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A statistical approach to the assessment of coarse fish populations

Science Report: SC030214/SR2

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Author(s):
R.Wyatt, R.Sedgwick and R.Burrough

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Research Contractor:
National Fisheries Technical Team,
Environment Agency
Mance House,
Arthur Drive,
Hoo Farm Industrial Estate,
Worcester Road,
Kidderminster,
Worcs DY11 7RA.
Tel: 01562 534 100 Fax: 01562 534122

Environment Agency's Project Manager:
Steve Axford, York Office

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Steve Killeen

Head of Science

Executive Summary

A statistical modelling approach to the analysis of coarse fish population dynamics is presented. This approach confers many advantages in understanding fish ecology and explaining the interrelationships between the fundamental processes of reproduction, growth and survival. The essential feature of the Population Dynamics Model (PDM) is its holistic or integrated structure, which means that each element of the analysis is performed having taken account of all the others. The outcome is therefore both extremely powerful and statistically efficient.

The PDM is uniquely able to address areas of uncertainty that have cast doubt on the reliability of earlier analytical methods. Inefficient and inconsistent sampling of juvenile fish has frequently led to data being discarded, while the implications of uncertainty in fish ageing as a result of scale reading error are so far-reaching that they permeate many areas of fish ecology. The model is extremely versatile and able to estimate capture efficiency, thereby utilising all the data to assess growth and survival rates. This flexibility also allows unbiased corrections to be made to age assessments and allows un-aged fish to be assigned ages, taking account of all available information.

Comparisons are made with the relative Year Class Strength (YCS) determinations of Frear and Cowx (2003) and reveal significant discrepancies in output. Since validation is an integral and natural component of the statistical modelling process, there is good reason to believe that the PDM results are far closer to the truth. The failure of earlier relative YCS methods to track long-term trends in population status is a particular drawback.

The PDM has wide-ranging application in coarse fish ecology. It is especially useful in the investigation of relationships between population parameters and environmental variables, which are the focus of much current biological research. There are natural links with Geographic Information System (GIS) models, offering the possibility of detailed exploration of the spatial dimensions of fish distribution. Also, specific aspects of environmental impact, such as the effect of endocrine disrupters on coarse fish fecundity, can be examined through simulation experiments.

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1 Introduction

This report describes work undertaken as part of Phase III of the project entitled “Factors Affecting the Recruitment of Riverine Coarse Fish”. It outlines the development and evaluation of a new method for performing population assessments of coarse fish from data obtained during routine electric fishing or netting surveys. The need for this development arose from the results of Phase II of the project (Frear and Cowx, 2003) in which a mechanism for calculating year class strengths (YCS) from single survey data was proposed. Unfortunately, the method, like those before it, is recognised to be sensitive to errors in the assessment of fish age. It is also limited by some of its assumptions and procedures to the extent that there is uncertainty over the accuracy and applicability of the outputs.

The concepts of YCS and recruitment in coarse fish populations have received detailed attention elsewhere (Musk and Britton 2006) but both are poorly defined constructs that can lead to misunderstandings and confusion when they are treated as fundamental biological variables. Relative cohort abundance is likely to change with time so that the observed pattern of YCS has meaning only in relation to the time of sampling. Furthermore, there is increasing evidence that difficulties in determining the true age of a fish from its scales, leading to misreading, can produce widely different patterns of YCS. Consequently the conclusions drawn from attempts to relate these patterns to environmental variables, made in Phase II of the coarse fish recruitment project, must be regarded as extremely tentative. Clearly no such relationships can be established with confidence until there is sufficient verification that YCS estimates represent an accurate reflection of the truth.

The methodology outlined here addresses some of the problems that afflict all fish population assessments, and represents a significant step forward in understanding coarse fish population dynamics. It is not another YCS method, but has a much wider remit. However, there are no radical developments in analytical methodology or software involved, simply the application of modern statistical methods to the analysis of coarse fish population data in a way that does not appear to have been attempted previously. Other areas of biological research, including marine fisheries (Hilborn and Walters, 1992), have been quicker to embrace these methods.

Like many modern statistical analyses, the process involves the construction of a statistical model. In contrast with previous YCS assessments, which have concentrated specifically on calculating cohort abundance, the statistical model addresses the fundamental biological processes of reproduction, growth and survival. Consequently it may be seen more accurately as a population dynamics model (PDM) from which cohort abundance can be derived as one of many possible outputs. In this context, direct comparison with earlier YCS methods is perhaps unrealistic. However, where appropriate,

the advantages gained by adopting the statistical modelling approach are highlighted and then summarised in the conclusions (Section 5.5).

2 Model development

All statistical models are built from data, and the datasets examined for this exercise comprise a time series of length, scale-reading and abundance data for dace and chub from the upper River Stour (Anglian Region). In final form, the model comprises a series of components or sub-models, each addressing a different aspect of the analysis. These sub-models are shown graphically in Figure 2.1, configured as a concentric hierarchy, which serves to illustrate their relationships with each other. The specific objectives of the modelling exercise were to produce statistical estimates of the three primary processes driving the population dynamics of coarse fish (central ellipse, Figure 2.1). Accordingly estimates were required for

1. annual recruitment, expressed as the abundance of 0+ fish
2. annual survival rate
3. annual growth rate.

Secondary components (outer ellipse, Figure 2.1) include factors such as age-selective sampling and scale reading, and other data sources such as removal estimates of abundance. These are included in the modelling process to improve the estimation of the primary population dynamics parameters.

The representation in Figure 2.1 illustrates the various processes involved in the analysis, but it masks an important feature of all such probabilistic models. All of the component sub-models are inextricably linked with each other and information is exchanged simultaneously in all directions. There is no hierarchy, nor any sequential element in the process, which means that all parameter estimates are made synchronously taking into account all the information in the dataset. This integrated and holistic approach is much more efficient and powerful than a sequential or stepwise procedure (such as that proposed in the Frear and Cowx (2003) YCS method), where information is frequently lost or distorted at each step through averaging, clipping, rounding or ignoring sources of error. Furthermore, stepped procedures can rarely take account of interaction effects, whereas the integrated analysis includes the influence of all interactions between all the variables. It is a difficult process to envisage but can be thought of in terms of balancing competing probabilities in order to produce the most likely outcome given all the information available.

The PDM is most accurately viewed as a modelling approach, rather than a single model. There is unlikely to be a single model that is appropriate for all species in all waters. Rather, statistical modelling involves iterative cycles of model fitting, testing, validation and modification for each dataset.

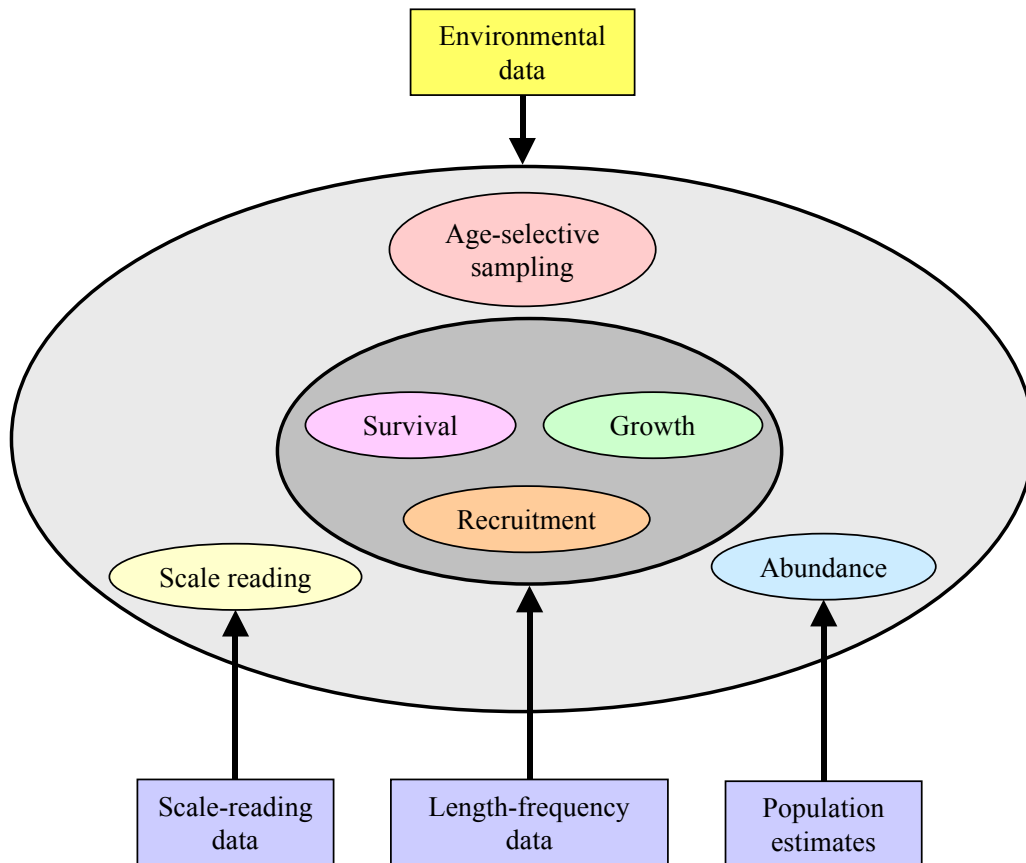


Figure 2.1 Components of the statistical population dynamics model.

The primary population dynamics components of recruitment, survival and growth will be considered in more detail in section 3, and the secondary components that are necessary to compensate for errors and biases in the sampling data are considered in more detail in section 4.

3 Primary model components

3.1 Introduction

The population dynamics 'core' is built around models of 0+ recruitment, survival and growth that track fish abundance and length data through time.

The description of the population dynamics sub-models will be illustrated with data for dace from the Suffolk Stour, collected between 1980 and 2002. There is a general perception amongst anglers that dace have declined in the River Stour, as in many other locations (G. Peirson, personal communication). If so, these changes should be apparent in the survey data, and the PDM may provide clues to the underlying causes.

The perception of poor angling performance is frequently related to a decline or absence of larger and therefore older fish. Their disappearance from the populations has a number of possible origins:

- poor recruitment
- poor survival (chronic)
- poor survival (acute)
- poor growth
- a combination of these factors

Outputs from the recruitment, survival and growth sub-models should help to elucidate the mechanisms for the declines on the Stour.

3.2 Recruitment sub-model

"Recruitment" is here restricted to mean the addition of new individuals to the population measured in terms of numbers of 0+ fish (fish in their first year) at the time of year when the surveys occurred. However, the PDM can also allow recruitment to be expressed at other ages.

Biological interpretation of the estimated recruitment depends on the time of year the surveys were performed. The datasets used here were collected between August and November. Recruitment in this context therefore represents fry surviving at the end of the first summer of life, but no adjustments have been made for the likely differences in survival between August and November.

The recruitment sub-model assumes that annual recruitment varies randomly around a "stock-recruitment" function. A range of stock-recruitment functions can be assumed, from a simple horizontal line (i.e. recruitment is independent of stock), to more realistic functions such as the Beverton-Holt model

(Beverton and Holt, 1957; Figure 3.1). This illustrates the interdependence between the sub-models, since the number of spawners in each year is estimated from the survival model (section 3.3), their length from the growth sub-model (section 3.4), and their fecundity from an external fecundity model (Mann, 1974). There will be considerable uncertainty in the estimated numbers of spawners and 0+ recruits in any year, and for many data sets, there is likely to be little evidence of stock size limiting recruitment (Figure 3.1).

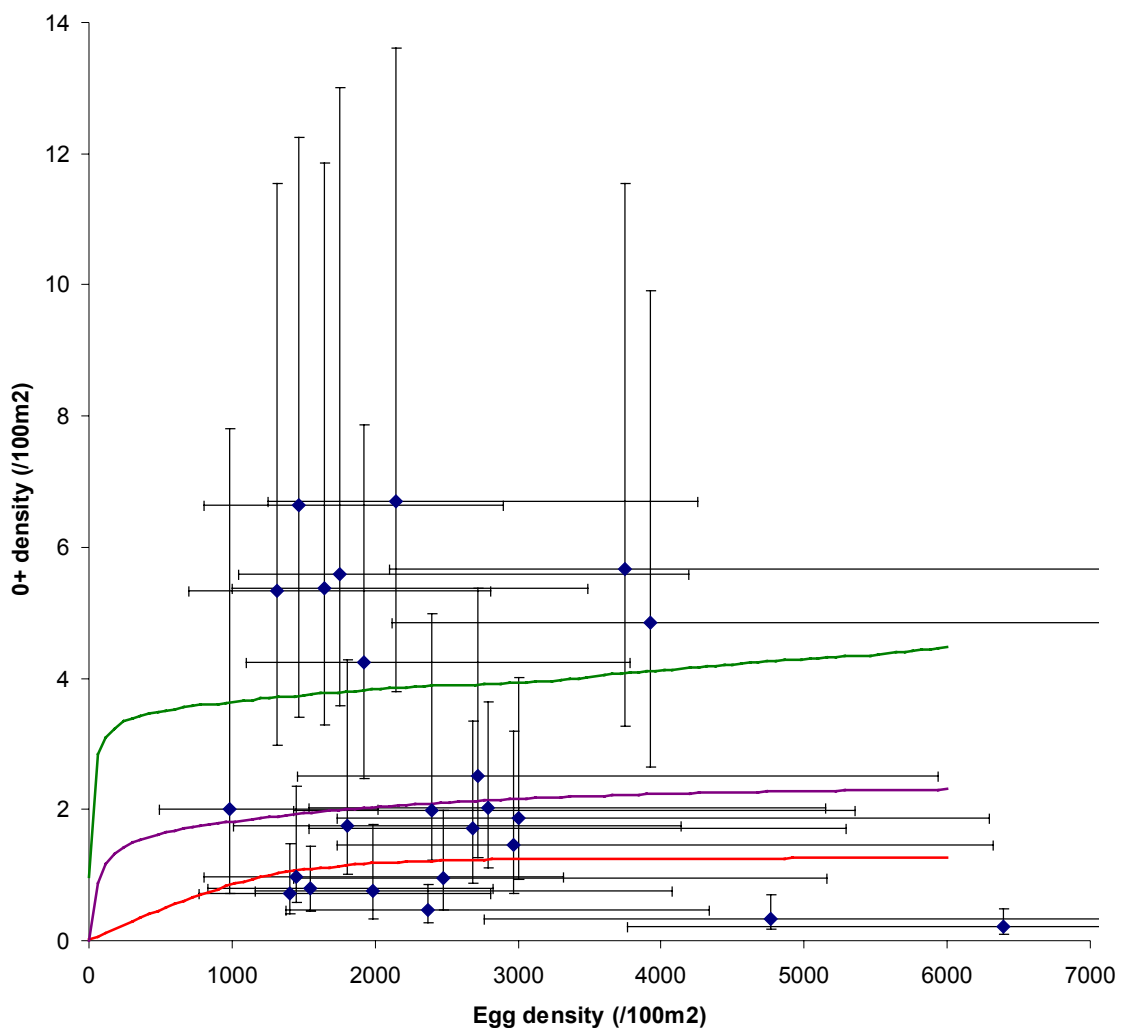


Figure 3.1 Stock-recruitment relationship for dace in the upper Stour. Points show annual estimates (with 95% confidence intervals) and curves denote the underlying relationship (mean with 95% confidence intervals).

When plotted through time, the annual estimates of 0+ recruitment provide the PDM equivalent of arithmetic year class strength indices (Figure 3.2). The abundance of 0+ dace provides evidence of poor recruitment in the early 1980s but thereafter a progressive recovery was evident and this continued into the next decade. Although there were years of poor recruitment, the data do not indicate that this is the root cause of the problem.

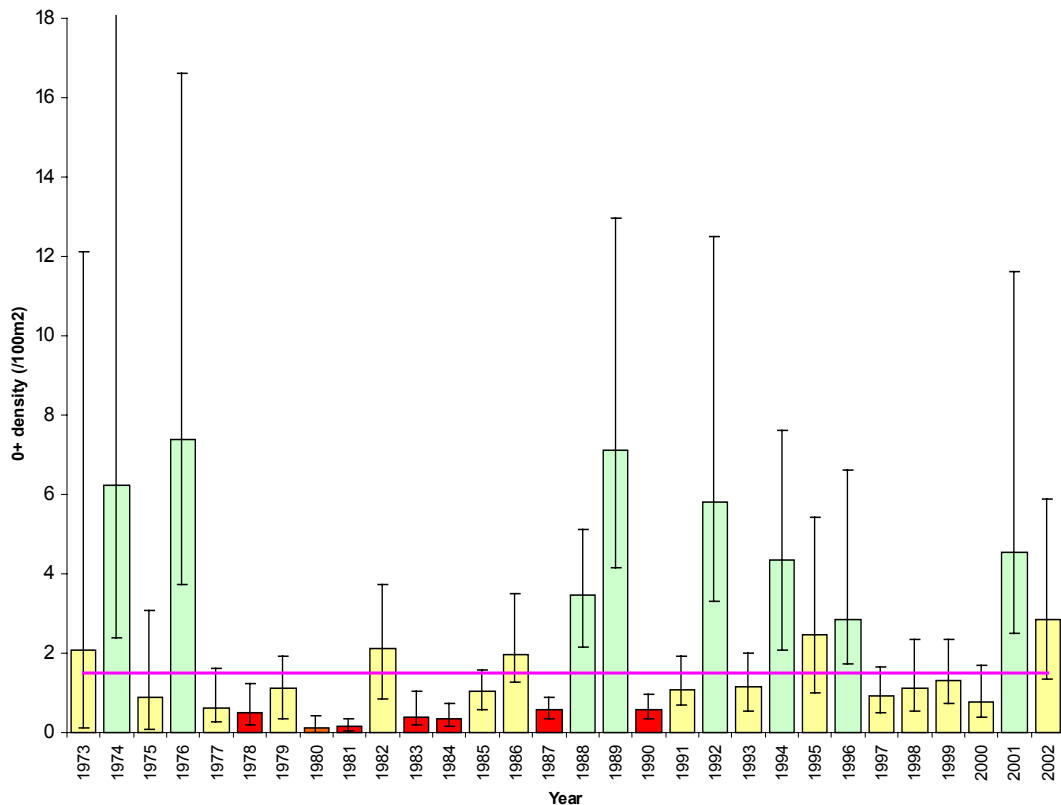


Figure 3.2 Annual recruitment of 0+ dace in the upper Stour. Vertical lines give 95% confidence intervals, and bars are coloured according to whether they are significantly above (green) or below (red) average.

3.3 Survival sub-model

The sub-model structure allows survival rates to vary between cohorts, between years, or both. Currently available datasets do not provide sufficient temporal information to investigate both aspects simultaneously, but as more data are accumulated from the National Monitoring Programme, this will change. For now, variation in survival between years has been estimated in preference, since seasonal abiotic factors are thought to be more influential

than inherited characteristics. While this means that cohorts are assumed to die at similar rates within a particular year, the overall survival for a cohort will depend on which years the fish live through.

The annual dace survival rate for the years 1980 - 2002 followed a clear downward trend over the whole of this period (Figure 3.3). Such a persistent reduction in survival is bound to have had an impact on the density of older fish and appears therefore to hold the key to the declining fishery performance. The analysis has thus identified an area of concern, although it does not provide evidence of the cause.

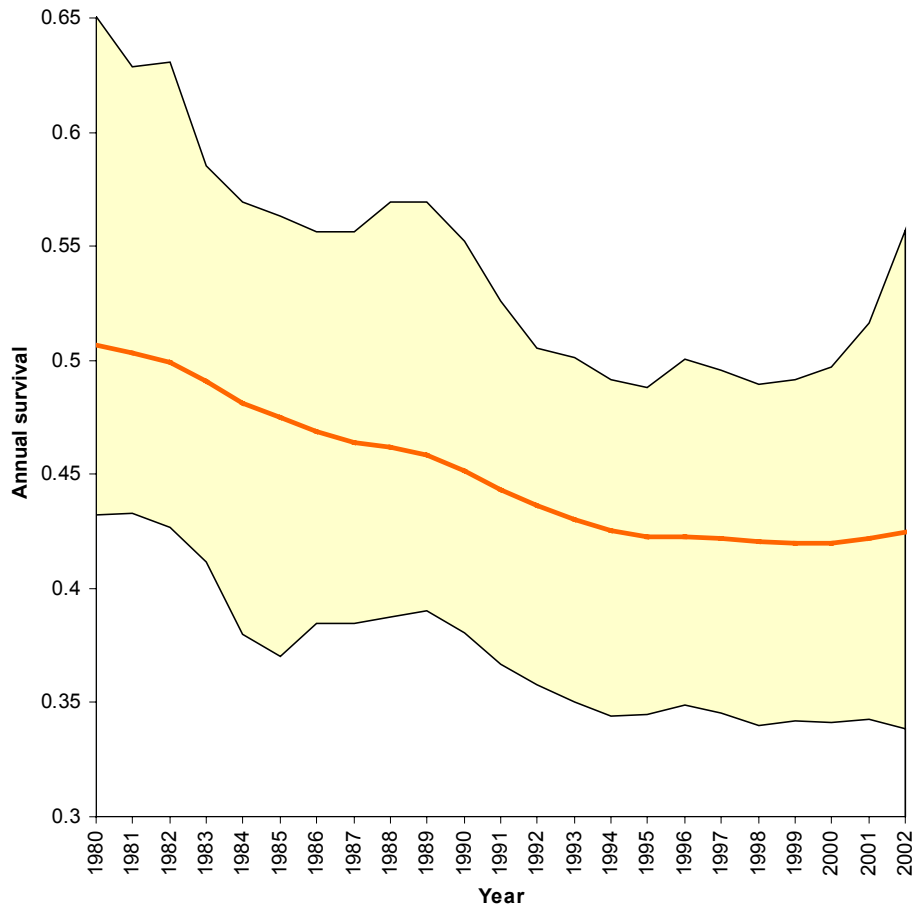


Figure 3.3 Annual survival (as a proportion) of dace in the upper Stour. Shaded area denotes 95% confidence intervals.

The effect can also be seen in the estimates of cohort abundance taken over all age groups from 0+ to 7+ (Figure 3.4). In this diagram, the density estimates for these groups are connected by survival curves for each of the successive cohorts. In the early 1980s, the period of poor recruitment of 0+ fry, already seen in Figure 3.2, is a prominent feature and is still discernible in the cohorts 7 years later. However the recovery in 0+ recruitment since the 1980s is not reproduced at age 7+, because these fish have suffered increased mortality over the same period. This is also reflected in a clockwise rotation of the survival curves.

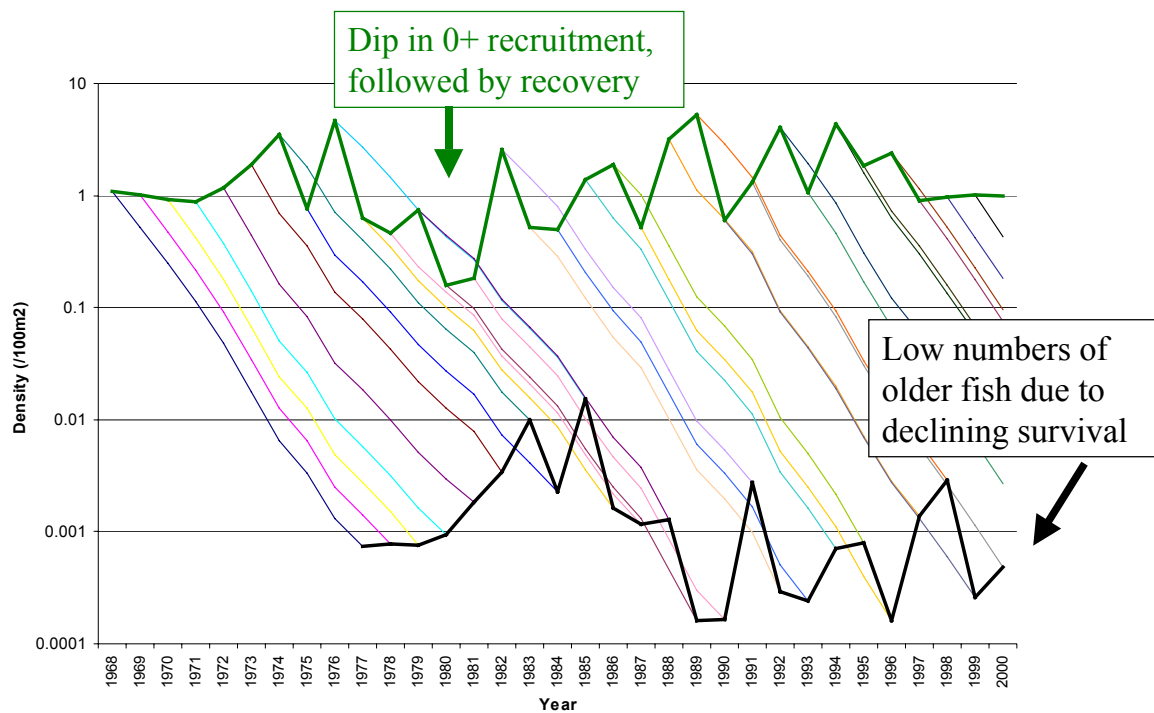


Figure 3.4 Density of dace in successive cohorts in the upper Stour. Upper green line = 0+ fish, lower black line = 7+ fish. The slope of the lines linking the two represents the survival of each cohort.

3.4 Growth sub-model

The growth sub-model can utilise any standard non-linear growth function, such as Gompertz, Logistic or Von Bertalanffy. As with the survival model, the instantaneous growth rates can be assumed to vary between cohorts, between years, or both. Furthermore, the distribution of lengths at a given age can follow a range of distributions including uni-modal, or bi-modal where multiple-spawning is evident. The growth of dace, assuming a Von Bertalanffy growth, uni-modal length frequency and growth rates varying between years, is shown in Figure 3.5. The growth curves suggest a decline in mean length for older fish during the mid 1980s followed by a recovery, but insufficient change to explain a decline in the numbers of larger fish.

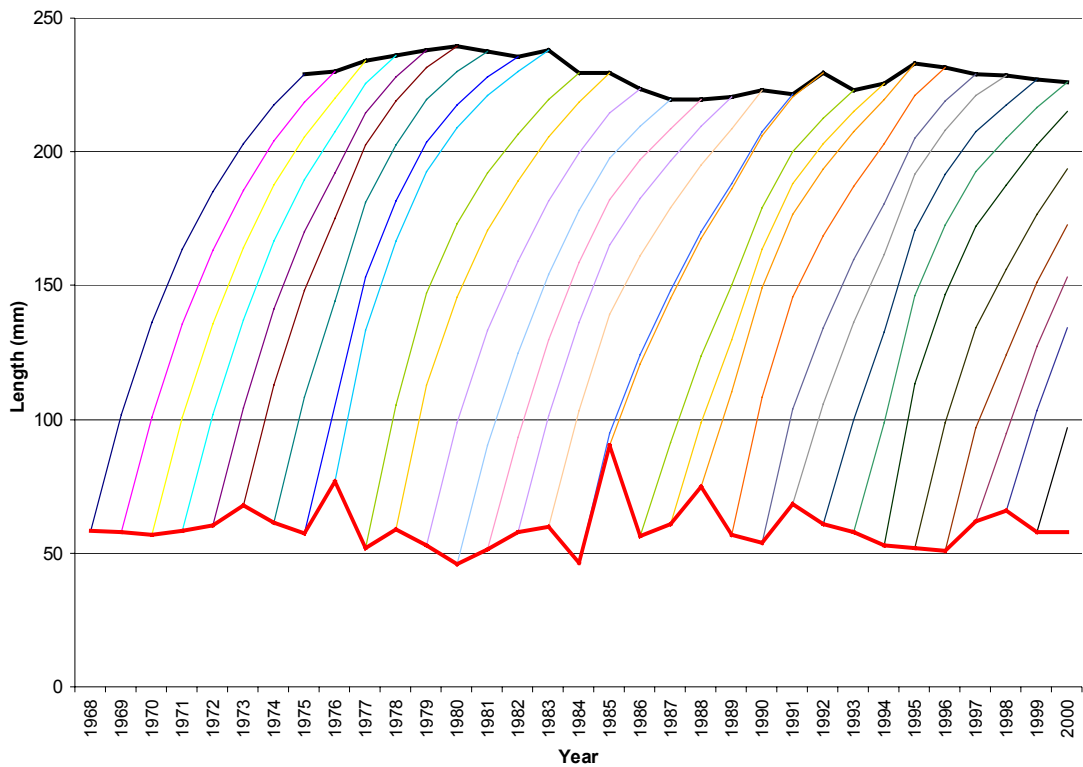


Figure 3.5 Annual growth of dace in the upper Stour. The lower line is the mean length of 0+ fish, the upper line is the mean length of 7+ fish.

The combination of the recruitment, survival and growth sub-models can provide predicted length frequency distributions for any year, irrespective of whether a survey was undertaken in that year. Observed and predicted length frequency distributions for dace on the upper Stour are compared in Figure 3.6. Following the sequence of predicted changes shows the fate of each annual cohort as it moves through the years.

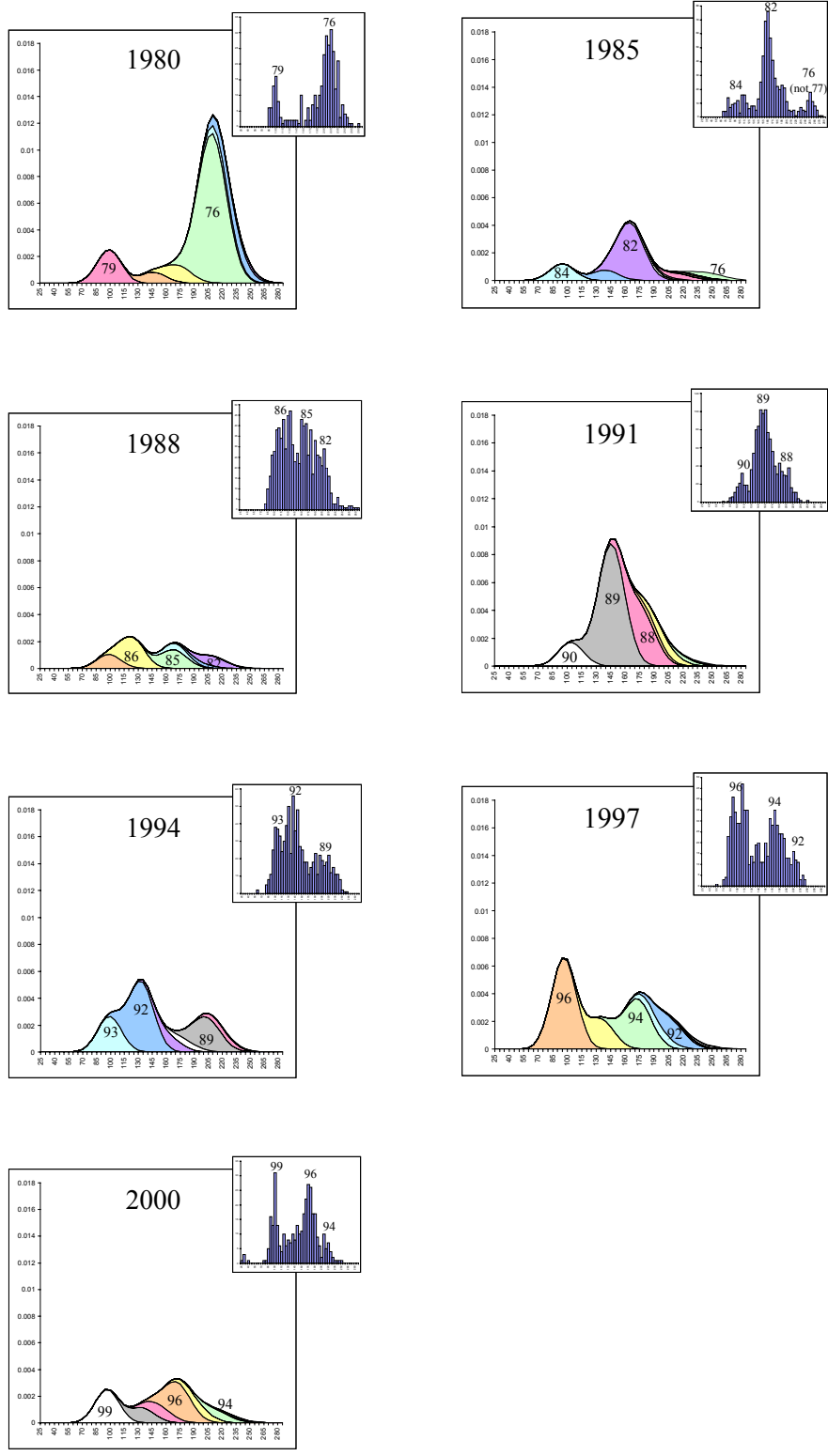


Figure 3.6 Predicted length-frequency distributions for dace from the PDM estimates of recruitment, survival and growth. Coloured areas under the curves represent different annual cohorts. Inset graphs show observed length-frequencies. Length (mm) is on the horizontal axes, frequency is on the vertical.

4 Secondary model components

4.1 Introduction

The peripheral sub-models (Figure 2.1) modify the data input in order to accommodate uncertainty associated with size-selective sampling and in determining ages from scale readings. The outputs are also directly linked with independent population estimates, input separately as data, so that cohort abundance is produced in absolute as well as relative terms. In this section, the sub-models are illustrated with data for chub from the upper Stour.

4.2 Age selective sampling sub-model

Age selective sampling is primarily a size rather than an age related phenomenon, and all practical methods of capture and removal of fish tend to be size biased, even discounting the tendency for gear operators to unwittingly target larger fish. Nets are selective according to their mesh size and do not effectively sample fish smaller than this. However, even small mesh nets may produce bias if they become clogged and difficult to manoeuvre, giving large fish more opportunity to escape. The size selectivity of electric fishing in favour of large individuals is well known. In addition, small fish tend to shoal closely in size groups and are more restricted in their habitat than most larger fish. Consequently, catches of small fish may be more variable than larger fish, depending on how shoals are encountered by the fishing gear, even if they can be sampled efficiently. Overall, there is a tendency for the abundance of younger age (size) groups to be underestimated in comparison with their older (larger) counterparts when using standard survey techniques. This is often apparent in length-frequency distributions for juvenile fish, which may exhibit a mode around the size at which sampling efficiency is maximal. Beyond this size, although sampling efficiency may change little, the numbers of fish caught will decline progressively, reflecting the loss of individuals through the natural processes of mortality, such as predation and disease. The typical form of the age/abundance distribution that might be expected if recruitment and survival were consistent from year to year is illustrated in Figure 4.1 using simulated data.

In order to estimate the abundance of 0+ fish, the usual practice is to extrapolate the declining numbers of fish in each age group back to a figure for year zero. This procedure cannot normally include the inefficiently and inconsistently sampled juveniles, and so these data are usually omitted from the analysis altogether.

Statistical modelling can address this problem by including the efficiency of sampling as a parameter within the model and estimating its effect at each age. Beyond some predetermined age, which can be based on prior knowledge, sampling may be assumed to remain consistent. As a result, the survival curve is not ‘pulled down’ by the data for juveniles, allowing the extrapolation to zero age to be made realistically while at the same time maximising the use of all the data that are available from young fish (Figure 4.1).

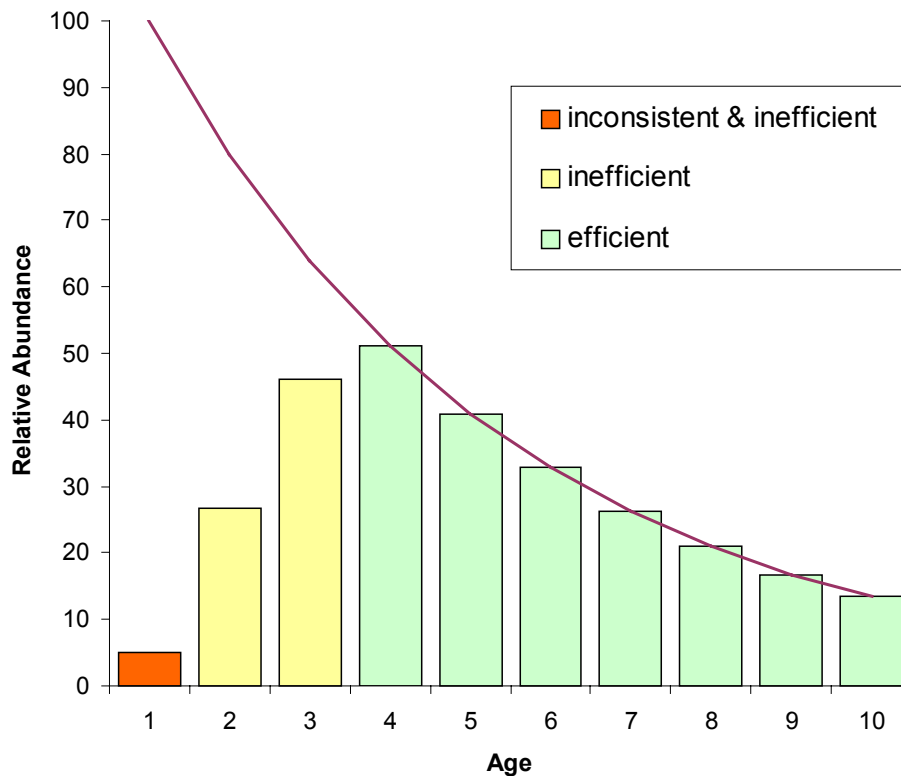


Figure 4.1. Illustration of a theoretical observed age structure (bars) compared to the actual abundance (curve). Bar colours show sampling efficiency.

4.3 Abundance sub-model

Previous methods for determining YCS have involved the calculation of cohort abundance in a form relative to some average value derived from the data itself, such as the overall mean YCS taken over several years. Annual YCS values are then expressed as relative indices centred around this mean, which is set to an arbitrary value, usually 100 (Mann, 1973; Linfield, 1981; Frear and Cowx, 2003). This practice appears convenient but only allows a limited degree of comparison, which is further restricted if the data are obtained from just one survey. More seriously, relative YCS results can give entirely misleading impressions of the population status since they are insensitive to shifts in mean abundance which are not captured within the

scope of the dataset. They can lead to the false conclusion that populations are declining when they are improving and *vice versa*.

The abundance sub-model avoids these pitfalls by relating cohort abundance directly to available population estimates from the source sites taken over the period of the investigation. This determines that the output is expressed in absolute terms and will reflect changes that take place over time. Relative values, where they are useful, can be easily derived around any convenient fixed reference point.

For example, the population size of chub on the upper Stour has been increasing over the period 1980 to 2000 (bars, Figure 4.2). The PDM utilises this information, and ensures that the estimates of recruitment and survival are consistent with both the age structure in each year, and the overall trend in abundance. As a result, the PDM gives estimates of recruitment that increase over the period 1980 to 1994 (Figure 4.3b), and predicts an increase in population size over the same period (centre line, Figure 4.2). In contrast, relative year class indices, such as that produced by the Frear and Cowx method, cannot accurately track underlying trends, and for the upper Stour chub, this method suggests a decline in recruitment over the same period (Figure 4.3a).

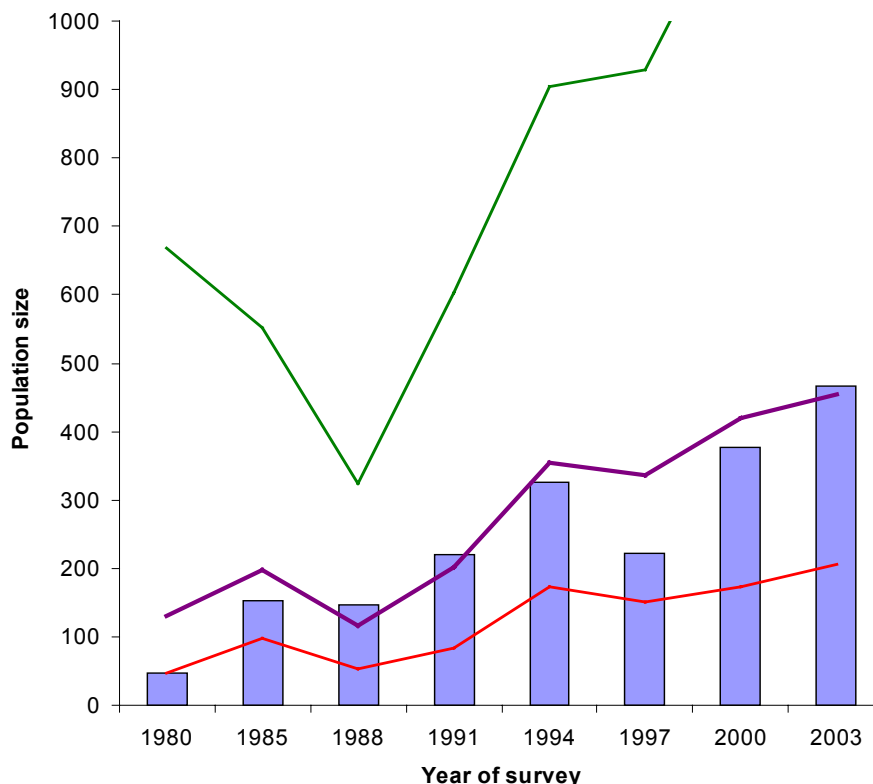


Figure 4.2 Observed (bars) and predicted (lines) abundance for chub in the upper Stour. Upper and lower lines give 95% confidence intervals for predictions.

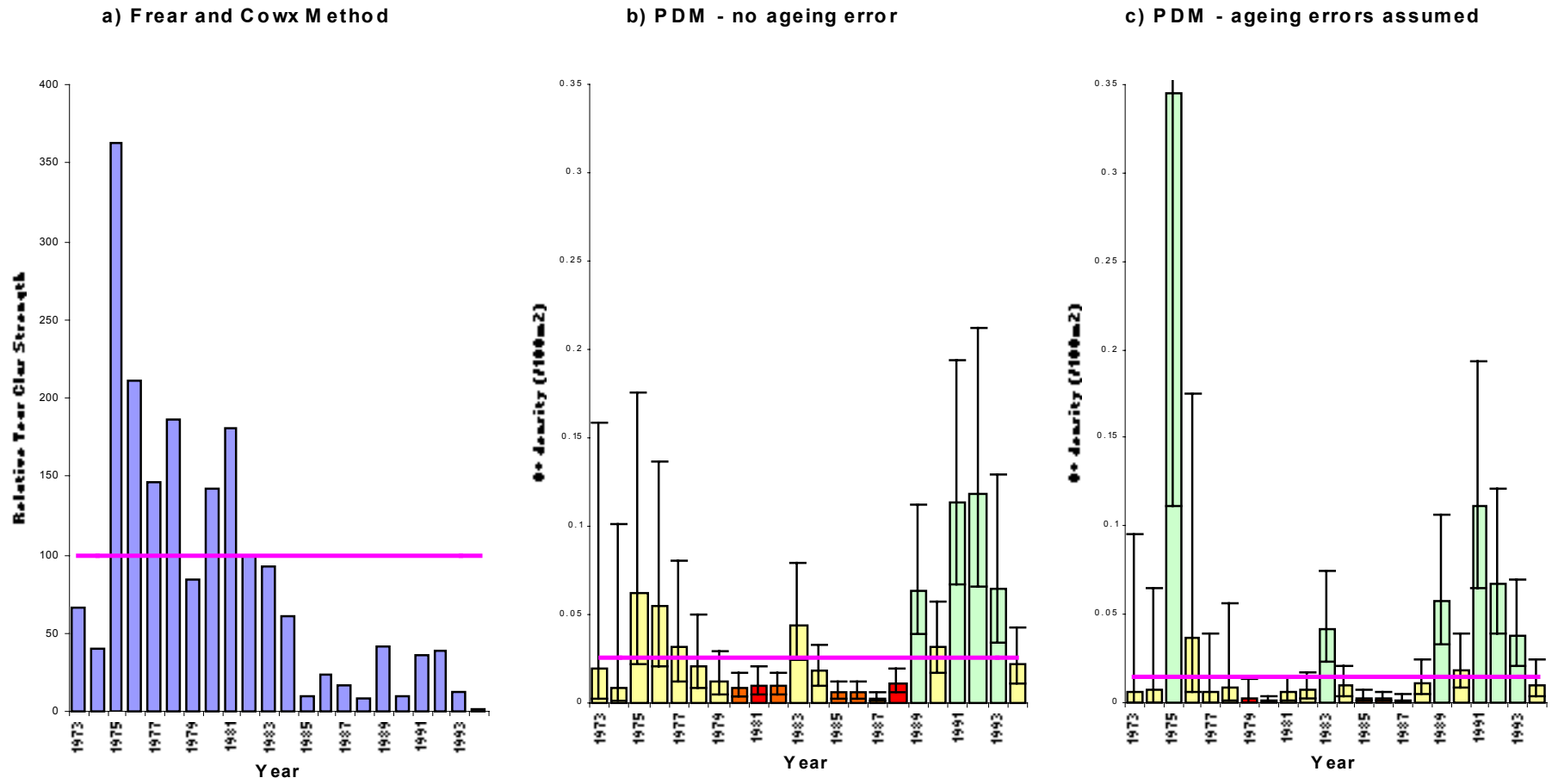


Figure 4.3 Cohort abundance (year class strengths) for chub on the upper Stour: a) Frear and Cowx method b) the PDM assuming age determination is perfect c) the PDM assuming ageing errors exist.

4.4 Scale reading sub-model

4.4.1 Causes of scale reading errors

Few fisheries scientists would claim that ageing fish from scale readings is a simple and objective process, and the causes of ageing errors have been considered by Musk and Britton (2006). Scale reading errors can be random i.e. occurring equally in either direction as a result of inconsistent interpretation, or systematic when the error is predominantly in one direction. A distinct pattern of errors is also apparent in relation to age. Young fish are generally aged more accurately than older fish, but where errors occur they may either result in underestimation of age due to indistinct first annuli, or overestimation of age through the misinterpretation of false checks. In contrast, older fish are frequently aged incorrectly because annuli become congested and scale erosion can remove a significant proportion of the outer edge leading to under-ageing. Since it is not possible to determine the true ages of the fish absolutely, “error” is used here in the statistical sense in which an observation is regarded as an estimate of the unknown true age, and therefore may be expected to differ from it by some extent.

4.4.2 The consequences of scale reading errors

Given that scale readings are quite likely to be in error (Mann and Steinmetz, 1985), it is surprising that much research has continued on the assumption that age determinations are accurate without having validated or tested these assumptions. Measurement errors in fish age can severely distort even simple analyses of growth or survival (Appendix A). The effect that the errors may have in distorting and clouding judgements is illustrated in the estimation of cohort abundance. If ages are wrongly assigned it becomes impossible to trace cohorts accurately through time and, strong year classes may appear apparently from nowhere, giving the impression that whole age groups have been missed in previous routine surveys. There is also a tendency for ageing errors to cause strong cohorts to become spread over several years, suggesting that favourable spawning conditions have persisted across time when in reality they were prevalent in only one season. It is obvious how misleading this would be if an attempt were made to establish temporal relationships with environmental variables. Such effects have been recognised as the phenomenon of ‘ageing drift’ but little attention has been given to resolution of the difficulties causing it.

4.4.3 Possible solutions to scale reading errors

These problems can be reduced by imposing a quality assurance approach involving cross-checks by ‘expert’ scale readers. However, this cannot be a complete solution in the absence of independent validation, because indistinct

first annuli, strong false annuli and edge erosion may cause even expert judgement, based on scale reading alone, to be incorrect. Another approach is to undertake more sophisticated data analyses to correct for the biases introduced by scale reading errors (Appendix A).

To make an informed judgement, an expert reader may take into account all the available information that might contribute to assessing the true age of a fish. This would include the length frequency distribution of the sample, the growth pattern of the population, previous survey data and the visual interpretation from the scale itself. With all the evidence assembled, a balanced judgement could be made, which is more likely to resemble the true age. However, for large samples the process could become prohibitively time consuming, and subjectivity would still remain.

The scale reading sub-model performs the procedure just described, except that a computer replaces the expert. Taking instantaneous and simultaneous account of all the relevant data without any subjective bias for potentially thousands of scales is what technology does best, and the outcome is the most probable age for the individual fish in the circumstances as they are known. For simple examples, estimating the age of a fish from different, and sometimes conflicting data sources, can be undertaken using simple probability theory. The method is outlined in Appendix B.

4.4.4 Quantifying scale reading errors.

To estimate the age of a fish from scale reading, length and abundance data, the model requires information on the likely magnitude of scale reading errors. Figure 4.4 shows a simplified version of the matrix format in which this information is presented to the model. For each age of fish (row), the probability is given that a particular scale reading (column) will be observed. Where scale reading is assumed to be perfect (i.e. there are no ageing errors), the matrix will comprise a diagonal row of ones (Figure 4.4a); there is certainty that the true age will be identified from the scale. At the other extreme, a complete lack of faith in scale reading would be indicated by a particular scale reading for a given age being just as likely as any other (Figure 4.4b). Whilst the scale reading sub-model could in theory include either of these two scenarios, in practice they are unrealistic and should only be viewed as extremes of a complex array of possible scenarios. More realistic scenarios would reflect that under-ageing is more likely than over-ageing, with the magnitude of ageing error increasing with age (Figure 4.4c&d). The scope given to re-ageing is controlled by the information on likely scale reading error rates, and would normally reflect what is known about scale reading errors for the species or population in question.

Information on scale reading errors can impart not only the extent of error likely to occur (Figure 4.4), but also the degree of uncertainty associated with this estimated error. For example, the scales may be read by a range of individuals, including inexperienced personnel where the likelihood of misreading could be high (Figure 4.4d), and experienced personnel where the

likelihood of misreading would be low (Figure 4.4c). Alternatively, uncertainty may reflect differences of opinion among fisheries scientists as to the likely magnitude of scale reading error, from the optimist (Figure 4.4c) to the pessimist (Figure 4.4d). Whatever the cause, the uncertainty associated with the likely magnitude of scale reading errors needs to be taken into account in the scale reading sub-model. The way in which this has been achieved in the PDM is beyond the scope of this report.

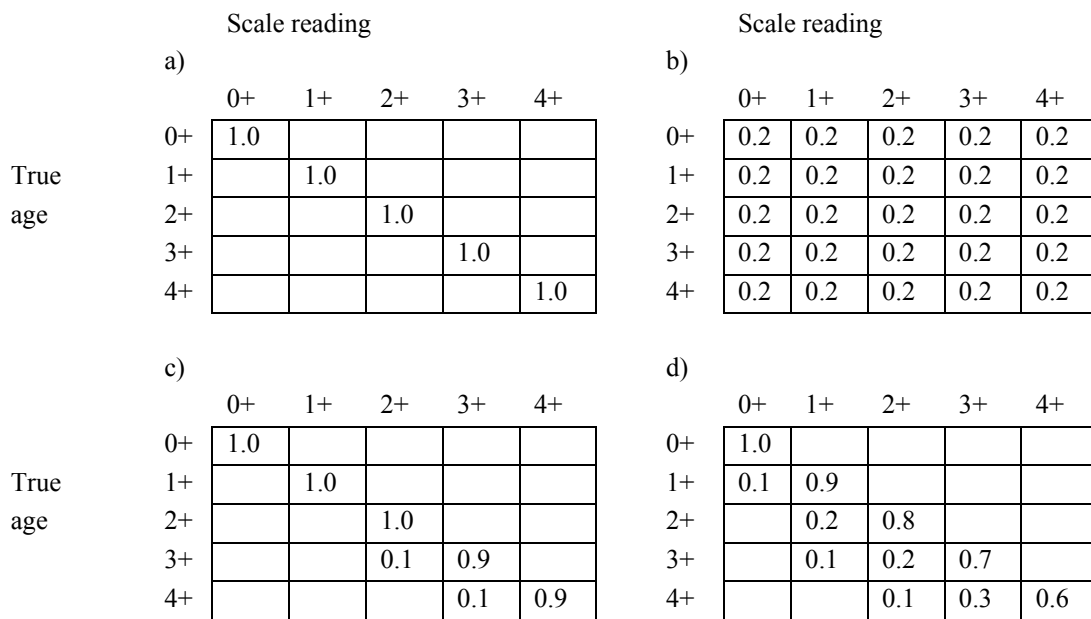


Figure 4.4. Probabilistic representation of a range of scenarios for ageing errors.

At first sight, it may appear that the scale reading sub-model introduces a degree of subjectivity when compared to previous YCS methods. However, it is important to realise that previous YCS methods make the implicit assumption that scale readings are perfect, and that confidence in this assumption is absolute. This in itself represents strong prior information that is not only highly subjective, but also totally unrealistic. Whilst the PDM could adopt this assumption (Figure 4.4a), it can also adopt far more realistic assumptions (e.g. Figure 4.4 c&d), and allow for the uncertainty associated with such assumptions.

4.4.5 Benefits of correcting for scale reading errors

Acknowledging the possibility of scale reading errors means that for every fish, age is estimated in a probabilistic way that balances the evidence from scale reading, length and abundance data (Appendix B). For some individual fish, the age will be estimated with a high degree of certainty, where scale reading error rates are believed to be low, and the scale reading, length and abundance data all tell the same story. However, for other fish there may be

considerable uncertainty, particularly where scale reading and length data are contradictory, as for fish number 4 in Appendix B, and for some of the chub in the upper Stour (see below).

The primary motivation for correcting for scale reading errors, however, is not for age estimation itself, but for the improved estimates of recruitment (section 3.2), survival (section 3.3) and growth (section 3.4) that are obtained. Even for the simplest data sets, allowing for the likely errors in the explanatory variables (e.g. age), will result in dramatic improvements in the analysis (Appendix A).

Use of the scale reading sub-model means that data from fish that have not been aged, but for which lengths have been measured, can be incorporated into the analysis and assigned ages by exactly the same process (e.g. fish number 2, Appendix B). These un-aged fish will contribute valuable information to the assessment of population dynamics in the form of their length-frequency distribution. Furthermore, the probabilistic basis for the scale-reading sub-model allows for the uncertainty associated with assigning an age to a fish with no scale sample, something not possible with an age-length key.

4.4.6 Illustrative examples from the River Stour

Figure 4.3 shows cohort abundance for chub from the upper Stour, estimated from three different methods: a) a conventional arithmetic year class strength index (assuming scale reading is perfect), b) the statistical PDM (also assuming scale reading is perfect) and c) the statistical PDM (assuming a realistic degree of scale reading error). Two detailed examples demonstrate how the model handles scale reading errors, and the consequences for estimates of recruitment.

The first example illustrates the phenomenon of “ageing drift”, as described by Frear and Cowx (2003). A number of large chub in the upper Stour in 1985 of similar and overlapping length distribution have been read as either 8, 9 or 10 years (Figure 4.5). If these scale readings are assumed to be correct, then the recruitment in 1975, 1976 and 1977 are estimated to be strong (Figure 4.3a&b). However, the 1976 and 1977 cohorts were relatively scarce in earlier surveys, and on the basis of all the information available (scale reading, length, abundance), the model estimates that there is a high probability that some of these fish have been under-aged. The result is an increase in estimated recruitment in 1975, with a corresponding decrease in subsequent years (Figure 4.3c).

The second example is less common, and involves possible scale reading errors for younger chub caught in the upper Stour. Figure 4.6 shows scale readings (left hand panels), and ages estimated from the model (right hand panels) in 1991, 1994 and 2000. According to the scale readings, the chub in 1991 appeared to have an unusually wide length range in which the 2+ fish completely envelop their older 3+ siblings. In this case, taking account of all

the evidence, the model has divided the fish into two distinct age groups with very little overlap in length. Whilst this appears to be a rather drastic process of re-ageing, the underlying reasons are seen when the length frequency distribution is viewed in the context of data from subsequent surveys in 1994 and 2000. It is immediately apparent that the bimodal distribution of 2+ fish in 1991 is anomalous, not being reproduced in subsequent surveys and that the second mode corresponds closely with the expected length for 3+ fish as judged from the later data. If the scale readings for 1991 fish were correct this would represent extraordinary growth for a single cohort in a single year and would be incompatible with the overall growth rate estimated on the basis of all the data available to the model. Given that scale readings are subject to a degree of uncertainty, the most probable resolution is that the scales in 1991 were wrongly aged (see Appendix B). In stark contrast, the degree of scale reading errors in all other surveys was estimated to be minimal. Whilst the magnitude of scale reading error may have been high in 1991, in this example, there is relatively little consequence for the assessment of recruitment. Estimated recruitment of the 1988 cohort (i.e. the 3+ fish in 1991) is increased from significantly worse than average (red, Figure 4.3b) to average (yellow, Figure 4.3c).

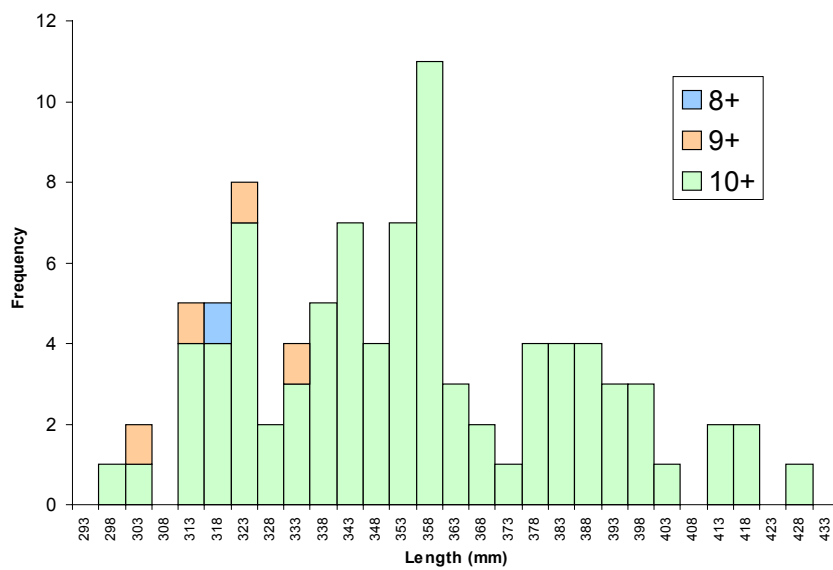
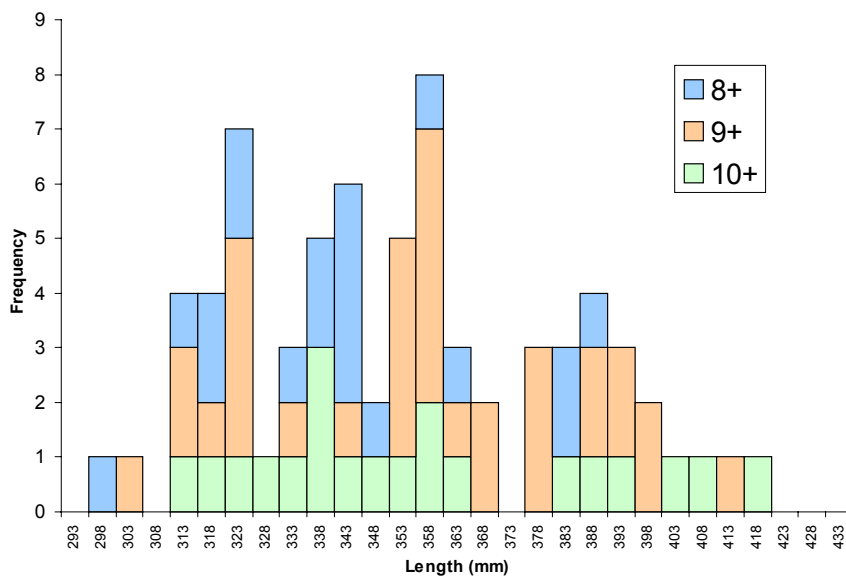


Figure 4.5 Scale reading (top) and model-estimated age (bottom) for chub on the upper Stour in 1985.

Scale reading

Age estimated by PDM

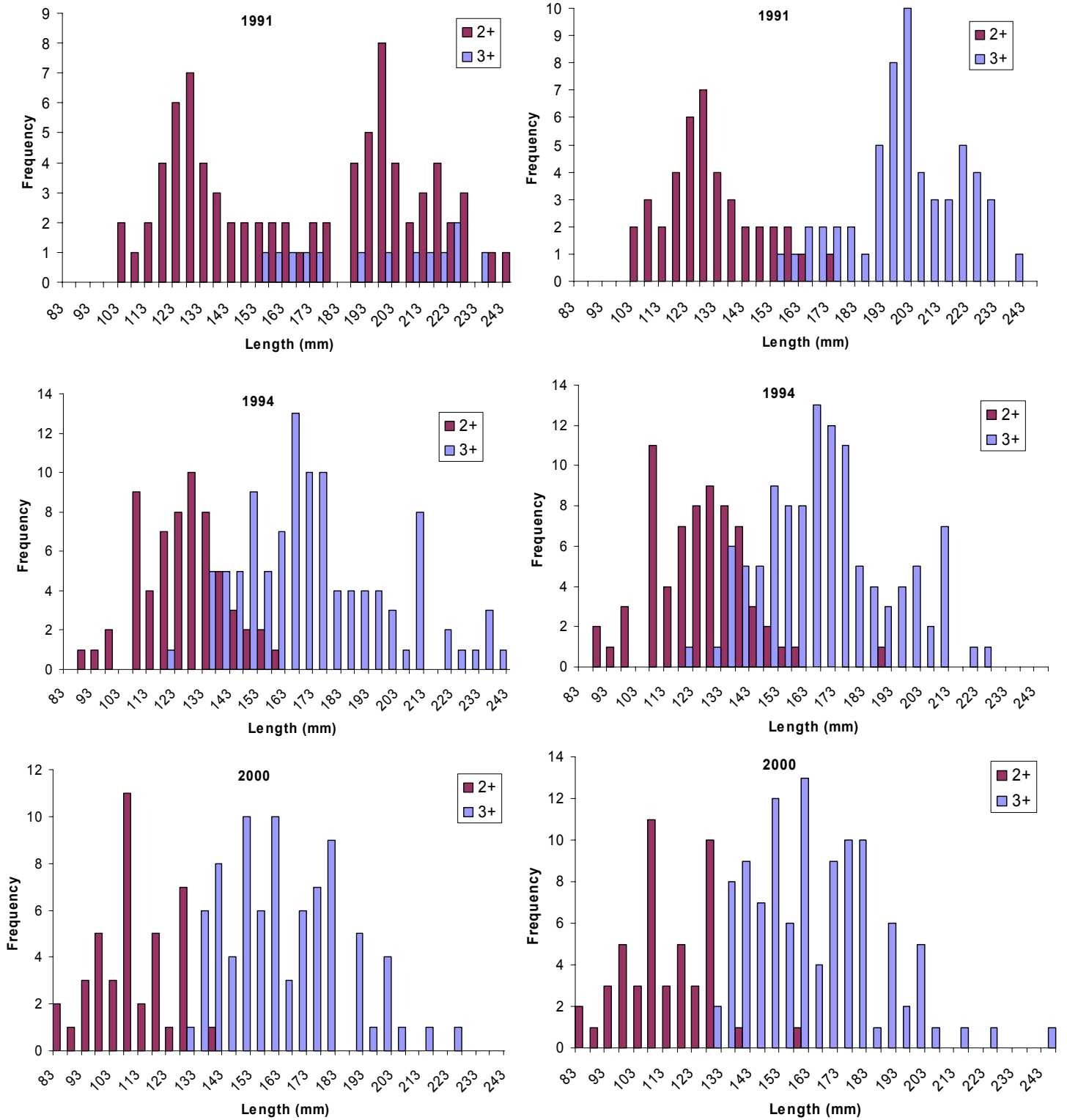


Figure 4.6. Scale reading and model-estimated age of chub in the upper Stour in 1991, 1994 and 2000.

5 Discussion and conclusions

5.1 Validation

Remedial actions to restore a fishery can take many forms, but they are generally expensive undertakings. If they are prompted by the findings of operational investigations then, quite rightly, there is a responsibility on the part of the investigator to demonstrate that the findings are correct and accurate as far as this can be established. Unlike many other investigational tools, statistical modelling includes the process of validation (model checking) as an implicit and integral part of the analytical procedure. All outputs are produced with estimates of uncertainty so that their accuracy can be assessed. However, for complex models a more comprehensive evaluation is required.

Statistical models are created from the data input and so a natural and logical validation is achieved by direct comparison between the model predictions and the raw data from which they were derived. This should be carried out for all parts of the model to gain confidence that the overall fit is good.

5.2 Implementation

There is good reason to believe that the PDM not only produces reliable estimates of cohort abundance required for assessing the factors affecting recruitment, but also that it has the potential to form the central processing tool for almost all aspects of coarse fish ecology. Statistical models are versatile and their development is mainly limited by human intellect and imagination, and available computer processing power. However they require appropriate data in sufficient quantities to produce outputs that can lead to identification of management options. At present, suitable long-term datasets are few, but the Environment Agency's National Monitoring Programme now produces annual population estimates for coarse fish over a wide range of rivers across England and Wales. Within a short time, sufficient annual cycles will have been completed to allow in-depth analysis of data from any rivers yielding samples large enough for modelling purposes. The simultaneous development of powerful analytical tools and the collection of high quality datasets should mean that the Environment Agency will soon have the opportunity to unlock many of the current mysteries of coarse fish ecology. Application of this knowledge should lead to better management of fisheries and improved angling opportunities, while maintaining the conservation value of our rivers.

At present, the widespread adoption of this approach to evaluating fish population dynamics is constrained by the need for some understanding of statistical modelling methods and familiarity with the specialist software involved. These skills are not widely available within the Environment Agency

and so dissemination as a routine procedure is unrealistic. Furthermore, when handling large datasets, estimation of parameters may take many hours. It is likely, then, that for the immediate future PDM fisheries assessments will have to be undertaken by specialists within the Statistics and GIS Group.

Improving statistical skills within the Fisheries Function is a training priority and it is expected that this will instil sufficient competence and confidence in some individuals to run the models themselves. Also, it may be possible that a simplified version could be operated to generate specific limited outputs, without full understanding of the mathematical details behind the methodology. Such usage carries inherent dangers of misinterpretation, and under-utilises the full potential of the model but may have valuable application in routine operations. In time, developments in computing power will inevitably reduce run times.

5.3 Application to management

The primary purpose of understanding the ecology of coarse fish populations is to improve their management. Fisheries assessments should have the ultimate aim, therefore, of informing management decisions. Since the PDM outputs are direct measures of reproduction, growth and survival, the fundamental processes which effect changes in abundance, they can be easily translated into management actions.. For example PDM outputs can identify and quantify long-term impacts such as the progressive loss of older dace from the river Stour. However by gaining an understanding of the relationship between recruitment, growth and survival the underlying causes of the impact may become clear. Such insights can then help to focus on the most appropriate management response.

5.4 Future development

The development of the PDM means that the effects of environmental variables on fish ecology can now be examined reliably. Statistical models are amenable to the evaluation of such variables (known as covariates) because they can be incorporated within the model and thus become an integral part of the analysis. Their effects can be estimated having taken full account of other factors in the model, including other covariates, and that interactions between different environmental variables can be explored. This is a much more efficient and powerful statistical process than the conventional approach of determining relationships in a separate or secondary analysis. Clearly there is extensive scope for evaluating the effects of water quality, habitat, climatic and biotic factors on coarse fish populations.

The full value and potential of the PDM is only just beginning to be realised. The fundamental dynamic processes of reproduction, growth and survival, applied to each cohort, together define the past, current and future status of any fish population. By understanding the way that these processes respond

to biotic and abiotic factors there exists the ultimate possibility of predicting abundance for a species in almost any circumstances where the data are available. Statistical models can be modified, developed, extended and even condensed to meet the peculiarities of virtually any datasheet. It is already apparent that the PDM can be utilised to address some existing areas of particular concern.

Two examples include the natural link with Geographic Information Systems to help map the spatial distribution of fish populations, and predicting the population effects of endocrine disrupting substances in sewage effluents. Natural links with GIS models hold out the possibility of National scale mapping of fish distribution and relationships with catchment features. The River Fisheries Habitat Inventory (RFHI) project for coarse fish will encompass much of this work and will benefit from, and build on, the development of the PDM. The impairment of effective fecundity through exposure to endocrine disrupting substances potentially threatens to undermine the population status of many aquatic vertebrate species in the vicinity of STW's. Estimating and predicting the severity of feminisation in males or androgenic effects in females required to elicit population decline could be achieved by development of the PDM and running simulation experiments.

5.5 The advantages of a statistical model

The application of models in fisheries ecology has a long history but in most cases the models have been deterministic (mathematical) rather than stochastic (statistical). Although recent developments in software have brought statistical models within the reach of many fisheries scientists the advantages for in depth analysis of fish population data have not been fully exploited. Consequently, particularly in the field of freshwater coarse fisheries, analytical approaches and methodologies have remained essentially unchanged for several decades. The development of the PDM represents a concerted effort to rectify this situation within the Environment Agency by the application of modern statistical methods to the analysis of freshwater fisheries survey data.

The conventional approach to analysis addresses each facet of the dataset as a separate entity. Where analyses are linked it is through averaging, summation or the creation of an index. Often implied or unstated assumptions underlay these manipulations. The great strength of statistical modelling lies in formally linking all parts of the analysis in a probabilistic manner so that all information is mutually shared. The assumptions regarding data structure are an integral feature of the analysis. It means that all parameter estimates, and their associated uncertainties, are generated having taken account of all others. This is a far more powerful, intuitive and meaningful approach, which offers the prospect of much deeper comprehension of the complexities of coarse fish ecology. The growth, survival and recruitment models, which form the central feature of the PDM, provide a particularly good illustration of this

concept since the processes are inextricably linked and generated from essentially the same data.

Probabilistic linking of component submodels allows elaborate and complex analytical systems to be constructed, which share information and take each other into account. They exhibit, moreover, great analytical flexibility and versatility since submodels can be introduced or removed from the system to suit the requirements of any particular line of enquiry.

Statistical models come into their own in dealing with difficult or incomplete data sets which may pose intractable problems for conventional analyses. Thus non-consecutive sampling, unaged, misclassified or even unmeasured fish can be accommodated easily and the increased uncertainty involved estimated. Recruitment of 0+ fish can be linked with population estimates so that outputs track natural trends in abundance and are, therefore, absolute in nature, rather than simply relative to the overall mean. Absolute data find application in many other areas of investigation e.g. in the exploration of density dependence through the development of stock–recruitment relationships.

All statistical models are constructed from data with the objective of reproducing as faithfully as possible the original form of the dataset. Successful modelling rests on the principle of goodness of fit between model predictions and data. Unlike most conventional analyses model checking and validation are an integral part of the process.

The advantages of statistical modelling may be summarised as:

- The statistical model is comprehensive and flexible, addressing all areas of coarse fish ecology and not just one aspect such as year class strengths.
- It is a modern statistical approach and employs recognised methods for estimating parameters, not the calculation of ad hoc indices relying on unwarranted assumptions.
- It estimates parameters associated with fundamental biological processes of survival, growth and reproduction.
- Uncertainties are quantified and assumptions are explicit.
- It utilises all the data available; including inefficiently sampled size/age groups.
- It allows un-aged fish to be included without the risk of potential bias arising from non-statistical approaches.
- Sub-models are linked dynamically, so that all information is shared and taken into account.

- Potential outputs are extensive.
- It is amenable to modification and development, or even simplification, to suit the available datasets – limited only by computing power.
- Covariates, such as environmental variables can be easily accommodated in the model.
- It indicates and allows correction for ageing errors incurred in scale reading and other errors of measurement and transcription of data.
- Validation can be achieved by direct comparison of observed and predicted data.

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Appendix A: consequences of scale reading error.

The consequences of ignoring scale-reading errors can be demonstrated using regression analysis. Simple regression analysis assumes that random variation is only associated with the y variable, and that the x variable is measured without error. This is illustrated in Figure A1 in which the data for all six graphs have been randomly generated around a regression line with a true slope of one, and a true intercept of zero. The top left graph (Figure A1) shows data generated with random variation only affecting the y variable. The assumptions of regression analysis are therefore correct, and the fitted line has a slope and intercept close to one and zero respectively. Subsequent graphs have an increasing degree of measurement error associated with the x axis, which results in the true underlying relationship between x and y becoming increasingly obscured. Simple regression analysis, assuming no measurement error for x, fits an increasingly horizontal line as the mismatch between the actual and assumed level of measurement error becomes greater.

In the context of coarse fish ecology, analyses of growth, survival and recruitment will require assessments in which the x variable (age) is subject to measurement error. Even if these errors occur randomly, the result will be to underestimate growth rates, over-estimate survival, and blur the distinction between strong and weak cohorts. In practice, the patterns of scale reading errors are more complex, with older fish being more difficult to age than younger fish, and under-ageing being more common than over-ageing. The implications for stock assessment are also more complex and give rise to phenomena such as “ageing drift”.

These problems arise not just because of scale reading error, but because of the mismatch between the actual situation (i.e. scale reading errors occur) and the assumptions made in the analysis (i.e. scale reading is perfect). The solution is to modify the analysis, replacing the incorrect assumption with a more realistic assumption reflecting the likely magnitude of scale reading errors. Figure A2 shows what happens when the regression analysis incorporates error in the x variable as well as the y variable. The top left graph in Figure A2 is the same as the bottom right graph in Figure A1, and shows data which have been generated around a regression line with a slope of one, an intercept of zero, and a high degree of measurement error in the x values. Subsequent graphs in Figure A2 show exactly the same data set, but the analysis allows for an increasing degree of measurement error in the x variable. As the mismatch between the actual and assumed measurement error decreases, the regression line is restored to the true position of a slope of one and an intercept of zero.

Of the eleven analyses shown in Figures A1 and A2, only two are correct: where the actual and assumed measurement errors are both ± 0 (top left,

Figure A1), and where the actual and assumed measurement errors are both ± 5 (bottom right, Figure A2). Clearly the first of these two situations is preferable, where the actual measurement error is zero, resulting in a precise analysis with narrow confidence intervals around the regression line. In the context of coarse fish assessments, quality assurance procedures can reduce scale-reading errors, but the subjective nature of scale reading means that scale-reading errors will remain. It is therefore essential that the correct assumption about scale reading errors is made in any assessment of growth, survival or recruitment. The Population Dynamics Model (PDM) achieves this using a probabilistic assessment of the possibility of scale reading errors (Appendix B).

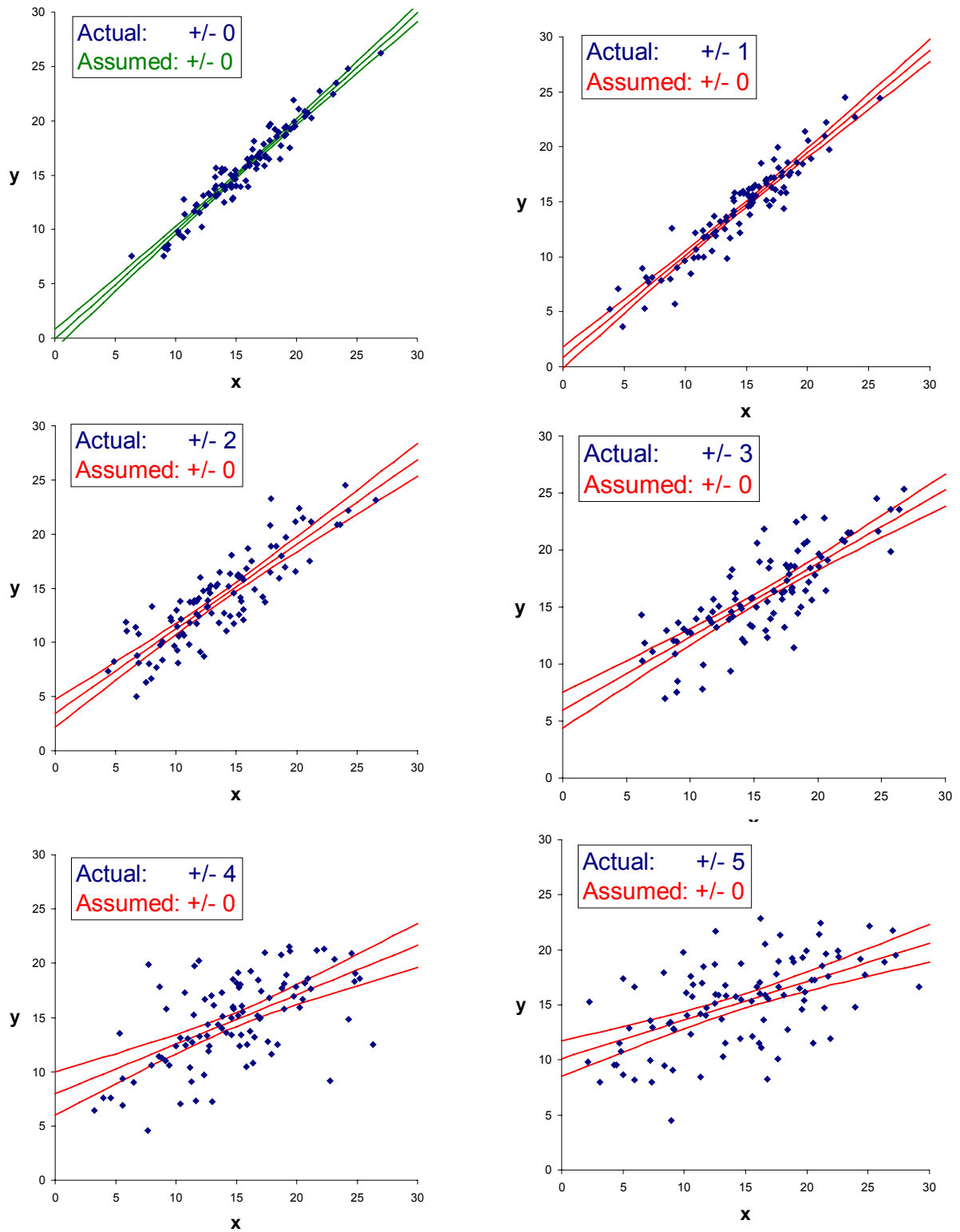


Figure A1. Simple regression analysis for data generated with increasing levels of random error in the x variable.

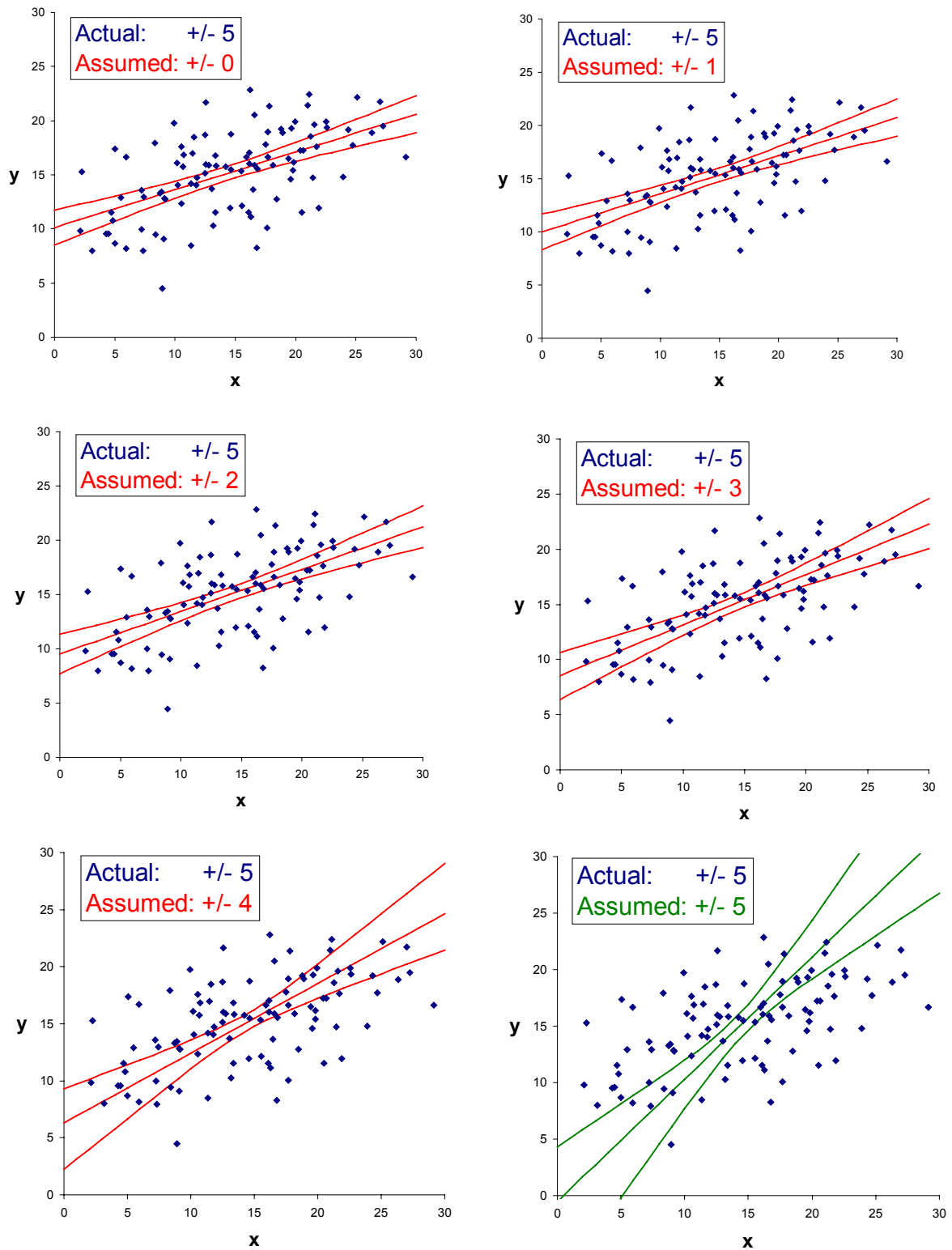


Figure A.2 Regression analysis that assumes an increasing magnitude of measurement error in the x variable.

Appendix B: fundamentals of estimating fish age

For many aspects of fish stock assessment, an age will need to be estimated for every fish captured in a survey. However, this is not always straightforward, since scale samples are unlikely to be taken from every fish and scale reading can be subjective and may not provide an accurate assessment of the true age of a fish. There are three sources of information that may be used to help estimate the age of an individual fish: a) the length of the fish, b) the scale reading and c) the age-frequency of the population.

The Population Dynamics Model (PDM) provides a probabilistic estimate of the age of every fish captured in a survey, regardless of whether a length measurement or scale sample has been taken. This can be a cause for confusion, particularly when the PDM estimates that the most likely age for a fish is different to that suggested by the scale. To help understand the underlying concepts, this appendix shows how the age of a fish can be estimated from different sources of information, using simple probability theory.

Consider the hypothetical situation of a pond stocked with fish of two ages, one-year-olds (a_1) and two-year-olds (a_2). The proportion of these fish is known to be 60% one-year-olds and 40% two-year-olds. It is also known that the mean length of the one-year-olds is 4 (standard deviation 1) and the mean length of the two-year-olds is 6 (standard deviation 1). The corresponding length-frequency distribution is shown in Figure B1.

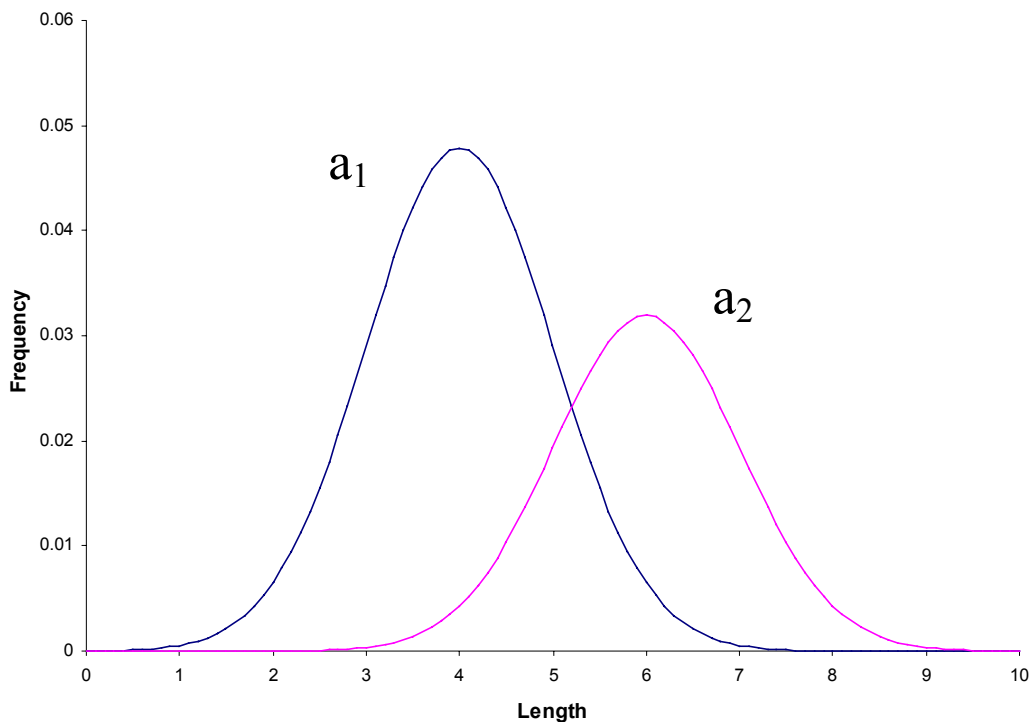


Figure B1. Hypothetical length-frequency distribution for two ages of fish.

Consider the situation where four fish are selected at random and different measurements are taken from each.

Fish 1. No length or scale sample.

If the length is not recorded, and a scale sample not taken, then the probability that the fish is a particular age will simply reflect the relative abundance in the population, and so the probability that the age is 1, $\Pr(a_1)$, is 0.6, and the probability that the age is 2, $\Pr(a_2)$, is 0.4.

Fish 2. Length = 6, no scale sample.

To estimate the age of a fish from its length requires the calculation of conditional probabilities. From the length-frequency distribution (Figure B1), we can estimate the relative probability that a fish will be a particular length, conditional on knowing its age ($\Pr(l | a)$). Assuming the lengths follow a Normal distribution, then $\Pr(l | a)$ can be calculated from the equation for the Normal distribution. For example, the relative probability that a fish will be of length 6, conditional on it being age 1, can be readily calculated in a spreadsheet package such as Excel, using the expression:

`=NORMDIST(6,4,1,FALSE)`

where 6,4,1 correspond to the length of the fish, the mean length at age, and the standard deviation of the lengths respectively. This gives $\Pr(l | a_1) = 0.054$, and similarly, $\Pr(l | a_2) = 0.399$.

A simple equation will convert the relative probability of a particular length, conditional on the age ($\Pr(l | a)$), to the probability of a particular age, conditional on the length ($\Pr(a | l)$). For example, the probability that the fish is age 1, given the length, is given by:

$$\Pr(a_1 | l) = \frac{\Pr(l | a_1) \Pr(a_1)}{\Pr(l | a_1) \Pr(a_1) + \Pr(l | a_2) \Pr(a_2)}$$

Substituting the values given above into this equation we get:

$$\Pr(a_1 | l) = \frac{0.054 \times 0.6}{0.054 \times 0.6 + 0.399 \times 0.4} = 0.169$$

Thus the probability that the age is 1, given its length is 6, is 0.169, and so the probability that the age is 2, $\Pr(a_2 | l)$, is 0.831.

Fish 3. Length not measured, scale reading = 1.

The estimated age will depend on the degree to which scale reading is believed to provide an accurate assessment of age. Scale reading error rates can also be expressed in terms of probabilities. Table B1 shows the situation where the probability of over-ageing a fish (false checks) is 10%, and the probability of under-ageing a fish (missing checks) is 20%.

Table B1. Illustrative probabilities of obtaining a particular scale reading for a given age ($\Pr(s | a)$).

True age	Scale reading			Total
	s ₁	s ₂	s ₃	
a ₁	0.9	0.1	0.0	1.0
a ₂	0.2	0.7	0.1	1.0

As before, we need to convert the probability of a particular scale reading, given the age ($\Pr(s | a)$), to the probability of a particular age, given the scale reading ($\Pr(a | s)$). The probability of the true age being 1, when the scale reading is 1, $\Pr(a_1 | s_1)$, is given by:

$$\Pr(a_1 | s_1) = \frac{\Pr(s_1 | a_1) \Pr(a_1)}{\Pr(s_1 | a_1) \Pr(a_1) + \Pr(s_1 | a_2) \Pr(a_2)}$$

Substituting the above values into this equation we get:

$$\Pr(a_1 | s_1) = \frac{0.9 \times 0.6}{0.9 \times 0.6 + 0.2 \times 0.4} = 0.871$$

Thus the probability that the age is 1, given the scale reading, is 0.871, and so the probability that the age is 2, given the scale reading, $\Pr(a_2 | s_1)$, is 0.129.

Fish 4. Length = 6, scale reading = 1.

In the situation where we have both a length and a scale reading, the calculations are a simple extension of those given above. The probability of the true age being 1, with a scale reading of 1 and length l , $\Pr(a_1 | s_1, l)$, is given by:

$$\Pr(a_1 | s_1, l) = \frac{\Pr(s_1 | a_1) \Pr(l | a_1) \Pr(a_1)}{\Pr(s_1 | a_1) \Pr(l | a_1) \Pr(a_1) + \Pr(s_1 | a_2) \Pr(l | a_2) \Pr(a_2)}$$

Substituting the above values into this equation we get:

$$\Pr(a_1 | s_1, l) = \frac{0.9 \times 0.054 \times 0.6}{0.9 \times 0.054 \times 0.6 + 0.2 \times 0.399 \times 0.4} = 0.477$$

Thus the probability that the age is 1, given the length and scale reading, is 0.477, and so the probability that the age is 2, $\Pr(a_2 | s_1, l)$, is 0.523. The most likely age is 2, despite the scale reading being 1.

The results for the four fish are summarised in Table B2.

Table B2. Summary of results for fish ageing exercise.

Fish	Data		Probability of age		Most likely age
	Length	Scale reading	Age = 1	Age = 2	
1	-	-	0.600	0.400	1
2	6	-	0.169	0.831	2
3	-	1	0.871	0.129	1
4	6	1	0.477	0.523	2

The calculations illustrated here are very similar to those used by the PDM, although the PDM is more complex. With the PDM, the age structure ($\Pr(a)$) is given by the recruitment (section 3.2), survival (section 3.3) and age-selective sampling (section 4.2) sub-models, the length at age ($\Pr(l | a)$) is given by the growth sub-model (section 3.4) and the scale reading errors ($\Pr(s | a)$) are given by the scale reading sub-model (section 4.4).

Furthermore, the PDM allows for uncertainty in all of these probabilities. For example, the age structure and growth rates of the population are not known

exactly because of sampling errors, and the scale reading error rates are also subject to uncertainty.

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