stock assessment of both finfish (e.g. Schaefer, 1954, 1957) and shellfish (e.g. Pereiro and Fernandez, 1974; Maigret, 1977; Polovina, 1989) and are still extensively used (e.g. Yoshimoto and Clarke, 1993; Stefánsson et al., 1994; Breen and Kendrick, 1998; Cadrin, 2000). Biomass is modelled simplistically as a function that combines life processes (recruitment, growth and natural mortality) and takes no account of population age or size struc-

ture. The biomass model is linked to the exploitation history of the fishery by an abundance index, often catch per unit effort (CPUE), assumed proportional to biomass, although fishery-independent indices may be used. Historically, the models were often fitted assuming equilibrium, but this method often performs poorly and time-series fitting using maximum likelihood or non-linear least squares minimisation is now the generally accepted approach. There may be confounding between parameters unless the stock has an exploitation history covering a wide range of biomass and fishing effort levels (Hilborn and Walters, 1992) as was noted during a preliminary assessment of the edible crab, *Cancer pagurus*, in the English Channel (ICES, 1998). If non-linear least squares minimisation is used for fitting, the objective function can be modified to take account of additional data using a weighting parameter as developed originally for catch-at-age analysis (Fournier and Archibald, 1982; Deriso et al., 1985), which can be useful in overcoming problems of parameter confounding.

Simplicity is both a strength and weakness of biomass dynamics models. They require few data (time-series of catch and abundance index), are straightforward to implement and extend, and few assumptions render them relatively transparent. They provide a useful tool for evaluation of management actions (Hilborn, 1997). However, their simplicity precludes insight to the dynamic processes (growth, stock recruitment relationship) and inability to address age- or size-specific issues (e.g. changes to selection pattern, minimum landing size (MLS), discarding practice) limits their utility for evaluating technical measures.

Three classical models are widely used: the Graham–Schaefer model (Graham, 1935; Schaefer, 1954, 1957; Ricker, 1975; Fletcher, 1978; Gulland, 1983), the Fox (1970) model and the Pella and Tomlinson (1969) model. The Schaefer model is based on the logistic equation and biomass declines linearly with fishing mortality, whereas in the Fox model, based on Gompertz growth, biomass declines exponentially with fishing mortality. Pella and Tomlinson (1969) introduced a third parameter to modify the shape of the function thus providing more flexibility but at a cost, as the model may be volatile and lead to estimates with high variances and parameter confounding.

Traditionally, biomass dynamic models were based on the differential equation governing resource biomass,

$$\frac{\mathrm{d}B_t}{\mathrm{d}t} = g(B_t) - qf_t B_t \tag{1}$$

where q is the catchability coefficient and f_t the effort in year t. However, the relationship is more often used in its discrete form:

$$B_{t+1} = B_t + g(B_t) - C_t \tag{2}$$

where B_t is (exploitable) the biomass at time t, $g(B_t)$ the biomass dynamic function in terms of current biomass, and C_t the catch during time t to $t + 1$. The three classic models are

- Schaefer model:

$$g(B) = rB\left(1 - \frac{B}{k}\right) \tag{3}$$

- Fox model:

$$g(B) = rB\left(1 - \frac{\ln(B)}{\ln(k)}\right) \tag{4}$$

- Pella–Tomlinson model:

$$g(B) = \frac{r}{p}B\left[1 - \left(\frac{B}{k}\right)^p\right] \tag{5}$$

where B is the current biomass, r the intrinsic rate of growth, k the average unexploited equilibrium biomass (carrying capacity) and p a shape parameter.

Fig. 1 illustrates some behaviours of Schaefer, Fox and Pella and Tomlinson models. Butterworth and Punt (1992) advise that the sensitivity to the shape parameter should be evaluated. Prager (2002) found that a generalised model, where the shape parameter was estimated, was more sensitive to outliers than the logistic model and concluded that unless a good estimate of model shape was available, the logistic model was more suitable for routine assessment. Other models have been proposed (Shepherd, 1982a; Ludwig and Hilborn, 1983) using the Ricker (1954) and Shepherd (1982b) functions originally developed for stock recruitment relationships.

Biomass dynamics models provide estimates of a number of reference points; maximum sustainable yield (MSY) and its associated family; fishing mortality for achieving MSY (F_{MSY}), fishing effort at MSY (f_{MSY}); biomass at MSY (B_{MSY}) as well as the unexploited (virgin) biomass. The Schaefer and some Pella and Tomlinson parameterisations permit estimation of the fishing mortality that will lead to stock collapse (F_{crash}). These may be useful in assessing the health of stocks and in framing management rules, but are sensitive to model choice.

The constant catchability assumption (i.e. that biomass is proportional to abundance index) may be modified using relationships such as a power model with catchability dependent on population size (Cooke, 1985), or stochastically modelling catchability as a random walk to account for random variability
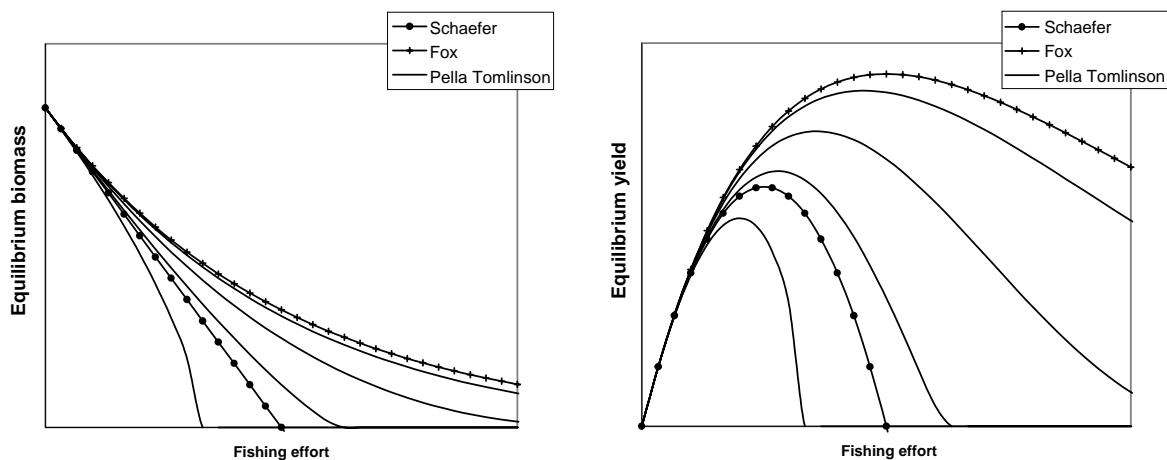

Fig. 1. Relationships between equilibrium biomass and fishing effort and equilibrium yield and effort for Schaefer, Fox, and Pella and Tomlinson (with a range of shape parameter values) biomass dynamics models.

or technical creep. However, Punt and Hilborn (1996) warn of caution in shaping the relationship between catch rate and biomass. Nonetheless, the constant catchability assumption may be violated over time, a problem common to much fisheries assessment, as well as due to spatial and behavioural (Frusher et al., 2003) characteristics commonly exhibited by crustacea. Poorly estimated catchability coefficients may result in spurious estimates of absolute stock size or fishing mortality. The ratios of biomass at time t (B_t) to B_{MSY} and fishing mortality at time t (F_t) to F_{MSY} (i.e. B_t/B_{MSY} and F_t/F_{MSY}) have been found to be more robust than absolute values of biomass and fishing mortality and are generally recommended for use in management (Prager, 1994, 2002; Cadrin, 2000).

The methods of using equilibrium assumptions or average effort (Fox, 1970) for fitting have been shown to perform poorly and generally are not recommended. Transformations into dynamic, or analogous difference, equations solved by multiple linear regression have been carried out (Hilborn, 1976, 1979; Schnute, 1977), but most recent applications have used time-series fitting, using maximum likelihood or non-linear least squares minimisation. Error can be considered as either process, occurring as a result of stochasticity in the processes of the model while observations are made without error, or observation where error occurs in the observations and the model is considered to be deterministic (Punt and Hilborn, 1996). The latter is the more commonly used and generally recommended approach. A recent development has been the use of state space models which account for both measurement and process error and have been implemented in a Bayesian framework in order to overcome the need for simplifying assumptions required for fitting using likelihood or Kalman filtering (Meyer and Millar, 1999a). Meyer and Millar (1999a) used a freely available software package, BUGS (Bayesian inference using Gibbs sampling) (Thomas et al., 1992; Spiegelhalter et al., 1996), to implement a Schaefer production model as well as more complex age-structured models (Millar and Meyer, 2000).

Prager (1994) reviewed estimation techniques and developed the ASPIC computer program (Prager, 1995), which includes extensions for handling missing and extra data, bootstrapping to obtain confidence estimates, bias and forecasting. Monte Carlo simulations have been used extensively to assess and address bias in biomass dynamics model parameters (Hilborn, 1979; Uhler, 1979; Mohn, 1980; Roff and Fairbairn, 1980; Roff, 1983; Breen and Kendrick, 1998; Cadrin, 2000) and are considered essential by Hilborn and Walters (1992), although Punt and Butterworth (1993) showed bootstrapped confidence intervals may be optimistic. A comparison of methods and measuring uncertainty is provided by Polacheck et al. (1993) for finfish species and rock lobster.

2.1. Extended or modified biomass dynamics models

Explanatory data may be used to extend biomass dynamics models to model the effects of external factors on stock dynamics. Freon (1988) considered pristine biomass and catchability coefficient parameters for the Schaefer, Fox and Pella–Tomlinson models as functions of an environmental variable and produced software for such analysis (Freon et al., 1990).

Stefánsson et al. (1994) carried out an assessment of *Pandalus borealis* in Icelandic waters using a production model extended to include a recruitment index and juvenile cod biomass estimates as a predation index. Subsequently, the model has been used by the ICES *Pandalus* Assessment Working Group (ICES, 2001b) to take account of the high levels of shrimp predation by cod and compared with the standard age-based assessment.

Polovina (1989) linked biomass dynamics models for three isolated stocks of Hawaiian slipper lobster and assumed the intrinsic rate of population growth (i.e. biological parameters) was the same, thus enabling a reduction in the number of parameters requiring estimation from very sparse data.

Production models can also be extended to include age structure (e.g. Punt, 1994; Restrepo and Legault, 1998), but ageing problems currently limit application in crustacean stock assessment.

3. Delay-difference models

Delay-difference models extend biomass dynamics models by including biologically meaningful and measurable parameters and considering time delays in the biological processes (Hilborn and Walters, 1992). They differ fundamentally from the aggregate biomass function of biomass dynamics models by

explicitly modelling age-structured dynamics and the lag between spawning and recruitment, but by making simplifying assumptions regarding growth, survival, fecundity and selectivity they avoid the complexity of formal age-, size- or stage-structured models. Key assumptions are that fish recruit to the fishery and spawning stock at the same age, have the same natural mortality rate and all exploited fish are fully vulnerable to fishing.

Minimum data requirements for estimating delay-difference model parameters include time-series of catch and relative or absolute abundance. Other additional biological information, exploitation rates or recruitment indices may be included as data or modelled. Parameter confounding is common and successful estimation requires auxiliary information on growth, natural mortality and/or the form of the stock recruitment relationship. It is then possible to obtain estimates for the remaining parameters with reasonably small standard errors and correlations (Quinn and Collie, 1990).

The models were developed initially by Deriso (1980) and elaborated by Schnute (1985, 1987), Kimura et al. (1984), Kimura (1985), Fogarty and Murawski (1986) and Fournier and Doonan (1987), the latter adopting a Bayesian approach to allow the inclusion of prior knowledge. Early derivations assumed growth was linear and dependent on the mean weight of the previous age, but Horbowy (1992) presented three models which, depending on the growth functions used, corresponded to von Bertalanffy, Brody or logistic growth models (Quinn and Deriso, 1999). Schnute (1985) and Fournier and Doonan (1987) recommend use of a 3-parameter stock recruit relationship (SRR) with a shape parameter (Deriso, 1980), but Hilborn and Walters (1992) suggest that there is little gain from this and recommend using Ricker or Beverton and Holt SRR models. In common with biomass dynamics models, delay-difference models permit estimation of the MSY family of reference points, unexploited biomass and F_{crash} which, although sensitive to model choices, provide an indication of relative stock status and a framework for management.

The delay-difference population dynamics can be expressed by the following two equations in terms of biomass and numbers:

$$B_t = s_{t-1}\alpha N_{t-1} + s_{t-1}\rho B_{t-1} + \mathrm{Wt}_{\mathrm{Recruit\,age}} R_t \qquad (6)$$

$$N_t = s_{t-1} N_{t-1} + R_t \qquad (7)$$

where B is the biomass, N the population number, R the recruitment, $\mathrm{Wt}_{\mathrm{Recruit\,age}}$ the weight at age of recruitment and t an index of time. α and ρ are parameters of the growth equation:

$$\mathrm{Wt}_{\mathrm{age}} = \alpha + \rho\,\mathrm{Wt}_{\mathrm{age}-1} \qquad (8)$$

Survival rate (s) is the product of a constant natural survival rate (φ), which is neither time nor stock size dependent, and a time varying survival rate due to harvesting ($1 - h_t$), where h_t is the annual harvest rate:

$$s_t = \varphi(1 - h_t) \qquad (9)$$

Various fitting methods have been suggested (Deriso, 1980; Schnute, 1985; Fournier and Doonan, 1987; Jacobsen et al., 1987; Walters, 1987; Kimura et al., 1996; Meyer and Millar, 1999a,b); including non-linear least squares minimisation, Kalman filtering and Bayesian approaches. Quinn and Deriso (1999) note that simple estimation procedures are often unsuccessful and describe Monte Carlo Markov Chain (MCMC) and Kalman filter methods for combined error model fitting. Moguel and Lara (1998) used a Bayesian framework to compare a range of models including a delay-difference model for *Panulirus argus* stock assessment.

Simulation studies based on delay-difference models permit a structured insight into the responses to perturbation or the effects of particular biological processes. They are relatively easy to implement and provide a good framework for dynamic analysis of management measures and an aide to understanding of age structure and temporal effects under non-equilibrium conditions (e.g. Tyler et al., 1985; Hall, 1997; Fogarty, 1998; Walters et al., 2000).

However, where data are relatively scarce, delay-difference models offer little or no advantage over biomass dynamics models for parameter estimation because of their demands for extra information, and may result in multiple solutions or spuriously good fits. Punt and Hilborn (1996) suggest that age-structured dynamic models are less restrictive and preferable to delay-difference models if more complex models than biomass dynamics models are required.

4. Depletion methods

4.1. Closed system depletion models

Depletion methods provide a useful means of stock assessment when data are scarce. They examine how measured removals of fish (catch) influence the relative abundance of remaining fish, the latter being estimated by an abundance index, often catch rate (CPUE) normally considered proportional to population size. With a closed population, no recruitment or natural mortality, the problem equates to predicting how large a cumulative removal is required for abundance index to reduce to 0. Closed system depletion methods provide a snapshot of population abundance or other stock parameters without insight into the stock dynamics over time and, therefore, do not permit estimation of biological reference points. The exception to this is if they are used to estimate biomass in a fishery's early development phase, when the biomass estimate may be used as an approximation to the unexploited biomass reference point.

The classical depletion methods are attributed to Leslie and Davis (1939), DeLury (1947); other works include Moran (1951) and Zippin (1956, 1958) and earlier works by Helland (1913–1914) and Hjort et al. (1933). The simplest depletion estimator consists of dividing the fishing period into two halves, assuming the population is closed and that catch rate in each period is proportional to abundance (Seber and Le Cren, 1967). Catch (rate) in the second fishing period is expected to be lower since abundance was reduced by the catch already taken. The Leslie and Davis estimate uses cumulative catch (K) prior to time t and an abundance index (U), which may be independent of the fishing process:

$$U_t = qN_1 - qK_{t-1} \tag{10}$$

where N_1 is the initial population size and q the catchability coefficient.

The DeLury method assumes all fish are equally vulnerable and that fish and fishing effort are randomly distributed. The abundance index (U) is CPUE, measured over short time periods such that population size is proportional to CPUE:

$$U_t = qN_1 \, \mathrm{e}^{-qE_t} \tag{11}$$

where q is the catchability coefficient and E_t the cumulative effort up to time t.

Both the Leslie and Davis, and DeLury models have a linear form and can be fitted graphically or by linear regression (Fig. 2).

Where fishing is intense over a short period of time, depletion methods are powerful tools for estimating initial abundance, although caution regarding catchability assumptions may be appropriate and simulations
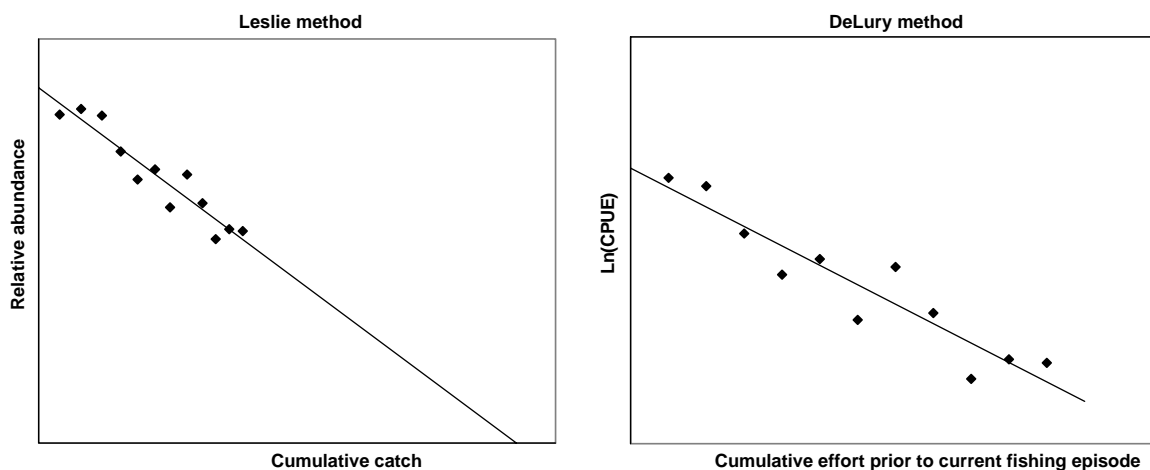

Fig. 2. Graphical illustration of Leslie and DeLury estimators. In both cases catchability is estimated by the slope, but population size is estimated by the intercept on the *x*-axis in the Leslie method and by the formula e^a/b, where a is the slope and b the intercept with the *y*-axis, in the DeLury method.

to estimate reliability are recommended (Hilborn and Walters, 1992). Measurement error in the independent variable (cumulative catch or effort) may cause catchability (q) to be negatively biased and initial stock size overestimated especially for the DeLury model. The Leslie and Davis model is more flexible and robust to this. Ricker (1975) suggests variability in q is probably the greatest source of error, with q a function of population size, declining as the population is depleted. The possibility of some animals not being available to the fishery ($q = 0$) for technical, spatial or behavioural reasons may also cause problems, and variability in q is of particular concern when the methods are applied to crustacea (Miller, 1990). Variability in q biases q upwards because catch is dominated by more catchable animals and hence population size is biased downwards. The presence of large number of animals with low catchability may be detected by curvature of the depletion regression if at least 10 time periods are used (Hilborn and Walters, 1992). Bias may also occur with depletion models because the same fishing episode is often used to provide cumulative catch and CPUE estimates that are not independent, although maximum likelihood estimation has been used to overcome the problem (Zippin, 1956; Schnute, 1985). Morgan (1974) found DeLury estimates of *Palinurus cygnus* density to be underestimated by 75% when compared with tag-recapture estimates, while Morrissy (1975) found that Leslie estimates of freshwater crayfish were underestimated by between 47 and 61% when compared with counts taken after the pond was drained. Simulation studies have shown large biases in DeLury and Leslie estimates if q was overestimated and moderate biases if q was underestimated (Bratten, 1969; Miller and Mohn, 1989).

The terms removal and index removal (IR) may be used to distinguish between fishery derived and independent catch rates. IR (and change in ratio (CIR), see below) methods (e.g. Petrides, 1949; Seber, 1982; Routledge, 1989; Pollock and Hoenig, 1998) are common in wildlife literature but have received less attention in fish stock assessment. Chen et al. (1998) developed formulae for estimating variance and bias in population estimates and related parameters. Simulation studies showed paired sample design, i.e. using the same sample stations for each survey, performed better than random samples and always produced feasible estimates with minimal bias and small standard

error. Chen et al. (1998) applied the methods to snow crab in Newfoundland but estimates of population size were rather variable, because catch was a small fraction of the stock and resulted in small changes in catch rate. Frusher et al. (1998) applied IR (and CIR) methods to Tasmanian rock lobster and estimated exploitation rates, consistent with the distribution and effort of the fishing fleet. Bootstrapping sample data showed wide variation around the estimated exploitation rates, attributed to the non-random distribution of lobsters. They recommended that the methods should be restricted to fisheries with high exploitation rate and relatively uniform size composition over the survey area.

4.2. Change in ratio

The CIR rationale (Kelker, 1940; Paulik and Robson, 1969) has been applied primarily in mark recapture analyses, but the method is included here since CIR and IR are often used together (e.g. Dawe et al., 1993; Chen et al., 1998; Frusher et al., 1998) and CIR has similarities with depletion methods. The method works by dividing the population into two distinct components and observing the change in their ratio following a known removal of animals. Formally, the model is expressed by the following equations:

$$N_{xy} = \frac{R_x - P_2 R_{xy}}{P_1 - P_2} \tag{12}$$

and

$$N_x = P_1 N_{xy} \tag{13}$$

where N_{xy} is the initial population estimate for both x and y components, R_x the number of x type animals removed, R_{xy} the total number of animals removed, P_1 the proportion of x type in the initial survey and P_2 the proportion of x type in the subsequent survey.

Eberhardt (1982) and Dawe et al. (1993) recognised the importance of replicate CPUE samples for estimation of empirical variances of the component proportions. The population is assumed closed or factors affecting the population (migration, natural mortality, etc.) are assumed to apply equally to the two components. Relative catchability of the two components is assumed to be constant, although actual catchability can change between episodes. The method has recently been applied to a range of crustacean stocks,

including *Homarus americanus* (Comeau and Mallet, 2001), *Pandalus platyceros* (Bishop et al., 2000) and *Chionoecetes opilio* (Dawe et al., 1993; Chen et al., 1998).

4.3. Open system depletion models

As depletion models have been generalised to open systems by making assumptions regarding stock dynamics (Allen, 1966; Chapman, 1974; Sainsbury, 1982), they have become similar to production models. The models have been further developed to include stage- and age-structure (Collie and Sissenwine, 1983). The two stage model of Collie and Sissenwine, often referred to as catch survey analysis (CSA or C–S analysis) has been widely used for crustacean assessment (e.g. Conser, 1991; Kruse and Collie, 1991; Conser and Idoine, 1992; Collie and Kruse, 1998; Cadrin, 2000) often using indices for undersized and legal sized animals. Data needs for CSA are catch data, survey abundance indices, covering both pre-recruits and exploited ages, and an estimate or assumption of natural mortality. The model, assuming catch is taken in mid-year, can be summarised by the equation:

$$N_{t+1} = [(N_t + R_t)\, \mathrm{e}^{-0.5M} - C_t]\, \mathrm{e}^{-0.5M} \qquad (14)$$

where N is the population number, R the recruitment, C the catch, t an index of time and M the natural mortality rate. The relationships between abundance indices and population and recruitment numbers are

$$n_t = q_n N_t \quad \text{and} \quad r_t = q_r R_t \qquad (15)$$

where n is the abundance index for adults, r the abundance index for recruits, q_n the catchability coefficient for adults and q_r the catchability of recruits.

The model of Collie and Sissenwine (1983) smoothed the abundance index and used a Kalman filter (Kalman, 1960) to partition error into observation error and process error. Catchability was overestimated if catch was assumed to be taken at the start of the year, but a model analogous to Pope's cohort analysis approximation (Pope, 1972) was considered adequate if catch occurred evenly through the year. Catchability was also sensitive to natural mortality; underestimating natural mortality caused overestimates of catchability and vice versa. Collie and Kruse

(1998) tested a modified version of CSA using simulated data and for realistic levels of measurement and process error, bias in abundance estimates was <5%. Some recent applications have used non-linear minimisation assuming observation error rather than the Kalman filter approach advocated by Collie and Sissenwine (1983).

Cadrin (2000) carried out a comparative study on Gulf of Maine shrimp, *P. borealis*, using stage-based CSA and the ASPIC biomass dynamics model by simulating catch and survey data with a range of coefficients of variation (CVs). CSA performed well when CVs were low (<10%) but broke down as CVs increased, and was unreliable when CVs exceeded 40%. ASPIC performed less well, with frequent convergence problems even for moderate CVs (>20%) on input data. Performance was best if the input data had a wide range of contrast. The CSA process equation may be robust to different population dynamics, but CSA is sensitive to incorrect model assumptions (e.g. natural mortality, length selectivity of the fishery, relative survey catchability of pre- and post-recruits) when applied to American lobster (Conser and Idoine, 1992) and king crab (Collie and Kruse, 1998) fisheries. Correct definition of the pre-recruit and fully recruited size classes is very important.

Age-structured depletion analysis is essentially a series of depletion experiments, each on an individual cohort and providing information on catchability, which can be compared across cohorts present at the same time and should therefore permit better estimation than aggregate models. However, problems in ageing Crustacea limit its application at present.

5. Equilibrium length-based methods

5.1. Jones length cohort analysis (LCA) and length-based linearised catch curve analysis

Length-based cohort analysis (Jones, 1981, 1984) produces estimates of abundance and fishing mortality at length given growth parameters, assumptions regarding natural mortality and a catch length frequency distribution from a population assumed to be at equilibrium. The duration of time spent in each length class is calculated using the growth parameters.

Estimates of the population number entering each length class are made either by Pope's cohort analysis approximation or by numerically solving the catch equation (Sparre et al., 1989). The process continues recursively estimating fishing mortality and number backwards along the 'pseudo-cohort'. The model can be summarised using the catch equations modified to take account of the time spent in each length class:

$$N_{l+1} = N_l\,e^{-(F+M)\,\delta t} \tag{16}$$

and

$$C_l = N_l\frac{F}{F+M}(1 - e^{-(F+M)\,\delta t}) \tag{17}$$

or using Pope's mid-year approximation:

$$N_l = (N_{l+1}\,e^{(M/2)\,\delta t} + C_l)\,e^{(M/2)\,\delta t} \tag{18}$$

where N is the population numbers, F the fishing mortality, M the natural mortality, l an index indicating length class and δt the time spent in a length class, given after manipulation of the von Bertalanffy growth equation by:

$$\delta t = \frac{1}{K}\ln\left(\frac{L_\infty - L_1}{L_\infty - L_2}\right) \tag{19}$$

where L_1 and L_2 are the upper and lower limits of the length class, L_∞ the asymptotic length of a fish and K the growth parameter determining how rapidly fish approach the asymptotic length.

LCA builds on linearised length-based catch curve analyses (van Sickle, 1977; Jones and van Zalinge, 1981; Pauly, 1983a,b, 1984a,b; Sparre et al., 1989), which were modified forms of age-based catch curve analysis (Edser, 1908; Heincke, 1913; Ricker, 1975; Sparre et al., 1989; Hilborn and Walters, 1992; Quinn and Deriso, 1999). In catch curve analysis the relationship between catch and age is linearised over the fully exploited ages in the population, and total mortality (Z), assumed constant over these ages, is estimated by linear regression. Catch curve analysis can be carried out using the proportion of fish in the catch and is therefore applicable for use with survey data, whereas VPA methods require the total catch, which is assumed to be measured without error, as input. Catch curves provide an estimate of constant total mortality with confidence intervals, whereas by assuming M

is known and accounting for all the catch, LCA provides deterministic estimates of both population numbers and fishing mortality at length. Bannister (1986) compared estimates of fishing mortality obtained using LCA and catch curve analysis for lobsters in different regions of the UK.

Hilborn and Walters (1992) note that the equilibrium assumption is critical and results can be misleading unless the stock is in equilibrium, or at least recruitment and exploitation rates have been stable without trend. They suggest that the method is a poor alternative to age-structured virtual population analysis (VPA), a view shared by Lai and Gallucci (1988). Nevertheless, LCA has been and still is quite widely used (e.g. Bannister and Addison, 1986; Addison and Bennett, 1992; Cadrin and Estrella, 1996; Garcia-Rodriguez and Esteban, 1999; ICES, 2001a) because, in conjunction with Thompson and Bell (1934), or length-based yield per recruit analyses it provides a framework for management evaluation in species where age-based data are unavailable.

5.2. Yield, spawner and egg per recruit models

Yield, spawning stock biomass (SSB) and egg per recruit models are not strictly assessment models but provide a framework for evaluation of management measures. They were developed as an age-based method, but have been generalised to use size-structured data and are commonly used following LCA. Data requirements for yield per recruit analysis are size-specific weight, natural mortality and exploitation pattern, whereas maturity and fecundity by size are additionally required for SSB and egg per recruit analyses. The yield per recruit model (Beverton and Holt, 1957) works by assuming an arbitrary number of recruits and projecting them forward based on fishing and natural mortality to estimate numbers in each size class during the lifetime of the cohort. Numbers are subsequently divided by the number of recruits to obtain the 'per recruit' estimates. Weight, proportion mature and fecundity by size are applied to estimate yield, SSB or number of eggs by size class, which are summed over all classes. Per recruit models are extensively used in crustacean fisheries (Bannister and Addison, 1986; Ebert and Ford, 1986; Fogarty and Idoine, 1986, 1988; Hobday and Ryan, 1997; Mohan, 1997; Pitcher et al., 1997). The length-based

yield per recruit model may be summarised as:

$$YPR = \sum_{l=\text{First length}}^{\text{Last length}} e^{-\sum_{i=\text{First length}}^{l-1}(F_i+M_i)\,\delta t_i} Wt_l$$

$$\times \frac{F_l}{F_l + M_l}(1 - e^{-(F_l+M_l)\,\delta t_l}) + YPR_{PG} \quad (20)$$

where F is the fishing mortality, M the natural mortality, Wt the average weight for a length class, l an index indicating length class and δt the time spent in a length class. The yield in the plus group (YPR_{PG}) may be treated simplistically since δt tends to infinity and all fish will die before reaching L_∞. However, if the final length class is far below L_∞ this will lead to under estimation of the yield in this length class.

Fogarty and Murawski (1986) listed four central assumptions: growth and natural mortality rates are unrelated to stock density; constant recruitment; fishing mortality is distributed over the entire exploitable stock; population dynamic processes can be integrated over a series of annual cycles to provide a cumulative evaluation of the yield potential of cohorts. They noted that these assumptions are clearly deficient for a variety of invertebrate stocks and that accounting for probabilistic annual moulting frequency and discontinuous growth of crustacea in the growth function is a major requirement for more realistic yield models. They extended yield per recruit models incorporating density dependent growth, or moult probability and increment, for surf clam and American lobster, respectively.

Per recruit models assume equilibrium, indicating long term changes in yield, SSB or egg production, but short to medium term consequences are not explained. They are straightforward computationally and useful in judging the impacts of changes in size limits and fishing mortalities on yield and egg production (Hilborn, 1997). As recruitment is assumed constant, only information regarding growth over-fishing is provided; the effects of stock density on recruitment are not taken into account. Combining per recruit analysis with a versatile stock recruitment function allows comparison under different characteristic stock recruitment assumptions (Shepherd, 1982b; Bannister and Addison, 1986; Addison and Bennett, 1992).

Reference points commonly estimated include fishing mortality corresponding to the maximum of the yield per recruit curve (F_{max}), fishing mortality where the slope of the yield per recruit curve is 0.1 times the slope at the origin of the curve ($F_{0.1}$), the unexploited SSB per recruit (virgin SPR) and fishing mortalities corresponding to various percentages of virgin SPR (e.g. $F_{35\% \text{ SPR}}$). If historic stock recruit data are combined with spawner per recruit analysis then further reference points may be estimated including F_{low}, F_{med} and F_{high}, which represent the fishing mortality corresponding to the 10th, 50th and 90th percentiles of the reciprocal of historic recruitment/SSB ratios transformed to F using the spawner per recruit function. Fitting a stock recruitment relationship and combining it with per recruit models allows estimation of the MSY family of reference points, unexploited biomass, F_{crash}, or its proxy F_{loss}, the latter utilising a non-parametric smoother connected to the origin by a straight-line when SSB is less than the lowest observed SSB as a stock recruitment relationship. These approaches could be used for crustacea when good stock and recruitment data are available and stock recruitment relationships have been estimated (e.g. Fogarty and Idoine, 1986; Ennis and Fogarty, 1997). Estimation problems may occur in crustacean fisheries, however, due to a long pre-recruit phase in the life cycle and recruitment occurring across several ages/years in some species and a lack of detailed knowledge regarding stock identity and the dispersal dynamics of larvae.

5.3. Dynamic length-, stage-based methods—Leslie matrix models

Dynamic length- and stage-structured models were developed from the age-structured matrix representation of Leslie (1945) and statistical catch-at-age analyses (Doubleday, 1976; Fournier and Archibald, 1982; Deriso et al., 1985; Gudmundsson, 1986, 1994; Kimura, 1989). These were generalised allowing the model to be framed in classes representing size, developmental stage, sex or area (Usher, 1966, 1971; Sainsbury, 1982; Caswell, 1989; Sullivan et al., 1990; Sullivan, 1992). Dynamic size-structured models provide a means of explicitly modelling moult-increment growth processes and have been widely applied recently to assessment of Crustacea and other invertebrates (Bergh and Johnston, 1992; Walters et al., 1993; Punt and Kennedy, 1997; Lai and Bradbury, 1998; Zheng et al., 1995, 1998).

The models have a high degree of biological realism and can be applied to policy and risk evaluation, but are computationally complex and need a high level of technical expertise to develop. Their technical complexity may also result in a lack of transparency to biologists and managers (Hilborn, 1997). They require considerably more data and biological assumptions than most other methods; size frequency data are the basic input, but assumptions regarding biological processes (growth, maturity, natural mortality) require extensive supporting data, and additional assumptions regarding catchability or selection pattern may be required. Population dynamics may be linked to the observed system by minimising differences between modelled and observed abundance indices or size frequency distributions, the latter an alternative to the assumption of constant catchability which is inherent in most assessment methods.

Dynamic length-based models require many assumptions and are specifically tailored to particular species and/or stocks. We provide two examples of such models.

Zheng et al. (1998) estimated abundance of Tanner crab using a probabilistic moult frequency and increment model for growth in separate sex length-based models incorporating shell hardness. Parameters were estimated assuming log-normal observation error and minimising least squares differences between observed and modelled length frequency distributions. The length-based approach incorporated survey, fisheries and tagging data and linked abundance estimates from multiple years through a population dynamics model. Modelling population dynamics filtered survey measurement error resulting in year to year abundance estimates that were less variable than independently considered swept area estimates.

Punt et al. (1997) used tagging experiments and maximum likelihood to estimate a transition matrix for monthly growth of size disaggregated populations of *Jasus edwardsii*. The matrix represented probabilities that an animal in a particular size class would grow into another size class in the model time step. These data were used in a dynamic length-structured model, within a Bayesian framework utilising the Metropolis algorithm (Hastings, 1970; Gelman et al., 1995), to estimate recruitment and fishing mortality parameters and for risk analysis of potential management measures (Punt and Kennedy, 1997).

In these two examples of dynamic length-based methods, the common reference points mentioned previously were not estimated. Zheng et al. (1998) primarily considered historic trends in recruitment, whereas Punt and Kennedy (1997) estimated the yield required to maintain biomass at its present level (replacement yield) and compared current egg production with virgin equilibrium egg production. However, given that dynamic length- and stage-structured models can be used to estimate exploitation pattern and historic time-series of biomass and recruitment it may be possible to calculate the standard reference points outlined in the yield, spawner and egg per recruit models section.

6. Age-structured methods

The use of statistical catch-at-age and VPA-based methods for crustacean assessment is limited by problems with ageing, but age-structured methods have been applied to crustacean stocks, e.g. *Nephrops* (ICES, 2001a) and *Pandalus* (ICES, 2001b).

Catch-at-length data can be converted to catch-at-age data using knife edged length slicing (ICES, 2001a) prior to assessment. Age-structured methods can then be applied including VPA (Gulland, 1965; Pope, 1972; Hilborn and Walters, 1992; Darby and Flatman, 1994), separable VPA (Pope, 1977, 1979; Pope and Shepherd, 1982; Shepherd and Stevens, 1983; Darby and Flatman, 1994), extended survivors' analysis (XSA) (Shepherd, 1992; Darby and Flatman, 1994), the adaptive framework (ADAPT) (Parrick, 1985; Gavaris, 1988; Conser and Powers, 1989; Conser, 1993) and integrated catch analysis (ICA) (Patterson and Melvin, 1996; Patterson, 1999). VPA-based methods, assume catch data are measured without error and as length slicing may introduce error and/or reduce contrast between ages and years, age-structured methods are not widely applied to longer lived crustacean species.

Catch-at-age-based methods can be used to estimate reference points as discussed in the yield, spawner and egg per recruit models section.

Numerous statistical catch-at-age and VPA-based methods are described in the literature. Hilborn and Walters (1992) and Quinn and Deriso (1999) provide many relevant references.

7. Consideration of uncertainty

Uncertainty is inherent in all forms of stock assessment and has a variety of causes and effects. Uncertainty may be due to measurement (observation) error or process error caused by random effects around the deterministic value. It may consist of random noise or it may have systematic pattern. Further error, often bias, may be introduced into the assessment process by model mis-specification. Uncertainty in results (estimated parameters and summary statistics) may be considered in terms of the distributions of the results, which encompasses the expected value, dispersion and bias, or in terms of the sensitivity of results to the input data, models and assumptions. It is important to consider not only the confidence intervals for the statistic of interest, but also the drivers for the result. A further consideration is interaction between parameters formally expressed in terms of covariance. Fortunately, many methods estimating dispersion metrics of parameters will also provide information regarding covariance.

Patterson et al. (2001) considered three approaches for considering uncertainty: frequentist, Bayesian and likelihood.

Frequentist approaches assume that parameters are exact and confidence intervals are derived from multiple analyses of the distribution of the data. Frequentist approaches do not offer a cohesive approach to the incorporation of prior information, but do offer non-parametric techniques and thus relaxation of assumptions regarding error distributions. Bias resulting from estimation is admitted and techniques to adjust for it have been developed.

Bayesian methods, on the other hand, consider parameters to have a (posterior) probability distribution, dependent on the prior probability distribution and the likelihood of the parameter given the data. The posterior distribution of a parameter in a Bayesian analysis is integrated over all possible values of the other parameters. Prior probability distributions provide a formal method for inclusion of knowledge from other sources and are formally distinguished from data, but specification of prior distributions is not trivial, results may be sensitive to the assumed prior distributions and the methods are computationally intense. Non-parametric analogues of Bayesian

techniques are not available, and methods to deal with bias have not been investigated.

Likelihood methods formally describe the probability of alternative model parameters given the data and are conceptually attractive. The probability distribution of the parameter of interest is conditioned on the maximum likelihood values of the other parameters. Likelihood methods become complex if interest parameters are not formal model parameters (e.g. variances or transformations) and as the number of parameters increases. This tends to restrict the approach to simpler fisheries models. Non-parametric approaches are not available.

Fig. 3 presents a variety of methods for evaluating uncertainty in stock assessment and projection. The text below elucidates; numbers in parentheses refer to Fig. 3.

Bayesian (1) or likelihood (2) frameworks formally express parameters in terms of their probability distribution given the data and uncertainty in the data is not acknowledged. Punt and Kennedy (1997) provide an example of a length-structured assessment for rock lobster utilising a Bayesian framework.

What follows is primarily a frequentist approach in which the methods are grouped into four broad categories of uncertainty: sampling variability, differences between modelled and observed data, model performance and sensitivity analyses.

7.1. Sampling variability

If data consist of multiple samples (or can provide replicate estimates by assuming a parameter is constant over time), then by making assumptions regarding error distributions, analytical estimates of uncertainty (3) can be produced (e.g. population estimates of snow crab from CIR methods (Chen et al., 1998) or standard error of survivors estimates from XSA (Darby and Flatman, 1994)). Alternatively, random draws (with replacement) and recombination of the samples can be used to generate multiple datasets and subsequently an empirical estimate of parameter distribution (4). We refer to this method as a non-parametric bootstrap of the data. It has the advantage that no assumptions need to be made regarding the distribution of the data, which are considered to be representative of the population. Frusher et al. (1998) used this technique to evaluate CIR and IR assessment
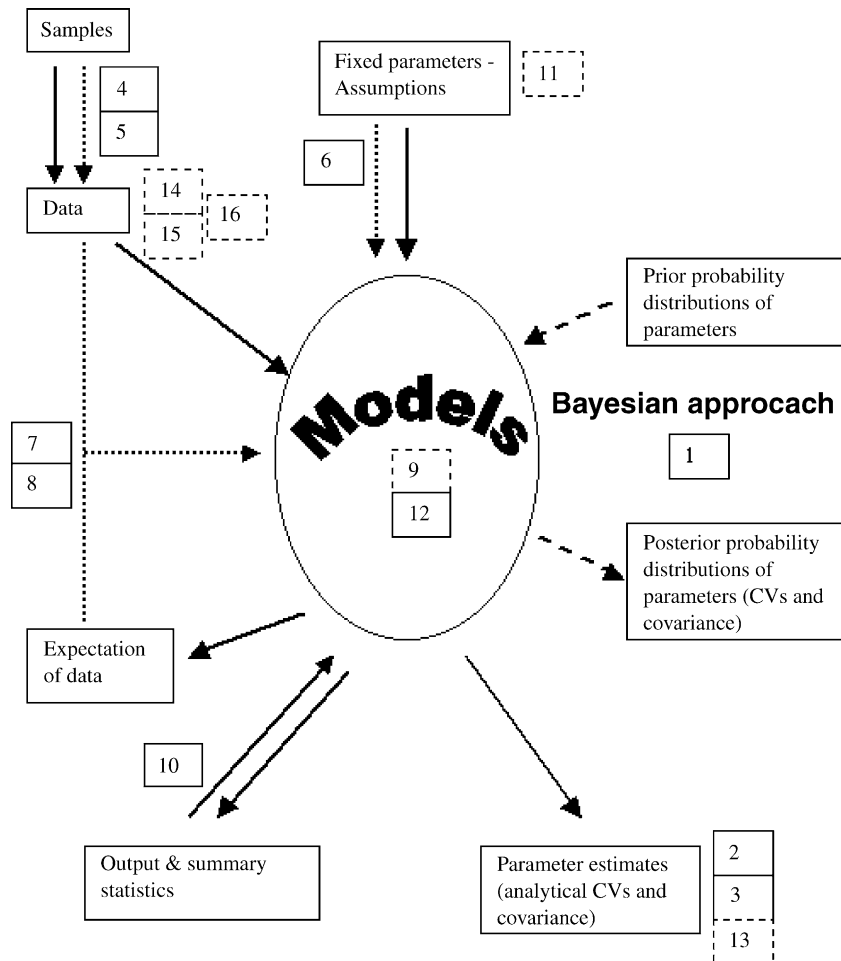
Fig. 3. Schematic representation of methods for evaluation of uncertainty in stock assessment and projection. Dashed lines indicate stochastic processes, and dashed boxes indicate sensitivity analyses: (1) Bayesian estimation of posterior probability distributions; (2) likelihood profiling; (3) analytical variance and covariance estimates; (4) non-parametric bootstrap of the data; (5) parametric bootstrap of the data; (6) Monte Carlo simulation of assumed input parameters; (7) non-parametric bootstrap of the model fit; (8) parametric bootstrap of model fit; (9) model testing on simulated systems; (10) scenario modelling with feedback; (11) sensitivity to range of discrete input parameters; (12) stochastic modelling of trends in parameters (e.g. random walks); (13) analytical calculation of derivatives; (14) numerical estimation of derivatives (perturbation analysis); (15) jack-knife of data points and (16) retrospective analyses.

of lobsters in Tasmania. For a parametric bootstrap of the data, the input data are modelled parametrically using the mean and variance of the samples and an assumption regarding the distribution of the data. Random deviates drawn from this distribution provide the multiple datasets required for estimation of a distribution for the parameter of interest (5).

Even if data are not available (or not directly used) it may still be possible to make some informed deci-sion about the level and distribution of an input pa-rameter and by generating random deviates of the in-put parameter estimate a distribution for statistic of interest (6). This type of approach might be used to investigate the effects of variability in natural mortal-ity. When the deviate is based on assumption we refer to the method as a Monte Carlo simulation, but if the deviate is based on modelled data it would be termed a parametric bootstrap of the data (5).

7.2. Differences between modelled and observed data

An alternative method is to generate an expectation of data from the fitted assessment model and bootstrap (Efron, 1981, 1982, 1985, 1987) differences between the observations and the expected data to provide multiple datasets. As when bootstrapping the data, the residual bootstrap could be non-parametric (7) where randomly redrawn residuals between observed and expected data were reapplied to the expected value. Alternatively, the expected data could be modelled parametrically with an assumed error distribution and random deviates sampled from this distribution to provide the multiple datasets, a parametric bootstrap of the model (8). Methods (4) and (5) were dependent only on the data or assumptions regarding them, but methods (7) and (8) incorporate assumptions regarding the stock or fishery dynamics to model the expectation of the data. Methods (7) and (8) can be used assuming either process error where the modelled data are considered to be stochastic and the observed data measured without error, or assuming observation error, in which case the modelled data are considered deterministic and the observed data stochastic.

7.3. Model performance

Simulating the biological system allows the performance of different assessment methods to be evaluated dependent upon the assumptions of the simulation model (9). Chen et al. (1998) evaluated CIR and IR estimators using paired and random sampling designs to sample from a simulated system, while Cadrin (2000) generated replicate sets of abundance and biomass indices, based on a recent shrimp assessment with differing levels of log-normally distributed measurement error, to compare the performance of CSA and biomass dynamics models. Building on this technique leads to scenario models (10), which combine stochastic system models (stock dynamics, fishery) and models of the management process (sampling, assessment, regulation) that feed back into the system model with explicit time structure. Scenario models allow comparative evaluation of management strategies within an experimental framework, which also allows alternative

model choices for robustness testing and may also provide valuable insight into assessment performance and bias.

The methods above have generally produced results that can be expressed in distributional terms. However, for sensitivity or robustness analyses, a series of experiments that evaluate effects of discrete parameter settings (11), or different models, or sub-components of the overall assessment model (9), may be used. Comparison of results over different options might suggest that results are robust to various plausible models or parameter values, in which case management can be applied, or sensitive to model/parameter choice, in which case the need for more research in this area is highlighted. As all models are by definition a simplification of the real system, this approach provides comparative information on the effects of model mis-specification. This type of approach has been used to explore the effects of different hypothetical stock recruitment relationships using a yield per recruit framework (Bannister and Addison, 1986; Addison and Bannister, 1998). Stochastic modelling of trends (12), for example, by using random walks, may be useful for modelling parameters that are thought to be 'more or less' constant, perhaps changing gradually in response to environmental conditions or gradually increasing as a result of technical improvements.

7.4. Sensitivity analyses

Sensitivity of results may be formally stated in terms of derivatives with respect to a particular variable, or a matrix of partial derivatives with respect to input variables, the Jacobian matrix. This gives information on the rate of change of the statistic of interest relative to change in the input variable. Derivatives may be analytically calculated (13), or numerically estimated by perturbation analysis (14), where each data point is sequentially varied and the change in results used to estimate partial derivatives. Barbeau and Caswell (1999) used perturbation analysis to evaluate management scenarios for survival of seeded populations of scallops. Jack-knifing (15) (Efron, 1981, 1982) involves sequentially excluding each data point and re-estimating the results providing estimates of dispersion and the relative influence of each data point. Retrospective analyses (16) were originally developed

to evaluate uncertainty in the final year estimates from VPA-based methods and relied on the convergence properties of VPA. They generally consist of re-running an assessment a number of times using the same model structure and successively removing the final year's data, but comparison between successive 'best assessments' employing slightly different model structures may also take place. Retrospective analysis provides an evaluation of the sensitivity of results to the time-series of data and can reveal bias and skew in terminal estimates (Sinclair et al., 1990; Cadrin and Vaughan, 1997; Mohn, 1999). Retrospective analyses can been applied to any methods utilising time-series of data, including biomass dynamics models and CSA (e.g. ICES, 2002). They provide a valuable tool for identifying model mis-specifications and/or inconsistency in estimates of catchability.

In summary, existing methods provide a flexible array of tools to investigate the sources and outcomes of uncertainty. However, their use and statements regarding uncertainty must be considered carefully. Simulation envelopes derived by bootstrap or Monte Carlo simulation depend on assumptions and may not represent the true confidence intervals. Stochastic processes may have been omitted and the simulation envelope underestimates true variability, or conversely co-varying variables may have been modelled independently resulting in overestimation of variability. No method can make up for poor data, the adage 'garbage in, garbage out' being particularly relevant because better sampling is likely to both reduce uncertainty and provide better quantification of it. Similarly, no method can overcome the issue of conflicting sources of data. The best approach may be to conduct separate analyses and present the alternatives to decision makers (Richards, 1991; Schnute and Hilborn, 1993).

Patterson et al. (1999) concluded that stock assessments and management forecasts depend on the principal assumptions underlying the structural model (e.g. whether or not catch is assumed to be exact), time-dependence in catchability, modelling of natural mortality, recruitment, and growth, and the basis for probability inference (Bayesian, bootstrap, etc.). Choice of assumptions depended on a variety of factors including the purpose of the analysis, the institutional framework for method development and usage, and availability and customary usage of software tools. No particular consensus appeared to

exist among fisheries scientists as to the most appropriate choices, and implications of different approaches were rarely examined. Despite much recent progress in method development, the extent to which probability distributions, estimated for management purposes, adequately represent the probabilities of eventual real outcomes is largely unknown and therefore statements regarding the probability of outcomes should be couched in relative rather than absolute terms.

8. Concluding remarks

In this paper, we have summarised a range of stock assessment methods that are available to the crustacean biologist, and reviewed techniques that are currently available to evaluate uncertainty in the whole assessment process. We conclude by suggesting a number of ways in which crustacean stock assessment methodology may develop in the future.

8.1. Dealing with uncertainty

Perhaps, most importantly, rapid development of computer technology means that previously computationally prohibitive methods are becoming common. This trend seems set to continue and will promote routine use of complex and stochastic models such as Bayesian analyses or spatially structured models. However, current practise still leaves room for improvement. Elements of the assessment process are often fragmented, outputs from one analysis providing input to the next, and whereas variance may sometimes be accounted for, covariance is usually ignored. There is, therefore, scope for development of integrated packages encompassing the complete assessment and projection process and retaining relationships between variables within each stochastic realisation. Evaluation of management strategies for actual stocks, or based on archetypal stock dynamics, may identify robust management regimes and provides useful insight into bias induced by assessment and management process, and application of simulation models to investigate the full management process seems set to expand. Managers are now accustomed to probability statements attached to metrics of interest in the decision making process and development and

refinement of methodologies to produce these is set to continue.

8.2. Model choice and comparison of performance

Any assessment or management evaluation must make assumptions and use simplified models of the true system. There is a trade off between the number of parameters to be estimated and assumptions made for simple and complex models. Comparative studies have demonstrated that simpler methods may sometimes perform as well as, or better than, complex models (Richards and Schnute, 1998). Simple models that retain biological realism should not be overlooked because generally they are more transparent than complex methods and likely to produce robust conclusions. Punt and Hilborn (1997) recommended Bayesian methods for decision analysis, but also emphasised the need to apply a number of alternative methods, noting that results that are robust to model choice will carry more weight.

8.3. More biologically realistic models

Most of the models described in this paper were developed as tools for assessing fin fish stocks, and may not be entirely appropriate for use in crustacean stock assessment. We foresee future developments in crustacean-specific models that incorporate aspects of crustacean biology such as stepwise growth more explicitly, or that allow variable or explicitly modelled trends in catchability. A major problem with most stock assessment methods is that they are age- rather than size-based, and the current inability to routinely age crustaceans limits the range of assessment models that can be used. However, recent advances have been made in techniques for ageing crustaceans (Sheehy et al., 1995, 1998, 1999; Ju et al., 2001) which, provided they can be developed sufficiently to allow routine ageing, promise to open up a wide range of assessment models.

The second major area of development in crustacean stock assessment models that is likely in the near future is the explicit modelling of spatial structure of crustacean populations. Spatial structure can be incorporated at two scales. In crustacean species, larvae dispersal between geographically defined stocks may suggest a metapopulation modelling approach where several sub-populations are linked by dispersal (Hanski, 1999), an approach applied for example, by Fogarty (1998) for *H. americanus*, and by Botsford et al. (1998) for *Cancer magister*. Spatial structure may also be incorporated by considering the spatial distribution of individuals within a sub-population and the consequent spatial distribution of the fishing effort that targets those individuals (Caddy and Seijo, 1998; Orensanz et al., 1998).

8.4. Independent parameter estimation

Finally, no amount of bootstrapping will get round the "garbage in, garbage out" problem. Ultimately, the quality of advice must depend on the quality of the underlying data. Sensitivity analyses can show where results are robust to model or data deficiencies and help to direct resources towards improving those areas lacking in knowledge. Fishery-independent methods have an important role in stock assessment for the provision of management advice and also by providing independent estimates for some parameters in stock assessment models and 'ground truthing' dynamic models. The development of fishery-independent methods is likely to expand, particularly incorporating technological developments such as remote sensing (e.g. telemetry, thermal/sonic imaging, underwater TV), automated data capture and transmission systems (e.g. satellite imaging and data transmission), and computer-aided analysis tools (e.g. image analysis).

Acknowledgements

Appendix A. Methods, data requirements, advantages and disadvantages

Method	Data requirement	Advantages	Disadvantages	Reference
Biomass dynamics models				
Biomass dynamics models	Time-series of catch and abundance index	Minimal data requirements and assumptions. Framework for management evaluation. Easily extended	Earlier fitting methods made equilibrium assumptions. Need contrast in the data to get meaningful fit. Aggregate dynamics do not provide insight. Unable to address age/size based issues	Graham (1935), Schaefer (1954, 1957), Pella and Tomlinson (1969), Fox (1970), Ricker (1975), Fletcher (1978), Shepherd (1982a), Gulland (1983), Hilborn and Walters (1992), Prager (1994, 1995), Punt and Hilborn (1996), Quinn and Deriso (1999), Cadrin (2000)
Extended modified biomass dynamics models	Time-series of catch, abundance index plus auxiliary data, e.g. recruitment index, predator index, environmental signal, trend in q	Relatively low data requirements and assumptions. Able to address specific issues	Greater data requirement and more assumptions than above	Freon (1988), Hilborn and Walters (1992), Stefánsson et al. (1994), Punt and Hilborn (1996), Quinn and Deriso (1999)
Age/stage structured production models	Aggregate time-series of catch and abundance index. Age-structured data or assumptions for biological parameters (growth, maturity natural mortality) and selection pattern	Age structure taken into account. Flexible framework for evaluation of management and technical measures, without the complexity of fully age-structured methods	More complexity, data requirements and assumptions. Problems with ageing Crustacea	Hilborn (1990), Punt (1994), Punt and Japp (1994), Punt and Hilborn (1996), Restrepo and Legault (1998)
Delay-difference models				
Delay-difference models	Time-series of catch and abundance index. Growth and stock recruitment models. External information on growth, natural mortality, recruitment and form of SRR may be required to avoid parameter confounding	Explicit consideration of age structure in models. More biological realism and temporal structure in the model	Parameter confounding common, unless some parameters fixed or estimated externally. More data requirements and assumptions than biomass dynamics models	Deriso (1980), Schnute (1985), Fogarty and Murawski (1986), Fournier and Doonan (1987), Hilborn and Walters (1992), Quinn and Deriso (1999)
Depletion methods				
Closed system depletion methods—Leslie and Davis, DeLury	Time-series of catch and catch rate (catch/effort) usually taken in a short period of time	Computationally straightforward and with minimal data requirements and simple assumptions	Provides snapshot estimates without account of dynamics. Assumption of closed system limits applicability. Requires frequent surveys in relation to fishing. Fishing intensity must be high	Leslie and Davis (1939), DeLury (1947), Zippin (1956), Seber and Le Cren (1967), Ricker (1975), Hilborn and Walters (1992)
Closed system depletion methods (IR)	Sampled catch rates before and after significant catch	Computationally straightforward with minimal data requirements and assumptions. Dispersion statistics available	As above	Petrides (1949), Eberhardt (1982), Seber (1982), Routledge (1989), Roseberry and Woolfe (1991), Dawe et al. (1993), Chen et al. (1998), Frusher et al. (1998)
CIR	Catch rates by component before and after significant catch by component	Computationally straightforward with minimal data requirements and assumptions. Dispersion statistics available	As above	Kelker (1940), Paulik and Robson (1969), Seber (1982), Pollock (1991), Dawe et al. (1993), Chen (1995), Chen et al. (1998), Frusher (1998), Pollock and Hoenig (1998)
Open system depletion methods (C–S or CSA)	Time-series of catch, abundance index, recruitment index, or age-structured data	Useful for crustaceans as discontinuous growth stages can be accommodated. Error can be partitioned into observation and process by using Kalman filter for fitting	More data and assumptions required for open or age/size-based systems. Sensitive to assumptions of natural mortality, relative catchability and size/age of recruits	Allen (1966), Ricker (1975), Hilborn and Walters (1992), Collie and Sissenwine (1983), Conser (1991), Kruse and Collie (1991), Conser and Idoine (1992), Collie and Kruse (1998), Cadrin (2000)

Appendix A. (*Continued*)

Method	Data requirement	Advantages	Disadvantages	Reference
Equilibrium length-based methods				
LCA/VPA	Length composition, growth model and parameters. Assumed natural mortality rate (M)	Relatively low data requirements. Provides length-based exploitation pattern and basis for evaluation of technical measures. Convergence of population numbers and fishing mortalities if F is high relative to M	Equilibrium assumption may often be violated, which can produce misleading results	Jones (1981, 1984), Lai and Gallucci (1988), Sparre et al. (1989), Hilborn and Walters (1992), Quinn and Deriso (1999)
Yield, spawner and egg per recruit models (YPR)	Selection pattern, natural mortality and weight by age/length. Maturity/fecundity by age/length for spawning biomass/egg per recruit	Computationally straightforward and can be extended to model stock recruitment relationship and density dependent growth under equilibrium assumptions. Provides a framework for evaluation of management measures	Not an assessment method. Cannot account for variability in recruitment and growth. Stock recruitment relation and density dependent growth effects not modelled in basic model. Provides information only on equilibrium conditions, not short-term effects	Beverton and Holt (1957), Gulland (1983), Quinn and Deriso (1999)
Stage-based YPR	Size/stage-based moulting probability and increment or growth rate. Fishing mortality rates	Relatively straightforward computationally. Provides a framework for evaluation of management measures	As above and difficult to get crustacean growth rates	Fogarty and Murawski (1986)
Dynamic size-structured methods				
Dynamic size-, stage-structured models (Leslie matrix models)	Size/stage disaggregated time-series of catch. Abundance indices or selection pattern. Natural mortality and growth rates from external sources or assumed. Stock recruitment relationship or time-series of recruitment	Explicit consideration of stage, size and temporal structure, provides framework for technical measures evaluation. Can model discontinuous growth processes. Good biological and selection pattern data provide an alternative to fitting using catchability model	Many assumptions, high data and technical knowledge requirement. Computationally complex and may lack transparency	Leslie (1945), Usher (1966, 1971), Sainsbury (1982), Rosenberg and Beddington (1988), Getz and Haight (1989), Caswell (1989), Methot (1990), Sullivan et al. (1990), Sullivan (1992), Bergh and Johnston (1992), Walters et al. (1993), Punt and Kennedy (1997), Zheng et al. (1995, 1998), Lai and Bradbury (1998)
Age-structured methods				
VPA/cohort analysis/separable VPA	Time-series of catch-at-age data. Assumed M at age. Terminal population (or F) estimates for VPA/cohort analysis. Selection pattern assumed fixed in separable VPA	Age and time structured estimates of numbers and fishing mortality. Convergence of population numbers and F's at age if F is high relative to M. Provides the basis for evaluation of management and technical measures	High data requirement. Catch-at-age data assumed exact. Assumptions regarding M and terminal numbers may not apply	Gulland (1965), Pope (1972, 1977, 1979), Pope and Shepherd (1982, 1985), Shepherd and Stevens (1983), Hilborn and Walters (1992), Darby and Flatman (1994), Quinn and Deriso (1999)

Tuned VPA (ADAPT, ICA, XSA)	Age-structured time-series of catch and abundance indices (aggregated abundance index may be used by ICA). Assumed values for M at age	Advantages of VPA plus able to include extra data. Explicit age-structured models for many variables. Able to weight and smooth variables	Many assumptions, high data and technical knowledge requirement. Complexity may mask the assessment drivers	Parrick (1985), Gudmundsson (1986), Gavaris (1988), Conser and Powers (1989), Shepherd (1992), Conser (1993), Darby and Flatman (1994), Patterson and Melvin (1996), Patterson (1999)
Statistical catch-at-age analysis	Age-structured time-series of catch and abundance indices. Assumed M at age	Age-structured models and able to include extra data. Statistical consideration of error on variables	Many assumptions, high data and technical knowledge requirement. Parameter confounding may occur if the data do not have contrast	Doubleday (1976), Paloheimo (1980), Fournier and Archibald (1982), Deriso et al. (1985), Gudmundsson (1986, 1994), Kimura (1989), Methot (1990), Hilborn and Walters (1992), Quinn and Deriso (1999)

Appendix B. Some examples of the application of stock assessment methods to crustacean (or other shellfish) stocks

Type	Method	Authors	Genus
Biomass dynamics models	Biomass dynamics	Morgan (1979), Saila et al. (1979), Yoshimoto and Clarke (1993), ICES (1998), Breen and Kendrick (1998), Cadrin (2000)	*Panulirus*, *Cancer*, *Homarus*, *Jasus*, *Pandalus*
Biomass dynamics models	Extended biomass dynamics	Stefánsson et al. (1994)	*Pandalus*
Delay-difference models	Delay-difference models	Fogarty and Murawski (1986), Hall (1997), Moguel and Lara (1998), Fogarty (1998)	*Jasus*, *Homarus*, *Panulirus*
Open system depletion models	Catch survey analysis (C–S or CSA)	Conser (1991), Kruse and Collie (1991), Collie and Kruse (1998), Conser and Idoine (1992), Moriyasu et al. (1998), Cadrin (2000)	*Homarus*, *Paralithodes*, *Chionoecetes*, *Pandalus*
Closed depletion models	Leslie and Davis, DeLury, IR	Morgan (1974), Morrissy (1975), Dawe et al. (1993), Chen et al. (1998), Frusher et al. (1998)	*Palinurus*, *Cherax*, *Chionoecetes*, *Jasus*
Closed depletion models	CIR	Dawe et al. (1993), Chen et al. (1998), Frusher et al. (1998), Bishop et al. (2000), Comeau and Mallet (2001)	*Chionoecetes*, *Jasus*, *Pandalus*, *Homarus*
Equilibrium length-based methods	LCA/LVPA	Addison (1986), Bannister and Addison (1986), Addison and Bennett (1992), Garcia-Rodriguez and Esteban (1999), ICES (2001a)	*Homarus*, *Cancer*, *Aristeus*, *Nephrops*
Yield per recruit analysis	Length-based YPR	Addison (1986), Bannister and Addison (1986), Fogarty and Idoine (1986, 1988), Addison and Bennett (1992), Spedicato et al. (1995), Hobday and Ryan (1997), Mohan (1997)	*Homarus*, *Cancer*, *Aristeus*, *Jasus*, *Panulirus*
Yield per recruit analysis	Stage-based YPR	Fogarty and Murawski (1986)	*Spisula*
Dynamic size-based methods	Dynamic length-based methods	Bergh and Johnston (1992), Starr et al. (1997), Punt and Kennedy (1997), Zheng et al. (1995, 1998), Lai and Bradbury (1998)	*Jasus*, *Paralithodes*, *Chionoecetes* (*Strongylocentrotus*)
Age-based methods	XSA	ICES (2001a,b)	*Nephrops*, *Pandalus*
Age-based methods	VPA, separable VPA	ICES (2001a)	*Nephrops*

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