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Australian Society for Fish Biology Workshop

The MEASUREMENT of AGE and GROWTH in FISH and SHELLFISH

Lorne • 22 – 23 August 1990

editor:

D. A. Hancock

Department of Primary Industries and Energy
Bureau of Rural Resources

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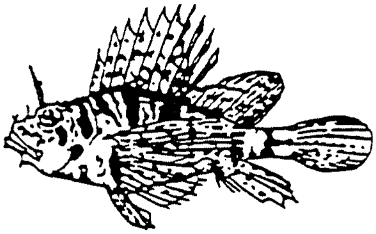

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The Bureau of Rural Resources within the Department of Primary Industries and Energy was established in October 1986. It provides scientifically objective advice to the Commonwealth Government in the rural sector. The Bureau's mission statement is "to promote efficient and sustainable use of Australia's agriculture, forestry and fisheries resources by providing scientific and technical advice to government".

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FOREWORD

J. P. Glaister

President, Australian Society for Fish Biology

The workshop on "The Measurement of Age and Growth in Fish and Shellfish" was held on August 22-23 1990 at Erskine House, Lorne, courtesy of the Victorian Department of Conservation and Environment. Its purpose was to try to resolve some of the controversy about what constitutes a validated age series, together with the estimation and comparison of growth. It was convened prior to a workshop on "Legal Sizes and their use in Fisheries Management" and preceded the Annual Conference of the Australian Society for Fish Biology (ASFB). Funding for the workshops and administrative resources was provided by the Fishing Industry Research and Development Council (FIRDC), the workshops coordinated by Dr Don Hancock (ex W.A. Fisheries) with publication of the proceedings made possible by the Bureau of Rural Resources (BRR).

The Society considered the topic to be both timely and of some urgency to Australian fish biologists researching (and publishing results of that research) age and growth. Interest ranged through freshwater and marine, fish and shellfish, isolated population studies and commercial fisheries.

The Society was fortunate in securing the services and long experience of Dr Richard Beamish, Director of the Pacific Biological Station, Nanaimo, Canada, as keynote speaker. The program was designed around several key themes each chaired by a scientist with particular expertise. Drs David Smith (Determination of Age), Keith Sainsbury (Inferences About Growth and From Growth) and Peter Young (General Discussion and Summing Up) ensured the Workshop ran smoothly and "worked". The basic procedure was for panel speakers to bring out the main points, followed by more general discussion from participants. Dr Kay Radway Allen provided the comprehensive summary with pointers to future directions at the conclusion of the workshop.

The success of the format and the general support for the concept has encouraged the Society to plan to include such workshops as a regular feature of its Annual Conference. The aim would be to act as a catalyst for national fish and fisheries expertise to give specific attention to technical areas as subjects of current or perceived national or regional significance.

The Society is most appreciative of the support of FIRDC, BRR and research institutions throughout Australasia. Publication of these proceedings was made possible by the Bureau of Rural Resources and its editorial staff. The Society is also indebted to the host State, Victoria, for the excellent arrangements for the meetings.

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SESSION 1

Introduction

Rapporteur: A. D. M. Smith

OPENING ADDRESS: SHOULD THERE BE A CONTEMPORARY ROLE FOR SOCIETIES SUCH AS ASFB?

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I would like to thank the organisers for the opportunity to speak at the opening of this workshop. As you all know this is one of two workshops which will run in conjunction with the 17th Annual Meeting of the Australian Society for Fish Biology.

Before formally opening the workshop I would like to make just a few brief comments about the role of societies such as this one. I hope that after you have considered my opening address, members might give due consideration to the question of an appropriate contemporary role for societies such as this one.

If a questionnaire were to be done amongst current members, about the role of the ASFB I would suggest that the bulk of responses would probably describe the ASFB as a body which brings together persons with a common interest in fish biology, and which essentially organises information exchange. Some responses might recognise a training role for the more junior members and might in fact see a workshop such as the one which will begin in a moment, as a demonstration of that training role.

I would hope that a few of the responses might see a role of the ASFB as one which also focused upon community education and active participation in public debate about issues which do, or might at some future date, impact upon fish biology, dynamics, distribution etc.

I wish to suggest that the small number of professional/technical societies whose members' interests are with aquatic resources, habitat etc, ought to give more consideration to assuming such a role and working through a longer term strategy to develop and achieve this.

Currently there are a range of inquiries and debates going on in this country and indeed even tactical responses being worked out by governments.

My list is not exhaustive but included on such a list would be:

- The House of Representatives inquiry into protection of the coastal environment.
- A proposed inquiry by the Resource Assessment Commission into coastal planning.
- The Southern Blue Fin Tuna debate.
- The Greenhouse Effect and responses by governments both state (territories) and federal to this issue.

- In Victoria, a Parliamentary inquiry into commercial and recreational fishing in bays and inlets.

- The Commonwealth Sustainable Development Paper.

- Proposed large scale pulp and paper manufacture in this country.

- The Commonwealth Policy Paper on Commercial Fisheries Management and the proposal to establish a Statutory Authority to manage commercial harvesting of a common property resource.

- A proposed reduction in Commonwealth research funds for fisheries research by at least 50%.

From where I sit, the input by the various aquatic societies to these inquiries and their contributions towards these debates has to date been a deafening silence. I wish to suggest that societies such as this one must begin to become active in these debates and inquiries and this should become one important contemporary role.

The members of course have every right to decide that this should not be a major role of such a society. If they come to that conclusion then I think there is a real risk and, collectively they ought to be aware of that real risk. The real risk, I suggest, is that the discipline ceases to be seen as one which is important and relevant to contemporary society and the institutions which govern it.

While such a situation may not pose a threat to the more established members who will attend the next few days of meetings, there is a possibility that the more junior members will find themselves on the same endangered species list as some of the fish species which will be discussed at these very meetings.

Let me finish with a few brief remarks about a contemporary role for societies such as this as a community educatory. I don't believe that anyone would deny the fact that the general public are fascinated by aquatic biology. Television has exposed them to aquatic biology through a range of programs put together by pioneers such as Jacques Cousteau and later by David Attenborough and David Suzuki as well as organisations such as the National Geographic Society and others. These have usually depicted marine species in their habitats and raised issues about the impact of mankind. The same degree of focus on freshwater species and habitats has yet to be achieved.

The more recent development of highly sophisticated public aquaria and the clear demonstration that thousands of people are prepared to pay to enter and experience these facilities, suggests to me that this public interest is not declining. Despite this the very professional and technical people who investigate, monitor and analyse so as to produce the data and descriptive information about what is exhibited to the public are currently in what I call "bunker mode". The symptoms of "bunker mode" are:

- A steady decline in financial support which has now been evident across Australia for several years.

- A serious and widespread de-skilling problem the end of which is not yet in sight.

- Ageing infrastructure in many of the institutions where work is being carried out.

- An inability now of the discipline to capture many of nations top-scoring students be they school leavers or graduates.

- The various societies must collectively address the following question. Despite clear public interest and a wide range of public concerns (look at the number of government inquiries) why is financial support of the aquatic disciplines so far down on the priority list?

I suggest furthermore that the time has arrived when collectively, the societies must do something about it.

Ten or so years ago I was working in medical research. At that time in Australia, medical research was in exactly the same situation as I am suggesting the broad aquatic discipline is in now. The various specialist groups such as cardiology, diabetes, etc, pooled their efforts and over ten years they have essentially reversed that situation. Last week was medical research week in Melbourne and the various societies no doubt held their individual meetings. However, running in parallel with these was a series of popular talks about medical science, public health, etc. These took place in Melbourne's Concert Hall and they drew in city commuters who had just finished a working day. The chairperson at each session was not an eminent scientist. Indeed media personalities like John Jost took up the challenge.

The importance of this community education process and its ability to generate public support should not be overlooked.

Finally I am delighted that the ASFB is running these workshops and I wish you all the best over the next few days of conference.

INTRODUCTION

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Ladies and gentlemen, welcome to the 1990 National Workshop series of the Australian Society for Fish Biology.

During preparation and planning of the Workshops, many long discussions were held with Don Hancock on ways and means of truly making these three days "Workshops". One is always faced with the worry that a series of seminars (or worse) may result. Invariably, the "Irresistible Force from the West" (Hancock) would fix me with a steely gaze and an exhortation "John, we must get them to *talk*!"

And so I sought inspiration in the Oxford Shorter: "*Worker*" was defined as "a non-fertile female in a colony of social insects". Not really us, I thought. "*Workshop*" looked closer, but was described as "a place of manufacture", while "*Workhouse*" was "an institution administered by Guardians of the Poor, in which paupers are lodged and the able-bodied set to work". This was closer, but Erskine House somehow did not convey the right atmosphere of a sweatshop. But there, buried on page 2449, under "Work", was the gem of why I think we are here, and that is "to do something involving effort (of body or mind); to exert oneself for a definite purpose especially in order to produce something or effect some useful result".

So here, at the seventeenth conference in 1990, we have two workshops. Also, for the first time we have had financial assistance from the Fishing Industry Research and Development Council (FIRDC) and I must acknowledge we are happy to welcome FIRDC Councillor Dr Bob Kearney as a participant in both workshops. In applying for support, our application included the following objectives:

(i) To promote the opportunity during the Australian Society for Fish Biology annual conference for the national fisheries research expertise to focus on a technical area or subject of current or perceived national or regional fisheries significance. Such area or subject to be identified by the membership of the Society *or by the Council* as appropriate.

(ii) To support *where appropriate* visiting fisheries scientists of acknowledged expertise in the workshop subject area to offer a national or international perspective.

(iii) To assist in the publication of workshop proceedings as a benchmark document of current knowledge in the workshop subject area.

(iv) As a result, to identify and define research questions of national fisheries significance.

I am sure you will agree that the topics for both our workshops look certain to achieve these objectives. I would ask all members and visitors over the next few days to consider possible topics for next year's conference.

We all owe a debt of thanks to Dr Don Hancock and Dr Kay Radway Allen, for the planning for these workshops. Australian fisheries science is fortunate in having the benefit of their advice and knowledge. Thanks are also due to Albert Caton (as always!), David Smith, Keith Sainsbury, Rob Lewis and Richard Tilzey. Richard conducted a survey of age determination studies in Australia and the results will be published as part of the proceedings.

Our first workshop will be the "Measurement of Age and Growth in Fish and Shellfish" and will continue over two days. The second is entitled "Legal Sizes and Their Use in Fisheries Management" and will comprise the third day. I'm sure members will agree the Bureau of Rural Resources Proceedings series has done a magnificent job in publishing the Proceedings from previous workshops. Gregg Berry of BRR deserves our especial thanks. For these workshops, separate proceedings will be published for each. Additionally, more than a third of this year's Conference papers are on Age Determination and Growth and with the concurrence of authors, abstracts will be published as an appendix to the proceedings.

Our first workshop will consist of three sessions. The first will be the "Determination of Age" and will be chaired by David Smith and summarised by Bob Kearney. Tomorrow we will participate in "Inferences about Growth and from Growth" to be chaired by Keith Sainsbury. The last session is to be chaired by Peter Young and will include a general discussion and summing up followed with a concluding discussion by Kay Radway Allen. We do urge all workshop participants to be vigorous and provocative in their participation and to assist rapporteurs in recording proceedings, please identify yourselves clearly before casting your pearls.

KEYNOTE ADDRESS
THE IMPORTANCE OF ACCURATE AGES IN FISHERIES SCIENCES

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Abstract

Structures used for age determination grow as a fish grows. In general there is an annual growth pattern with a period of rapid growth and a period of slow growth. Age determination is the recognition of the annual growth pattern on a particular structure, not the identification or counting of zones that form in a regular manner.

In the past the emphasis on zone counting rather than studying growth resulted in serious misinterpretations of the biology of commercially important species. Many species were seriously under-aged because it was not recognised that the pattern of growth of the structure used changed as the fish aged. Frequently this problem resulted from a failure to validate the age determination method for all age groups.

As a direct consequence of a failure to validate ages, natural mortality estimates were overestimated for some species resulting in overharvesting. Other consequences were the loss of time series data bases and the development of biological theory based on inaccurate information. In particular, little attention was paid to longevity because the importance of strong year classes was underestimated. As long as most fish were believed to be quite young (usually 5-15 years), there was little need to study longevity. Understanding longevity is important because it appears to be an important and neglected variable in the theory of stock and recruitment. As we learn more about recruitment patterns in long-lived fishes we may find there is a relationship between longevity and the relative importance of the environment in recruitment.

In 1983, Gordon McFarlane and I published a paper on the importance of obtaining accurate ages in fisheries science (Beamish and McFarlane 1983). There were two reasons for writing this paper. Firstly, we believed that incorrect ages were becoming common in the scientific literature and secondly, I was having trouble getting one of my papers on age determination published. I argued with an editor that the paper was not "just another paper on age and growth". The paper was important, I suggested, because it described how several methods of age determination could be used to assess the accuracy of estimated ages. Assessing accuracy was necessary because few people validated age estimates and the commonly used scale method produced serious underestimates of age. The editor of this well-known journal was understandably suspicious about this accusation that ages obtained from scales could be wrong. Eventually I agreed to write a paper describing the concerns I had about the accuracy of age estimates and he agreed that my paper was publishable.

I am told that the 1983 paper convinced many fisheries biologists and some editors, that the determination of the age of a fish is not a simple, unequivocal process. In fact, studies of age and growth are almost popular again as evidenced by the number of papers presented at this workshop and in the recent scientific literature.

Despite this renewed interest in obtaining accurate age determination estimates, I think the use of incorrect age estimates is still a serious problem in fisheries science. Perhaps you will agree with me by the end of this presentation.

I have a few opinions I would like to pass on now, in case I forget to talk about them later. The first, is that the need to validate ages should not mean that non-validated ages cannot be published. Validation must be considered, but it should not be a prerequisite for publication. I am confident that the peer review process, properly applied, will ensure that age estimates will not be used improperly. This does not mean that editors and reviewers should be less militant about the importance of validation. Any report that uses age estimates directly or indirectly should consider how ageing error affects the conclusions. By "any report", I include the more quantitative or modelling studies, especially stock assessments and studies correlating age class strength and environmental parameters.

My second thought is that it is important to centralise age determination staff into one unit. These talented and good-natured people cannot work in isolation. Accuracy and precision will improve in relation to the amount of daily discussion that occurs about age determination problems. These people also ought to be paid well because their age determinations are fundamental to sustaining fisheries. It seems to be an international phenomenon that practitioners of quantitative science are thought to be worth more than those of us that observe and record.

Finally, I think our inability to produce accurate ages has affected our thinking about the importance of the environment in the stock and recruitment process. This is where I want to end, so let me return to the beginning.

We started ageing fish late in the 1800's (Maier 1906) and we started the science of fisheries management in the mid-1900's with the publications by Ricker (1954) and Beverton and Holt (1956). I don't think we started ageing fish accurately until the 1980's. This doesn't mean that ages were wrong before this, only that it was recently that we recognised that our procedures for age determination were susceptible to significant errors. The scale method was probably the basis for our problems in age determination. The problem with the scale method is not that annuli are difficult to identify; it is that annuli are too easy to identify. The facility of interpreting annual growth patterns convinced many investigators that ages could be determined easily and that many fish were young (relative to something old - like ourselves).

One example of this problem with the scale method of age determination comes from some studies of the age of a freshwater fish in Central North America. Annuli on the scales of the common white sucker (*Catostomus commersonii*) are a classic example of scale annuli. The annulus is identified in the anterior quadrant of the scale where the first circulus that forms after a period of reduced growth, grows around the incomplete circuli that stopped forming when the fish growth was reduced. The annulus also is characterised by a change in the spacing of circuli. The scale in Figure 1A was estimated to have 5 annuli, but was from a fish that had been tagged at age 5 and was at liberty for 8 years. Once the fish was known to be older, an older estimate of age could be made (Figure 1B) but not by using the established criteria.

The problem with the use of the scale method for this species is that the pattern of scale development changed abruptly. The change apparently occurs when growth in length is reduced. Because the scale protects the fish, it is logical that scale growth must be reduced when the fish virtually stops growing. If the scale continued to grow, fish would look like swimming armadillos.

If early investigators had validated their estimates of all ages they would have realised that the pattern of annuli formation on the edge of the scale for older fish was different from the pattern in the centre of the scale.

The common white sucker is best aged using sections of fin rays. The fish represented in Figure 2 was aged using pectoral-fin-ray sections and was age 5 when tagged (Figure 2A) and age 13 when recaptured (Figure 2B). We now know that the maximum age for this species is at least 23 years; more than twice the previously accepted maximum age that was determined from scales.

We also should not assume that one structure can be used to age a particular species for the entire life span of the species. We should not assume any age is accurate unless it is proven to be accurate. The problem illustrated by the application of the scale method to age common white suckers is really the more general problem of validating age estimates. It is just as important to prove that younger ages are accurate as it is to validate older ages. To do this, it may be necessary to use more than one method of age determination. I use a number of structures whenever I need to estimate the age of a new species and sometimes a new population. I use the scale method even though most people now are suspicious of it; it can be useful for younger fish and some fish from heavily exploited populations. Sections of fin rays are often useful. The particular fin and the best rays from a fin will not be the same for all species; so it is necessary to look at all fins initially. Vertebrae can be useful, particularly sections of vertebrae. Other bones can be used, but I prefer the ones mentioned. Some investigators use a length-frequency analysis. I suggest the use of this kind of analysis only for very young fish. After lengths of age groups overlap, ageing fish with a length frequency analysis is little better than guessing.

The most dependable method seems to be the otolith method. I like to identify two otolith methods; the otolith surface method and the otolith cross-section method. In general, the otolith cross-section method is necessary for older fish. Cross-sections can be thin sections through the nucleus, or the otolith can be broken or cut in half through the nucleus. Burning the surface with the flame from an alcohol lamp usually improves the contrast of the annual growth pattern (alcohol should be used because other fuel can leave a carbon residue).

The importance of looking at a variety of structures is best illustrated by the attempts to age walleye pollock (*Theragra chalcogramma*) and Pacific cod (*Gadus macrocephalus*). The walleye pollock fishery currently is the largest in the world. Between 7,000,000 and 11,000,000 t were caught in the North Pacific in 1989. The scale is of little help for age determination even though it is still used by some investigators (Figure 3A). Sections of pectoral fins are excellent for some populations (Figure 3B) but are not useful for others (Figure 3C). When a broad translucent zone forms on the edge of the section (Figure 3C) it is an indication that the pectoral-fin method should not be used. This broad zone is a clear sign that another method is required. In a recent paper, Gordon McFarlane and I (in press) used broken sections of otoliths (Figure 3D) to estimate age of walleye pollock and we found ages could be about twice as old as previously thought. I will discuss the importance of this observation later.

Off the west coast of North America we have a rapid-growing cod that is a close relative of the Atlantic cod. Because the Pacific cod is a relatively short-lived, fast-growing fish it was aged using length frequencies after it was realised that otoliths and scales were of little use. In a recent comparison of ages from a length frequency analysis and from pectoral fin-ray sections, we concluded that both methods are subject to error (Beamish *et al.* in press). The length frequency analysis appeared to provide a general description of the age composition of a catch but did not accurately represent the age composition. The fin-ray method was difficult for some Pacific cod because a translucent zone formed late in the year, followed by a period of winter growth followed by another translucent zone. The annulus, therefore was the two translucent zones with an opaque zone in the middle. If the opaque zone in the middle was very wide, it was difficult to identify an annulus (Figure 4).

For older fish, it is almost always necessary to examine cross-sections of otoliths. You may not know if a fish is older so cross-sections need to be made as a matter of course. In some cases, the otolith section will reveal a pattern consisting of closely spaced zones toward the interior, usually these zones are most obvious on either side of the sulculus groove or the interior edge. The debate a few years ago was whether or not these zones were annuli (Figure 5A, age 6; Figure 5B, age 56y, both from Pacific Ocean perch). Many people now accept that they are annuli and the problem now is how to interpret these closely spaced zones. Before I discuss the relevance of this problem, let me review the evidence that proves that fish are much older than previously thought. There are two methods that have been used to show that these older ages are accurate, oxytetracycline (OTC) injections and radiochemical assays.

The injection of OTC produces a mark in the otolith that fluoresces under ultraviolet light. When the tagged and injected fish is recaptured, the amount of otolith growth beyond the OTC mark is compared to the estimated amount of yearly growth. The amount of OTC injected can affect the prominence of the mark and can cause mortality. In an earlier study (McFarlane and Beamish 1987) we produced a nomogram that allows investigators to select an appropriate dosage (Figure 6). In a more recent study (McFarlane and Beamish 1990) we observed that the tag can also affect growth (Figure 7) and mortality. Thus tagging and injecting fish with OTC may adversely affect the normal growth pattern for younger fish. Despite this problem, the pattern that forms in the otolith will be representative of the pattern that formed prior to the injection. In the examples that follow, the OTC injection confirmed that the zones identified as forming annually did form once a year. In the first example (Figure 8A), a sablefish (*Anoplopoma fimbria*) was tagged and injected at age 26 and recaptured 5 years later. The amount of otolith growth during the 5 years was similar to the amount in the 5 years before the OTC mark. A rock sole (*Lepidopsetta bilineata*) recaptured 2 years after marking, clearly shows 2 years growth on the otolith surface, distal of the OTC mark (Figure 8B). A yellowtail rockfish (*Sebastes melanops*) otolith section shows that the 2 annuli that formed after the OTC mark were similar in width and appearance to the annuli that formed before the mark (Figure 8C). The final example (Figure 8D) shows that the OTC mark can be used to mark fin rays. The section from a fin ray of a lingcod (*Ophiodon elongatus*) confirmed that the zones identified as forming annually, did in fact form once a year.

The second method is the use of a radiochemical assay. This method of assessing the general age of animals has been used by a number of investigators, but was first applied to the fish ageing controversy by Bennett *et al.* (1982). The basis for a radiochemical age determination is the incorporation of the calcium analogue ^{226}Ra into the otolith. ^{226}Ra decays radioactivity to ^{210}Pb (half-life of 22.3 years). The ratio of ^{210}Pb to ^{226}Ra in the otolith core is a measure of time that can be related to estimates of fish age because the rates of decay are known. Campana *et al.* (1990) used this method to confirm that the Atlantic redfish (*Sebastes mentella*) live to an age of 75 years. Their study indicated that current management of Atlantic redfish could be suboptimal because management plans did not recognise that this species was so longlived.

We have looked at a number of species and now believe that it is common to find species that are considerably older than previously thought (Table 1). Many people are disturbed when they see these ages. Accepting that a rockfish is 140 years in someway is not what one would expect. However, if you consider that in the past, we seldom proved that fish were young, it should not disturb us when we finally validate age estimates and find that fish can be very old.

Once we accept that fish are older, I think we will reconsider how we view stock and recruitment. In particular, we need to assess the consequences of ageing error in our understanding of population dynamics. We are beginning to study the consequences of ageing error and we are discovering that the errors can have dramatic consequences. For example, Lai and Gunderson (1987) examined the effect of ageing error on the population dynamics of walleye pollock by using 4 methods of age determination. They assumed ages from the surface of otoliths were the reference estimates and examined how parameters used in population dynamics would be affected when age estimates from the other methods were used. In general, the scale method and the fin-ray method produced ages that were younger than the otolith surface ages and the ages determined from the otolith cross section were the oldest. Growth curves generally were affected the least by ageing error. Under-ageing caused an increase in the mean length of younger age-classes, a decrease in the mean length of older year-classes and a decrease in the proportion allocated to a strong year class. The von Bertalanffy parameter L_∞ was only slightly affected by ageing error; K was affected, but survival (S) was most affected. Under-ageing could affect survival estimates by 20 to 40 %. It was interesting that in their study, over-ageing (using otolith cross sections) did not have much of an effect on von Bertalanffy parameters. They also found that under-aging had a significant effect on optimal fishing mortality and estimates of yield per recruit. A surprising result was the effect of the magnitude of the coefficient of variation (C.V.) on all of the parameters. Error in C.V. are errors in precision and are usually normally distributed. Lai and Gunderson (1987) showed that as C.V. increases, the erroneous parameter estimates became worse. The problem of incorrect parameter estimates is particularly relevant to catch-at-age analysis such as virtual population analysis. If M is too high when reconstructing stock size, a multiplication error is introduced in the starting year class size. This error will be present in the percentage age composition figures resulting in an overestimate of recruitment. In another study, Bradford and Peterman (1990) showed that if mortality was overestimated by 25% or 50% there was a very low probability of reconstructing a stock trend using VPA analysis for normal fishing mortalities.

These and other studies clearly show that under-ageing, resulting in over estimates of M, has serious effects on our understanding of the population dynamics. Overfishing clearly will occur if management strategies are based on such erroneous information.

I believe that ageing errors should always be estimated when we age fish. Errors in precision or the amount of normal variation about an age estimate can be determined by having several readers estimate the age of a sample, maintaining standard samples that are aged each year and having other agencies age samples. Estimates of the errors associated with accuracy are much more difficult. Even if a method is validated, there is an interpretation problem associated with the closely spaced annuli. Perhaps the best method of assessing the importance of ageing error is to carry out sensitivity analysis for any assessments that use age estimates that may be inaccurate.

The consequences of using erroneous ages in stock assessment appear to be serious. However, I believe, an equally serious or perhaps more serious problem is the failure to recognise the importance of strong year classes and underestimating longevity. I can best illustrate this problem by examining the age estimates from catches of two species discussed earlier.

As mentioned, the walleye pollock fishery is the largest in the world. Walleye pollock are fished by a number of countries, including USSR, Japan, Poland and USA. It is used primarily for surimi but some of the product is frozen and consumed as fillets. Recent studies indicate that walleye pollock are older than previously thought (McFarlane and Beamish in press). Age estimates using this new interpretation show that the fishable population in the Central Bering Sea consists of 3 strong year classes or periods of strong year classes (Figure 9). Two of these year classes or periods of strong year classes (1972-73 and 1977-78) make up almost 70% of the recent catch. Recruitment, therefore, is irregular and natural mortality rates are lower than used previously.

A more dramatic example of how ageing error obscured the importance of strong year classes is found in the study of Pacific ocean perch (*Sebastes alutus*). The age composition of commercial catches in the mid-1960's was determined from the surface of otoliths. These estimates indicated most fish ranged in age from 10 to 20 years and the age frequency was approximately normally distributed (Figure 10A). There was some evidence that one year class was more abundant than others, but the stronger year classes could only be identified for a few years. Ages produced using the otolith cross-section method are more than twice as old as ages produced by the surface method. New ages produced show a dramatically different age frequency of commercial catches from the same area (Figure 10B). The new age composition of the catch is no longer normally distributed. The new ages show that 3 strong year classes make up a large percentage of the catch. Strong year classes occurred in 1976, 1970 and 1952. The 1952 year class is the dominant age class in the catch, 32 years after it was produced.

When you look at the age compositions of these and other species that are aged using the otolith cross section method, you begin to have new insights into the stock and recruitment process. The dominance of strong year classes that form at different intervals clearly indicates that the environment plays a key role in the recruitment processes. The environment is not a factor that exerts a constant and minor effect on recruitment as often believed. For some species, at least, it appears that environmental effects may override spawning stock size effects because strong year classes result from small spawning biomasses; at least within the ranges of stock sizes for populations that are not seriously overfished. Looking at the age compositions in Figure 10, it is difficult to believe that incremental increases in spawning stock size will result in incremental increases in recruitment.

One also develops a new respect for longevity. There has to be a reason some fish live to be very old. It is possible that the longevity of a species has evolved to optimise recruitment in relation to the length of the period of unfavourable environmental conditions in the particular habitat of that species. If this is true, then longevity is an important parameter in stock assessments because it may be an indicator of the relative importance of the environment. The longer some species live, the greater the importance of strong year classes in the recruitment process.

I believe ageing errors have obscured the importance of strong year classes and caused us to concentrate on the importance of spawning stock size in the regulation of recruitment. Accurate estimates of age indicate that the influence of the environment on recruitment needs to receive more attention in fisheries science. We need to develop new models that recognise irregular recruitment patterns and perhaps identify minimum stock sizes. This new approach is not only important, it is urgent if you are a believer in global warming as I am.

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Table 1. Estimates of maximum ages of fishes in the commercial fisheries off Canada's west coasts. Revised from Chilton and Beamish 1982.

FAMILY AND COMMON NAME	MAXIMUM YEAR (AGE)
Anoplopomatidae	
Sablefish	70
Gadidae	
Pacific cod	8
Pacific hake	23
Walleye pollock	28
Hexagrammidae	
Lingcod	21
Pleuronectidae	
Arrowtooth flounder	22
Rock sole	25
Dover sole	45
English sole	22
Scorpaenidae	
Rougheye rockfish	140
Pacific Ocean perch	90
Shortraker rockfish	120
Silvergray rockfish	80
Darkblotched rockfish	47
Widow rockfish	58
Yellowtail rockfish	64
Bocaccio	36
Canary rockfish	75
Redstripe rockfish	41
Yellowmouth rockfish	71
Harlequin rockfish	43
Sharpchin rockfish	45
Squalidae	
Spiny dogfish	80

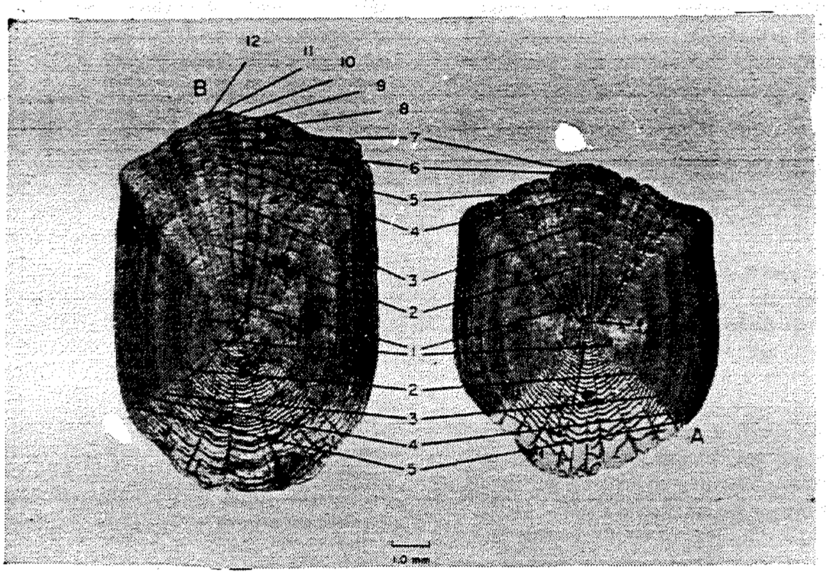

Figure 1. Scales from a common white sucker (A) before tagging and releasing, and (B) after recapture 8 years later. Both scales were estimated to be 5 years old using the standard definition of the scale annulus for this species (Beamish and McFarlane 1983).

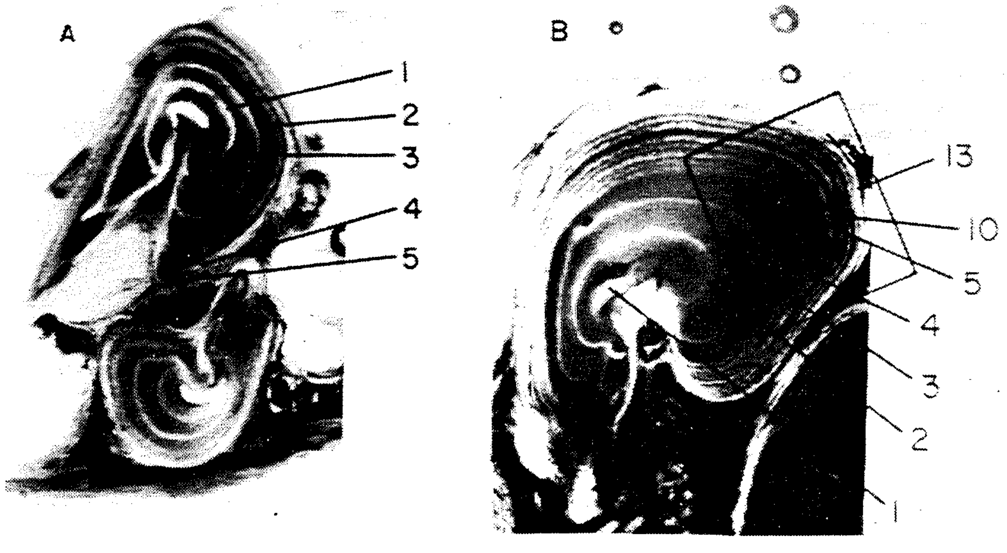

Figure 2. Sections of pectoral-fin-rays from the same fish in Figure 1. The fin-ray-annuli clearly show the fish was (A) age 5 when tagged, and (B) age 13 when recaptured. The use of more than one method of age determination provides an assessment of accuracy when a valid age determination method is not available (Beamish and McFarlane 1983).

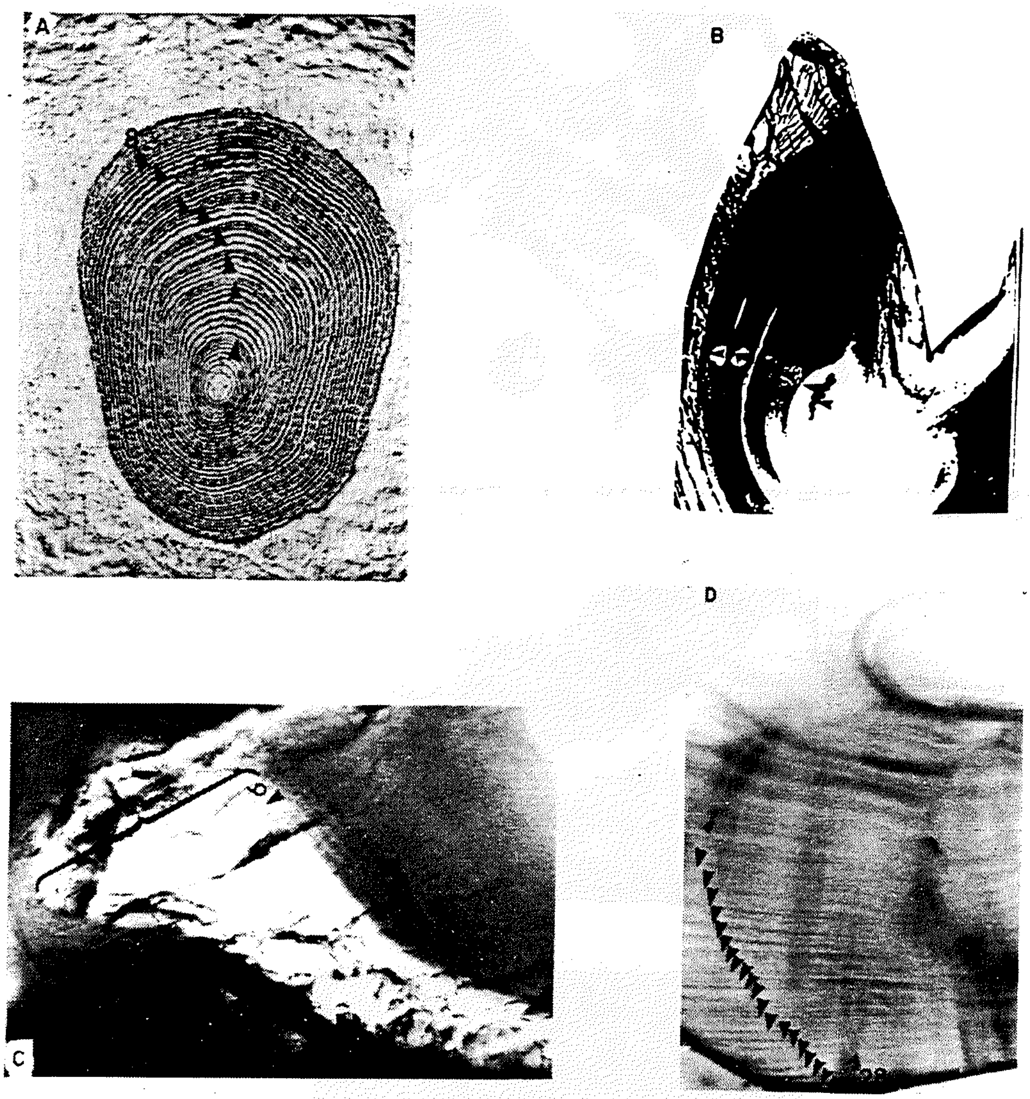

Figure 3. Methods used to age walleye pollock; (A) scale, (B,C) pectoral-fin-ray sections, (D) broken otolith section showing 28 annuli (McFarlane and Beamish in press).

Figure 4. Section of a dorsal-fin-ray of a Pacific cod showing a large amount of opaque winter growth between 2 translucent zones. The annulus is best defined as the 2 translucent zones and the opaque zone (Beamish *et al.* in press).

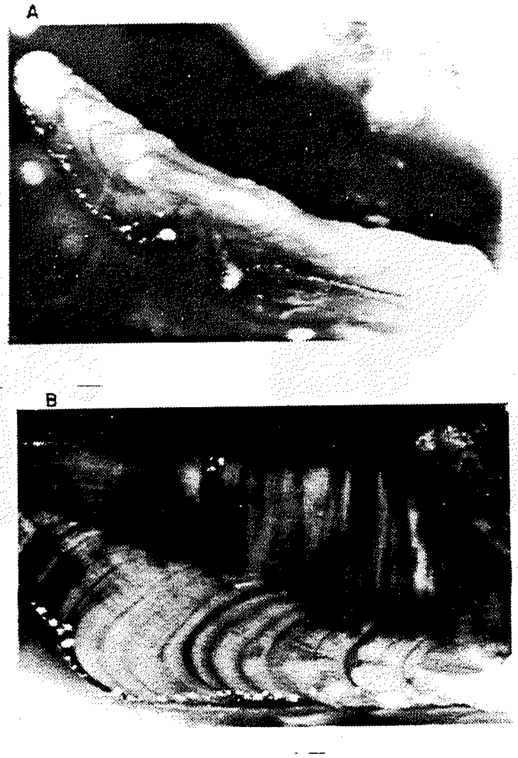

Figure 5. Broken and burnt cross sections of Pacific Ocean perch (*Sebastes alutus*) otoliths, showing the change in the appearance of the annuli as the otolith grows. 5A, age 6; 5B, age 56 years. The closely spaced zones towards the edge in 5B are now recognised as forming annually but exact counts of these zones can be difficult.

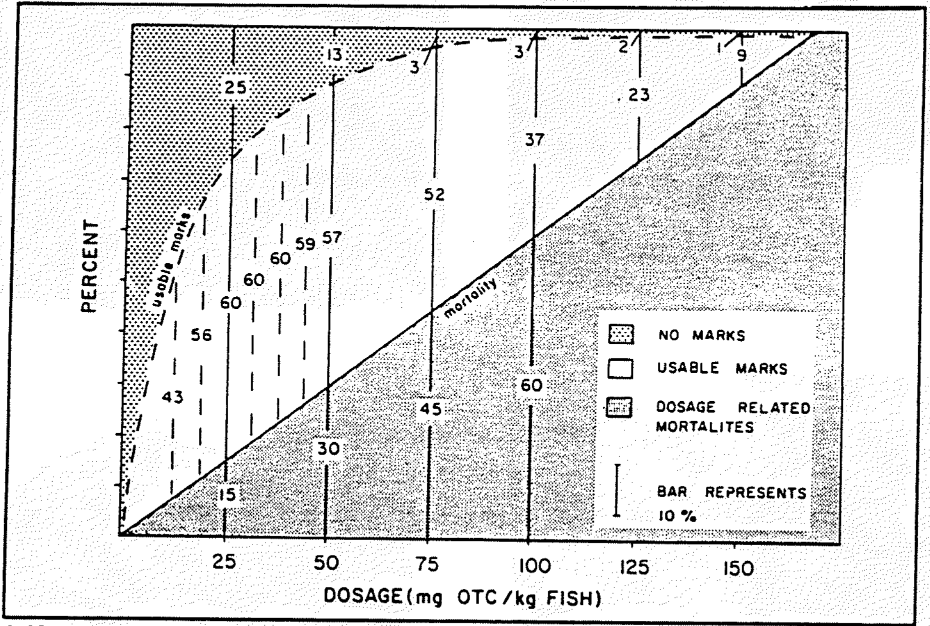

Figure 6. Nomogram showing the percentage of useable marks and percentage of mortalities that can be expected for various dosages of oxytetracycline for sablefish (*Anoplopoma fimbria*) (McFarlane and Beamish 1987).

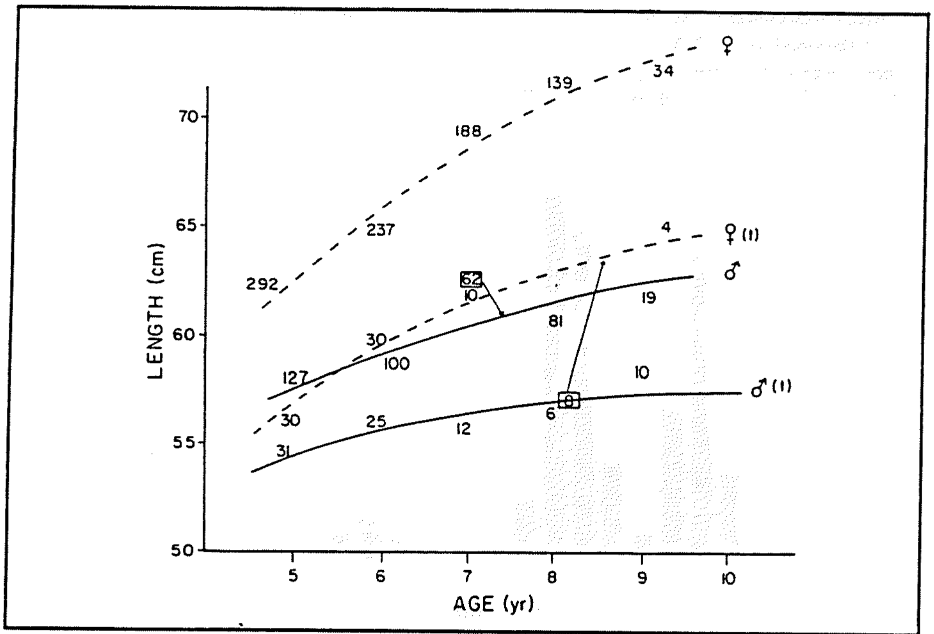

Figure 7. Growth curves of tagged (t) and untagged sablefish from the same year class. Tagged fish were significantly smaller for both sexes.

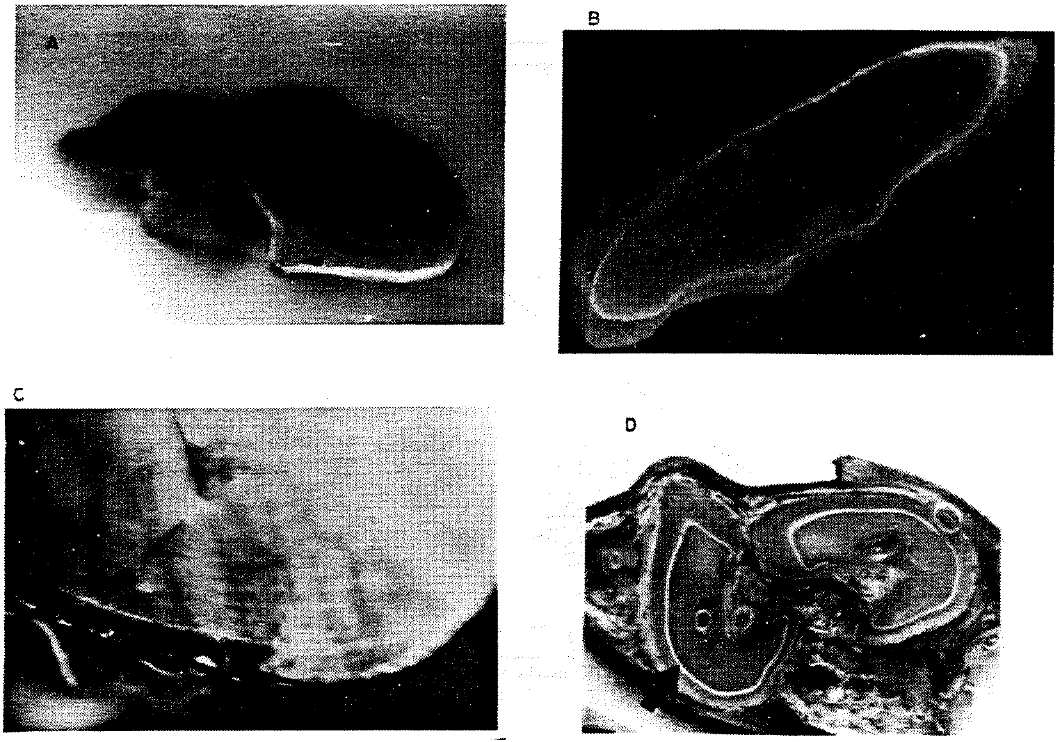

Figure 8. Examples of oxytetracycline marks in structures used for age determination.
(A) sablefish (Beamish *et al.* 1983).
(B) rock sole (Fargo and Chilton 1987).
(C) yellowtail rockfish (Leaman and Nagtegaal 1987).
(D) lingcod (Cass and Beamish 1983).

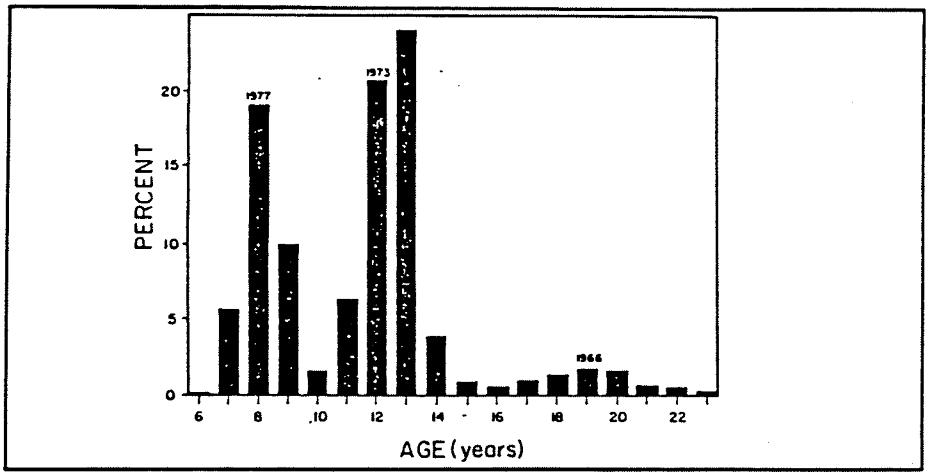

Figure 9. Age composition of walleye pollock sampled in February 1985 by Polish scientists in the international area of the Bering Sea (n = 299). Abundance of age groups was determined using an age-length key to convert length-frequency distributions into age frequency distributions. Relative year-class strength is in percent.

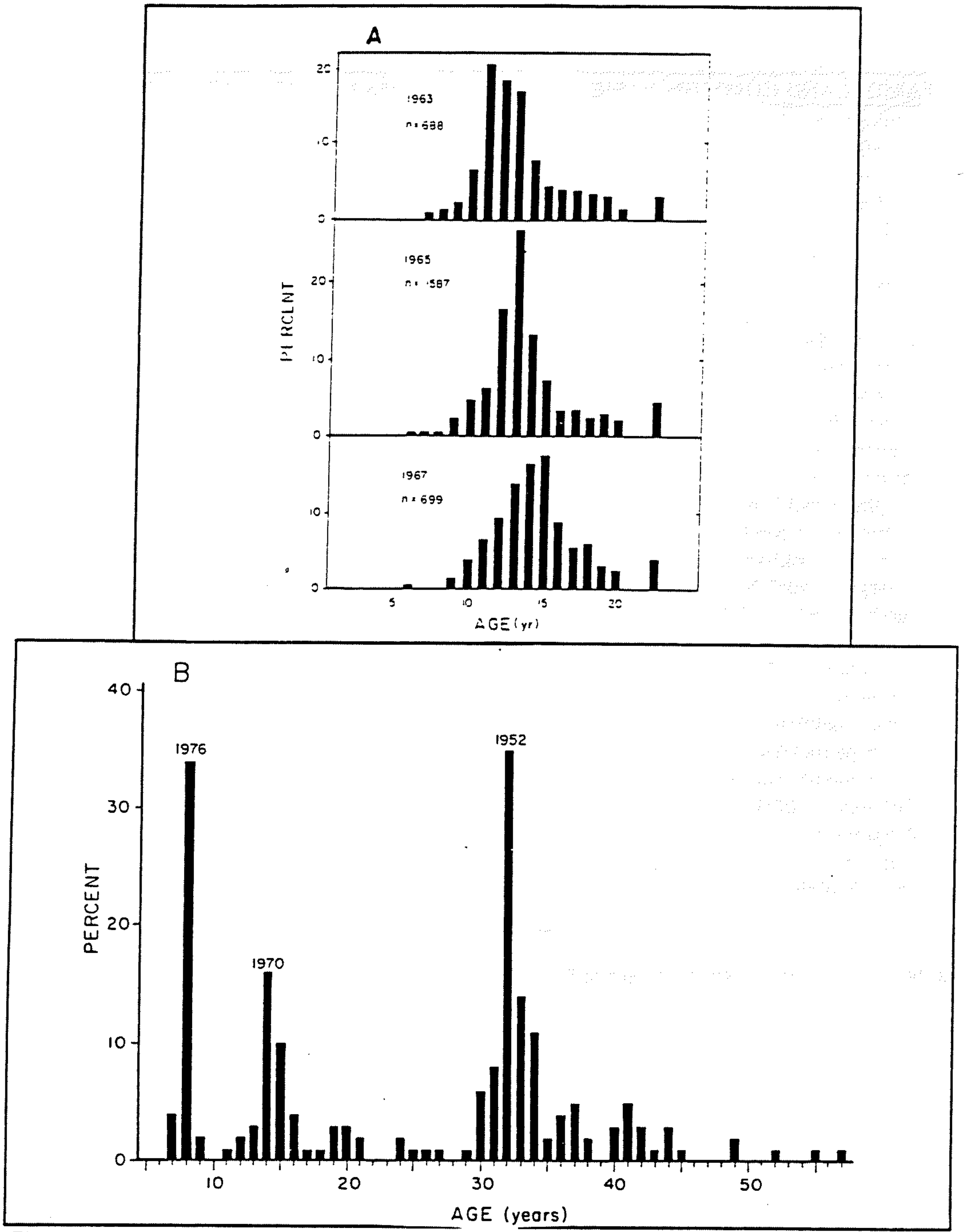

Figure 10. Age composition of commercial catches of Pacific Ocean perch off the west coast of Canada, (A) otolith surface ages (Westrheim 1973), and (B) ages from broken and burnt otolith cross-sections (Leaman 1988).

FAMILY AND COMMON NAME	MAXIMUM YEAR (AGE)
Anoplopomatidae	
Sablefish	70
Gadidae	
Pacific cod	8
Pacific hake	23
Walleye pollock	28
Hexagrammidae	
Lingcod	21
Pleuronectidae	
Arrowtooth flounder	22
Rock sole	25
Dover sole	45
English sole	22
Scorpaenidae	
Rougheye rockfish	140
Pacific Ocean perch	90
Shortraker rockfish	120
Silvergray rockfish	80
Darkblotched rockfish	47
Widow rockfish	58
Yellowtail rockfish	64
Bocaccio	36
Canary rockfish	75
Redstripe rockfish	41
Yellowmouth rockfish	71
Harlequin rockfish	43
Sharpchin rockfish	45
Squalidae	
Spiny dogfish	80

Table 1. Estimates of maximum ages of fishes in the commercial fisheries off Canada's west coasts Revised from Chilton and Beamish 1982.

DISCUSSION OF KEYNOTE ADDRESS

Recorded by A.D.M. Smith
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The Keynote Speaker, Richard Beamish, agreed with Peter Young that the apparent shrinkage of very old fish was explained by increased fishing effort in recent years, leading to higher growth rates in younger fish. Peter Gehrke wanted to know how much of the new ageing work is based on finding new marks and some new events to explain them, compared with physiological understanding of cause and effect. He was told that currently work is directed towards identifying annual patterns and deriving implications for ageing. Not much work is being done on the physiological basis of the patterns, and Richard Beamish asked why there should be. Peter Gehrke responded that we need to know whether it is an annual event at a particular time each year, and wanted to know how an increase in temperature will affect the formation of marks. Richard Beamish replied that the current major issue in age determination is to account for the small zones shown on his slides. In other words, are the fish 40 or 80 years old? Validation is expensive and difficult and cannot be done for every age. He further stressed the need for an age determination unit in Australia, for it to be well funded, and its staff well paid.

John Anderson asked what new technologies of ageing or validation are on the horizon, and was told that there are not a lot at present, although there may be some prospect with the work on the biochemical basis of protein ageing. Iain Suthers inquired about the value of weighing otoliths, to which Richard Beamish replied that a nice curve of weight increase with age can be obtained. However, if very accurate and important information is needed e.g. was 1941 or 1945 a good year class, then it is of no use.

John Kalish asked about modal progression for age validation with long time series, and was told that it works well for young fish for ages up to the point where frequencies overlap. Keith Sainsbury wanted to know whether the existence of the very old year classes shown in the graphs was consistent with the catch statistics of those fisheries. Richard Beamish responded that there was good internal consistency. Pacific hake are relatively short - lived and there hadn't been a strong year class for four or five years. One of the problems, however, is that many of the data bases are so poor that there isn't often a long time series. For walleye pollock in the Gulf of Alaska, you don't see the strong 1978 year class, but stocks have declined to give 10% of what are considered acceptable catches. For many species, the fishery today depends on strong year classes.

Keith Sainsbury was told that the species with the three strong year classes was Pacific Ocean perch. Richard Beamish was not sure what its exploitation rate had been over the past 20 years but was sure it had been low. To Sandy Morison the 1960's data for ocean perch seemed to show a clear case of modal progression, despite the mis-ageing, but this was the reason why people had believed in the ageing method. However, all the ages were incorrect.

Wayne Chamley commented that most of the current methods of ageing are very labour-intensive and therefore expensive. Micro-densitometry is automatable and lends itself to mass processing of sections. Can it be done? Richard Beamish agreed that many people are trying to do it at the moment but was not sure whether they would be successful.

Frances Laurenson wanted to know how understanding about the age of *Sebastes* has been affected by the fishery north of 54 degrees where fishing pressure has been low. She was told that this was the standard problem of a long-lived schooling species which is easy to catch. Fishermen did not believe the scientific advice that they could be fished out, so that when an area was set up for free fishing and they did in fact fish it out, they claimed that the reason they did not go back there was because it was "too expensive on fuel". You can't win!

Murray Macdonald asked about the use of lipoprotein and metabolic products in, for example, crustacea. Richard Beamish had read the papers but still needs to be convinced that it will work, especially above a certain age.

Rob Day inquired about environmentally induced strong year classes as to whether the speaker was suggesting that we dispense with the idea of managing on the basis of changing stock levels or is the need to adjust to changing year class strengths. Richard Beamish told him it was the latter. There is a need to set minimum stock sizes and to fish down surges of recruitment by decreasing quotas, i.e. saw tooth fishing. This required some knowledge of productivity and recruitment pulses. His final comment was that the adaptive basis for longevity may be related to the maximum period of unfavourable conditions over the evolutionary history of that species.

SESSION 2

Determination of Age

Chairperson: D. C. Smith

CHAIRPERSON'S INTRODUCTION

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This is the first national age and growth workshop to be held in Australia. It is particularly timely. Management of fisheries in Australia is moving towards output control measures based on age-structured stock assessments. The determination of accurate ages is, therefore, crucial for these assessments and the evaluation of the effectiveness of management strategies.

I would like to stress that determining age is difficult and one of the hardest areas is that of validation. The question of validation has been an issue of some controversy in Australia. We hope to address this during the workshop and to establish a broad framework of methods and terminology. The aim is to establish an agreed glossary of terms for ageing methods by the end of the workshop.

There are three sub-sessions. The first two deal with current usage and validation - for fish and sharks, and for commercial invertebrates. In the third sub-session panellists will discuss future directions and problems encountered. Finally, Bob Kearney has agreed to the onerous task of reviewing the whole session.

Each panellist has been allocated 5-10 minutes and there will be time for general discussion at the end of each sub-session. This is a workshop *not* a series of seminars so we hope the session will be as "interactive" as possible.

Before I introduce the first panel member, I would like to quickly mention the current status of the Central Ageing Facility. The main objective of this facility is to ensure the coordinated long-term collection of age composition data. Eventually, once costings have been worked out, it will also be available for fisheries agencies to use on an *ad hoc* basis as well. FIRDC has provided us with establishment costs, ie microscopes, computers, preparatory equipment etc. Running-costs, in the short term, will come from industry levies administered by the Australian Fisheries Service. Discussions are on-going but I am confident that before the end of the year the Facility will be a reality. [The Central Ageing Facility commenced operation at the Marine Sciences Laboratories, Queenscliff, Victoria, during July 1991.]

Sub-session A

Current Usage and Validation - Fish and Sharks

Panellists:	K. R. Rowling A. J. Fowler J. R. Anderson T. I. Walker P. L. Moulton J. M. Kalish R. E. Thresher
Rapporteur:	D. Huber

AGE DETERMINATION OF SOUTH EASTERN DEMERSAL TRAWL SPECIES

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The purpose of this paper is to briefly review methods of age determination which have been reported for the main species taken by the South Eastern Trawl Fishery (SETF), with the exception of orange roughy *Hoplostethus atlanticus* which will be the subject of a separate paper at this workshop. A summary of the results of the review of published and semi-published age determination studies is presented in Table 1.

Tiger flathead *Platycephalus richardsoni* is the only SETF species with any history of age determination studies, which date back to the mid 1930's. All the studies on flathead have used whole otoliths for age determination and the methodology has been reasonably well documented. Although there has been some recent disagreement regarding interpretation of the innermost circuli on the otoliths, resulting maximum ages and von Bertalanffy parameters for these recent studies are very similar.

Ageing studies on the other species have been restricted to the last decade, except for some early work on jackass morwong *Nemadactylus macropterus* by Han (1964) using scales. This study was in agreement with a result widely reported in the literature that the use of scales for age determination tends to lead to an underestimation of the abundance of older age classes in the samples. All the studies carried out in the past decade have used either whole otoliths, or sectioned otoliths for those species which have thicker otoliths. Various techniques of clearing and/or charring whole otoliths have been investigated; however, most workers have found such techniques to be very time consuming, with little or no improvement in clarity of the circuli.

Validation of the ages determined has been attempted in all the recent studies, generally using marginal increment and/or length frequency modal progression methods. In many cases this validation has succeeded over a limited range of ages; however, for some studies validation has been completely unsuccessful. In some cases, the results of tag/recapture experiments have been used to attempt to validate ageing studies. However, while generally providing support for the estimated growth rates, such studies have also failed to fully validate the ageing techniques over the whole of the range of ages in the exploited population, as the tagging experiments have primarily been designed to yield information on mortality rates. Proper validation of age determinations can thus be seen to be one of the major problems encountered in these studies.

While not wishing to deal in any great detail with the actual results obtained in each of the studies, it is interesting to note that the maximum estimated ages of the main SETF species fall between about 10 and 30 years, which indicates that they are mostly moderately long lived species. The need for proper validation of these reported ages is therefore considered to be very important, before use is made of the results of age determinations in any modelling of stock dynamics.

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Table 1. **Summary of age determination studies reported for south eastern demersal trawl species**
T_{max} - maximum reported age (years); L_∞ - asymptotic length (cm); K - growth constant (yr^{-1});
t_0 - hypothetical age at length zero (yr); F - Female; M - Male

Species	Reference	Method(s)	Validation	Problems	Results			
					T_{max}	L_∞	K	T_0
Tiger flathead	Dakin 1939	Whole otoliths	Hyaline/opaque regular periodicity	First study tentative ages only	6-8yrs	No von Bertalanffy parameters reported		
	Fairbridge 1951	Whole otoliths	% Opaque edges	False annull, otolith interpretation	7 (+) yrs	No von Bertalanffy parameters reported		
	Huston 1955	Whole otoliths	None reported	No validation, seasonal variation	8 (+) yrs	No von Bertalanffy parameters reported		
	Montgomery 1985	Whole otliths	Marginal incriment	Incomplete validation	F:12yrs M:8yrs	76.6 58.9	0.122 0.178	-0.65 -0.63
	Wankowski *et. al* 1986	Whole otoliths	(Expected) marginal increase	Indistinct 1st annulus on some otoliths	F:12 yrs M:10 yrs	58.8 48.2	0.160 0.178	-1.22 -1.69
Jackass morwing	Han 1964	Scales	None reported	Small sample, older ages under-represented	9 yrs	No von Bertalanffy parameters reported		
	Smith 1982	Whole otoliths	Marginal increment tagging	Juvenile otoliths not available	F:16 yrs M:11yrs	51.1 45.5	0.125 0.167	-3.17 -3.51
Gemfish	Withell and Wankowski 1989	Whole otoliths	Marginal increment length freq. modes	Unsuccessful validation small sample size	13 yrs	112.3	0.153	-0.89
	Rowling 1990	Whole otoliths	Length freq. modal progression to 3 yrs	Incomplete validation	F:16yrs M:11yrs	109.4 97.5	0.180 0.212	-0.61 -0.52
Blue grenadier	Kenchington and Augustine 1987	Whole otoliths <8 yrs, sectioned otoliths	Length freq. modal progression <60 cm	Only validated to 3 yrs	25 yrs	F:99.3 M:90.7	0.203 0.256	-1.48 -1.21
Ling	Withell and Wankowski 1989	Whole and sectioned otoliths	Marginal increment Length freq. modes	Unsuccessful validation small sample size	21 yrs	135.5	0.095	-1.41
Redfish	Diplock 1984	Whole otoliths	Marginal increment, % opaque edges, tagging	Incomplete Validation	F:16 yrs M:11 yrs	40.4 35.5	0.146 0.182	-0.35 -0.17
Ocean perch	Withell and Wankowski 1988	Scales <5 yrs, whole and sectioned otoliths	Length freq, modes, marginal increment	Unsuccessful validation small sample size	F:30 yrs M:35 yrs	44.7 43.2	0.107 0.115	-0.163 -0.285

ATTEMPTED VALIDATION AND AGEING OF SMALL TROPICAL FISH USING OTOLITHS

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Abstract

The usefulness of otoliths in the determination of age of two closely-related species of damselfish collected from the tropical central Great Barrier Reef was assessed. *Pomacentrus mollucensis* had sagittae which when sectioned, demonstrated a pattern of increments of alternating opaque and translucent bands which were validated to be formed yearly. Therefore, a count of such increments translated directly into an estimate of the age of the fish. These sections were generally interpreted in the same way on different occasions. For *Pomacentrus wardi*, collected from the same habitat, the sectioned otoliths were most often uninterpretable as they did not present a clear pattern of increments. This between-species comparison is relevant to the dogma that has surrounded the applicability of direct ageing to tropical fish.

Introduction

The usefulness of the hard bony structures of fish such as otoliths, for the ageing of tropical species remains unresolved. The dogma states that such methods do not work for tropical fish because there is insufficient seasonal variation to induce a seasonal pattern of growth in such structures (Pannella 1980; Brothers 1982). However, in recent years some tropical species have been successfully aged using such techniques (Loubens 1978; Johnson 1983; Brothers and Mathews 1987; Manooch 1987; Samuel *et al.* 1987; Hill and Radtke 1988; Dee and Radtke 1989; Morales-Nin and Ralston 1990). Therefore, for a study of age and growth of tropical fish, it should no longer be initially assumed that direct ageing is inapplicable, and that it is necessary to apply such techniques as tag/recapture studies and length frequency analysis. Pilot studies should be done to assess the usefulness of direct ageing for such species, and particular attention should be paid to otoliths, as these are the most often preferred anatomical structure (Bagenal 1974; Pentilla and Dery 1988).

In this study several criteria were assessed to determine the usefulness of otoliths for ageing two congeneric and co-habiting species of damselfish from the central section of the Great Barrier Reef. Studies were done to assess the presence of a utilisable internal structure that could be useful for ageing and to assess the interpretability of such structures. To this end, the specific aims addressed were to:

- determine if otoliths demonstrated an internal structure of increments;
- assess the precision of the interpretation of otolith structure;
- determine the period of increment formation.

Materials and Methods

Fish Collection

Specimens were collected from large micro-atolls in the lagoon of John Brewer Reef (18° 38's, 147° 04'E) on the central Great Barrier Reef. Collections were made on four occasions; 16th March, 3rd September, 3rd November 1988 and 26th February 1989, by spearing and with the fish anaesthetic quinaldine. Fish were preserved in concentrated ethanol and dissected as soon as possible after the field trip, to minimise the potential degradation of the otoliths. Prior to dissection, fish were weighed (preserved weight to mg) and measured (Standard Length to mm). After dissection, the sagittae were cleaned, washed in distilled water and stored dry in small, numbered glass vials.

Preparation of Sections

Thin transverse sections of sagittae were produced by grinding using a gem-faceting machine (Gemmasta Model GF4). Initially each sagitta was embedded in Spurr's histological resin to form a small, hard block. This block was then mounted in a grinding jig and ground down close to the central core of the otolith, using different grades of wet and dry paper (120, 1000). The ground surface was then polished using a graded series of lapping film (9, 3, 1 mm). This polished surface was glued to a microscope slide (using Spurr's resin) and the block was ground and polished from the other direction, resulting in a polished section of otolith between 50 - 100 mm thick.

Sections of otoliths were examined using a Leitz compound microscope on which was mounted an Ikegami high resolution, black and white video camera connected to a Commodore Amiga personal computer with a high resolution colour monitor. With the image of the otolith displayed on the monitor the increments could be counted and measured using the computer.

Precision

The interpretability of otolith structure was assessed in two ways. Firstly, the repeatability of the counts of increments in transverse sections was assessed. For each species a number of otoliths was examined and the increments counted on two occasions separated by periods that ranged from days to months. Precision was assessed by comparing the second count of all otoliths with the first count.

The second method for the assessment of precision was based upon classifying each otolith according to the ease of interpretation of the otolith structure. There were four classes defined as follows:

Class 1 - Otolith structure was uninterpretable, and no estimate of the number of increments was possible;

Class 2 - Increments were difficult to distinguish, and a count was obtained, however the confidence that could be placed in its accuracy (i.e. reflecting the real number of increments) was low;

Class 3 - Increments were distinguishable, although their clarity was intermediate;

Class 4 - Increments were very clear and the otolith was easy to interpret.

Validation

The rate at which increments are deposited in otoliths was assessed by marking otoliths *in situ* with tetracycline (Kobayashi *et al.* 1964, Fowler 1990). On 26-27th March 1988 individuals of *P. mollucensis* associated with isolated colonies of the hard coral *Pocillopora damicornis*, and individuals of *P. wardi* living in the adjacent micro-atoll matrix were captured with quinaldine. Each fish was injected with a volume of tetracycline/saline solution determined by its size, and then released at the capture site. Injection was done with a 1.0 mm syringe and a 26 gauge needle (0.45x13 mm) which was inserted through the skin, under the mid-lateral, post-pectoral scales into the coelomic cavity.

Fish were treated with a dose of tetracycline that was approximately equivalent to 50 mg/kg body weight (McFarlane and Beamish 1987), although it was necessary to use SL (standard length) to approximate weight in the field. This was based upon the relationship between SL and weight which was initially determined by taking a small sample of approximately 20 individuals of a broad size range of each species and weighing and measuring these fresh specimens. The concentration of the solution administered was 5.0 mg tetracycline ml^{-1} of sterile saline.

On 3rd September 1988, 24 *P. mollucensis* and 20 *P. wardi* were collected from the area in which marking with tetracycline had taken place. On 26th February 1989, a further 59 *P. mollucensis* and 55 *P. wardi* were removed. On each occasion these potentially-marked fish were treated according to the procedures described above, although after dissection otoliths were stored in the dark.

Sections of otoliths from these collected fish were examined on two occasions under white, reflected light and the number of opaque increments counted, and their distance measured from the edge along several axes. The otoliths were then examined in the dark using incident UV light. When a tetracycline band was evident the distance from this to the edge of the otolith along two axes was measured (at x400), to determine the absolute growth of the otolith over the time between treatment and capture. By comparing the respective measurements, the location of the tetracycline circulus was determined relative to the location of the opaque circuli.

Results

Descriptions of Sections

The transverse sections of sagittae from *Pomacentrus mollucensis*, when viewed under reflected light, each displayed a central, dense, opaque region (Figure 1a). The region around this decreased in opacity and the larger otoliths then had alternating sequences of thin opaque lines and wider translucent areas. The opaque lines were counted as circuli. In sections of 0.05 - 0.1 mm thickness, opaque increments were thin relative to the clear regions they separated and sometimes were continuous from the ventral to the dorsal tips (for orientation refer to Pannella 1980). Often, however, their clarity was disrupted in various axes and counting was generally done along one or two axes.

The transverse sections of sagittae from *Pomacentrus wardi* also had a dense opaque central region which eventually gave way to a clear region (Figure 1b). In some otoliths more opaque regions were discernible; however, in general these were difficult to distinguish from the background matrix and rarely were they as clear as for the otoliths of *P. mollucensis*. The otoliths of both species shared approximately the same growth patterns relative to SL; those of *P. wardi* were at the larger end of both distributions and those of *P. mollucensis* at the smaller end (Figures 2a, 2b). Despite this similarity in growth pattern the otoliths of *P. wardi* contained less defined and precise macrostructure, as the distinction between opaque lines and translucent regions was generally poor.

Precision

For *Pomacentrus mollucensis* the counts of opaque circuli in sections of otoliths of 124 fish were compared between two occasions. Of these a small percentage were rejected as unreadable on one or both occasions (Figure 3a). For the remainder, differences varied between 0 and 3, but with a decreasing relationship here (Figure 3a). Generally, these results suggest that otoliths were interpreted in the same way on both occasions. However, since some otoliths were less clear and more difficult to interpret than others, there were some differences in the counts. For

Pomacentrus wardi a total of 112 sectioned sagittae were examined twice. Of these the majority were rejected as unreadable on one or both occasions (Figure 3b). Of the remaining minority, the difference between counts was generally zero indicating that when structure was evident it was interpreted consistently on both occasions (Figure 3b).

For *Pomacentrus mollucensis* only a small percentage of sections were rejected as unreadable (Figure 4a), and the majority were classified as either Class 3 or 4 (Figure 4a). Therefore, the confidence that could be placed in the estimate of the number of increments was relatively high. Alternatively, for *P. wardi* most sections were classified as either Class 1 or 2, which meant that they could either not be interpreted at all because of the lack of any consistent macrostructure, or where some macrostructure was present, very little confidence could be placed in the accuracy of its interpretation (Figure 4b).

Validation

Collections were made twice from the vicinity of the reef from where fish had been treated with tetracycline. Of 24 *Pomacentrus mollucensis* collected in September, 5 had been treated with tetracycline and of 59 collected in February 1989, 18 had been treated (for photos refer to Fowler (1990)). These fish had been at large since treatment for periods of 168 and 335 days respectively. Of the five fish collected in September, the four smallest (22.7-30.6 mm SL) had no opaque increments when viewed under reflected, white light. The fifth and largest fish (36.5 mm SL) had one opaque increment that was closer to the otolith centre than the tetracycline band, indicating that it had formed prior to treatment. Therefore, no fish had formed an opaque circulus in the 168 days between late March and early September 1988.

The 18 fish collected in February 1989 ranged in size between 30.5-55.1 mm SL and their otoliths varied in size accordingly. Each displayed one opaque increment between the tetracycline band and the edge of the otolith (Figure 5) which therefore, formed in the 335 days since treatment with tetracycline. The results from both collections of fish suggest that formation of circuli occurred once per year at some time between September and February. From this, the otolith macrostructure can be interpreted to give an estimate of age of the fish.

In total only eight *Pomacentrus wardi* were recaptured which had previously been treated with tetracycline, four of which had been on the reef for 168 days and four for 335 days since treatment. The interpretation of these otoliths was ambiguous because of the difficulty in distinguishing or interpreting the macrostructure of the otoliths under either reflected or transmitted white light. This, in combination with the low number of recaptured treated individuals, has prevented the successful validation of the period of increments.

Discussion

The two congeneric species of fish considered in this study were both small coral reef fish, which co-habited on the same lagoonal patch reefs. Furthermore, their otoliths had a similar shape and appearance, and demonstrated similar growth patterns with respect to standard length. However, despite these similarities, their otoliths presented remarkable differences in their internal structure. One species demonstrated an alternating sequence of opaque/translucent bands which could be interpreted to give an estimate of the age of the fish in years. Alternatively, for the second species, the internal structure was generally too indeterminate to confidently interpret in terms of the age of the fish.

Pomacentrus mollucensis joins a growing list of tropical species that have defied the dogma regarding the inability to age them because of a supposed lack of seasonality in their environment (Loubens 1978; Longhurst and

Pauly 1987). On the contrary it is most likely that the fish considered in this study had experienced considerable seasonal variation through their lives. Water temperature in shallow habitats of the reefs of the GBR can display seasonal variation of as high as 10°C, due to such factors as insolation during the day and cooling by evaporation and irradiation at night (Potts and Swart 1984; Gladstone and Westoby 1988). This by far exceeds the 4 - 5°C seasonal range suggested as being necessary to cause the formation of a discernible increment pattern (Longhurst and Pauly 1987).

On the other hand, *Pomacentrus wardi* has conformed to the expectations determined by the dogma by failing the criterion regarding the formation of a clear internal structure of increments. The otoliths rarely contained an interpretable pattern of increments, despite the considerable seasonality in their environment, as indicated above. This suggests that these fish did not respond so deterministically in their physiology to the seasonal variation at John Brewer Reef as did *Pomacentrus mollucensis*.

This study has contributed to the debate regarding the direct ageing of tropical fish by indicating that there is no simple generalisation that can be made. That one species conformed to the dogma and another closely-related species defied the dogma indicates the complexity of the situation. This is further exacerbated by the results from another on-going study which suggests, not surprisingly, that the structure of otoliths of individuals of the same species but collected from different geographic regions of the GBR, also vary considerably (Fowler, unpublished data). Therefore, it is unwise to generalise about ageing tropical fish, and this should be assessed for each species and region for which age and growth information is required. Such assessment can be done reasonably quickly by removing a small sample of fish, preparing sections of their otoliths and examining for an interpretable pattern of increments.

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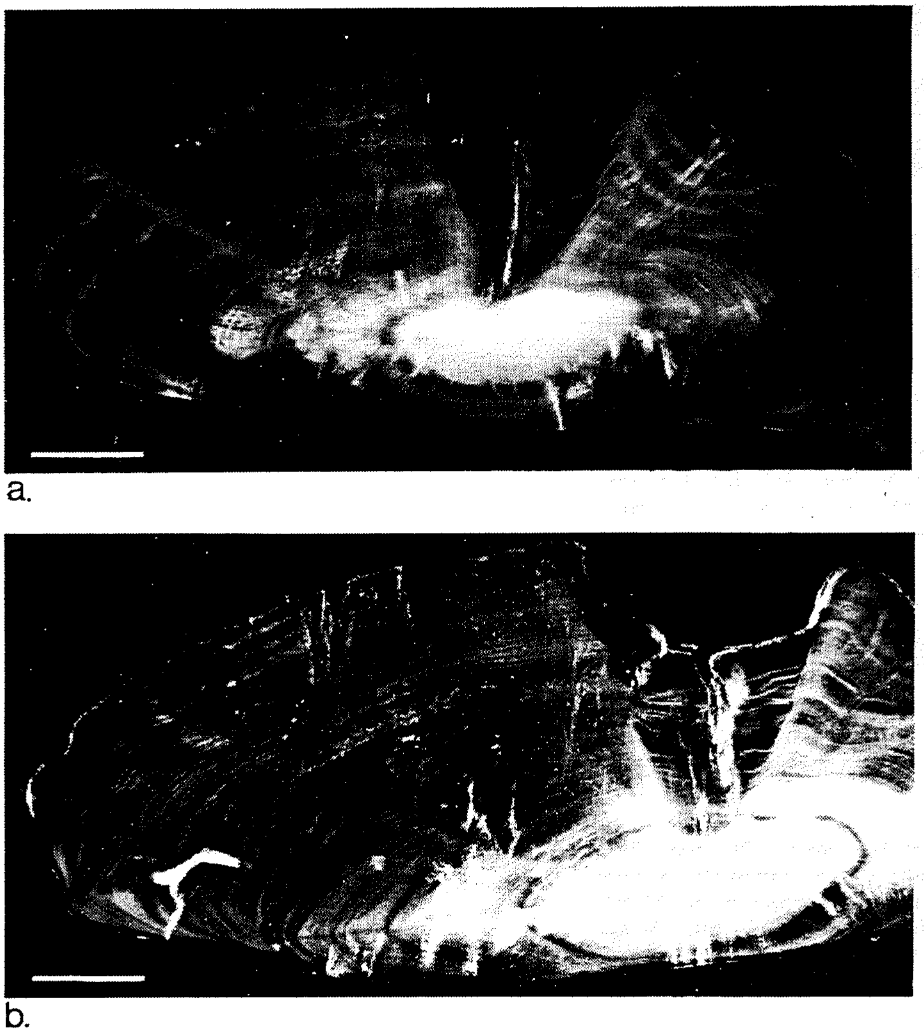

Figure. 1. *Pomacentrus mollucensis* (a), *P. wardi* (b). Photographs of sections of sagittae illuminated by white incident light. (Both scale bars = 200 µm).

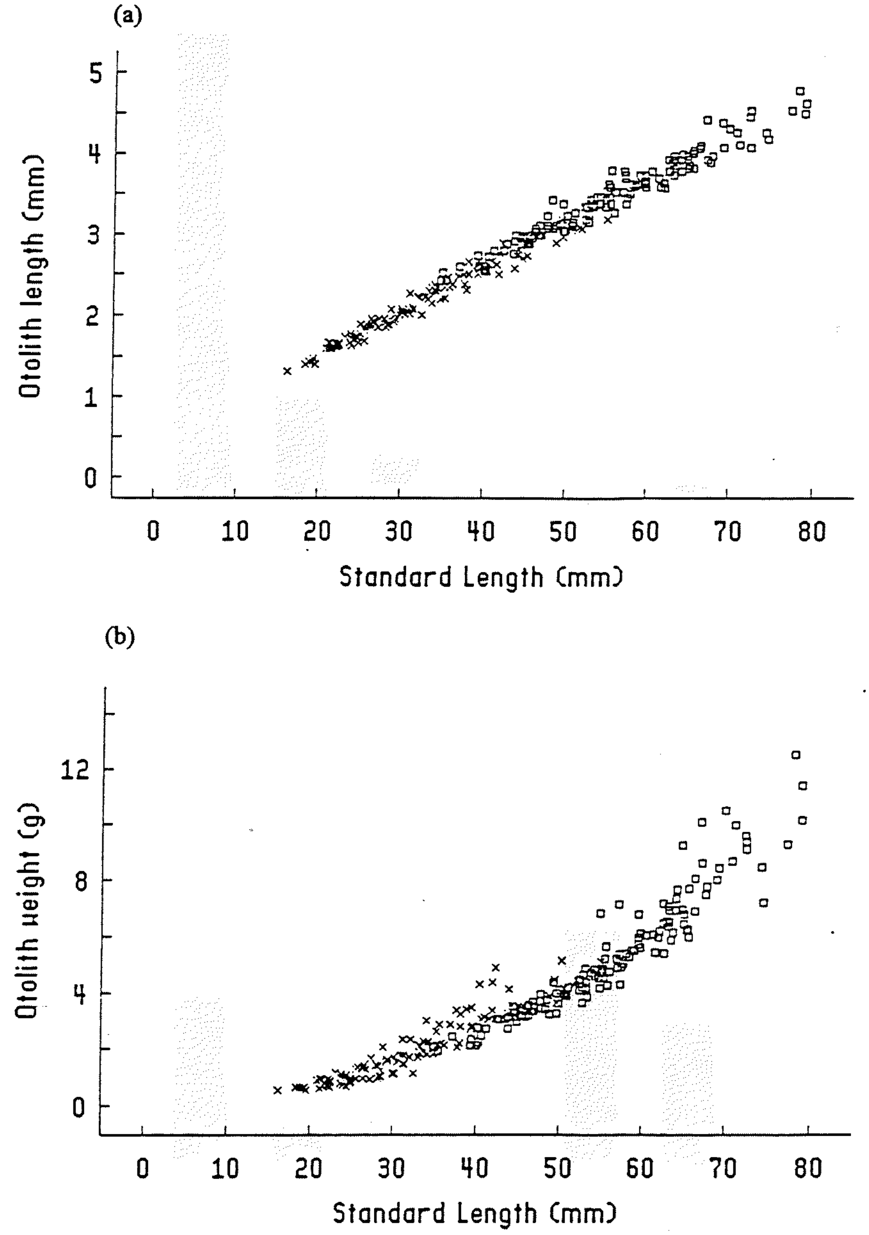

Figure 2. *Pomacentrus mollucensis* (crosses), *P. wardi* (open squares). (a) Relationship between otolith length and SL. (b) Relationship between otolith weight and SL.

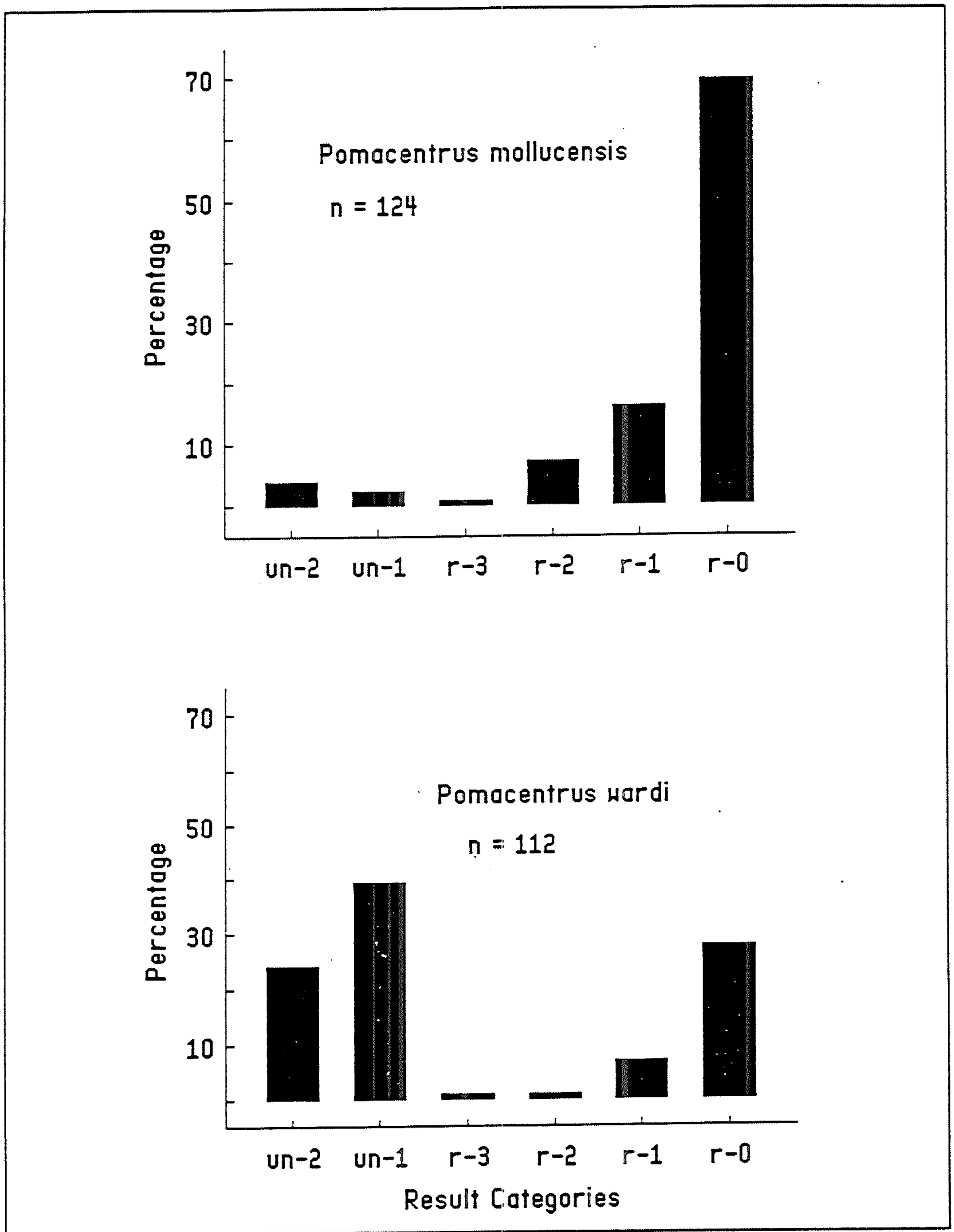

Figure 3. *Pomacentrus mollucensis, P. wardi.* Results from the assessment of precision. (un-2) unreadable on both occasions, (un-1) unreadable on one occasion, (r-3) otoliths readable but counts differed by three, (r-2) counts differed by 2, (r-1) counts differed by one, (r- 0) counts did not differ.

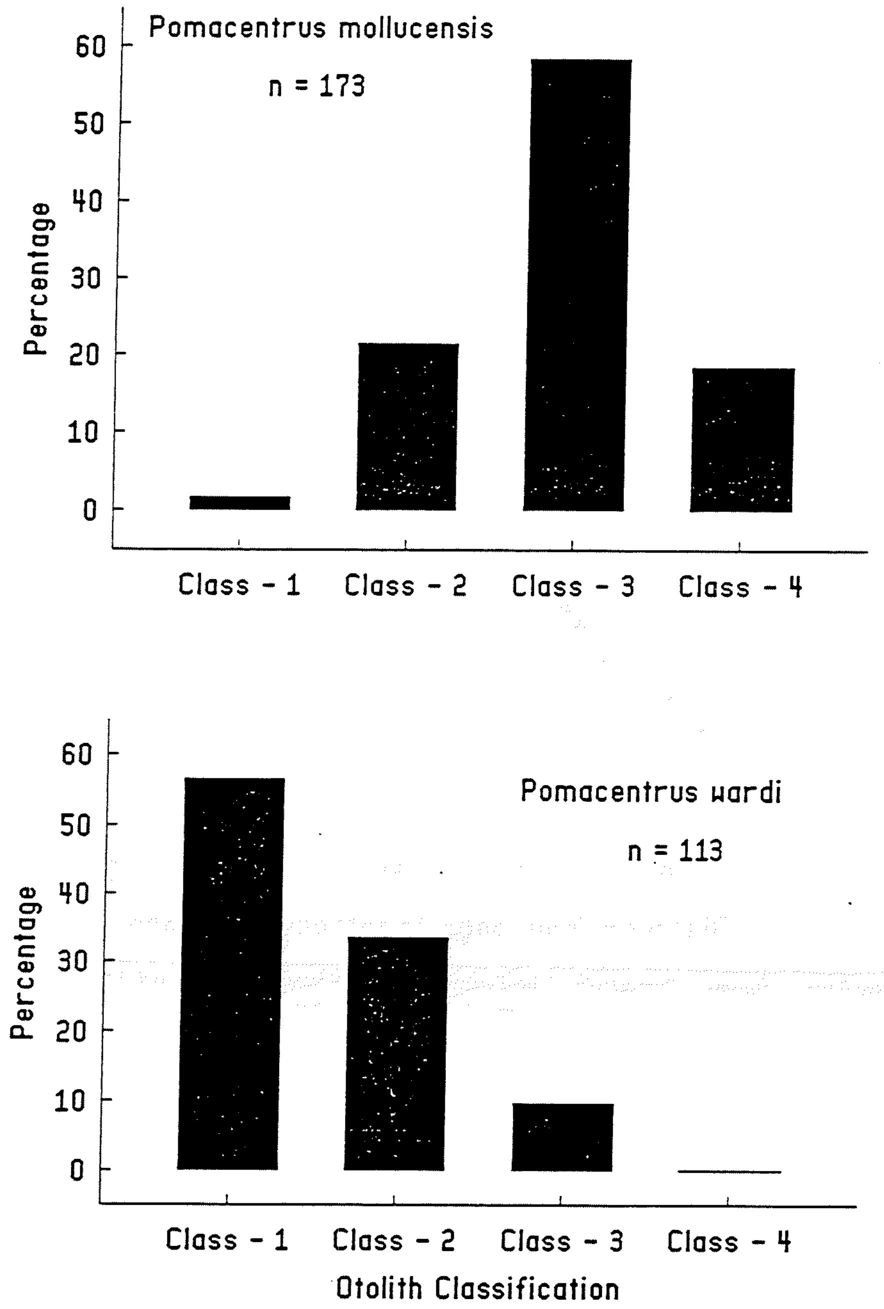

Figure 4. *Pomacentrus mollucensis, P. wardi.* Results from the classification of the quality of sections of sagittae (for definition of classes refer to text).

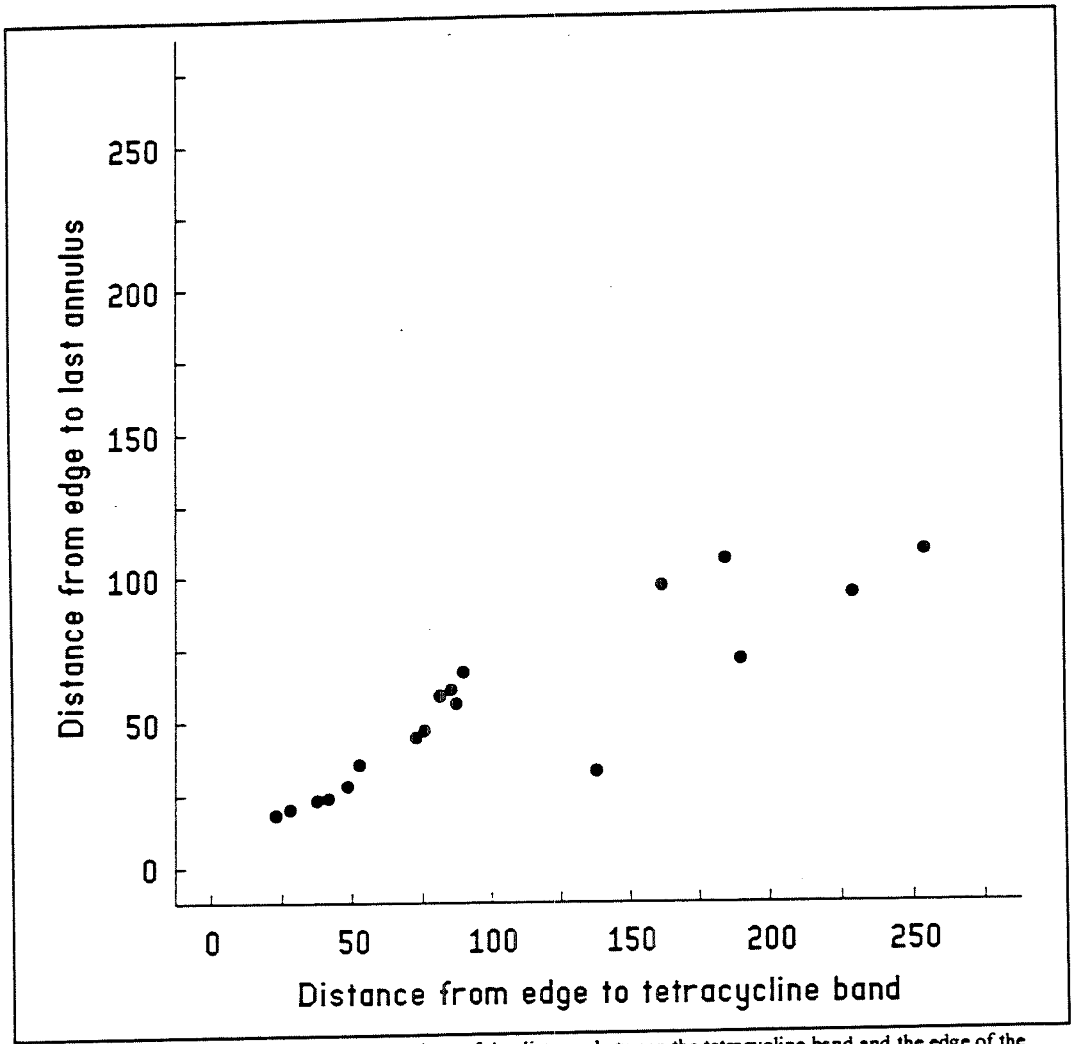

Figure 5. *Pomacentrus mollucensis*. Comparison of the distance between the tetracycline band and the edge of the otolith (to ventral apex) and the distance from the last formed circulus to the edge, along the same axis.

AGE DETERMINATION FOR NATIVE FRESHWATER FISH IN THE MURRAY-DARLING BASIN

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Introduction

The aim of this paper is to review the status of age determination methods and their application and validation for native freshwater fish species occurring in the Murray-Darling Basin. The review includes published work, unpublished studies, theses, and work currently being undertaken by various groups working on the species. It is intended that this review will provide a reference for various groups interested in ageing particular species, both by providing a review of existing information, and contacts for work currently being undertaken by various groups already working on the species. The review will also avoid unnecessary duplication and wasted effort caused by individuals attempting methods which have already been shown to be ineffective or unreliable. The review also provides guidelines for future research in identifying gaps in our current knowledge of age determination methods, verification, validation and analysis for species endemic to the Murray-Darling Basin, and some consideration of the key problem areas for age determination. While every effort has been made to include all past and present work in this review, any omissions are regretted but inevitable with such a review.

Definition of Terms

The following definitions are provided for terms used throughout the text:

Check: stoppage, pause or slowing down or interruption, in bone formation producing a mark or ring on a bony structure.

Annulus: is a zone, mark or pattern produced by a periodic growth-check which interrupts growth and bone formation and produces a ring which is considered to be annual in occurrence (= annual ring or check).

Validation: to establish the accuracy of the technique (i.e. establishing exact conformity with a standard or with the known true age).

Calibration: correlation of readings with standards of known age, in order to establish the reliability of an ageing method and procedures in identifying annuli.

Verify: to confirm the reliability of the readings by checking against known standards or against age estimates derived in other ways or by other groups.

Precision: the reproducibility of the readings made by different readers or using different techniques.

Status of Age Determination Studies

Table 1 provides a summary of the current status of age determination studies for fish occurring in the Murray-Darling Basin. Not every entry applies to studies carried out within the Basin itself, the selection criteria being that representatives of the species occur within the Basin. The sources are listed either as references to published information or thesis (Reference list), or as contacts for unpublished work and for work currently being undertaken or planned (Contact list; e.g. Gooley, VICFISH). Appendix 1 provides addresses for the contacts listed.

Of the 28 species currently recorded as occurring in the Murray-Darling Basin (Appendix 2) only 12 species have so far been studied for age determination. Most species studied grow to a larger size and are important for commercial or recreational fisheries. The limited number of published and validated age determination methods highlights once again the general lack of biological information on freshwater fish in the Murray-Darling Basin despite the value of the resources.

Published and Validated Age Determination Methods

Validated age determination methods have been published for only 2 species: freshwater catfish (*Tandanus tandanus*) using thin sections of dorsal spines, with validation using marginal increments, known-age fish and tagging studies (Davis 1977), and for Macquarie perch (*Macquaria australasica)* using scales and whole otoliths, with validation using marginal increments and length frequency distributions (Cadwallader 1984). Both studies were site-specific, with the freshwater catfish confined to the Gwydir River (New South Wales) and Macquarie perch to fish in Dartmouth Dam on the Mitta River (Victoria). Age determination of bony bream (*Nematolosa erebi*) in the Lower Murray River using scales has been undertaken by Puckeridge and Walker (in press) to determine age at maturity. The method was validated using length frequency analysis and the periodicity of annulus formation (marginal increments). This study was also site-specific relating to populations in the Lower Murray River which are at the southern extremity of the species' distribution.

The remaining age determination studies are either theses, unpublished past work or current work (Table 1).

The recent studies of age determination of Australian bass (*Macquaria novemaculeata*) using sectioned otoliths, with validation using known-age fish and marginal increments (Harris 1985), are relevant even though this species is absent from the Basin, as it relates to the closely related species golden perch (*M. ambigua*) and Macquarie perch (*M. australasica*).

Methods of Age Determination

Scales

Of the hard parts used for age determination, scales are usually tried first because of their ease of collection and the traditional acceptance of this method. Various early publications provide descriptions of native fish scales and some evaluation of their use for age determination for species in the Murray-Darling Basin (e.g. Llewellyn 1966; Lake 1967; Jones 1974). However, apart from Macquarie perch (Cadwallader 1984) and river blackfish (*Gadopsis marmoratus*) (Jackson, QLDFISH) scales have mostly been found to be unreliable or unreadable for most freshwater fish in the Murray-Darling Basin (e.g. Jones 1974) and are not currently the method of choice. Generally, many overseas studies have shown that scales become unreliable for older fish when both somatic growth and scale growth slows and the checks or annuli become more difficult or impossible to read reliably (Beamish 1973; Beamish and McFarlane 1983; Sikstrom 1983). This limits the use of scales as a reliable method despite their advantages in terms of ease of preparation and the opportunity for multiple sampling during tagging studies.

Otoliths

Otoliths are widely used for age determination of both freshwater and marine fish (Williams and Bedford 1974; Erickson 1983). The method has been validated experimentally (Schramm 1989). Several recent papers have shown that otoliths continue to increase in thickness and reliably have annuli laid down as somatic growth slows in older fish (Wright *et al.* 1990; Reznick *et al.* 1989). Most current methods in the Murray-Darling Basin are directed at establishing and validating otolith methods using whole or sectioned material for annual and daily increment determination (Table 1). Otoliths (generally sagittal) have been examined either whole (Battaglene, NSWFISH; Jones 1974; Cadwallader 1984), as burnt and polished, half sections, (Gooley, VICFISH; Jones 1974; Rowland 1985) or as thin sections (Anderson and Morison, VICFISH)(Table 1). Whole preparations are obviously easier to prepare but the reading becomes more difficult and less reliable with older fish (Hoyer *et al.* 1985). Nevertheless, whole otoliths have been shown to be suitable in some locations (eg. for golden perch in impoundments by Battaglene, NSWFISH). Burnt and polished half-sections provide good results, and the technique is still very widely used despite the considerable time and effort required to prepare each sample (eg. Gooley, VICFISH, Table 1). The technique of preparing otolith thin-sections by cutting otoliths embedded in polyester resin using a thin diamond impregnated saw as described by Bedford (1983); Augustine and Kenchington (1987); Kenchington and Augustine (1987); Withell and Wankowski (1988; 1989), appears to offer the best potential for future work (Anderson and Morison, VICFISH). The end result is similar to that for polished half-sections but is less labour intensive. The method appears to provide clearly visible 'checks' and 'annuli' without the need for staining or burning. The technique is simpler and easier than using half-sections and can be readily adapted for large batches of samples (Bedford 1983). Preliminary work has confirmed that the age estimates for Murray cod using thin sections and the estimates obtained using burnt and polished half-sections are identical (Anderson and Morison, VICFISH; Gooley, VICFISH, personal communication). Several studies are currently being conducted to verify the use of this technique for Murray cod, golden perch and to describe its use for other species in the Murray-Darling Basin (Anderson and Morison, VICFISH) . The method is also useful for sectioning dorsal spines of freshwater catfish and other species (e.g. Macquarie perch, silver perch, trout cod) without the need for de-calcification (Anderson and Morison, VICFISH).

Figures 1 and 2 show examples of otolith and dorsal spine thin sections for Murray cod, golden perch, silver perch, Macquarie perch and freshwater catfish. This illustrates the potential value of this technique.

Otoliths have also been used for obtaining daily age estimates (Essig and Cole 1986; Secor and Dean 1989; Tzeng and Yu 1989; Schramm 1989). Several groups are currently examining the usefulness of the technique for various species in the Basin (Harris and Thorncroft, NSWFISH; Pierce, SAFISH; Table 1). The aim of this work is to estimate daily ages of larvae and juvenile fish, to validate yearly age estimates using other methods, and to use the pattern of growth and daily 'checks' induced naturally, or induced artificially, in a hatchery as a means of identifying stocks derived from different sources and subject to different environments during the first months of life. It is hoped that this method may enable juvenile stocks in the Lower Murray derived from various sources such as the Darling River, the upper Murray River, or local recruitment in South Australia to be identified as an aid to fishery management in the lower Murray River (Pierce, SAFISH).

Fin Spines and Rays

Dorsal spines are the preferred method for ageing freshwater catfish (Davis 1977). Care is needed to account for the first year's annuli which may be obscured or lost as the core of the spine becomes hollow with age. Several early studies have briefly examined the use of fin spines for Murray cod and golden perch (Llewellyn 1966; Jones 1974). Anderson and Morison (VICFISH) are also examining the use of spines and rays as an alternative to otoliths for Murray cod, golden perch and silver perch and other species. The method has the advantage of being non-destructive. It may be possible to simply clip off the dorsal spine with minimum damage to the fish which can then be released during routine survey work or used as part of a tagging exercise to validate ageing methods. This is preferable to killing large numbers of fish to collect otoliths, particularly when monitoring stocked populations, or remnant populations, of endangered or threatened species.

Fin rays have not been examined for age determination of fish in the Murray-Darling Basin (Beamish 1981). Beamish and McFarlane (1983), Cass and Beamish (1983), discuss the value of fin rays and the method needs to be examined for use with fish in the Murray-Darling Basin, given its success with other species.

Opercula, Vertebrae and Other Hard Parts

Various authors have examined the use of opercula for age determination (e.g. Rowland 1985; Jones 1974), but the method appears to be generally unreliable and the patterns are difficult to read beyond the first few years of life. Nevertheless, it may be useful to verify other methods, for example verifying the ageing of Murray cod using otoliths (Jones 1974).

Validation

Most validation has been made using changes in marginal increments to confirm that the 'checks' seen are 'annuli' and that they correspond to annual growth cycles linked to seasonal temperature changes. Generally in conducting this analysis the various 'age classes' or 'check groups' have been grouped together and the data presented as a combined data set. The potential problems with this procedure are discussed later. Length frequency analysis and modal progression studies have also been used (Table 1). The recommended recognised methods for validation (Beamish and McFarlane 1983) using fish of known age, or various mark and recapture studies (using oxytetracycline or conventional tagging methods) have not been used except by Harris (1985), Davis (1977) and Rowland (1985). The range of known-ages are very limited with these studies and this generally restricts the absolute validation of the method to the younger fish. Known-age fish are being used for current validation work (eg. Anderson and Morison, VICFISH; Gooley, VICFISH; Battaglene, NSWFISH etc.).

Current Work

Work currently under way will hopefully improve the dismal current situation with respect to the lack of published and validated age determination methods for species in the Murray-Darling Basin. Gooley (VICFISH) is working to validate the use of polished half-sections of otoliths to age Murray cod. Anderson and Morison (VICFISH) are currently working to validate the use of otolith thin sections for ageing golden perch and Murray cod. Battaglene (NSWFISH) is working towards validating the use of whole otoliths for ageing golden perch. Various other studies are being made for other species in the Basin (Table 1).

These current studies will improve the present situation and will enable native fish management in the Murray-Darling Basin to be more effective, and more soundly based on age and growth models including the implementation of universal fishing restrictions throughout the Basin (Pierce 1988; Lawrence 1990) which depend on knowledge of the age structure of populations and age at maturity.

Daily Age Determination

Otoliths have been used to estimate daily ages (Essig and Cole 1986; Tzeng and Yu 1989; Radtke 1989). Attempts to verify daily growth increments in larval golden perch and silver perch, using otoliths, has been undertaken by Harris and Thorncroft (NSWFISH). The aim of this work is to verify annual age estimates and also to evaluate the use of experimental manipulation of day-length and temperature as a means of stock identification or tagging by 'imprinting' patterns in the daily checks on otoliths. Likewise Pierce (SAFISH) is hoping to use daily increments on native fish otoliths for stock identification in the Lower Murray to identify the spawning location of golden perch, silver perch and Murray cod. The initial work is being conducted using purple-spotted gudgeon (*Mogurnda adspersa*), flat headed gudgeon (*Philypnodon grandiceps*) and rainbow fish (*Melanotaenia fluviatilis*). The method also has application for validating annuli in older fish. Various attempts have been made to identify daily growth rings in *Galaxias olidus* (eg. Cowden 1988).

Problems of Age Determination Studies in the Murray-Darling Basin

The review presented in Table 1 highlights a number of problems with age determination of native fish endemic to the Basin:

1. Lack of published and validated methods

The general lack of published and validated methods restricts age determination. The studies completed on freshwater catfish, Macquarie perch (and bony bream) have been site-specific and require verification in other waters.

2. Smaller catch rates and absence of commercial catch makes validation difficult

Small populations of fish in the Murray-Darling Basin and lack of commercial catches makes it difficult to obtain the numbers of fish required for effective validation. This restricts the vigorous application of the marginal increment method to each 'age class' identified and generally restricts the ability to determine the accuracy and precision of the age determination methods. Many of the species under study, such as trout cod, Murray cod and freshwater catfish, are regarded as endangered, or threatened in one or more states. The remnant populations are often too small to be regularly and destructively sampled. Likewise the capture of large numbers of fish is unacceptable to recreational anglers for populations specifically established for recreational angling purposes. The lower numbers of fish available, the smaller catch rates and lack of commercial catch for collection of samples make it more difficult to obtain the material to verify and validate age determinations. This places greater emphasis on 'calibration' and 'verification' when seeking to apply a validated technique developed in one area, to other areas throughout the Basin as it may be impractical to validate the technique in each sub-catchment or area.

3. The preference for the use of otoliths for age determination restricts the use of mark and recapture for validation

The use of mark and recapture methods to validate age determination is restricted because the best ageing method using otoliths involves the killing of fish. Conventional tagging studies or the use of oxytetracycline are restricted because recaptures are low and finances are not available for major mark and recapture studies.

4. While the annual *temperature variation* would be expected to produce clear 'checks' or 'annuli' the other *variations in the environment* would also be expected to influence growth rates

Annual mean monthly water temperatures throughout the Murray-Darling Basin vary from about 22-30°C in summer to 8-9°C in winter. These temperature changes would be expected to produce pronounced variation in growth with season and hence the expectation of reliable annuli on the hard parts. However, the habitat and environment throughout the Basin is variable both temporally and spatially. Drought and floods have been mentioned as possible problems affecting the reliability of age determination in the Murray-Darling Basin (Llewellyn 1966; Davis 1977). River regulation has reduced the variance of flows in the major streams but has probably had little effect on the extreme events of major droughts and floods and such events may produce checks which could be confused with annuli. Native fish growth is very variable even within the one waterbody (Anderson and Morison, VICFISH, unpublished data) and even for intensively reared fish held under identical control conditions (Gooley, VICFISH, personal communication). Likewise, there are major variations in habitat throughout the basin likely to affect growth rates and the pattern of annuli or checks. For example, it is known that growth of native fish in reservoirs, impoundments or natural lakes can be very rapid compared with that in rivers and streams. Likewise growth patterns in upland high altitude streams would be expected to be different for the same species inhabiting lowland streams. Spawning times of native fish such as Murray cod and trout cod may be delayed by a month or more in Victorian hatcheries (Snobs Creek) compared with NSW hatcheries (Narrandera) (G. Gooley, VICFISH, pers comm.) because of differences in seasonal temperatures. Similar differences would be expected in the wild and this difference in 'birthday' can affect size at age during the first few years of life.

Major differences in size at age can be expected in lake populations compared to populations in river or stream habitats because of differences in food availability and growth rates. This is likely to cause problems when trying to apply a technique developed in one habitat type, such as a lake, to a different habitat type, such as a river or stream. Age estimates may be inaccurate because of these differences in growth. Criteria to recognise and describe 'false annuli' produced by food shortages or environmental change from true annuli are not available. Also it is difficult to know when to expect habitat and climate changes that are likely to produce these 'false annuli' (eg. the effects of drought or flood). This highlights the need for 'verification' and 'calibration' through frequent exchange of material between different groups working in different habitats in different parts of the Basin.

5. Marginal increments not adequate as sole validation method

Marginal increment measurements are assumed to provide adequate validation over a broad range of age classes. However, the confirmation that the observed 'checks' are produced annually is a necessary but not sufficient condition for the validation. The estimated ages may be inaccurate despite the apparent consistency in the seasonal pattern of marginal increment development and the derivation of a 'birthday'. This is particularly true when estimates are obtained from a large range of fish with different numbers of 'checks' and the data have been lumped together in the analysis. For example, failure to properly read the first one or two annuli, or the consistent inclusion of a 'false check' produced by environmental conditions, or maturity, may produce errors in age determination which will not be detected by these methods. Only rarely is every year class examined using marginal increments in terms of when every check assumed to be an annuli, forms. While it may be difficult or impossible to obtain data for marginal increments for each 'age class' because of the difficulty in obtaining the required numbers, other supportive evidence is needed to verify and establish the accuracy of the age determination method.

6. Reader biases

There is a need to avoid biases associated with the reader knowing the length of the fish being aged. Whilst this can be avoided by ensuring that the readings are done 'blind' (i.e. without knowing the details of the fish), the size of the fish can still be inferred from the size of the otolith itself and this cannot be overcome easily, so the bias remains. There is then an expectation by the reader that an otolith of a particular physical size will have come from a fish of a particular age. These problems are especially relevant for freshwater fish, whose growth rates would be expected to vary considerably in different habitats because of variations in temperature, food availability and water quality. Consequently fish of a given size from different areas and populations would be expected to have different ages. This again emphasises the need for appropriate 'calibration' and 'verification' and for regular exchange of material between different groups working on the same species in different parts of the Basin.

Calibration and Verification

Even when an age determination method has been described, validated and published by one group of workers, there may be major problems when other less experienced groups try to apply the technique, particularly in different parts of the Basin. The need for each group to individually validate each age group cannot be justified; yet the problem of ensuring the age determination is accurate and reliable remains a major issue. This is especially relevant in the Basin when fish numbers are small, resources are limited and there is an expectation of variation in growth in different habitats and under different conditions. There is, therefore, a need for a method of overcoming these problems. One solution lies in the provision of adequate material for 'calibrating' the age determination method and for cross-checking ages by having other groups verify the readings. This will require the regular exchange of material and is best serviced by the establishment of a 'verification referee' as outlined in Figure 3. Under this scenario particular groups who have established the verified age determination method would act as a source of reference material for 'calibrating' other groups, and would undertake to 'verify' some of the age estimates made to ensure the results were reliable and consistent and that the method was being appropriately and accurately used. This would not obviate the need for validation, but it would mean that the use of marginal increments may be considered acceptable as validation without other supportive evidence and it would ensure consistency. The success of this approach depends upon the adoption of identical or comparable techniques and the willingness of particular groups to act as the referees and to exchange material. Various groups within the Murray-Darling Basin are willing to participate in such a scheme. This scheme offers the best hope of achieving accurate, consistent and reliable age determination methods throughout the Murray-Darling Basin, by establishing an Age Determination Reference Facility for the native freshwater fish in the Murray-Darling Basin.

It is proposed that one or more groups in the Murray-Darling Basin assume the role of a Reference Facility, maintaining validated reference material for each of the species, and act as "verification referees" for material submitted to them. Initially, each group may only wish to deal with one or two species, but it is proposed that eventually the reference collections be collected together and administered by the one agency, perhaps the Murray-Darling Commission, or the Age Determination Reference Facility proposed for marine fish in Victoria.

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Table1. Review of age determination studies for native fish species occurring in the Murray-Darling Basin

Terms: Hist. / Disc., historical descriptive paper ; Oto., otolith; Marg. Inc., marginal increments; "Birthday", change in marginal increments used to establish a birthday for fish corresponding to outer edge of the annuli; Known age, validation based on the use of fish of known age; Unpub. work, age study partially or completely finished but not published; Current work, studies currently being carried out.

Species	Status	Time	Methods	Validation	Age	Source
Murray Cod	Hist./Desc.	Annual	Scales, Otoliths dorsal fin rays			Llewellyn (1966) Lake (1967) Jones (1974)
	Thesis	Annual Opercula	Scales, Oto(whole) Marg. Inc.	Known Age "Birthday"	0-7	Rowland (1985)
	Current work	Annual	Oto(Polished half)	Known Age "Birthday" Marg. Inc.	0-5	Gooley (VICFISH)
	Current work	Annual	Oto(thin sections)	Known Age	0-3	Anderson & Morison (VICFISH)
Golden perch	Hist./Desc.	Annual	Scales, Fin spines, rays Oto(whole), opercula			Llewellyn (1966) Lake (1967) Jones (1974)
	Current work	Annual	Oto(whole)	Known Age (?)	(?)	Battaglene & Thurston (NSWFISH)
	Current work	Annual	Oto(Thin-sect) Fin spines	Known Age "Birthday" Marg. Inc.	0-5	Anderson & Morison (VICFISH)
	Current work	Daily	Oto(Thin-sect)	Known Age	juven.	Harris & Thorncroft (NSWFISH)
Freshwater eel	Publication	Annual	Oto(whole)	Marg. Inc. Length / Freq.	0-5	Sloane (1984)
River blackfish	Unpub. work	Annual	Oto(whole)			Beumer (QLDFISH)
	Unpub. work	Annual	Scales	(?)	(?)	Jackson (QLDFISH)
	Unpub. work	Annual	Scales	Mark / recapture	(?)	Koehn (VICFISH)
Australian smelt	Publication	Growth of known age fish		Known Age	0-2+	Milton & Arthington(1985)
	Publication	Growth of known age fish		Monitored populations length / freq.		Hume *et al.* (1983)
Bony bream	Publication	Annual	Scales	Marg. Inc. Length / Freq.	0-3+	Puckeridge & Walker (1990)
Galaxias olidus	Hon. thesis	Daily	Oto(whole)	Marg. Inc. Length/Freq. OTC Mark / recap.		Cowden (1988)
Rainbow fish, Flat-headed gudgeon	Current work	Daily	Oto(Thin-sect)			Pierce (SAFISH)
Macquarie perch	Hist. / Desc.	Annual	Scales		0-5	Lake (1967)
	Hist. / Desc.	Annual	Scales		0-5	Bishop & Tilzey (1978)
	Publication	Annual	Scales Oto(whole)	Marg. Inc.	0-5	Cadwallader & Rogan (1978)
Silver perch	Current work	Daily	Oto(thin sect.)	Known Age	juven.	Harris & Thorncroft (NSWFISH)
	Current work	Annual	Oto(thin sect.)			Anderson & Morison (VICFISH)
Freshwater catfish	Publication	Annual	Dorsal fin spines	Marg. Inc.		Davis (1977)

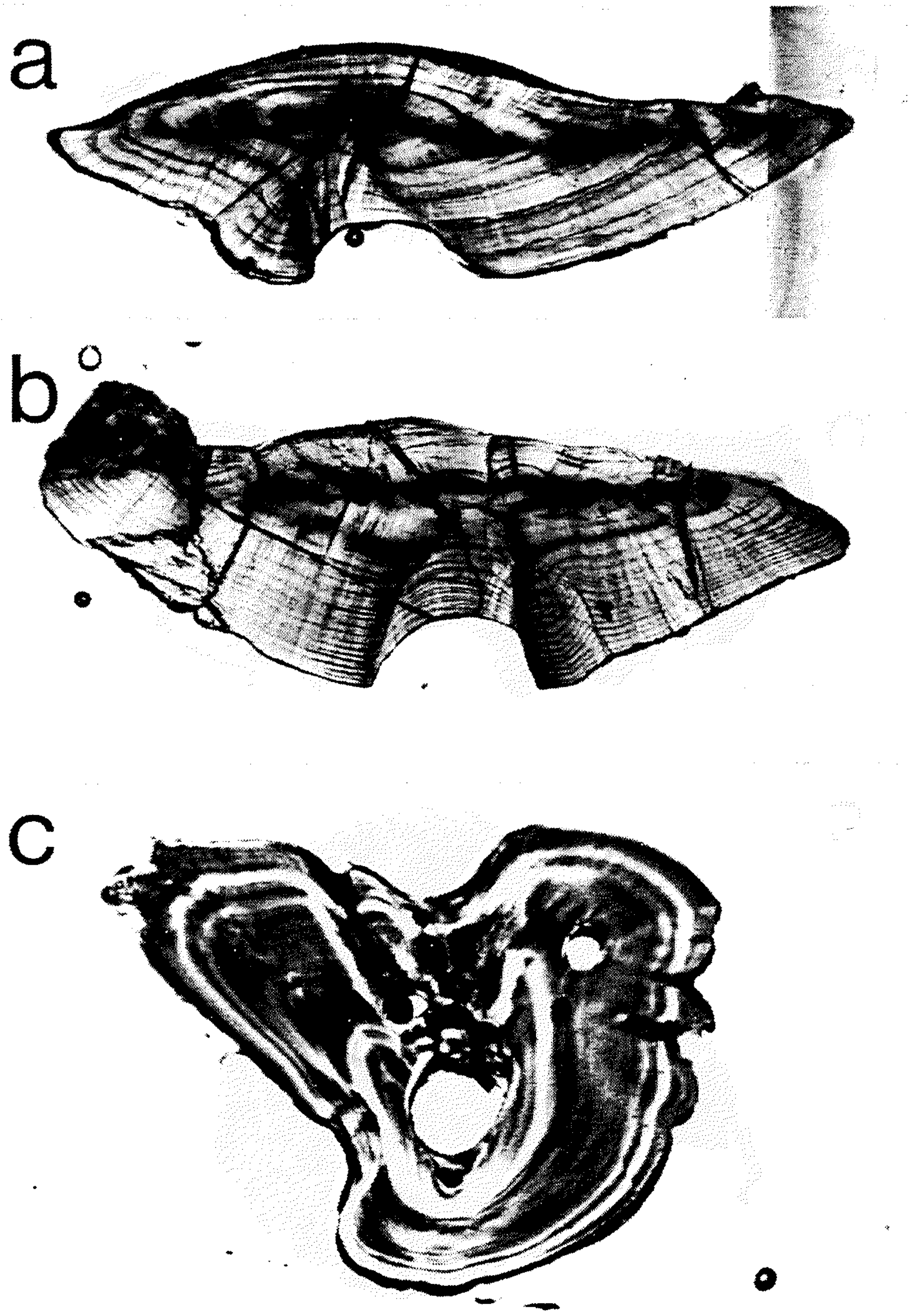

Figure 1. Photographs of otolith and dorsal spine thin-sections using transmitted light; (Anderson and Morison, VICFISH).

a) Golden perch otolith.
b) Murray cod otolith
c) Golden perch dorsal spine.

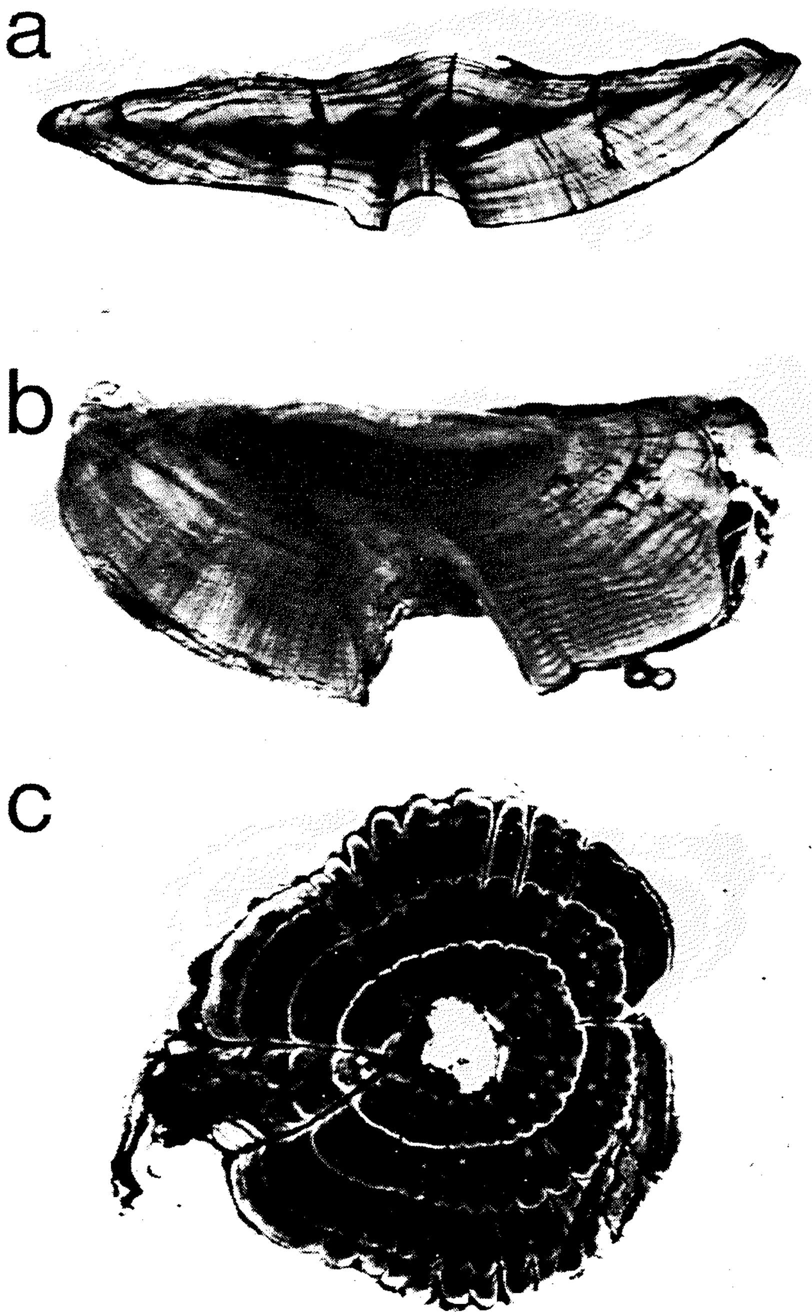

Figure 2. Photographs of otolith and dorsal spine thin-sections using transmitted light; (Anderson and Morison, VICFISH)
a) Macquarie perch otolith,
b) Silver perch otolith
c) Freshwater catfish, dorsal spine.

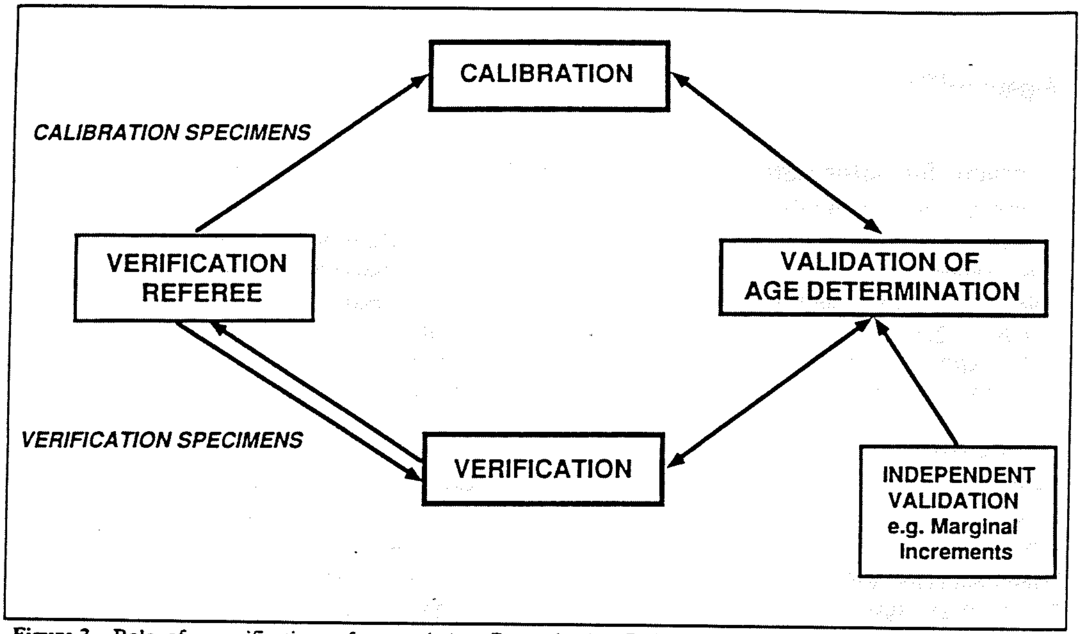

Figure 3. Role of a verification referee and Age Determination Reference facility in providing calibration and verification for age determination.

Appendix 1

Contacts for information on Age Determination of native fish species in the Murray-Darling Basin

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Appendix 2. **Native freshwater fish of the Murray-Darling System, excluding marine or estuarine species (after Anderson 1989)**

FAMILY	SPECIES	COMMON NAME USED IN TEXT
Clupeidae	*Nematalosa erebi* (Gunther 1868)	Bony bream
Galaxiidae	*Galaxias brevipinnis* (Gunther 1866)	Climbing galaxias
	Galaxias rostratus (Klunzinger 1872)	Flat-headed galaxias Murray jolly tail
	Galaxias olidus (Gunther 1866)	Mountain galaxias
Retropinnidae	*Retropinna semoni* (Weber 1895)	Australian smelt
Plotosidae	*Tandanus tandanus* (Mitchell 1838)	Freshwater catfish
Melanotaeniidae	*Melanotaenia fluviatilis* (Castelnau 1878)	Crimson-spotted rainbow fish
Atherinidae	*Craterocephalus stercusmuscarum* (Gunther 1867)	Freshwater hardyhead
	Craterocephalus eyresii (Steindachner 1881)	Lake Eyre hardyhead
Ambassidae	*Ambassis castelnaui* (Macleay 1881)	Western chanda perch
Percichthidae	*Maccullochella peeli* (Mitchell 1838)	Murray cod
	Maccullochella macquariensis (Cuvier & Valenciennes 1829)	Trout cod
	Macquaria ambigua (Richardson 1845)	Golden perch
	Macquaria australasica (Cuvier 1830)	Macquarie perch
Teraponidae	*Bidyanus bidyanus* (Mitchell 1838)	Silver perch
	Leiopotherapon unicolor (Gunther 1859)	Spangled perch
Kuhliidae	*Nannoperca australis* (Gunther 1861)	Southern pigmy perch
Gadopsidae	*Gadopsis marmoratus* (Richardson 1848)	River blackfish
	Gadopsis bispinosus (Sanger 1984)	Two-spined blackfish
Eleotridae	*Hypseleotris klunzingeri* (Ogilby 1898)	Western carp gudgeon
	Hypseleotris galii (Ogilby 1898)	Firetail gudgeon
	Hypseleotris spp.	Midgley's carp gudgeon Lake's carp gudgeon
	Mogurnda adspersa (Castelnau 1878)	Purple-spotted gudgeon
	Philypnodon grandiceps (Kreft 1864)	Flat-headed gudgeon
Diadromous species		
Mordaciidae	*Mordacia mordax* (Richardson 1846)	Short-headed lamprey

Appendix 2. (continued)

FAMILY	SPECIES	COMMON NAME USED IN TEXT
Geotriidae	*Geotria australis* (Gray 1851)	Pouched lamprey
Anguillidae	*Anguilla australis* (Richardson 1841)	Short-finned eel
Galaxiidae	*Galaxias maculatus* (Jenyns 1842)	Common galaxias
Bovichthyidae	*Pseudaphritis urvillii* (Valenciennes 1831)	Tupong

AGEING OF SHARKS FROM THE SHARK FISHERY OFF SOUTHERN AUSTRALIA

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Abstract

The structure of shark vertebrae and the methods used to stain and count the increment lines on the vertebrae are briefly reviewed. Results from ageing studies of gummy shark, *Mustelus antarcticus* Günther, and school shark, *Galeorhinus galeus* (Linnaeus), which provide most of the stock for the shark fishery off southern Australia are discussed.

A pairwise Student's *t* test on results obtained by two people interpreting and counting increment lines in stained (alizarin red S) vertebrae showed that these results for school shark were significantly different ($0.02<P<0.05$) but not the results for gummy shark ($P>0.05$).

Introduction

The shark fishery off southern Australia began in the mid-1920s and depends mainly on gummy shark, *Mustelus antarcticus*, and school shark, *Galeorhinus galeus*. The fishery now produces over 5000 tonnes, live weight, of shark valued at more than $25 million to fishermen in Victoria, Tasmania and South Australia.

Initially, fishermen targeted school shark and used several hundred baited hooks attached to a sinking main-line up to 10 km long. In 1964, fishermen introduced bottom-set gill nets into the fishery and by the early 1970s most of the catch was being taken by this method. Since adoption of gill nets, the gummy shark has become an equally important species in the shark catch.

During the 1940s and early 1950s the Commonwealth Scientific and Industrial Research Organisation undertook studies on school shark (Olsen 1953, 1954, 1959, 1984; Grant *et al.* 1979; Stanley 1988; Moulton *et al.* 1989). Later, during 1973-76, the then Fisheries and Wildlife Division of Victoria (now, the Fisheries Division) undertook similar studies on gummy shark (Kirkwood and Walker 1986; Walker 1984, 1989) and, to a lesser extent, school shark in Bass Strait and waters off eastern Tasmania. During 1986-87, the Fisheries Division studied school shark in Bass Strait and waters off South Australia to gather more information for management of the species. At the same time sampling of gummy shark in Bass Strait was repeated to determine whether the growth parameters for the same species might have changed in response to fishing or to a decline in population density (Walker 1988; Walker *et al.* 1989a).

Preliminary results from ageing studies on gummy shark vertebrae collected during 1973-76 have been presented by Walker (1984); revised results from these vertebrae using a different method and results from ageing studies on gummy shark vertebrae and school shark vertebrae collected during 1986-87 have been presented by Moulton *et al.* (1991).

In this paper we briefly review the structure of shark vertebrae and the methods adopted for ageing sharks from their vertebrae. We also discuss some of our work estimating the ages of gummy shark and school shark.

Structure of Shark Vertebrae

The vertebrae of sharks, and most other chondrichthyans, consist of a centrum with a neural arch attached dorsally; two transverse processes attached ventro-laterally in the trunk region of the axial skeleton, and a haemal arch attached ventrally in the caudal region. The adjacent concave faces of two neighbouring centra enclose an ovoid, almost spherical, mass of soft-tissue notochord acting as a 'ball joint'. The centrum is a short amphicoelous cylinder formed, in part, of concentric layers of cartilage around the notochord. In these concentric layers calcification usually occurs in characteristic but often complicated patterns (Ridewood 1921; Romer 1963).

Little work has been undertaken on the chondrichthyan endoskeleton to determine the fine structure, the chemical nature of skeletal mineral, the availability of minerals for growth and repair of the skeleton, and even the presence of bone. Physiologically, marine chondrichthyans have to prevent calcium in the environment from entering their bodies, and the role of the skeleton in mineral homeostasis has not been established, although chondrichthyans probably use calcium from their environment, as do other vertebrates, rather than calcium from their skeletons.

In the vertebrates all mineralised skeletal tissues except chondrichthyan enameloid have incremental lines which are persistent structural evidence of past events in the growth of a particular tissue or organ.

Most of the cartilage of chondrichthyans is not mineralised, but some cartilaginous tissue contains calcium phosphate deposited in two principal patterns: the tesserae pattern found in the mineralised tissues, such as the jaws, and the more complex internalised pattern found in the centra and their accessory cartilages (Clement 1986).

The pattern in a centrum is a series of incremental lines concentric about the centre. This pattern indicates that growth is on the edge of the centrum where diameter and length of the centrum, and, therefore the length of the shark, can increase. Clement (1986), applying photomicrograph, micro-radiograph and scanning electron micrograph techniques to *Squatina*, found distinct concentric walls of mineralised cartilage enclosing seams of unmineralised hyaline cartilage consisting of concentrically deposited fibres of collagen. He concluded that incremental lines visible on the articular surfaces of the centra are external manifestations of variations in internal deposition. As such, the number of increment lines on the concave surfaces and sections taken through several planes of vertebrae which represent changes in calcification through time have been used by many fisheries scientists as a record of shark ages.

Ageing Sharks from Vertebrae

Research on age determination of sharks and other chondrichthyans has focused on analysis of translucent and opaque 'bands' in calcified vertebral centra (Martin and Cailliet 1988). When sections of vertebrae are viewed with transmitted light, the bands are usually opaque (calcified) in summer months and translucent in winter months (Cailliet *et al.* 1983b; Cailliet and Radtke 1987; Martin and

Cailliet 1988). Cailliet *et al.* (1983b) defined a 'ring' as the narrowest kind of concentric mark (increment line) observed, and use the term 'band' to refer to wider concentric marks composed of groups of rings.

The bands can be heightened by chemicals which stain calcium or protein (collagen). Silver nitrate (Stevens 1975; Cailliet *et al.* 1983a, 1983b), alizarin red (LaMarca 1966; Gruber and Stout 1983; Moulton *et al.* 1991), crystal violet (Schwartz 1983), cobalt nitrate and ammonium sulphide (Hoenig and Brown 1988) stain calcium; mercurochrome (Schneppenheim and Freytag 1980) and ninhydrin (Schneppenheim and Freytag 1980; Davenport and Stevens 1988) stain proteins.

After assessing silver nitrate, alizarin red and ninhydrin as stains for vertebrae from gummy shark and school shark, we selected alizarin red in fresh solutions because of its ease of use and consistent results. Staining the increment lines with silver nitrate was particularly labour-intensive and often the stained lines were not readily distinguishable, particularly in the region near the outer edge, unless the vertebrae had been cleaned with boiling hexane in a Soxhlet apparatus for 24-48 h to remove fats from the surfaces of the centra.

Ageing of Specimens Collected during 1973-76 and 1986-87

A total of 1596 gummy sharks (328 during 1973-76 and 1268 during 1986-87) and 655 school sharks (during 1986-87), caught in bottom-set monofilament gill nets or on baited hooks attached to bottom-set long-lines, were dissected at sea and 4-6 anterior vertebrae from each shark were placed in a labelled vial which was stored at -15°C (the 1973-76 study) or at about -4°C (the 1986-87 study) during transfer to the laboratory.

In the laboratory the vials were stored at -22°C until the vertebrae were required for chemical treatment. Initial treatment involved separating the vertebrae and trimming off the connective tissue and the neural arch from each vertebra. The vertebrae were then immersed in a 0.25% sodium hypochlorite solution, and allowed to soak until fascial material could be removed easily; small vertebrae (3-5 mm diameter) could be cleaned effectively in 30-40 min whereas larger vertebrae (>15 mm diameter) often required soaking for 1-2 h. It was essential to avoid overbleaching which resulted in 'chalky' or partly decalcified vertebrae, and so adversely affected subsequent staining. The vertebrae were then placed under flowing tap-water for about 0.5 h to remove traces of sodium hypochlorite and then allowed to air dry.

During the study, several vertebrae from some of the sharks were embedded in a general purpose GP5A polyester resin and orientated so that a thin section about 1 mm thick would include the central embryonic region, as well as both or either of the two centra faces and a section of the longitudinal vertebral support column. A GEMMASTER^{TM} cutter with a 6-inch diameter blade 0.5 mm thick was used to cut the section.

For routine processing, whole vertebrae were immersed in a weak alkaline solution of alizarin red S stain prepared from a concentrated solution of the stain and 0.1% potassium hydroxide solution in the ratio of 1:9 (after Gruber and Stout 1983); the larger the vertebrae the longer the duration of immersion (1-5 h). The vertebrae were washed in tap water for 1 min. and the surface of one of the two centra of each vertebra was viewed immediately under a stereo microscope at appropriate magnification (x7-x14) using incident light.

Each vertebra was given a 'readability' rating of 1-4 on the basis of either or both the decreasing degree of differentiation effected by the stain or the increasing difficulty in interpreting the arrangement of the bands resulting from the staining of vertebral increment lines. Vertebrae were assigned a readability of 5 when the bands could not be counted.

At the centre of all vertebrae was a dark stained region, the 'core' (about 2 mm diameter). The first clear band outside the core was not visible on vertebrae taken from full-term embryos and new-born sharks, but was visible on vertebrae taken from sharks judged to be several months old. Presumably the first band is laid down at about the time of birth; hence the first band is referred to as the 'birth band'.

All stained vertebrae from each sample were examined and all the bands on the most evenly and clearly stained centrum. A few bands were either incompletely stained, or appeared as closely paired rings. Bands near the outer edge where the bands become highly compacted were often difficult to differentiate. Compacting tended to increase with the size of the vertebra and the difficulty of counting the bands was exacerbated by the vertebra's characteristic curvature towards the outer edge where new material is deposited during growth. The presence or absence of staining beyond the outermost discernible vertebral band was recorded.

By assuming one light stained band and one dark stained band are formed annually, and, by choosing, on the basis of studies of *in utero* growth of embryos (Walker 1984; Walker *et al.* 1989b), 1 January as the birth date, we estimated each shark's age from the formula:

age = number of dark bands + 1 (only if outer perimeter was stained) - 1 (birth band) + proportion of year between 1 January and capture date.

Between Reader Test

Two readers counted the bands in vertebrae collected during 1986-87. The two sets of results were not significantly different (pairwise Student's *t* test) for gummy shark (n=569, mean difference=0.040, SE=0.048, t=0.835, and P>0.05) but were significantly different for school shark (n=580, mean difference=0.112, SE=0.048, t=2.328, and 0.02<P<0.05). Because the mean differences and the standard errors of the results by the two readers were small, the results from both readers were accepted.

The percentages of samples in which counts by the two readers differed in the vertebral bands counted between the two readers are given in the following tabulation.

Species	Percentage of samples for each vertebral band count difference.									
	>+3	+3	+2	+1	0	-1	-2	-3	<-3	Total
Gummy shark	1.1	1.1	3.3	18.3	49.0	20.7	4.4	1.4	0.7	100
School shark	0.9	2.1	6.7	19.5	46.7	17.9	4.8	1.2	0.2	100

Future Work

Alternative potentially more accurate and less labour intensive methods, involving radiographic techniques (Cailliet *et al.* 1983b; Clement 1986; Yudin and Cailliet 1990; Natanson and Cailliet 1990), are being explored for routine ageing of sharks from the southern shark fishery.

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AGE DETERMINATION OF NEW ZEALAND FISHES: EXPERIENCES AND FUTURE DIRECTIONS

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Introduction

Despite the importance of age-based stock assessment to the successful management of commercially important marine fishes, relatively few species have been subject to ageing research in New Zealand, particularly in conjunction with rigorous age validation. This point has become more clear with the development of fisheries for several slow growing deepwater species over the last decade. In these species age information is vital to estimate the productivity of the resource, although extremely slow growth and variable recruitment may make Virtual Population Analysis (VPA) impractical and of little use. Alternatively, management of species such as snapper (*Chrysophrys auratus*) can be optimised through the implementation of age-based population studies. This paper will describe briefly several studies that have included a significant attempt to carry out age validation and discuss future directions for ageing research in New Zealand.

Ageing Studies

This section describes some of the ageing research, in conjunction with age validation, that has been completed in New Zealand. The selected studies are discussed chronologically. Where several studies have been completed on a single species, these are grouped for clarity. Theses have not been included because of the difficulty in obtaining this material and due to the lack of critical review.

A major portion of a study on the biology of the tarakihi (*Cheilodactylus macropterus*) considered age determination and validation (Tong and Vooren 1972). Age validation was done by both marginal increment analysis and, for juveniles only, comparison of annuli counts with the progression of cohorts over several years. For marginal increment analysis whole otoliths were immersed in cedarwood oil and examined with reflected light. The dorso-posterior portion of the whole otolith was examined for measurements of the marginal increment. Based on marginal increment analysis it was found that one opaque and one hyaline zone were formed annually with opaque zone formation beginning between late July and mid-September and hyaline material formation from March to July (Tong and Vooren 1972).

Collections of juveniles and construction of seasonal length-frequency distributions for tarakihi confirmed the growth rates estimated for juveniles from otoliths (Tong and Vooren 1972). Small juvenile tarakihi (<30 cm) collected from the Tasman Bay nursery grounds in February 1969 showed two distinct modes at approximately 9 and 17 cm. It was possible to follow these modes in subsequent samples collected in June and November 1969 and in February and June 1970. Using these data Tong and Vooren (1972) were able to confirm the juvenile ages and to determine that no hyaline ring was formed in the first winter of life in New Zealand tarakihi.

Further studies of tarakihi involving estimations of age and growth were made for fish from the East Cape Area, New Zealand (Vooren and Tong 1973) and from the west coast of the South Island and the waters surrounding the Chatham Islands (Vooren 1977). In comparing age and growth data for tarakihi from several areas it was found that there were significant differences in growth and mortality rates (Vooren 1977).

Age and growth of the pilchard (*Sardinops neopilchardus*) was investigated using modal progression from length-frequency data and by quantification of rings on scales (Baker 1972). Modal progression was effective in determining the ages and growth rates of these rapidly growing fish. Baker (1972) determined the season of scale annulus formation by quantifying the percentage of fish with a single scale annulus at different seasons of the year, a crude form of marginal increment analysis. He found that winter was the season of scale annulus formation with the first annulus being formed when the fish are actually 1.5 years old.

Marginal increment analysis was used to validate otolith ages in a study of growth in the sand flounder (*Rhombosolea plebeia*) and the yellow-belly flounder (*Rhombosolea leporina*) (Colman 1974). This technique was suitable for validating ages, but there was considerable variation in the times of opaque and hyaline ring formation. Otolith rings were subsequently used for back-calculation of fish lengths (Colman 1974).

Kahawai (*Arripis trutta*) ages were estimated from scales and otoliths and the occurrence of annuli was validated by marginal increment analysis (Eggleston 1975). Scales were determined to be unsuitable for estimating ages in individuals older than 5 years and, using otoliths, a maximum age of 22 years was found. Eggleston (1975) felt that adult kahawai otoliths were too thick to count annuli in whole otoliths reliably. After breaking, grinding and polishing followed by burning in an alcohol flame, it was possible to clearly distinguish annuli on all otoliths. Further work showed that suitable preparations for the observation of annuli could be made by burning whole otoliths and making counts of annuli on the medial ventral edge of the sagittae (Eggleston 1975).

Ages of red gurnard (*Chelidonichthys kumu*) were determined from broken and burned otoliths and validations were carried out by marginal increment analysis (Elder 1976). It was found that the period and extent of otolith burning was critical for distinguishing opaque and hyaline zones. After processing, otoliths were immersed in cedarwood oil and examined under reflected light. The marginal increment validation found that the "dark" (hyaline) zones were deposited annually starting in about December.

Snapper (*Chrysophrys auratus*) have been subject to the most intensive ageing research in recent years and further studies are continuing at present. Paul (1976) investigated age of snapper from scales and otoliths and validated the formation of annuli in these two structures using both marginal increment analysis and the seasonal progression of modes in length-frequency data. Additional validation for the formation of annuli in snapper otoliths was provided by Sullivan (1985) who followed strong year classes over a period of more than 10 years. Horn (1986) and others have investigated age and growth in snapper and it has been possible to compare growth among what are presumed to be separate stocks.

Ageing research on snapper is continuing. This additional research was instigated because of the continued debate at MAF Fisheries regarding snapper ages, particularly in relation to the use of the "daily increment" method for ageing. In 1986 a tagging experiment was undertaken with over 4000 snapper being tagged and injected with oxytetracycline hydrochloride (100 mg/kg of body weight). To date over 1100 fish have been returned (a recapture rate of over 25%) and otoliths from these fish have been used to validate the formation of annuli in fish estimated to be from 2 to 32 years old (personal communication, R.I.C.C. Francis, MAF Fisheries, Wellington). Otoliths collected from this experiment are being used to determine the rate of microincrement formation in snapper of different ages.

Several other studies have considered age and growth and have successfully validated ages by marginal increment analysis of otoliths. These include studies of trevally (*Caranx georgianus*) (James 1984), bluenose (*Hyperoglyphe antarctica*) (Horn 1988), and alfonsino (*Beryx splendens*) (Massey and Horn 1990).

Recently, the ages of small juvenile orange roughy (*Hoplostethus atlanticus*) have been validated (Mace *et al.* 1990). Little information had been obtained from reading otoliths of adult orange roughy and length-frequency distributions from biomass surveys were not revealing. In 1988 a survey on the Chatham Rise was undertaken to locate an aggregation of small juvenile orange roughy and follow the progression of length modes with time. Using a modified prawn trawl a suitable aggregation was located and the catches from three surveys in February, May and September 1988 resulted in a modal progression in juvenile length-frequency distributions that was suitable for the validation of annuli on the small juveniles (Mace *et al.* 1990). Hyaline rings were counted in whole otoliths from juveniles of less than 10 cm and these presumed annuli were distinct in most specimens. In previous studies of orange roughy ageing, these annuli were ignored and were considered settlement or metamorphic checks within the first annulus. Mace *et al.* (1990) found that orange roughy growth was exceptionally slow with standard lengths of 3.1, 5.5 and 7.6 cm after 1, 2 and 3 years, respectively. Three further surveys for small juvenile orange roughy have been carried out on the Chatham Rise and these data provide additional evidence for the formation of annuli in small orange roughy otoliths (unpub. data, MAF Fisheries, Wellington).

Future Directions

Subsequent to the above work there has been some reorganisation of MAF Fisheries with a research section dedicated to aging studies being formed. Previously, there had been no dedicated group working on fish age and growth in New Zealand. The goal of the new ageing section is to validate ages of commercially important marine species with research priorities being assessed on the basis of several criteria. The major criteria include monetary value, political value, potential impact of management based on population studies, potential value of age determination and the probability for success in carrying out an age validation study. Most ageing research will investigate age determination based on the use of otoliths, with age validation techniques based on mark-recapture, chemical, image analysis/processing and mathematical methods being considered. Successful validation would be followed by the establishment of a group for the routine ageing of a species as needed.

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AGE DETERMINATION BY MEANS OF DAILY INCREMENTS: USES AND ABUSES

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That fishes could be aged, more or less, by counting "annuli" in their otoliths and other hard parts has been a standard fisheries practice for many decades (Bagenal 1974). It was not appreciated until Panella (1971), however, that the much finer (µm) scale incremental structure in otoliths, at least, was often the result of daily cycles of calcification (Mugiya *et al.* 1981), and hence could potentially be used to age fishes to the day. Since Panella (1971), determination of ages and growth rates for larvae, juveniles and, occasionally, adult fishes by means of counting "daily" increments in their otoliths has become a standard procedure (Campana and Neilson 1985).

The key assumption in such ageing studies is that the increments counted, in fact, are formed daily. There are essentially four ways to validate this assumption: (1) examination of fish of known age (which usually means reared in captivity); (2) back-calculation to a known spawning date based on estimated age and date of capture; (3) measurement of diurnal changes in the width of the outermost increment; and (4) tag-and-recapture studies, in which the otolith is marked with, for example, tetracycline or strontium chloride. All of these techniques have been used successfully; none, however, are entirely straightforward. Validation based on laboratory-reared fish, for example, can be confounded by artefacts in the rearing conditions, as well as by the common observation that in many species the incremental structure of otoliths of laboratory-reared specimens does not match closely that of their wild brethren. Of the four commonly used techniques, tag-and-recapture studies are probably the most powerful. However, they can be subject to problems of sampling biases and the usually unquantified effects of handling and injection of marking chemicals on otolith growth and microstructure. These problems, and similar ones associated with other validation procedures, facilitate discounting negative results of a validation experiment. That is, the acceptance/rejection fields associated with experimental validation studies are not symmetrical; if the data fit the expectation, they are generally accepted uncritically, whereas if they do not fit expectations, the results can be easily, logically and "impartially" rejected on the basis of probable methodological problems.

For this reason, the increasingly large body of data which suggests that under normal circumstances an assumption of one increment per day is justifiable (literature reviewed by Campana and Neilson 1985) cannot be taken at *prima facie* value. Indeed, there are three specific concerns for worry (Thresher 1988).

First, validation studies are often rather perfunctory, involve relatively small sample sizes, and rarely determine the statistical power of the data to invalidate the hypothesis of one increment per day (Rice *et al.* 1985). Type II errors (the error of accepting a false null hypothesis) are doubtless common in the literature, but are overlooked because the conclusions are consistent with expectations.

Second, the hypothesis that increments form daily is rapidly achieving the status of a Kuhnian paradigm ("everyone knows it is true"). Consequently, studies that do not support the hypothesis are immediately treated as suspicious ("you did something wrong"). The relatively few studies that attempted rigorously to document non-daily increment formation (e.g., Geffen 1982) were so severely (and probably justifiably) criticised for methodological problems that subsequent workers are likely to either ignore data contrary to expectations (using the excuse of "probable methodological problems") or, if they do pursue it, will have trouble getting their results published. Consequently, the observation that the literature abounds with "validation" studies, but not with "invalidation" studies is likely to reflect human behaviour and biases as much as it justifies the assumption of daily increment formation in all instances.

Third, the limits of "normal" are rarely determined, despite being absolutely critical for application of the daily ageing techniques. Beyond what range of environmental variables (e.g., feeding rate, water temperatures) do visible increments cease to form daily? More importantly, is it possible to tell from the otolith microstructure itself that estimated ages are no longer reliable? "Growth hesitations", for example, are commonly features in otoliths. What do they mean? Are they really hesitations (and if so, for how long) or do they mark a major environmental event (nearly being eaten, for example) that highlights a particular increment without distorting the underlying daily rhythm? Even studies that rely heavily on the validity of hypothesis of daily increment formation do not adequately address these problems. It is not possible to assess using daily ageing to measure variability in growth rates in field populations, for example, without first demonstrating experimentally that over the range of growth rates measured (or likely to be measured) the hypothesis of one increment per day remains valid. Until such studies are undertaken, the use of daily age data in such field studies must be viewed with suspicion.

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DISCUSSION OF SESSION 2, SUB-SESSION A

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The Chairman invited discussion following each panel presentation and this has been recorded in sequence here.

Richard Tilzey commenced discussion on *Kevin Rowling's* presentation with the observation that most of the species mentioned were species scheduled for the introduction of Individual Transferable Quotas (ITQ). He deplored the lack of validated age information on these species, to be managed on an output control basis, and supported the call for a Central Fish Ageing Facility.

Bob Kearney commented on Kevin Rowling's point that tagging studies undertaken on South East Trawl Fishery species were of little use in age determination studies, and argued that it provided at least an indication of growth rates and age, particularly in situations where fish were recaptured after having been at liberty for considerable lengths of time. He asked the speaker if he could suggest alternative methods.

Kevin Rowling made mention of the radionuclide method, but expressed doubts as to its usefulness in the determination of age on a fine scale, for example in discriminating between fish of 20, 25 and 30 years of age. He thought that long-term tagging studies would provide useful information on age and growth, provided that these research projects were properly designed. He mentioned the success of redfish tagging in NSW, where fish were being recaptured after 4-5 years. Kevin Rowling also noted the positive results from the use of oxytetracycline (OTC) in tagging studies.

Peter Young asked Ron Thresher to what extent methodology was available for the use of oxygen isotope in the validation of otolith annuli, particularly when dealing with such small amounts of material. Ron Thresher replied that techniques were certainly available, but that these were quite costly. He also mentioned that, whilst being more specific than most ageing techniques, certain assumptions needed to be made about the absorption of this radioactive isotope. He warned against the sole reliance on any one ageing technique and called for validation against a number of ageing methods.

David Smith questioned the definition of validation and wondered if supportive results in a visual count of otolith rings and the radionuclide method would constitute proper validation. He questioned if every ring needed to be validated. Kevin Rowling was of the opinion that industry would like to see precise validation of every ring, but added that this was often not feasible.

Following *Tony Fowler's* paper, Rick Fletcher observed that the band width was approximately the same distance from the edge of the otolith in *P. wardii* and *P. mollucensis* and asked whether the two species had similar growth rates. He was told that *P. wardii* is a larger and faster-growing species and that this was reflected in a higher ratio of standard fish length versus otolith size.

Murray MacDonald questioned whether there were any obvious ecological or behavioural differences to account for differential growth rates in these two sympatric species.
Tony Fowler explained that one species is

herbivorous, the other planctivorous, but added that he had insufficient knowledge of the calorific value of those two food sources to explain the difference. He suggested that seasonal fluctuations of food abundance may be a contributing factor.

Iain Suthers wondered whether there were physiological differences between the two species, such as extended spawning periods, to account for differential growth rates. Tony Fowler replied that both species had similar spawning periods, from September/October to February, but he could not rule out physiological differences on that basis.

Bob Kearney was interested in the sixth point raised in *John Anderson's* presentation, that annulus reading was biased by otolith morphology, and asked whether readers could be given photographs instead of otoliths. The speaker responded that even photographs would still reflect morphological differences, such as otolith shape and thickness. Bob Kearney suggested that ageing might be done on vertebrae instead.

David Smith stressed the importance of reader bias, saying that whilst at the Marine Science Laboratories (MSL), Victoria, all otoliths were read "blind" (i.e. without prior knowledge of fish length), it was still difficult for readers to avoid making assumptions based on the visual dimensions of otoliths. John Anderson stressed the need for calibration and suggested that even the most experienced otolith readers should be subjected to periodic re-calibration, using material from a large size range of otoliths of known ages.

Frances Laurenson suggested that surface area determinations be linked to otolith weight to ascertain size-based biases in readers. She recommended the use of a computer program, developed by the U.S. Halibut Commission, to determine otolith/weight relationships. John Anderson acknowledged that this was common practice amongst researchers in the field, but pointed out that environmental conditions had a tremendous bearing on growth rates amongst freshwater fish and that frequently no constant otolith/weight relationships could be determined.

Campbell Davies asked if studies on aquarium-reared fish had been used for validation purposes. John Anderson warned against the use of aquarium-reared fish, which may be subject to stunted growth. Studies by his organisation had been made on fish, such as the Murray cod and golden perch, which had been stocked in ponds over a number of years and were of known age.

To a question on whether tetracycline had been used on wild populations, John Anderson responded that the return of tagged fish rested with anglers and that the return rate was quite low. He expressed his preference for working with stocked populations.

Mike Moran warned against the single use of marginal increment to validate age. It had been his experience that fish of a known common age show wide variation in marginal increment, readings of marginal increment ranging from zero to one, because fish tend not to grow in phase with one another. He warned against jumping to conclusions if a dominant pattern was ascertained for a given "year class". He pointed out that fish may lay down false rings or occasionally skip the formation of yearly rings and he stressed that environmental noise should be considered in the interpretation of data. John Anderson agreed that marginal increment was a necessary, but insufficient, validation of fish age.

Ian Brown was intrigued by the use made by *Terry Walker* of glycerine red stains on shark vertebrae, and questioned whether any other researchers had attempted to use this method on broken otoliths. David Smith responded by mentioning a scientific paper recently published on the range of stains available for otolith work. His own work at MSL supported the finding that staining is species specific and that the success of stain penetration was dependent on otolith preparation.

Stephanie Davenport commented that she had encountered difficulties in the use of protein stains in her shark work, to which Terry Walker replied that in his shark ageing research he only used calcium stains, as they produced clearer results.

Tony Fowler asked *Ron Thresher* whether he had a hypothesis to explain why temperate water fish species had clearer ring bands than tropical fish species. Ron Thresher responded that otolith bands in tropical fish showed greater longitudinal width in their marginal increment and that daily growth rings ranged from 5-10 microns. In contrast, temperate water fish species measured approximately 2 microns and tended to show a more compressed subdaily structure. He suggested that in faster growing fish the wider ring band provided more room for static and environmental noise.

Iain Suthers supported this finding from his microscopic otolith studies. He also drew to attention to recent calibration studies conducted in France, Denmark and Great Britain on herring and cod. In the case of cod, daily age determination was unequivocal, but in herring, daily age estimates varied by 10 days. He supported earlier suggestions for rigorous calibration of otolith readers.

Ron Thresher strongly endorsed the need for continuous and long term calibration. He mentioned one CSIRO program, which has been collecting blue grenadier larvae for 5 years, and stressed the importance of re-reading previously-read otoliths. He was of the opinion that as researchers' knowledge on daily growth expanded, it was crucial that the same criteria for otolith assessment be maintained and he advocated the use of computer programs for a routine approach.

Don Hancock asked whether the cause for daily ring formation was as obvious as it seemed. He drew attention to the phenomenon of double ring formation in cockles, which appeared to be associated with the mollusc's inability to feed at low tide. Ron Thresher pointed out that double ring formation had been cited in scientific literature, but that not much research had been conducted in this area. He indicated that a species' endogenous rhythm may be overridden by extreme environmental fluctuations. Experimental work by CSIRO has shown that in laboratory-reared fish, alterations in the diurnal exposure to light did produce significant results in the daily band formation in otoliths. It appeared to alter the pattern of optical density, and daily increments were not as strongly pronounced as they would ordinarily be. He was of the opinion that only severe disruptions of the diurnal light cycle would have marked effects on daily ring formation. He was however less certain about the effects of other environmentally induced stresses, such as starvation. He mentioned that it was not possible to gauge such stresses in laboratory-reared animals and cautioned against inferences based on strong increment formation under these conditions.

David Ritz questioned whether diurnal vertical migration of some fish larvae would affect daily ring formation. Ron Thresher had found no evidence of this in the blue grenadier larvae that he had studied. He suggested that vertical migration may be linked to feeding behaviour and data were as yet unavailable on the effects of feeding on daily ring formation.

Tony Fowler, commenting on John Kalish's presentation, said that he appeared to advocate the count of daily rings in order to validate annual bands. He pointed out that this approach was at odds with Ron Thresher's approach to ageing. Ron Thresher re-iterated that age could not be determined conclusively through light microscopic studies of otolith substructures, but added that better results may be achieved for fish that lived in a constant environment.

Campbell Davies inquired how long it would take between the tagging of fish with OTC and the appearance of fluorescent markers in the otolith structure. John Kalish responded that tagging effects were immediate and that a fluorescent effect in the otolith edge would be visible within 24 hours.

David Smith, in closing the subsession, commented on the apparent age difference between species aged in Australia and in New Zealand (where age estimates were higher). He questioned if these differences were due to variations in growth rates or an artefact of different ageing techniques. He called for the exchange of otolith material, and dual calibration experiments between the two countries.

Sub-session B

Current Usage and Validation - Commercial Invertebrates

Panellists:	B. F. Phillips D. J. Die W. J. Nash P. C. Young
Rapporteur:	P. C. Coutin

PROBLEMS IN THE ESTIMATION OF THE AGE OF SPINY (ROCK) LOBSTERS

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Abstract

Data on the growth of spiny lobsters usually are obtained from:

(1) measurements of moult frequency and increment of captive animals,

(2) mark and recapture studies,

(3) change in size frequency distribution from repeated samples of a population,

(4) determination of natural moult frequency combined with information on size increment from animals moulting just after capture,

(5) measurements of hard structures such as segments of the antennule flagella or ridges on the stridulating organ,

(6) the use of biochemical techniques such as fluorescent pigments (lipofuscin).

All of these data provided individual problems of analysis because of the sampling techniques used to collect them or biases caused by the environment in which the data were collected, such as the change from laboratory to field conditions. In addition, there is a long larval phase in spiny lobsters, the estimation of which is usually based on other techniques, and there are again errors in these data. No single method of analysis seems to provide satisfactory information, and a synthesis of various techniques may provide more accurate information.

THE CONCEPT OF ABSOLUTE AGE IN PENAEIDS

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Abstract

Like all crustaceans, penaeids can not be directly aged because they do not retain hard structures after they moult. Estimation of absolute age is always done by scaling relative age estimates to the timing of certain events in the life history of the prawn. Many of these key events, like spawning, larval settlement, or juvenile migration have large interannual variability in timing and duration. Estimation of absolute age depends on the level of knowledge of the timing and variability of all life history processes, and on the underlying assumptions about population structure, growth and individual variability.

Introduction

The correct ageing of animals is essential for most population dynamic and stock assessment analyses of aquatic animals. Unfortunately, penaeids, like all crustaceans, shed their cuticle at moult, leaving no hard tissue with marks that could indicate their age. Recent research on the accumulation of certain pigments in the nervous system suggest that in the future soft tissues may be used to age crustacean decapods (Sheehy 1989; in press). However, at this stage there is no reliable technique that can be used to assign ages to penaeids unless the animals have been completely reared in the laboratory. Length frequency analysis and tagging provide estimates of growth but not of age. However, these two techniques can give us an indication of the relative age difference between different sizes or life history stages.

If relative age estimates are combined with information on timing of life history processes like spawning, larval settlement and juvenile recruitment, some idea of absolute age can be obtained (Figure 1). This procedure has been used for penaeid species (Staples 1980a, 1980b), but it is difficult to validate. Therefore, it is important to understand what sort of assumptions are made when this method is used and whether age estimates may be biased if any of the assumptions of the method fail.

Assumptions Concerning Relative Age Estimates

Relative ages are estimates of age that can not be directly associated with the true birthdate of the prawn. In general they only indicate the age difference estimated for one or several individuals with unknown birthdates. For instance tagging data provide information on the relative age difference for an animal at two points in time, between release and recapture. On the other hand length frequency analysis produces estimates of the relative age difference between two cohorts or modes at two subsequent samplings. The following section will discuss assumptions of tagging and length frequency analysis that directly relate to age. Both methods have several other important assumptions relating to growth and population structure that have been discussed by other authors (Pauly and Morgan 1987; Hancock 1989).

Tagging

The assignment of relative ages with information from tagging experiments can be achieved in two ways. The first one is to use time at liberty as a measure of relative age difference. Unfortunately, doing so does not allow inferences to be made about relative ages in the population. The second way is to use a growth model to make inferences about age. Fabens' (1965) form of the von Bertalanffy curve, may be used for that purpose. i.e.

$$L_c = L_r + (L_\infty - L_r)(1 - e^{Kd}) \qquad (1)$$

where L_c is length at recapture, L_r is length at release, d is time at large, and L_∞ and K are the von Bertalanffy growth parameters. If an unweighted least squares procedure is used to estimate L_∞ and K, the implicit assumptions concerning age are:

1. Prawns of the same size at release have the same relative age,
2. The relative age of the prawns at recapture is equal to the relative age at release plus the time spent at sea.

Therefore note that the relative age of a prawn at release is assumed to be a direct function of its size, however at recapture it is not. For instance, two prawns that have spent the same time at sea but had different sizes at release will have, according to the fitted growth curve, different relative age differences between release and recapture.

Individual variability in growth parameters (Sainsbury 1980) may be introduced in the formula above, and,depending on the assumptions about the error terms, different models will arise. Consider for example one that assumes normally distributed individual L_∞ and a single K for all animals (Kirkwood and Somers 1984),

$$\Delta L = (L_\infty - L_r)(1 - e^{-Kd}) + \varepsilon \qquad (2)$$

where ΔL is the size increment between release and recapture and ε is a normally distributed error with mean zero and variance V, where

$$V = \sigma^2 (1 - e^{-Kt})^2 \qquad (3)$$

Under this new model, assumptions 1 and 2 above are still implicit. However, because of individual variability in L_∞, estimates of relative age for the recaptures are a function of individual growth patterns. Therefore two prawns that spent the same time at sea may have different or equal relative age differences between release and recapture, depending on their individual L_∞. However, because the model does not incorporate each prawn's individual L_∞ but rather the mean and variance of the population's L_∞, it will not be possible to assign a relative age to individual recaptures.

Seasonal effects in growth may be also introduced to Fabens' (1965) model. In general this is achieved by incorporating a sinusoidal oscillation in the value of K. Somers (1988) for example presented the following model,

$$\Delta L = (L_\infty - L_r)(1 - e^{-Kd - S(t) + S(t+d)}) \qquad (4)$$

where $S(t)$ is the sinusoidal function of the time at release t.

Again assumptions 1 and 2 above hold, however the relation that defines the estimated age at recapture is now a function of the date of the release and the date of the recapture. This implies that two animals that spent the same days at sea and had the same size at release, but were tagged at different times, may have a different estimated relative age difference.

If an even more complicated growth model is considered such as one that incorporates, individual variability in growth, seasonality and measurement error in length increments (Francis 1988) it is even harder to interpret what may be the relative age assigned to the recaptures.

In summary all growth models that analyse tagging data are only designed to model change in size. Therefore the true relative age difference between release and recapture, the time spent at sea, will never be retrievable from the estimates of the model parameters. Whether a growth model is of any use to compute relative ages from size composition will always depend on how well the assumptions above are met.

Length Frequency

Length frequency analysis does not provide any information on absolute nor on relative age. This technique makes even more restrictive assumptions about age and its relation to size than those made by tagging. It is also fundamentally different from tagging in that it provides information on growth of what it is perceived to be an age group or a cohort not of an individual. Models used to interpret length frequencies may be divided into those that make particular assumptions about growth and those that do not. The latter group could be associated with the following assumptions:

1. Size defines age, in the sense that modal groups identified in the length frequency can be associated with age groups.
2. It is possible to associate modal groups at different sampling times with the same age group.
3. There are defined age groups within the population.

Length frequency analysis models that make assumptions about the form of the growth functions can be easily related to the models presented in the previous section on tagging. The simplest model identifies peaks in the length frequency as peaks in the age frequency and ignores growth variability (Pauly *et al.* 1984). This generally implies that size determines age directly and therefore can only be applied to modal analysis of length frequency distributions. For these models differences in size necessarily represent differences in age, and animals present in the same sample with different sizes are assumed to have different ages.

Other models incorporate growth variability by expressing the distribution of length at age in a parametric form, such as a normally distributed function with a given mean length at age and a variance of length at age (Fournier *et al.* 1990). These models make the assumption that all size variability within an age group is assigned to growth variability, none to differences in birthdate. Both groups of models can accommodate seasonal effects.

Only assumption 2 above can be tested with tagging experiments in prawns. It is also difficult to reconcile the other two assumptions with the fact that many prawns have extended spawning periods suggesting that within an age group there may be a large range of birthdates. In fact most analyses assume that size differences within a length frequency group are only the result of either growth or age variability, not of both. It is interesting to see how much of these differences can be explained by birthdate variability, and seasonal growth. This is specially relevant in penaeids where growth seasonality and extended spawning times are common. It can be easily shown that growth variability can be mistaken with birthdate variability. For instance the same length frequency distribution can be the result of growth variability (Figure 2a), age variability (Figure 2b) or a combination of these two (Figure 2c). This can be shown to hold for both the non seasonal and the seasonal versions of the von Bertalanffy curve (Figure 2a-2c).

Assumptions Concerning Transforming Relative to Absolute Age

Absolute age is a measure of the time passed since the prawn was born. It can be estimated from relative age when there is information on the timing of certain life history events, and by tying this information into a general life history model for the animal. This is generally achieved by developing estimates of the time that it takes for a prawn to go from egg or larvae to a stage from which relative age estimates may be obtained. This latter stage should be a well defined period of the life history of the animal and should last the shortest possible time. The most commonly used stages are the time at which the postlarvae settle to the bottom from their pelagic existence, and the time at which the juveniles leave the nursery grounds and move towards their adult habitat.

Ageing prawns involves therefore the estimation of the time it takes for a prawn to go from egg to settling postlarvae and/or migrating juvenile. This is achieved by first estimating seasonal patterns of spawning, settlement and migration. The time differences between peaks in the intensity of these events are then taken as an indication of the average age difference between events in the life history of an animal. Unfortunately for many penaeid species, spawning (Crocos 1987; Rothlisberg *et al.* 1987; Blyth *et al.* 1990; Watson and Keating 1990), postlarval settlement (Young and Carpenter 1977; Staples 1980a; Turnbull and Mellors 1990) and juvenile migration (Staples 1979, 1980b; Staples and Vance 1987) are fairly spaced in time and have often several peaks. The problem then becomes one of identifying what peak in spawning may generate a particular peak in settlement and/or migration. More often than not this is achieved through subjective inference and not through appropriate hypothesis testing. Even if the identification and association between peaks is quite clear, the implications of ignoring the large variability present in the system are mostly ignored.

It is practically impossible to follow a batch of eggs up until they settle in the nursery grounds as postlarvae. However, it is possible to try to follow the peaks of newly settled postlarvae throughout their development until they migrate out of the nursery grounds and towards the adult habitat. This may be achieved by generating length frequency distributions of the population of prawns as they move from one habitat to the other (Staples 1980a, 1980b; Turnbull and Mellors 1990). This is the most objective way to determine the correspondence between peaks in settlement, migration and recruitment into the fishery. It requires intensive sampling for different life stages, in different habitats, with different gears (Staples 1980b).

There is an additional problem to be considered and that is the interannual variation in the timing of these events and their spatial component. The timing of these events changes from year to year and between areas, making it more difficult to establish a general life history model for the species. Settlement of postlarvae and migration of juveniles are heavily influenced by local environmental parameters like tidal currents, river outflow and salinity, at least in some species (Young and Carpenter 1977; Staples 1980a, 1980b; Staples and Vance 1987).

Summary and Conclusions

Due to the absence of permanent hard structures, ageing of penaeids is reduced to making inferences about its relation to size and about the timing of key events in the life history of the animal. Knowledge about population structure, growth, and the life history cycle is essential to understand whether inferences about age are correct. Because many of the assumptions implicit in length frequency analysis and tagging models can not be tested for penaeids, the estimation of absolute or even relative age is always open to subjective interpretation.

Extended spawning, postlarval settlement and juvenile migration periods complicate the interpretation of population structure from size frequency distributions. Growth variability, evident from results of tagging experiments in penaeids (Kirkwood and Somers 1984), complicates the matter further, and so does interannual variability. As a result, all estimates of age developed for penaeids at various points of their life cycle have generally a high degree of uncertainty. They represent at best only the average age at which each event takes place, and at worst an untestable hypothesis about the length of each life history stage.

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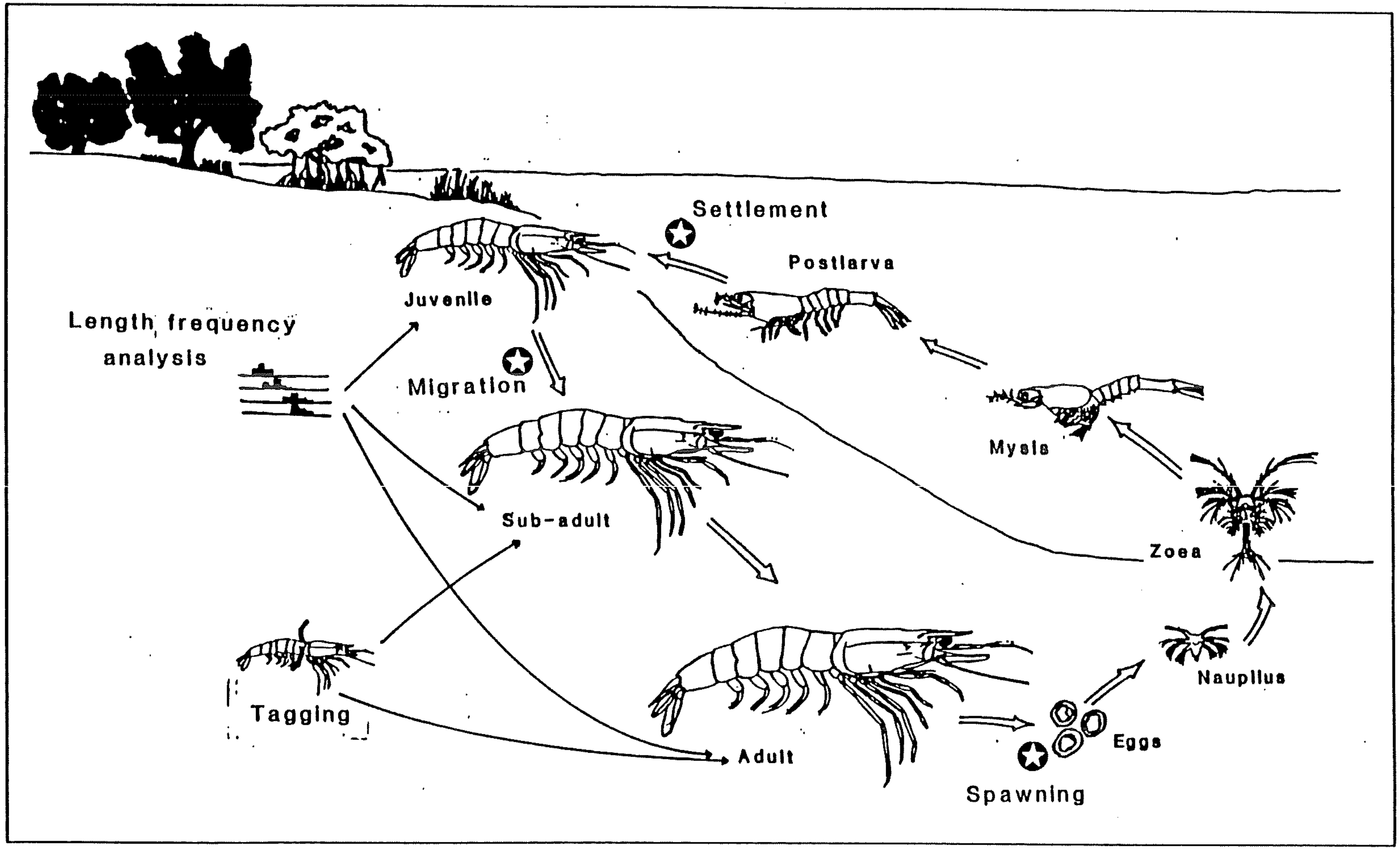

Figure 1. Life cycle of a penaeid prawn, key events used for rescaling relative age estimates and periods where length frequency or tagging information on relative ages can be obtained.

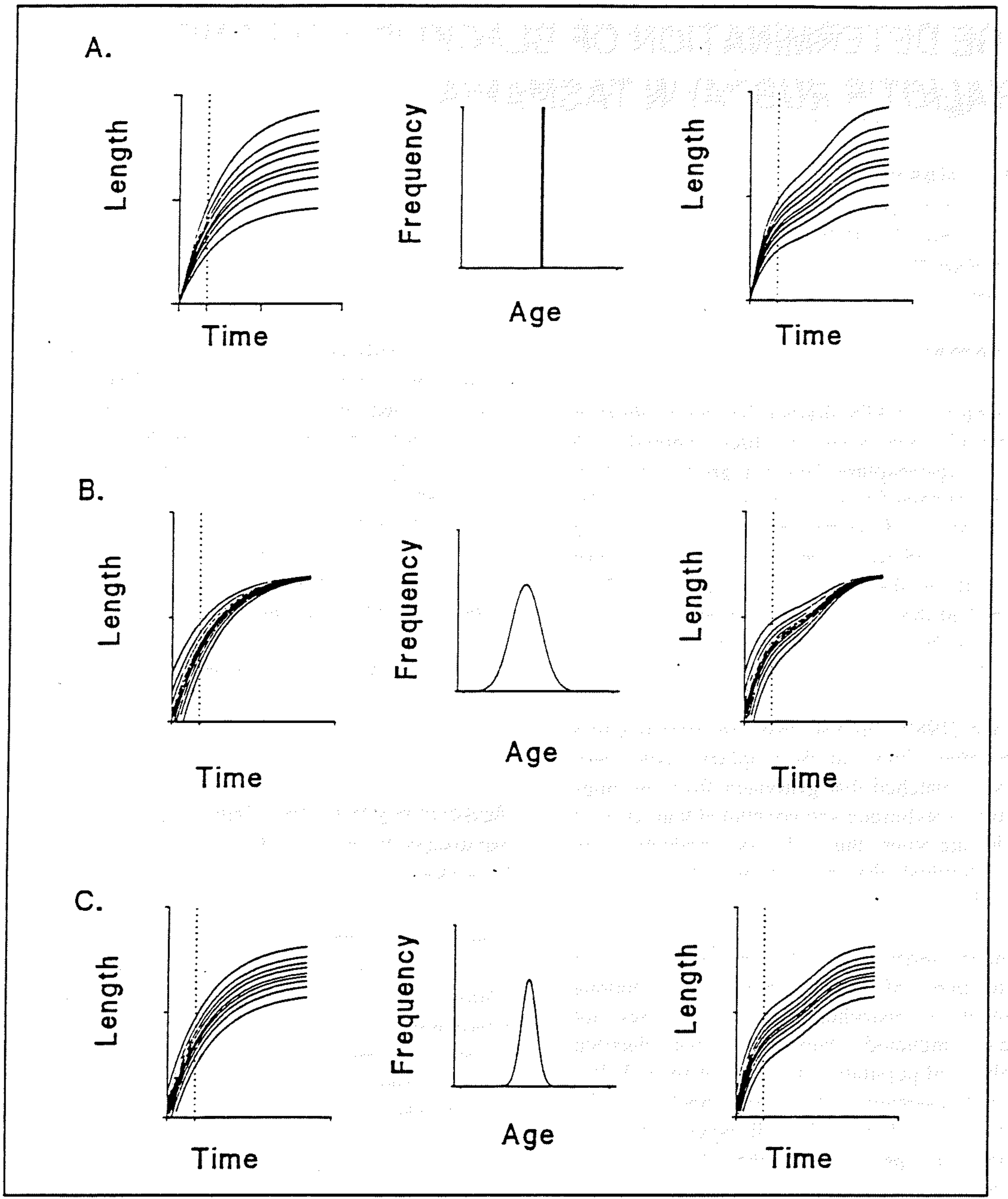

Figure 2. Representation of six simulated growth patterns for a hypothetical penaeid stock. All populations had the same length frequency distribution 85 days after their average birthdate. Left graphs represent stocks without seasonal growth, and right graphs with seasonal growth. Middle graphs represent the age distribution at 85 days. A. Stocks with only growth variability. B. Stocks with only birthdate variability. C. Stocks with both growth and birthdate variability.

AGE DETERMINATION OF BLACKLIP ABALONE (*HALIOTIS RUBRA*) IN TASMANIA

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Summary

Ageing of blacklip abalone (*Haliotis rubra*) in Tasmania has been by three methods: (i) fitting tag-recapture data to a growth function (von Bertalanffy or Gompertz); (ii) modal progression of length frequencies of young abalone; and (iii) counting of growth checks (layers) in the shell. Prince *et al.* (1988) identified three minor bands (shell layers) laid down within the first 16 months of life, after which the layers are deposited annually.

Prince (1989) showed that the growth curve generated from mark-recapture data very closely matched that generated from the ring-counting technique and concluded that, at least at the site where the study was conducted, age of individual abalone can be determined by counting growth layers in the shell.

Similar verification of the periodicity of deposition of shell layers in abalone populations elsewhere in Tasmania has not been conducted; however, since detailed analyses of population structure at several sites around Tasmania have been made on the assumption of annual shell layer deposition (Nash in press; unpublished data and manuscripts), it is desirable that this be done. Since the periodicity of deposition of both minor and major shell bands is only empirically based, the factors determining this need be determined. Methods for doing so include those used by Prince *et al.* (1988), tetracycline labelling of the shells, and reciprocal transplantation of abalone between stunted and non-stunted stocks.

Additional, independent, evidence of a close linear relationship between number of growth rings and age at all sites surveyed so far around Tasmania is given. The possibility that the number of layers deposited per year is more than one, or that it is variable, is also considered, and it is concluded that, on the basis of the results of our population surveys, the findings of Prince *et al.* (1988) are generally applicable throughout Tasmania. This conclusion notwithstanding, the ring-ageing technique should be tested rigorously on both stunted and normal abalone stocks throughout Tasmania.

Measuring the Relationship between Number of Growth Checks in the Shell and Age

Prince *et al.* (1988) compared the numbers of growth layers in the shell of blacklip abalone (*Haliotis rubra*) with the age of abalone, as determined by a combination of mark-recapture and modal progression of young age classes. They found that three minor layers were deposited in the first 16 months of life, with major layers being deposited annually thereafter. Based on the approximate time of the year that growth checks occur, Prince *et al.* (1988) concluded that the checks are related to temperature rather than to reproduction.

The number of minor rings present, and the time period over which they are deposited, were determined empirically; no reason for this pattern was shown, although it was suggested that it may be determined by changes in diet and habitat as the abalone grow.

Direct ageing of individual abalone allows detailed analyses of population structure to be made. However, this can only be done if the relationship between age and number of shell growth layers found by Prince *et al.* (1988) is applicable to populations of abalone other than those on which their study was conducted.

Possible doubts about the widespread application of the method have been raised. These are:

(i) that the frequency of growth layer deposition may be variable, particularly in slow-growth (stunted) populations, in which shell layers are deposited more frequently than once per year. Food supply to these populations may be only sporadic, and growth may be restricted to these occasions;

(ii) other workers (*e.g.* Sakai 1960) have demonstrated that growth checks in other abalone species are related to reproduction as well as seasonal temperature changes. If growth checks in *Haliotis rubra* were related to both temperature and reproduction, then the likelihood of discerning both layers would depend on the time interval between these two events; if abalone reproduce when temperatures begin to increase in spring/early summer (as evidence suggests), then only one growth check per year may be discernible.

A number of predictions arise from (i) above. By observing the patterns of longevity and apparent growth rate of populations around Tasmania, an initial evaluation of this hypothesis may be made. Assuming that stunted abalone have the same potential longevity as abalone with normal growth, then the *apparent* longevity (determined from growth layers) of stunted abalone would be greater if these stunted abalone deposit more than one layer. However, stunted populations would be less heavily fished than normal-growth populations (because of size limit regulations), and so would be more likely to contain more old animals anyway.

This problem may be avoided by examining the relationship between maximum length and maximum age attained in populations that are not fished. If the hypothesis in (i) above is correct, then the relationship should be an inverse one - that is, populations with lower maximum size should also exhibit greater apparent longevity. The unfished (or only very lightly fished) populations of the Bass Strait islands were used to examine this.

Contrary to predictions, the relationship is not an inverse one (Figure 1); there is a significant positive relationship (slope >0; $p<0.05$). These results therefore do not support the hypothesis that the frequency of shell layer deposition is greater in stunted populations. The hypothesis cannot be ruled out conclusively, however, because the assumption of equal longevity of all populations, regardless of the degree of stunting, may be invalid. If the rate of natural mortality were higher in stunted populations, then the positive relationship seen in Figure 1 may still exist because the true maximum age of the stunted populations may be considerably less than that shown.

Concerning proposition (ii) above: if reproductive growth checks occur, and are distinguishable from temperature-caused growth checks, then the number of growth layers deposited annually would be more than one for sexually mature individuals. The timing and periodicity of both reproduction and temperature-related growth need to be determined to answer this question. For example, if spawning occurs at about the same time as the seasonal temperature-related growth check is deposited, then the two growth checks may be indistinguishable, and therefore be interpreted as a single growth check. If, on the other hand, these two events occur several months apart, then the two types of growth checks would be more clearly distinguished.

Additional, independent, support for a close linear relationship between age and number of growth checks in the shell is that a significant difference exists between the lengths of immature and mature abalone of the same age (Figure 2). Unless the relationship between growth layers and age were a close linear one, this relationship should not be detectable. This pattern was found for all populations surveyed. By itself, this evidence does not allow the frequency of shell layer deposition (one or more layers per year) to be determined, but it does not support the hypothesis that the number of growth rings deposited annually is variable.

Age determination by counting growth rings in the spire may be biased because not all abalone shells can be aged. Those that have been severely bored by sponges or polychaetes are usually impossible to age. The prevalence of bored shells varies between sites, with abalone in exposed areas being less bored than those in sheltered embayments. The proportion of shells that cannot be aged ranges from 8 to 67 percent (Nash in press; unpublished results).

Since, within a site, the prevalence of boring is likely to increase with age of the shell, the proportion of shells that are ageable is likely to decrease with age. This may lead to an over-estimate of growth rates, since more young than old animals in each size category may be sampled. More importantly, it will bias the estimation of the age structure of the population, since the older age classes will be under-represented (Figure 3). Estimation of total mortality (*Z*) of the population by catch curve analysis will therefore result in over-estimation of *Z* (Nash in press).

Conclusion

If the age structure of abalone populations can be determined by direct counting of growth layers in the shell, then an understanding of some important population processes can be achieved rapidly. Despite the possible reservations described above, there is no clear evidence that the results of Prince *et al.* (1988) are not more widely applicable. Nevertheless, it is highly desirable that the age-growth ring relationship be examined from more populations, encompassing a range of temperature regimes and growth rates (stunted or non-stunted).

The methods for doing this would include those of Prince *et al.* (1988) (mark-recapture and modal progression analysis), and include a method of placing a mark in the shell (such as oxytetracycline labelling), with the regime of recapture of these labelled animals designed so that the frequency of shell layer deposition, as well as its underlying cause (temperature, reproduction, disturbance or a combination of these), can be determined.

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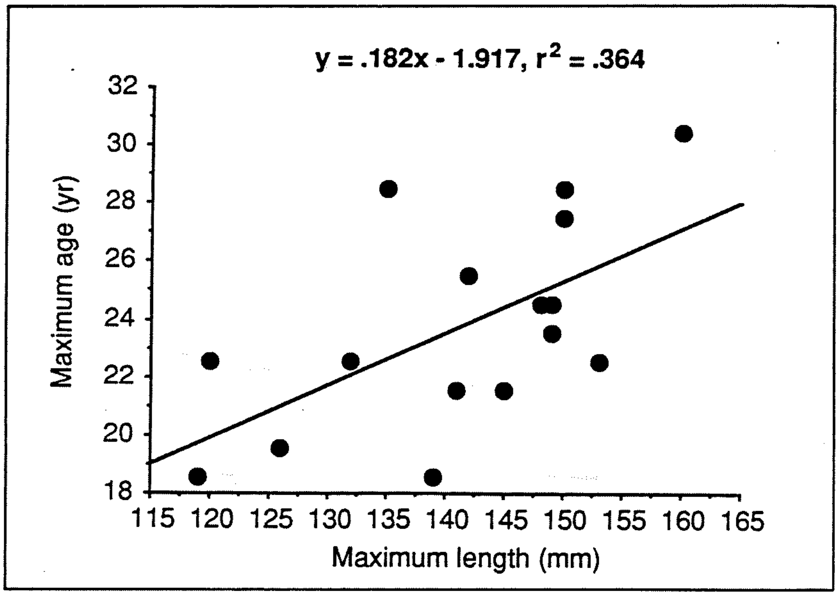

Figure 1. Relationship between maximum shell length and maximum age attained for blacklip abalone (*Haliotis rubra*) from Bass Straight island sites.

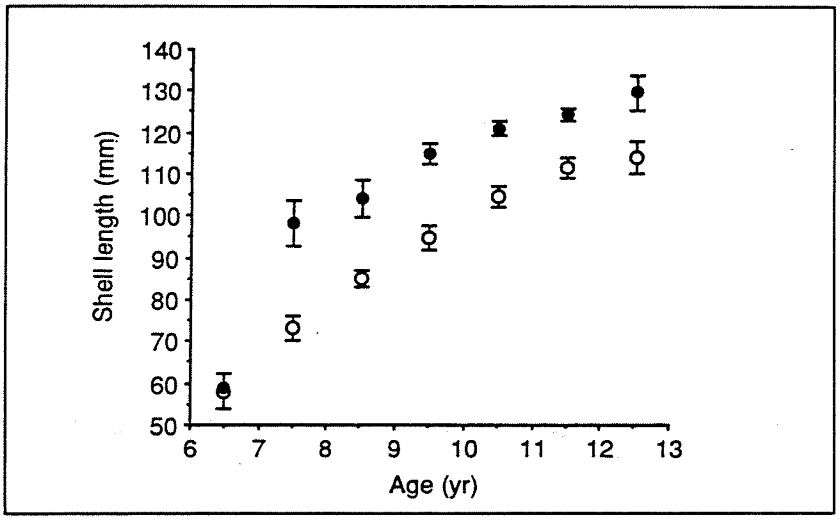

Figure 2. A comparison of the lengths of immature amd mature backlip abalone (*Haliotis rubra*) by age from Binalong Bay, north-east Tasmania. ● Mature abalone; ○ Immature abalone. Error bars are 95 percent confidence limits about the mean.

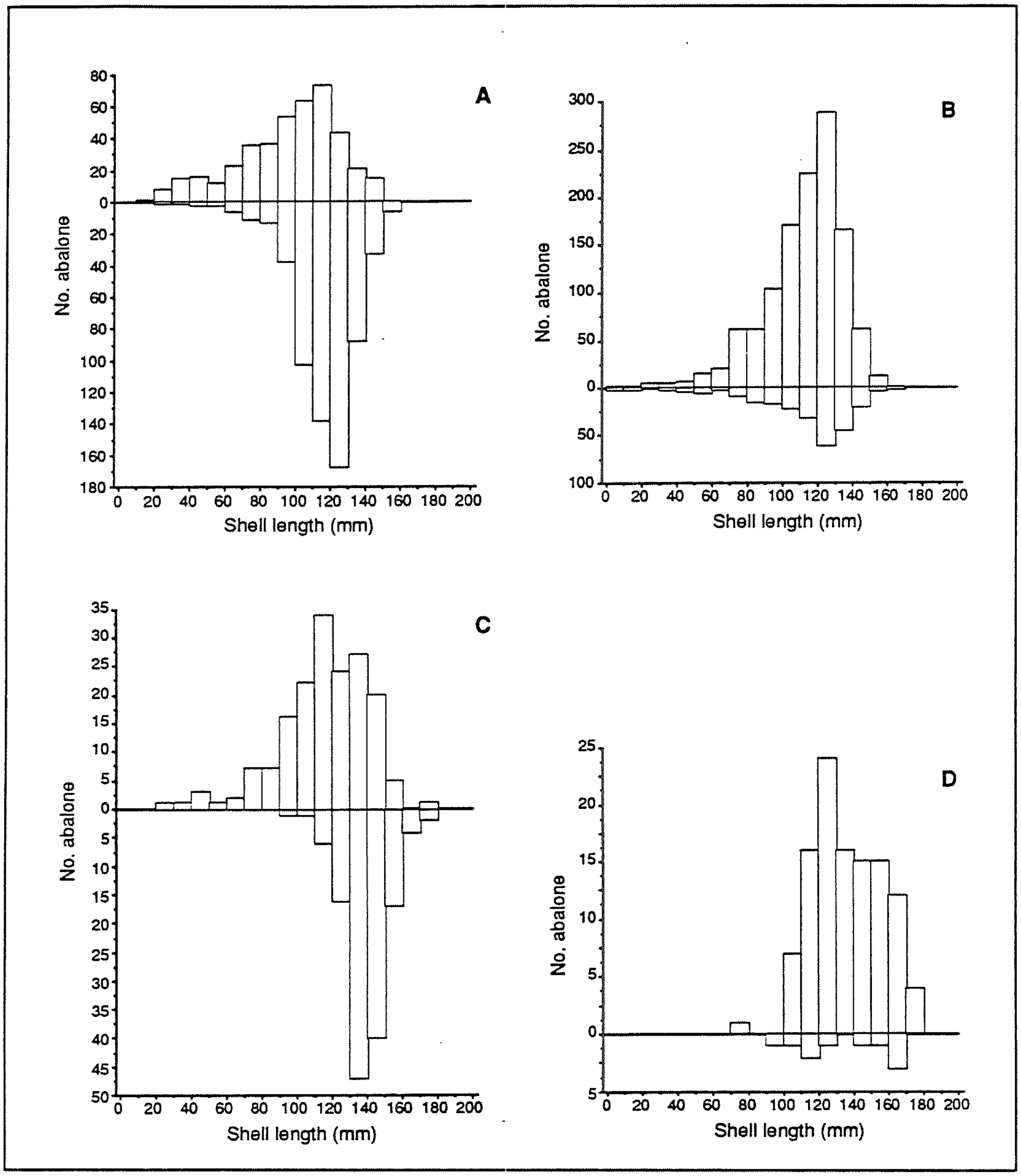

Figure 3. Length composition of ageable *versus* unageable *Haliotis rubra* from (A) Babel Island (all sites combined); (B) The Gardens (all sites combined); (C) Top Rocks; (D) Ketchem Bay. The ageable fraction is above the *x*-axis.(reproduced from Nash in press).

AGEING OF SCALLOPS

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The shell of bivalve molluscs consists of a proteinaceous matrix, which supports calcium carbonate deposition in the form of calcite or aragonite. As the mollusc grows, cells in the margin of the mantle secrete layers of calcium carbonate along the outer margin of the shell valves, thereby enlarging them. Shell growth is manifested as numerous small ridges or striae; these striae have been used as the basis for ageing individuals of several species. The two valves are joined dorsally by a flexible ligamentous hinge, which acts to oppose the closing action of the adductor muscle. This ligament also shows annular structure as a result of growth; it has been used for ageing individuals in a few species.

Larvae of the sea scallop *Placopecten magellanicus* kept in aquaria laid down their first growth line 3-4 days after fertilisation (Hurley *et al.* 1987). Annular rings were produced daily on the ventral outer margin of the shell, irrespective of the light regime (12 h dark: 12 h light, or 24 h light). However, when larvae were starved for 2-6 days and were reared at lower temperatures (11°C rather than 14°C), they showed fewer striae.

The daily deposition of rings on the shells of several species of scallops has been demonstrated in the laboratory; however it has also been demonstrated that deposition is affected by the conditions under which the animals are kept. Striae are also deposited on the outer margin of the shell of post-metamorphosis spat, and adult scallops. Wrenn (1972) suggested that in *Argopecten irradians* these striae were laid down each day, primarily in the late afternoon and evening. This observation was confirmed by Wheeler *et al.* (1975), who measured daily fluctuations in the incorporation of ^{45}Ca and ^{14}C-bicarbonate into the shell matrix. When adults were kept in the laboratory under ideal conditions they deposited one increment per day and the number of growth increments and the increase in shell height were strongly correlated. However, when conditions were poor, individuals tended to deposit slightly undersized increments and at less frequent intervals (Palmer 1980). Similar differences in the timing of deposition of striae were also noted by Clark (1968), who maintained *Pecten diegensis* in running sea water for about 50 days. He found that, while 6 out of 12 individuals formed shell striae that were compatible with daily growth increments, the other 6 produced fewer striae, which he attributed to a cessation of growth when individuals were disturbed.

Differences in the banding on the shells of individuals in wild populations have been attributed to variability in the shape and spacing of striae. Silina (1978) observed an alternation of zones of broad and narrow striae in shells of *Patinopecten yessoensis*. During winter (November-April, about 135 days), 18-28 zones form. Each zone, which consists of 10-12 faintly discernible narrower bands, is laid down over 5-7 days. During the remainder of the year 160-220 striae were laid down. Silina suggested that the striae became narrower after maturation. Franklin and Pickett (1980) described four types of shell banding in *Pecten maximus*: (i) a pigmentation band extending over several striae; (ii) an "interference" ring consisting of a deep cleft between two striae, usually with no difference in the width of striae on either side of it; (iii) protruding ridges made up of 20 or more striae bunched together, and probably due to longer term environmental change; and (iv) annual rings, which are preceded by closely grouped striae and followed by successively wider striae. The annual ring often consisted of thin, pale, overlapping striae laid down at the start of the new season's growth. These authors suggested that the number of striae after the annual ring approximated the number of days in the growing season (about 200), and that variability in growth is reflected in differences in the width of the striae.

Because both the type and causes of banding vary, visible rings on shells cannot be simply related to annual events, and even in individuals with clear banding, substantial interpretation is required. In *Placopecten magellanicus*, for example, Krantz *et al.* (1984) reported that growth rates determined from seasonally induced changes in $^{18}O/^{16}O$ ratios in shell calcite were twice those estimated by experienced readers counting shell bands . However, when Tan *et al.* (1988) repeated the experiment with individuals of this species from colder, more northerly areas, they found that shell bands were laid down annually. They suggested that the discrepancy could be attributed to the different hydrological regimes at the two collection areas which, in southern waters, may have resulted in growth checks being formed in summer as well as in winter.

Ageing using shell structure has been attempted with only two Australian scallop species. Joll (1988) used a tag-and-recapture study to show that pigmented striae on the shell of juvenile *Amusium balloti* were laid down daily. However, as the animals matured the rings became very tightly packed and difficult to count. The commercial scallop, *Pecten fumatus*, shows the same striae as other species, but their arrangement into visible bands is extremely variable. Fairbridge (1952) recognised both annual and disturbance bands in this species in southern Tasmania. He observed that the ring laid down by juveniles when they were about 30 mm shell height was the result of slowed growth in winter, followed by a spurt in August when individuals were about 1 year old. He also assumed later rings were annual. Our work has found one-year-old individuals of *P. fumatus* from Bass Strait are more likely to be 50 mm shell height (Martin *et al.* 1990) and that spat in collector bags will grow to 30 mm shell height in three months. Although disturbance rings are often seen on Bass Strait scallops, regular banding that could result from seasonal growth checks is much less obvious. This suggests that, in general, water temperatures in this region during winter are too high to significantly retard growth and produce externally visible rings on the shell. Because of these problems, a method that can be used routinely to age *P. fumatus* is yet to be found. Use of the shell ligament remains a possibility, for Merrill *et al.* (1966) found that, while annual marks were present on the ligament of *Placopecten magellanicus*, disturbance marks did not form in this structure as they did on the shell. Another approach might be to look for internal growth lines in shell cross-sections, such as have been observed in cross-sections of the shell of the Atlantic surf clam, *Spisula solidissima* (Jones *et al.* 1978). They were less variable than external lines, and Jones *et al.* inferred from marked and recaptured animals that they are laid down annually.

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DISCUSSION OF SESSION 2, SUB-SESSION B

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The Chairman invited brief discussion following each panel presentation, after which there was a time for more general discussion of the subject matter of Sub-session B.

The questions following *Bruce Phillips'* presentation covered the effects of tags on growth and the new methods of ageing crustacea using the parts of the cuticle and the accumulation of polonium 210. Steve Montgomery was told there was good evidence from micro-tagging experiments in Western Australia that tags reduced growth in lobsters. Information on the older and larger animals approaching L_∞ was difficult to get because the large animals are for various reasons not released with tags. Bruce Phillips was unaware of any current research in Australia on ageing lobsters using the polonium 210 method or the Japanese method of ageing crustacea using parts of the cuticle.

The problem of variability in the growth of tagged individuals was discussed following *David Die's* presentation. It was suggested that a particularly high or low growth rate observed during a tagging experiment may not be sustained throughout the life of a particular animal. Consequently, tagging results may not be representative. Steve Montgomery asked if the number of moults could be used to obtain a growth coefficient. David Die considered that it would not be useful because there was variability in both the intermoult period and growth. The intermoult period could relate more to environmental variability than size or age.

Warwick Nash answered questions on the problems of ageing abalone caused by boring organisms damaging shells and from stunted growth. Shells that were eroded were rejected for analysis. It was difficult to determine when shells stopped growing because ring deposition occurred on the inside of the shell and the annual growth increments decreased as L_∞ was reached.

There were no questions following *Peter Young's* paper on age determination in scallops.

During General Discussion Richard Beamish raised the issue of a standardised terminology for ageing methods as a criterion for publishing. David Smith also recognised the tendency to use different terms to describe the same feature such as growth rings, checks, annuli and increments. In order to improve scientific writing an attempt at defining terms was urgently needed. It was suggested that previous glossaries should be used as a starting point, and a revised glossary should be circulated to fish societies and editors of journals. A competing set of terminologies in different international journals that are mutually incompatible should be avoided at all costs. These sentiments were echoed by John Kalish, Peter Young, Keith Sainsbury, Ann Grant, Bruce Phillips, John Glaister, and Rob Day.

The session chairman, David Smith, continued the general discussion by requesting an account of the Canadian research on ageing invertebrates. Paul Breen responded by describing ageing techniques that were applied to a long lived species of freshwater clam. Acetate peels were taken from polished sections made through the scroll structure inside the umbo near the hinge of the bivalve. This method was validated by tagging hatchery-reared clams released into the wild, radio isotope ratios and the recovery of shells from an area that was completely dredged 25 years earlier. Ring counts indicated an age of up to 140 years and the average age was in the order of 60 years old. Richard Beamish added that analysis of ring sequences could be related to environmental fluctuations such as log jams in the rivers.

Referring to Warwick Nash's paper, Rob Day noted that growth checks of Japanese abalone were related to reproductive periods whereas elsewhere growth checks were related to low temperatures. Peter Young reiterated the problems of interpretation of the growth checks and ageing shellfish. In the UK, the spawning of scallops coincides with the end of winter and the combined effect produces a well-defined growth check. In contrast, the scallops in Bass Strait appear to be greatly influenced by periodic upwellings which cause the scallops to grow rapidly followed by interim periods of very little growth. Under the circumstances, the growth checks probably relate to upwelling time and nutrient input which may not be regular or annual. Don Hancock considered that it was necessary to examine species on a case by case basis. Referring to the cockle, a bivalve mollusc from the UK, he described a 6-month period of no growth during which a well defined ring was laid down. The development of the gonad started during the period of no growth. At the end of winter, spawning and the onset of growth occur at the same time. It was most likely that the growth checks were controlled by temperature because the one year old cockles, which were not ready to spawn for the first time, also laid down a ring like the two year olds which did spawn.

The discussion moved on to ageing methods for crustacea utilising the lipofuscin technique. Initial results have been very encouraging but highly influenced by temperature regimes. Murray MacDonald noted that fluorescence caused by formalin- preserved material introduced errors in the early stages of development of this technique. John Kalish considered that the basic problem was that lipofuscin is a pigment made up of a range of substances and consequently there was no clear cut-off point associated with UV excitation of the molecules. In order to address this problem, the first step would be to identify the pigments and determine the molecules in lipofuscin. This task was not really in the realm of fisheries biologists but biochemists. Once that had been done there were still a lot more problems to solve. The UV yield of lipofuscin could be investigated with spectrophotometers by homogenising the neural structure. The next step would be to observe the neurones directly and investigate the influence of factors such as temperature and stress which can influence the release of these substances. These sorts of problems still have to be resolved so the technique is still very much in the early stages.

Murray MacDonald followed up this discussion by asking whether the life span of Australian scallops has been correctly determined at an order of magnitude less than some Canadian marine bivalves. Peter Young replied that most of the species such as *Pecten maximus* have been given a maximum age of 20 years. These ages were determined during a large number of studies carried out in the 1960s. At that time, there was a lot of confusion as to what was being counted and nobody really agreed on the interpretation of the rings. The current estimate of maximum age of the local scallop of thirteen years was based on the work of Fairbridge. However, there was no long term validation of age from tagging studies to indicate how long the local scallops live. Modal progression has indicated that scallops grow for four years and there seems to be a general consensus around the world that scallops do not live to a very great age like the Canadian clams.

While there has been no suggestion that scallops live for enormous lengths of time, Richard Beamish added that Canadian rock scallops live to be well over 16 years old. Introduced Japanese oysters have been aged at over 30 years old because there was still evidence of the strong 1957 year class.

Keith Sainsbury considered that more validation of ageing studies was required. Although some length frequency and some tagging work have been undertaken, there have been very few attempts at validation of the ages of invertebrates. John Kalish suggested that radioisotopic methods have been widely used to obtain a maximum age of deep sea molluscs. The advantages of using these techniques on large bivalves was derived from the large amounts of calcium carbonate material in the shell. However this was a limitation when the method was applied to fish otoliths in which the amount of calcified tissue is very small. Peter Young agreed that where there was an annual cycle of temperature, the carbon radioisotope method would be a useful validation tool for shellfish.

Peter Young related the problems of validation of scallop ages by tagging experiments in Banks Strait. Over 20,000 scallops were tagged and only 12% were returned. The tagged scallops were in the water for 18 months and there was not a single return since then, despite the fact that scallops will hold a tag for a very long time. Estimates of fishing and natural mortality suggested that very few scallops in Banks Strait would have been left alive after the tagging period. The problem is that the population is exploited, and it is not possible to leave tagged scallops *in situ* for any length of time without them being removed by fishing.

Peter Young raised the issue of the relative importance of the large old individuals in comparison to the majority of the population. For instance, in Banks Strait, there is a small population of very large scallops, the size of dinner plates, which must be very old. As the average age of exploited populations is less than two years old, these very old large scallops represent a very small part of the population and biomass. However, they are an important component of the few remaining spawning adults in the stock. Part of the reason why there are such recruitment problems in the scallop fishery may be attributed to the lack of a sufficient number of large, old mature scallops in the exploited population.

Bruce Phillips remarked that animals aged at over 140 years far exceeded the working life of the average fish biologist! He considered that the difference between the relatively few very large and very old individuals and the large numbers in the rest of the population was so great that the very large ones could be considered as giants. There were examples of parasitised marine molluscs and facultative sterile lobsters which grew to exceptional sizes as energy was channelled into somatic growth rather than reproductive effort.

Richard Beamish considered that many of the very old fish were not particularly large and that there was no relationship between size and age of fish. For instance the Canadian rock fish which lived to a very old age and was not of a great size, reproduced every year at an age of 60-70. He found that it was really necessary to look at an unexploited population. He added that it was important to keep in mind the objectives of ageing studies. Usually it was to address a particular management problem. If animals live to a very old age, there was some genetic reason for the longevity. If scallops are being harvested at a very young age what does that say? What does that indicate? Is the population being overfished? He did not know anything about the Australian scallop industry. Is the scallop fishery in good shape here in Australia? So there is not going to be scallops for dinner tonight? Does that not say something? If an animal lives to be very old in the unexploited situation and we go back in time and we find that there used to be lots of old animals there, and now we are harvesting the animals that are only one or two years old, evidently we are putting our resource at tremendous risk if environmental factors play an important part in natural mortality and recruitment. This is what has happened with many of the over-exploited species around the world.

Sub-session C

Future Directions and Problems Encountered

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MICROCOMPUTER-BASED DIGITISING SYSTEMS FOR ANALYSING BONY STRUCTURES OF FISH FOR AGE AND GROWTH

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Abstract

The desire for accurate measurement of incremental structures in the hard parts of fish has led to the development of increasingly sophisticated methodologies. High resolution and precise measurement are particularly important when working with daily increments, which are often only a few microns apart. Speed and accuracy can be greatly increased when measurements are electronically digitised. These systems involve some method of projecting an image such that it can be electronically digitised using a microcomputer. The simplest and least expensive methods involve the use of a camera lucida or still micrographs to provide images which can be analysed with a hand held digitising pen connected to the microcomputer. A more accurate, albeit more expensive, method of projecting an image is with a video camera mounted on the microscope. The image can be projected onto a separate monitor and a digitising machine can be used in conjunction with a microcomputer to produce an inscreen cursor typically controlled by a "mouse". An alternative system which is simpler and less expensive is to interface the video image with the on-screen graphics of a microcomputer using "genlock" hardware.

Introduction

Knowledge of the age structure of fish populations is of undisputed importance in fishery science. However, the process of collecting and analysing data for ageing studies is time consuming, and the methods are open to significant levels of inaccuracy and imprecision (McGowan et al. 1987). Recent advances in microcomputer and video technology have provided the opportunity to decrease processing time and increase accuracy and precision of counts and measurements on bony structures of fish. In this paper I outline some of the methods presently available for use in analysing periodic structures in the bony parts of fishes and discuss their advantages and limitations.

Methods for Analysing Bony Structures of Fish for Age Data

Traditional Methods

A typical traditional method for analysing annuli in otoliths, scales or other hard parts of fishes would be to examine the bony structure under a stereo microscope, and use an ocular micrometer to make various measurements such as radius to each annulus. Measurements and counts would be then hand transcribed into a data log to be later entered into a computer data base. The main advantage of this method is that it is inexpensive, and most fisheries research laboratories would have stereo microscopes fitted with ocular micrometers. There are, however, a number of disadvantages of this method in terms of accuracy, precision and speed. The specimen and micrometer must both be sharply focussed which is difficult to achieve. Parallax errors may occur where the measurement extends to the extremes of the micrometer scale. The specimen may have to be repositioned to fit under the micrometer scale. It may be necessary to interpolate between micrometer divisions. Finally, the operator must look away from the specimen to record data. This method is particularly unsuitable for examining daily increments, because even at the highest magnification available with the light microscope, increments, which may be less than a micron apart (Campana *et al.* 1987), are extremely narrowly spaced in the field of view.

A variation on this method which may be more accurate but which is more time consuming is to outline periodic structures using a camera lucida and pen and paper and use this for making counts and measurements. A method which improves the accuracy and precision of counts and measurements, but which increases expense and is much more time consuming, is to take micrographs and make counts and measurements on these.

Modern Methods

The speed and accuracy of counting and measuring periodic structures on the hard parts of fish can be greatly increased with the aid of a microcomputer-based digitiser. The digitiser reduces operator error in reading measurement scales and where data are recorded directly into the computer, decreases overall processing time by eliminating data transcription and entry. Where a digitising tablet connected to a microcomputer is available this may be used in conjunction with micrographs (either prints or projected transparencies) or camera lucida image to digitise counts and measurements. The most convenient method of providing an image which can be digitised is to use a video camera. The use of a video camera to produce an image on a television or computer monitor, although initially more expensive than other methods, has the major advantage that the operator does not have to examine the specimen through the microscope to count and measure. This has major benefits in terms of operator fatigue and measurement accuracy. The major advantage over the micrograph method is that the time and expense of processing photographs is eliminated.

Two major types of video camera are available, the 2/3" tube camera and the charged couple device camera (CCD). Tube cameras are sensitive to low light and have very high resolution; however, they are extremely susceptible to damage by excess light, and repairs are very expensive. In contrast CCD cameras are very robust with respect to damage by light and are now approaching the same levels of light sensitivity and resolution as tube cameras. The price of each type is similar and at the present time a recent model CCD camera is recommended.

Once the image is projected onto a monitor it may be digitised in a number of ways. A simple method is to mount the monitor with the screen facing upwards and place a transparent sheet over it so that a digitising pen or "mouse" may be moved over the screen for counting and measuring. The disadvantages of this method are that parallax error and screen curvature may affect the accuracy of measurements. The most accurate way to digitise a video image is with an "in screen" cursor. One method of producing an "inscreen cursor" is to use a separate component of digitising hardware such as the H.E.C. Video Coordinate Digitiser. This produces a cursor which is incorporated into the video image on a television monitor. The cursor may be positioned with a "roller ball" attached to the digitiser or may be controlled with a "mouse". A television monitor with very high resolution, ie. 1000 vertical lines, can be used. The main disadvantage with this system is the expense; apart from the computer, video camera and separate monitor, the video coordinate digitiser itself costs over $5000 US. Perhaps the most elegant method to date to interface a video image with a microcomputer-based digitiser uses "genlock" technology. This inexpensive piece of hardware (about A$1000) allows the video image to be displayed on the microcomputer monitor overlain by the computer's graphical display, ie pull down menus, mouse cursor and other types display. This technology is well developed for the Commodore "Amiga" line of computers but is becoming available for other major PC types as well. This system requires no separate digitiser or television monitor, considerably reducing expense. The resolution of computer monitors is now approaching that of high resolution television monitors, so this is not the problem it once was. More sophisticated "genlocks" allow video images to be saved to disk, providing the potential for a library of otolith images to be stored on disk or magnetic tape. In general the "genlock" technology seems to provide the best option to date in terms of providing maximum accuracy and speed of digitising and data processing at a reasonable expense.

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A BETTER MOUSETRAP? USE OF IMAGE ENHANCEMENT FOR AGEING BASED ON HARD PARTS

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One of the standard, and most commonly applied procedures for ageing fishes is the counting of "growth increments", either annuli or daily increments. Despite the ubiquity of these procedures, there are several fundamental problems associated with them. First, incremental structure is often ambiguous, for several reasons. "False" increments, multiple growth increments and growth hesitations are common in hard parts. The number of conspicuous increments visible along one radius is often different from the number visible along other radii. And, in older fishes especially, increments are often so closely spaced that discriminating between them is difficult. Second, errors in counting are common, particularly with regards to daily growth increments. For older larvae and small juveniles, observers often need to discriminate between and count several hundred increments. An error of only a few percent can have a significant effect on reconstructed spawning cycles and estimated rates of larval and juvenile growth. Third, because counts are made by eye (albeit usually aided by a low power microscope or a scale-reader) and the decision as to what to count and what to ignore is often not easy, counts made on the same otolith often differ between observers, and even between days for the same observer. Hence, it is a routine practice for each otolith to be counted several times in order to determine an "average" age (which may or may not be accurate). When substantial differences remain between observers, otoliths are usually discarded. Counts are also routinely made by at least two observers, in an attempt to minimise subjective errors and to ensure that the basis for counting has not changed over time (which can happen as observers become more familiar with the otoliths being examined). There are no objective standards or reliable means of quantifying incremental structure, which could otherwise provide a way to define precisely what one decides to count and what to ignore. And fourth, current ageing procedures are time consuming, limiting the number of animals that can be routinely aged, and to an extent inherently imprecise. Measuring increment widths (as in, for example, validation by analysis of changes in the width of the marginal increment) by using a microscope reticule or holding a ruler up to the projected image, for example, is inefficient and prone to measurement errors. Ultimately, such difficulties affect the quantity and quality of the data on which, among other things, management decisions are based.

The widespread availability of small, powerful and relatively inexpensive microcomputers raises the possibility of a radical change in the procedures by which conventional age determination based on hard parts is carried out. Specifically, it makes possible application of relatively simple procedures for computer enhancement and processing to the examination and statistical analysis of the optical images routinely used to age animals by means of daily or annual increments. Image processing offers several extremely attractive and powerful advantages over conventional, non-computer-assisted ageing procedures, including vastly increased resolution of poor images, automatic (and near instantaneous), error-free counting and measuring of features in the images, and electronic magnification of closely spaced increments.

Image processing can be divided into two components: image analysis, which involves measurement of spacing, areas or some other quantitative aspect of the image, and image enhancement, in which computer-assisted procedures are used to improve the clarity of the image. The two processes are closely related and often can be done in conjunction with one another, eg image analysis almost always follows enhancement. Hardware and program needs, however, are very different. Image analysis is the easier and less expensive of the two procedures to implement, and several routines for the automatic or semi-automatic counting and measuring of incremental structure in hard parts have been described in the literature (e.g., Frie 1982; Campana 1987; Gandelin and Laval 1987). Image enhancement has not been as quickly incorporated into ageing studies. Historically, there are several reasons for this. First, although the computer programs involved in image enhancement are relatively simple in concept (see, for example, Baxes 1988), they can be difficult to implement. Programs tended to be expensive, and highly specialised. Second, the computer hardware required to undertake image enhancement ("frame grabbing", high-resolution digitising boards, large memory requirements, powerful processors to handle full image manipulation) have also been expensive (e.g., in the tens of thousands of dollars). And third, the relatively "clean" images routinely involved in industrial applications of image enhancement are not typical of "dirty" otoliths, for example, where background optical density varies widely and non-linearly across the image, and incremental structure is often "fuzzy". The complexity of the image, while on the one hand making it an ideal candidate for application of image enhancement procedures also renders useless quick and easy application of software not specifically designed for use in ageing.The logistical and cost problems of image enhancement are resolving themselves as technology advances. Current generation, inexpensive microcomputers, e.g., the Macintosh II series and the Amigas, are designed with high-resolution graphics in mind, and are therefore "pre-adapted" for image enhancement.

High-resolution "frame-grabbers" suitable for such computers are now widely available, usually for less than a few thousand dollars. Problems of software availability have altered even more dramatically. Recently, several very powerful image enhancement software packages, designed to run on, for example, the Mac II, have become available as public domain (e.g., free) "shareware", e.g., NIH Image (Lennard 1990). Although designed for general application, these image enhancement packages constitute a valuable and powerful resource base for development of software contoured specifically for ageing purposes.

The question of whether image enhancement offers a panacea for problems of subjectivity and inaccuracy in ageing based on hard parts is not yet answered. Like most technology dependent problems, the answer tomorrow is likely to differ fundamentally from that today. The difficulties in enhancing effectively "dirty" images, like otoliths, is far from insurmountable (NASA does it all the time, albeit with a budget slightly larger than that of most fisheries or academic institutions). It requires the marrying of statistical analysis (e.g., two dimensional, non-linear regression) to image enhancement. This step has not yet been demonstrably taken in fish ageing programs. Until it is, casual users of image enhancement procedures will continue to be disappointed with the results of simple enhancement programs and the potential of the technology will not be fully assessed.

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ELECTRON PROBE X-RAY MICROANALYSIS OF CALCIFIED TISSUES: AN ALTERNATIVE METHOD OF DETERMINING AGE OF FISH

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Effective fisheries management requires precise data on length-at-age distributions and growth rates. These data have traditionally been obtained from tag-and-recapture programs, modal analysis of length-frequency samples, and conventional ageing based on hard parts. All three techniques have a number of disadvantages when used for routine determination of age and growth. Tag-and-recapture programs provide the best and least ambiguous data on growth, for example, but are expensive to undertake, may be insensitive to changes in growth rate (unless the program is repeated at high frequency), and generally lack precision for older fish, which are rarely recaptured. Similarly, modal analysis of length-frequency data can produce very reliable and accurate estimates of population-mean growth rates for young, fast-growing fishes, in which length modes are usually well separated and movement of the modes is relatively rapid, but is imprecise and often wholly ineffective for mature fishes, in which the modes overlap extensively and growth rates have declined. Finally, 'conventional ageing', based on counting numbers of annual growth increments in calcified structures (e.g. vertebrae, otoliths, scales, and fin-spines) suffers from difficulties in resolving the outermost 'annuli' in older fish (the growth increments become more closely spaced due to the declining growth rates of most fish as they mature), as well as problems of subjectivity and, usually, poor validation for mature fish.

For these reasons, we have been examining an alternative method of accurately ageing fishes. Since 1987, we have been investigating whether the chemical composition of otoliths can be used, first, to provide information on fish movements and as a means of stock discrimination, and second, as a method of age determination. The concept of obtaining life-history information through the analysis of variations in the chemistry of mineralised/ calcified tissues of marine organisms is by no means new. The chemistry of mineralised tissues of marine invertebrates, including bivalves, gastropods and corals, has been studied extensively since the mid-1960's (Dodd 1965; Weber 1973; Buchardt and Fritz 1978; Smith *et al.* 1979; Rosenberg 1980; Schneider and Smith 1982). In a number of instances, the concentrations of a range of elements were noted to vary episodically along the growth axis of the tissue, suggesting regular ontogenetic or, perhaps, seasonal variability in composition. Subsequent studies have indeed linked changes in composition to both environmental factors, such as water temperature, pH, salinity, and food availability, and physiological factors, such as reproduction.

Episodic variability in composition has also been noted in the calcified tissues of teleosts and elasmobranchs (Calaprice 1975; Gauldie *et al.* 1986; Radtke and Cailliet 1984; Kalish 1989; Radtke 1989). In these studies (as well as most of those involving invertebrates), the principal element considered was strontium, which is thought to be physiologically neutral (i.e., it has no specific toxic or beneficial effects) and which substitutes for calcium into the calcium carbonate-protein or calcium-phosphate-protein matrices of calcified tissues. It has often been suggested that the level of substitution varies with water temperature (Sr:Ca ratio increases as temperature declines) (e.g., Dodd 1965; Smith *et al.* 1979; Radtke 1989), but the issue is by no means clearcut (Buchardt and Fritz 1978; Kalish 1989). Irrespective of whether or not water temperature is the primary determinant of Sr concentrations, most studies suggest that the cyclic variations in Sr, and some of the other elements, nonetheless represent seasonal cycles of deposition and therefore, that peaks in this ratio can be counted to determine age. For fishes, the validity of this ageing procedure has not yet been tested.

We are currently involved in such a validation study. To date, we have worked primarily on otoliths and primarily with southern bluefin tuna (SBT), *Thunnus maccoyii,* and jackass morwong, *Nemadactylus macropterus.* The standard procedure we have developed involves analysing composition at points every 20-25 mm across the full growth axis of an otolith, using a Cameca Camebax wavelength dispersive electron microprobe. A typical example of the cyclic patterns in the Sr:Ca ratio that we observe for *N. macropterus* is shown in Figure 1. For morwong, we have not as yet attempted to validate that these peaks represent annual events, but we also note that our age estimates, based on the number of peaks, agree closely with those predicted from length-at-age growth curves determined by other ageing methods (Smith 1982; Wankowski and Jolley 1986). The bulk of our ageing work, however, focuses on SBT. As in the morwong, we invariably find conspicuous episodic variations in chemical composition along the growth axis of tuna otoliths. Peaks in the Sr:Ca ratio can be clearly seen and are easily discerned, even in the outer margin area of sagittae from large *T. maccoyii* (Figure 2). This suggests two important advantages of this ageing technique over more conventional ones. First, the presence or absence of peaks in element concentrations can be determined statistically, thereby removing the subjectivity and uncertainty associated with conventional ageing by means of hard parts. And second, even peaks near the edges of otoliths of large fish are easily discerned and separated, whereas optical increments counted using conventional techniques are typically difficult to separate near the margin. Hence, if it can be made to work routinely, ages for large, mature tuna, and other fishes, can be determined much more accurately and precisely using probe microanalysis than is possible using conventional methods. The key, of course, is whether or not the peaks in concentrations represent annual events. For this validation, we are currently analysing the marginal composition of otoliths from *T. maccoyii* caught throughout a 2 year period, to test directly whether the pattern of element deposition varies during the year.

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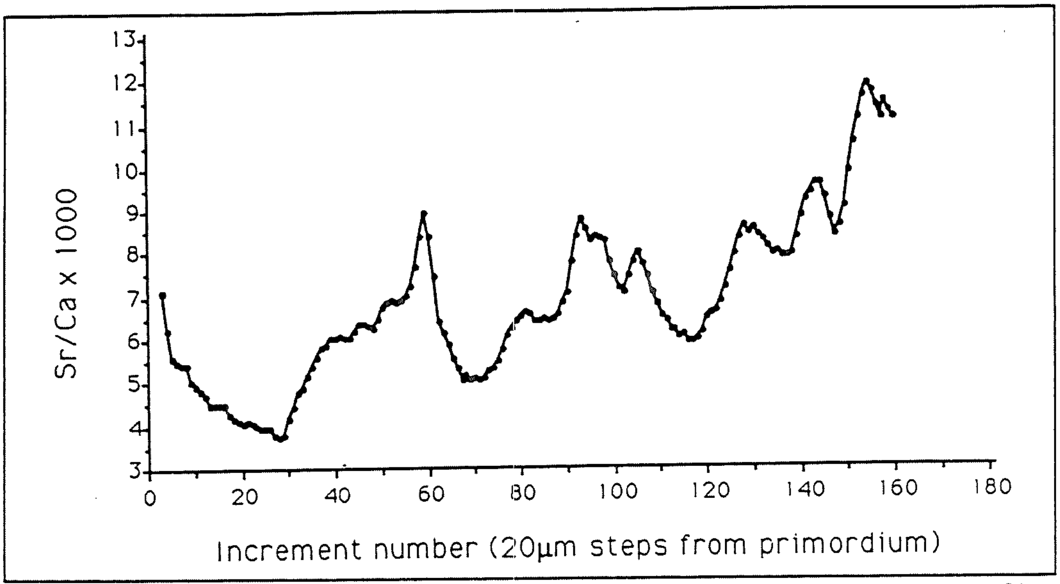

Figure 1. Life-history scan for Sr (expressed as Sr/Ca ratio) across a sagitta from *Nemadactylus macropterus* (34 cm S.L.) conducted on Cameca Camebax WDS electron probe (15 kV, 25 nA, 14 mm beam diam.).

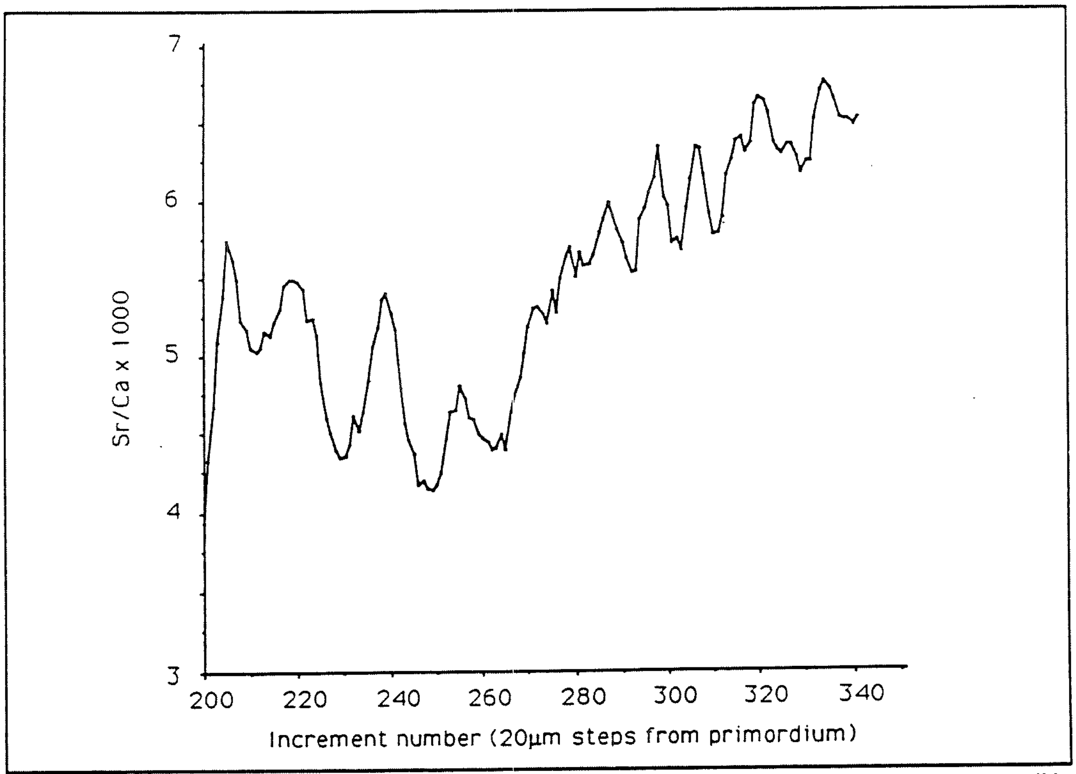

Figure 2. Life-history scan for Sr (expressed as Sr/Ca ratio) across the outer portion (ie.posterior region of the otolith section, near margin) of a sagitta from *Thunnus maccoyii* (177 cm F.L.) conducted on Cameca Camebax WDS electron probe (15 Kv, 25 Na, 14 mm beam diam.).

AGEING FISH USING RADIONUCLIDE ANALYSIS

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Introduction

Fisheries scientists need to know the age structure of fish populations for management purposes. Unfortunately many species (e.g. deep-sea and tropical species) are difficult to age using conventional methods,and validation of those ages very difficult to obtain. An alternative independent ageing method that has been showing considerable success in recent years is radionuclide analysis. Calcareous structures such as otoliths, shells and corals incorporate trace levels of radioactive elements from the uranium and thorium decay series during life which then decay at known rates. Therefore by analysing the very low levels incorporated it is possible to determine the age of the animal. There are several different isotope pairs (^{228}Th/^{228}Ra, ^{210}Po/^{210}Pb and ^{210}Pb/^{226}Ra) from the uranium and thorium decay series that are biologically useful. For example, the pair ^{228}Th/^{228}Ra, useful in the range 0-10 years, has been used to verify annual banding in modern corals (Dodge and Thomson 1974), to age vesicomyid clams growing in hydrothermal areas (Turekian *et al.* 1983) and to age the carapaces of spider crabs and the European lobster (LeFoll *et al.* 1989). The pair ^{210}Po/^{210}Pb useful for only 0-2 years, has been used to measure the growth rate of *Nautilus pompilius* (Cochran *et al.* 1981) and to age sharks (Weldon *et al.* 1987). The isotopes ^{210}Pb/^{226}Ra are potentially very useful, since they provide age data in the range 0-100 years. This pair has been used to age several teleost fish species and will be discussed in detail.

^{210}Pb/^{226}Ra Analysis

Radiometric age determination using ^{210}Pb/^{226}Ra is based on the fact that these isotopes are in radioactive disequilibrium when incorporated into an otolith. Thereafter they gradually approach the equilibrium state, where the rates of decay of the two nuclides reach equality, which in this case takes about 100 years. It is the extent of the disequilibrium that acts as a natural chronometer.

The analytical technique consists of cleaning the otolith or shell of any organic coating with "Fenton's Reagent" and then dissolving them in dilute HCl. At least 1 g of material is needed, therefore pooling of samples is often necessary. The chemical procedure is detailed in Fenton *et al.* (1990). ^{210}Pb is analysed via its alpha emitting grand-daughter ^{210}Po, and ^{226}Ra is measured directly, both by alpha-spectrometry. The radiochemical analyses require the best available ultra-low level techniques and equipment. Two samples can be analysed simultaneously with each radiometric analysis taking 2-3 weeks. An equivalent blank run is needed for each species analysed.

For the radiometric ages to be valid, several assumptions must be met. These assumptions have been discussed by Bennett *et al.* (1982) and Fenton *et al.* (1990) but it is important to re-state them here:

1) both ^{226}Ra and ^{210}Pb are taken up into the otolith at a rate always in constant ratio to the rate of mass increase of the otolith;

2) the rate of uptake of ^{226}Ra significantly exceeds that of any ^{210}Pb, i.e. allogenic ^{210}Pb is much less than ^{226}Ra and can therefore be distinguished from radiogenic (authigenic) ^{210}Pb;

3) no losses or gains of ^{226}Ra and ^{210}Pb occur after uptake, other than by radioactive decay or ingrowth.

Any violation of assumptions 1 and 2 can be identified from the results of the assays, particularly by analysing juveniles of the species. The specific activity (activity per unit mass) of ^{226}Ra in the otoliths should be invariant with increase in mass of the otolith, i.e. be invariant with age. The specific activity of ^{210}Pb would be a function of the decay of any allogenic ^{210}Pb and ingrowth of authigenic ^{210}Pb (from the decay of ^{226}Ra). Thus the specific activity of ^{210}Pb would be expected to increase with time. Assumption 3 is based on the observations of numerous authors (reviewed by Veeh and Burnett 1982) that ^{226}Ra and ^{210}Pb distributions in modern aragonitic corals are not compatible with any significant loss of ^{222}Rn, or other nuclides, in the ^{238}U decay chain between ^{226}Ra and ^{210}Pb.

These three assumptions were met in the study of *Sebastes diploproa* (Bennett *et al.* 1982) and for orange roughy (Fenton *et al.* unpubl. data) and ages determined. However, in a study where sharks were aged by ^{210}Pb, serious problems were experienced with violation of the "closed system" and "constant uptake" assumptions (Weldon *et al.* 1987). Of the 4 species of sharks analysed, the radiometric age for only two were consistent with estimates based on other methods. The variability they observed was thought to be due to both the analytical limitations of low-level radioactive analyses and physiological processes within the calcified cartilage of the vertebral centra used for analysis (Weldon *et al.* 1987). The assumption of constant uptake was also violated in blue grenadier (Fenton *et al.* 1990), probably due to the change in habitat between juvenile and adult life. Therefore, age determination was not possible for blue grenadier.

A recent study by Campana *et al.* (1990) avoided the problems of constant uptake of ^{226}Ra and knowledge of the mass growth rate of the otolith with the whole-otolith method by only analysing the central cores of the otoliths. Their study of the redfish *Sebastes mentella* demonstrated that ages determined by radionuclide analysis confirmed the ages obtained by using the criteria of Beamish (1979) for the interpretation of annuli in charred cross sections of the otoliths. Therefore by analysing the central core of otoliths the range of species suitable to age using radionuclide analysis is greatly increased. For example, this coring method would enable ageing of species where a habitat change occurs and secondly for species where only adult otolith material is available for analysis. However, drilling out the core of otoliths is not without problems. Apart from the extreme care required to remove only the oldest material and to avoid contamination there is the problem of pooling samples to obtain sufficient material to analyse i.e. about 1 g. Pooling samples is a potential problem particularly with the larger (and older) individuals of a species since a wide range of ages for fish of the same length would be expected and in the case of orange roughy this range can be in the order of 60 years (Fenton *et al.* unpubl. data). In this case pooling would provide an average age and not show true longevity.

Conclusions

Fish ages can be determined using radionuclide analysis of $^{210}Pb/^{226}Ra$ in otoliths. Two approaches, whole otolith and coring are possible. The choice of method depends on the species involved and samples available, for the reasons discussed. Radionuclide age determination offers the possibility of ageing fish species that are difficult or impossible to age by conventional methods.

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THE PROBLEM OF AGEING ORANGE ROUGHY

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Introduction

Orange roughy (*Hoplostethus atlanticus*) is now the major species in the South East Trawl Fishery (SET) and yields the largest finfish catch in Australia, with approximately 40,000 tonnes landed during the period May 1989 to April 1990. The species is also an important resource for the New Zealand deep-water trawl fishery. Orange roughy are caught predominantly in depths from 800 to 1100 m.

There remains considerable uncertainty regarding the key biological information necessary for the effective management of this valuable resource. Orange roughy have proven very difficult to age although otoliths do exhibit distinct translucent (hyaline) and opaque zones. Interpretation of these zones has led to considerably different estimates of the species' growth rates and longevity (Kotylar 1980; van den Broek 1983; Gauldie *et al.* 1989). Recently, however, Mace *et al.* (1990) have shown that the first three translucent zones on very small (<10 cm) orange roughy are formed annually, indicating very slow growth.

Because studies on orange roughy in Australian waters are being conducted by several fisheries agencies, an Orange Roughy Workshop was held in October 1987 to coordinate, and to avoid duplication of, research. Participants agreed that the Marine Science Laboratories (MSL) would have the main responsibility for ageing orange roughy by conventional methods.

In this paper, methods used at MSL and preliminary results are briefly described. The most suitable methods for ageing mature orange roughy are also discussed.

Ageing Methods

Prior to using otoliths all bony parts were examined for their suitability as material for ageing orange roughy. Generally all, except otoliths, showed little structure or zonation useful for ageing.

Otoliths were taken from orange roughy sampled during survey trawling between January 1987 and June 1989, from commercial landings (Smith *et al.* 1988), and from regular samples, particularly of small fish, provided by other institutions (Table 1).

Whole Otoliths

Greatest emphasis was given initially to small immature fish (< 25 cm) because the zonation pattern is most evident on their otoliths. Whole otoliths were "read" using a semi-automatic system to record relevant details and measurements. Otoliths were immersed in water against a black background and examined under low power (x6) using reflected light. Under these conditions translucent zones appear dark whereas opaque zones appear white. Some otoliths from larger fish required brief soaking in water to clarify the inner zones, but prolonged soaking reduced clarity at the edge.

Measurements for each otolith were taken using a 22x28 cm digitising pad (Kurta bitpad) and a LED cursor linked to an Olivetti microcomputer using custom software. A dissecting stereo-microscope and camera-lucida were used to superimpose the LED image on the microscope field of view. The centre of the nucleus was digitised first and the translucent zones were measured along the anterior/posterior axis in the anterior portion of the otolith. As far as possible each otolith was read blind, that is with no reference to the size of the fish.

A readability, or hardness, scale was used to assess and compare the clarity of each pair of otoliths:

1. otoliths very clear - good resolution between zones;
2. otoliths clear - resolution reduced but zones still discernible;
3. reduced clarity and resolution and/or zones only discernible in one area of the otolith;
4. zones could not confidently be interpreted - very poor resolution;
5. otoliths fragmented or broken - unreadable.

Only those rated 1-3 were used subsequently.

The appearance of the edge, whether translucent or opaque was also recorded.

These data were written automatically to two files; one containing summary information including "age", and the second, all data.

Otolith Morphometrics

A subsample of orange roughy, from 13-43 cm standard length (SL), was examined separately and otolith morphometrics including length, width and weight recorded.

Sectioning

Otoliths from fish covering a broad size range were embedded in a polyester resin and sections, 0.1-0.2 mm thick, were cut with a Gemmaster cutting saw with a 10 cm x 2 mm blade. The sections were first washed in water, to remove resin and otolith particles, and then in 100% ethanol. Sections were mounted on slides (DPX mountant) and protected with a cover slip.

Preliminary studies indicated that sections along the anterior/posterior axis of the otolith gave the best results (cf. blue grenadier where transverse sections are used).

The system used to read whole otoliths was also used to read sections.

Results and Discussion

Whole Otoliths

The results of a comparison between two readers indicates that counts are consistent and thus the level of precision is high; 92% of the counts were the same or had a deviation of only one translucent zone (Table 2).

If one translucent and one opaque zone are laid down each year then the youngest fish aged was 4 years (at 14 cm SL) and the oldest 28 years at 40 cm SL (Figure 1). Because length at first maturity for orange roughy is about 30 cm (Bell 1989) our results indicate an equivalent age of up to 20 years. Regular (i.e. monthly) samples of small (<15 cm) orange roughy were difficult to obtain and so the change in marginal increment could not be used to validate the ages of juveniles.

Our results for immature fish are consistent with those of Mace *et al.* (1990) and with those from radionuclide ageing conducted at the University of Tasmania (David Ritz pers comm).

There are, however, still problems with larger fish; counts on whole otoliths are not as high as might be expected (given the age at first maturity) and are much lower than the maximum age of more than 80 years indicated by the radionuclide analysis. The maximum "age" reported by Mace *et al.* (1990) was also less than 30 years although they do report surface counts up to 42 on fish not included in their Figure 5.

Such results show that whole otoliths are not suitable for the ageing of large, and presumably old, fish.

Otolith Morphometrics

Otolith length is linearly related to fish length ($r^2 = 0.96$). The relationship for otolith widths is similar. Otolith weight, however, increased rapidly after about 35 cm SL (Figure 2). Our results show that after maturity otoliths thicken rapidly. Therefore surface counts are unlikely to indicate the true age for mature orange roughy.

Sectioned Otoliths

Approximately 500 orange roughy otoliths have been sectioned and mounted on slides ready to "read". There are considerably more zones evident in sections than for whole otoliths with preliminary counts in excess of 70. We are now comparing counts for sectioned and whole otoliths of small fish in an attempt to develop a method for ageing mature fish.

Conclusions

Zone counts on whole otoliths from juvenile orange roughy give estimates of age which are consistent with those recorded by New Zealand researchers and for radiometric ageing methods.

Whole otoliths are of little use for ageing mature fish because otoliths thicken after maturity.

Preliminary results suggest that examination of sectioned otoliths may be the most useful method.

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Table 1. Orange roughly otolith samples, obtained during 1987-1990, shown as a composite year
MSL, Marine Science Laboratories, Victoria; DSF, Division of Sea Fisheries, Tasmainia; CSIRO, CSIRO Division of Fisheries; BRR, Bureau of Rural Resources (Great Australian Bight samples); FRI, Fisheries Research Institute, NSW

Institution	Number of otolith samples recieved during											
	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
MSL	1252	358	0	1719	2825	0	1373	701	0	0	872	0
DSF	35	620	2	71	77	2	244	24	13	48	0	0
CSIRO	82	0	83	60	0	0	0	0	0	0	0	0
BRR(GAB)	114	123	340	298	192	78	159	72	115	0	59	50
FRI	203	45	237	69	62	24	0	38	0	0	0	3

Table 2. Difference between primary and secondary readers' translucent zone counts from whole otoliths
Sample size 94; number unreadable 7; size range 18 - 32 cm standard length; "age" count range 8 - 21

Deviation in counts	Percentage deviation between readers
0	44
1	48
2	6
3	0
4	2

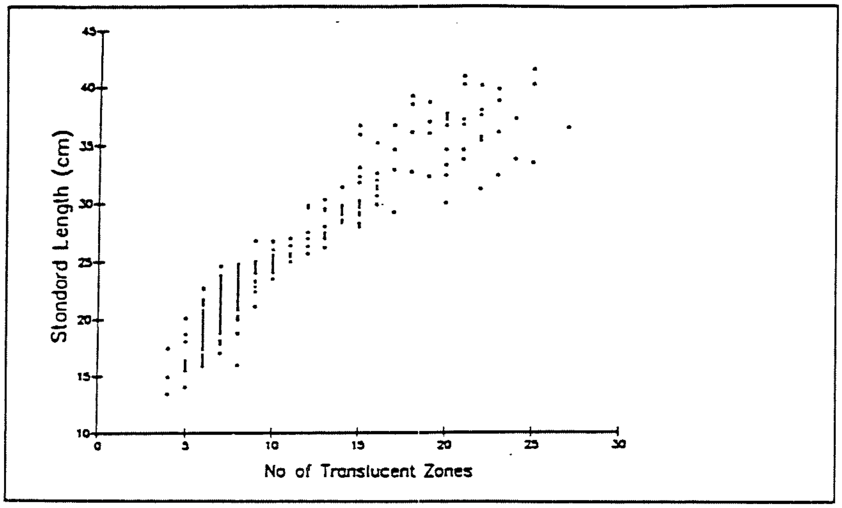

Figure 1. Relationship between fish length and the number of translucent zones - whole otoliths.

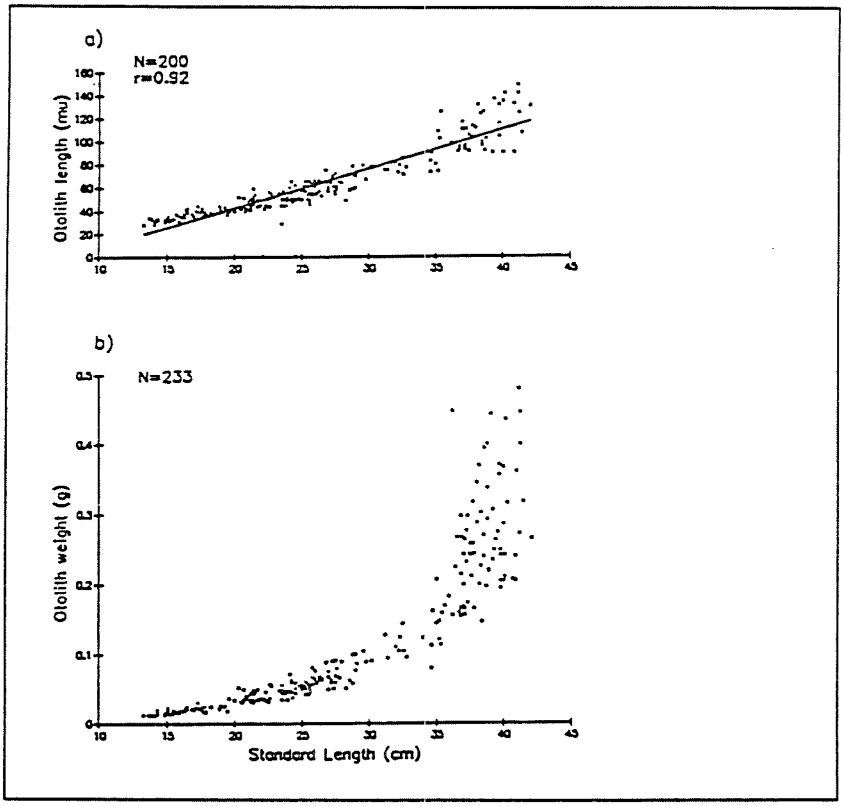

Figure 2. Otolith morphometrics - relationship between a) otolith length (micrometer units) and b) otolith weight and fish length.

PROBLEMS ENCOUNTERED AND FUTURE DIRECTIONS

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Right from Dick Beamish's opening talk it has been obvious that the science of ageing fish and invertebrates still has many shortcomings. Today, nobody has pretended otherwise. My conclusion from today's discussions is that the shortcomings in our science of growth and ageing are symptomatic of the lack of knowledge of fish and invertebrate biology in general. This in turn relates back to the problems of dealing with organisms which we often cannot even see in their natural state, and for which we often have little more than anecdotal information, and when we do have data they are often nothing more than a very small number of point estimates in a large time scale. It is also due, in part, to the tremendous individual variability within the species of organisms being researched, and the small proportion of the total population that has been sampled. On top of this we have the changes in the physiology of individuals with age and with natural fluctuations in their environment. There are then the population effects due to man's intervention. These include the important primary variables of pollution and habitat change, and draw attention to the tremendously important influence on growth that arises from density dependence, a factor which has not even been mentioned so far today.

On top of this series of variability in populations and individuals there are many experimental problems that plague all biological studies. A prominent uncertainty for age and growth studies is the question of whether our observations affect our estimates of age. Several examples have been presented where this does occur, most notably tagging often slows the growth of fish, and the extreme example where tetracycline treatment actually killed the fish being studied, and in other cases had sub-lethal consequences, for example Terry Walker's sharks where tetracycline turned them yellow. Who can answer the question: Is a yellow shark a happy shark?

It is obvious that ageing fish and invertebrates is extremely difficult and interpretation of our results is fraught with uncertainty. Unfortunately, like all fisheries research work, and for most experiments which are difficult to perform, research on age and growth is expensive, and as many of the species we need to study are not of major economic significance in their own right, it is often extremely difficult to obtain enough money to have even a first attempt at ageing. Of course when you have made this attempt and have a preliminary answer, it is often even more difficult to obtain funding to validate that estimate when financial managers find the repetition of an experiment far from their list of high priorities.

Moving from generalities to the specific points covered by individuals speakers, I refer back to Dick Beamish's opening address. Dick stressed the importance of validation of age determinations and of ageing techniques, and the need for quantification of precision, accuracy and errors, and acceptance of the many sources of variability to which I have already referred.

Dave Smith reminded us that in Australian fisheries we will, in the future, be relying even

more heavily on age structured models. He again reminded us that ageing is difficult and we should not expect too much from present techniques.
Kevin Rowling indicated the differences in age and growth between species in a single fishery, in this case the south east trawl fishery. The implications for management, particularly as we head towards ITQ (individual transferable quota) systems for each and every species, are daunting. If, as Dave Smith suggests, management relies increasingly on age-structured models for resource assessments, then the implications of many and varied age-structured populations within a single multi-species fishery are frightening. Kevin also highlighted the need to ensure that if tagging is to be used as a method for studying ageing or growth of fish, then the tagging experiments should be designed specifically for this purpose. This is unfortunately seldom the case and far too often tagging experiments are sold as being all things to all people.

John Anderson stressed the specific problems with the ageing of freshwater species and raised many points, the most important of which I felt was the concept of a verification reference centre. I found myself agreeing very strongly with John on this and wondered whether or not this could become a function of the Ageing Facility which we hope will be soon established in Victoria.

I have already referred to Terry Walker's problems with tetracycline and sharks. Terry highlighted the types of errors that can easily be made, and I was particularly impressed with his revelation that tagging work had indicated that school sharks were in fact twice as old as had been estimated by other methods of ageing. His reference to one shark known to be at least 40 years old but which had only 22 rings on its vertebrae left us all wondering. Terry also highlighted the valuable point of the need for species-specific stains when preparing hard parts for reading.

Ron Thresher outlined for us the problems of ageing larval fishes. I found his discovery that daily rings are easier to read in temperate rather than tropical species, most interesting. Ron also made the point that he felt that daily rings could not be used for fish over 200 days old. While this may generally be true, I believe it relevant to draw your attention to the work of Alex Wild of the Inter-American Tropical Tuna Commission who has been able to age yellowfin tuna up to five years by counting daily rings. His estimates have been validated against tagging and modal progression data.

John Kalish highlighted the differences between species, in this case, snapper and orange roughy. John demonstrated that otolith counts on snapper had been successfully validated by tagging work but he expressed grave concerns that orange roughy age estimates derived from otoliths appeared to significantly underestimate ages derived from other techniques.

The invertebrate section was opened by Bruce Phillips who introduced us to the problems of ageing crustacea. Bruce highlighted the lack of useable hard parts for these species and drew our attention to another major problem of this group of animals; this is the variability in time from the egg to settlement and to subsequent recruitment to the commercial fishery. From Bruce's figures it appeared that the variability from settlement to recruitment for lobsters was as much as 50% within the three year period it takes for recruitment. He also indicated that for one New Zealand lobster species there is a 22 month period between the time of spawning and subsequent larval settlement. These are major sources of variability and highlight the problems of ageing crustacea and of relating stock size and recruitment.

David Die stressed several problems with penaeids, similar to those covered for lobsters and emphasised the particularly important point that in most of our studies, particularly tagging and length frequency analyses, we are not measuring absolute age at all, we are actually only getting a measure of relative age.

Warwick Nash highlighted the problems with ageing abalone, but did acknowledge there is good news, that at least with this invertebrate we have a hard part that appears to be useable. Annual rings can be counted on abalone shells but validation is not yet conclusive. However, further good news is that modal progressions and tagging could both be used to solve this problem.

Peter Young was not so optimistic for scallops. He did however convince me that daily ring counts were at least a measure of minimum age and while Peter was loath to put too much weight on this finding, it is, I believe, extremely valuable for it at least anchors one end of the spectrum of alternatives. It may also have value as a measure of relative age which could be raised to an estimate of absolute age if appropriate validation can be perfected.

I thought that Keith Sainsbury's question at the end of the invertebrate section was particularly relevant. He asked "why, for invertebrates, has there been so little discussion of validation". This forced me to go back to terminology. It has always been my understanding that validation of age and growth does not relate to the use of any specific technique, but rather to confirmation that any technique which has already been used is giving a correct result. Therefore, the basic problem is that you must have a first estimate before you can validate it. It is therefore very hard to carry out experiments of validating the age of invertebrates if you don't have a first estimate to validate. This, in itself, highlights the problems with invertebrates; it is difficult enough to get one estimate, and in many cases, presently impossible to get two.

My apologies to the speakers in the last session, for there was simply not enough time for me to summarise their major findings. However, as their presentations are still fresh in your mind this should not pose a problem.

So much for the problems encountered. Where are we now, and what future directions should we take? It is obvious from the large number of people present here today, and from the variety of work on age and growth being carried out in Australia at present, that there is an enormous interest in this aspect of science, and a great deal of ongoing endeavour. Almost all of the studies on ageing individual species include a major component of trying to develop new techniques or improve on old ones. The types of improvements that have been discussed today range from increasing the understanding of the basic biology of the species to the digitisation and image processing of existing techniques, and on to the development of new techniques. Several relatively new techniques were in fact discussed, but I tend to agree with Dick Beamish that if a panacea is to be found for our "age problems" then most likely it will not come from a fisheries biologist. I believe a revolution in technique is most likely to occur if a scientist in another field discovers, or stumbles across, a method that allows the routine and rapid ageing of marine organisms. Such a breakthrough is most likely to happen if there is a major injection of funds for oceanographic or oceanic research. If, for example, space program type funding was to be directed at understanding our oceans, then major developments in technology could be anticipated.

While there is at present no panacea I am heartened by the great progress that has been made in the science of fish age and growth since the 1950's. Dick Beamish's references to the lack of even colour photography in the 1950's, and therefore to the changes we can expect in the next decades, should make us all optimistic. However, the chances of major breakthrough occurring is closely linked to the level of funding available for research. On this note I believe it is relevant to refer back to Wayne Chamley's opening remarks. Wayne expressed considerable concern about the recent cutbacks in the funding for fisheries science. I have already stressed that major developments are unlikely without some injection of capital, and obviously a cutback in funding will greatly lessen our chances of rapid progress. Wayne stated that Federal funding for fisheries research was likely to be cut by 50%. There will certainly be considerable cuts in funding unless industry support can be obtained to help meet the reduction in FIRDC allocations from 1% to 0.5% of the gross value of the Australian fishing industry. These are hard times for Australia but they are even worse for fisheries in Australia. In particular fisheries production in NSW and Victoria is declining, and if one then notes that the level of FIRDC funding is tied to the gross value of the fishing industry, then funding for fisheries research goes down as our fisheries decline. This, I believe, is absurd. Funding for research should be based more on needs and total resource potential, rather than the industry's ability to pay in any short period of time. If research funding is to be tied to the value of the industry then it should be tied to a proportion of the value that the industry should be worth if the resource was properly managed, not the industry's present value as a result of mismanagement. If we follow the existing practice, Government funding for fisheries research can be progressively reduced by overfishing the resource base to which funding is tied. The example of southern bluefin tuna is relevant: presently the resource is overfished with longline CPUE down to less than 5% of optimum levels and the value of the Australian industry down to $40 million per annum. At MSY the resource should yield at least four times as much. Research funding should be related to the maximum value - not the present reduced level which has resulted from mismanagement.

What new developments are we likely to see and what new directions should we take? I thought that Ron Thresher's suggestion that we may be able to replace tetracycline with strontium chloride had considerable merit. This is the type of innovative change that we must consider, as was Dave Ritz's comment on the possible use of polonium 210. Again this highlights the need to keep close contacts with other fields of science and to try and build on the leads which these other disciplines provide for us.

We certainly need to address the implications of the many problems we have discussed and not just confine ourselves to the identification of these problems. We need to look not only at the errors that occur in our estimates of age and growth but at what are the implications of errors in our estimates, and in the advice we provide for management. Far too often we know there are errors in our estimates, but because we are unable to quantify them, we do not fully explain their implications to managers. A recent example of a major problem in this area is the provision of assessment advice on southern bluefin tuna to the trilateral management meeting on this species. At the present time Australia, Japan and New Zealand use estimates of southern bluefin tuna populations which rely heavily on age composition of catches restructured from using a single growth curve. This growth curve was derived from tagging work carried out in the 1970's and published in 1983. More recent tagging work indicates that there has been a 50% change in growth since that time, (almost certainly a density-dependent change), but this change in growth is completely ignored in the analyses carried out by the scientists of all three countries, and the advice given to management does not even reference this major factor.

An additional problem arises through inconsistent use of terminology. It was noticeable right from the beginning of discussion this morning that there is confusion over what we mean by a ring or an annulus, or a mark, or a discontinuity, or a band, etc. This problem with terminology continues right through to the interpretation of our results for management. For example in this latter category we have the problem of what we mean by the time of recruitment. I have already discussed this briefly and refer again to the point Bruce Phillips makes about the 22 month difference between egg laying and settlement, and the further delays before recruitment to a commercial fishery. If we do not define recruitment correctly, then not only are we misusing words, but we are actually talking about totally different things.

Finally, I wish to go right back to the beginning and agree with Wayne Chamley's opening point. That is that this Society does play a key role in making other Australian scientists, and even bureaucrats, aware of the problems faced by fisheries researchers. I believe the Society has been backward in appreciating the role it could play in influencing research funding decisions, and in these times of budget cutbacks and declining fisheries resources perhaps we need to do more than just say we have problems.

DISCUSSION OF SESSION 2, SUB-SESSION C

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Each panel presentation in Sub-session C) was followed by a short time for questions, with the major emphasis on discussion being deferred until after the review of Session 2 by Bob Kearney.

John Glaister commented to the first speaker, *Greg Jenkins*, that he had seen systems in the USA that had their own statistics packages. Greg Jenkins replied that although his system did not have this facility, it was reasonably easy to put all the data onto one of the standard stats packages.

In answer to a question from John Glaister on the cost of the average micro computer-based system, Greg Jenkins advised that the all-up cost was around $10 000, with the microscope being the most expensive item. Mike Moran advised that WA has a system that cost $5,000, not including the microscope.

John Kalish thought that frame grabber software was definitely the way to go, because you then had a system that could store images. The only drawback was the amount of storage space required - you need one low grade floppy disk per otolith.

Peter Young wondered if *Ron Thresher's* work was compatible with satellite image processing, and raised the question of cooperation in this area. Ron Thresher advised that this was possible, although there were some language differences.

John Kalish commented that he considered PC-based systems to be better than the MAC11 because the PC frame grabber systems were better, and there is a better range of hardware and software available. Ron Thresher agreed, but thought the others were improving.

In response to a point of clarification raised by Barry Bruce, *Craig Proctor* advised that the increments on the horizontal axis on the graphs presented were not growth increments, but 25 micron jumps that are used when analysing the data. Tony Fowler then asked how the peaks that are measured relate to the opaque zones in the otolith. Craig Proctor felt that there was a very close relation between the two, although this has not been rigorously tested. Sister SBT otoliths will be examined for comparative age estimates.

David Smith invited *David Ritz* to give a ball park figure for how long orange roughy live, to be told that David Ritz was confident that they live to 70+ years old. He explained that one of the main problems is that not much is known about the mass-growth curve of orange roughy otoliths. If a linear relationship is assumed, 38-39 cm fish are 70+ years old. However if there is a two stage process that slows down after maturity, these fish would be very much older. Tony Smith asked David Ritz to clarify if he was saying that changes in weight of the orange roughy otolith decrease as the fish ages. David Ritz responded by saying that there was a wide range of values at the top end of the curve, and that he did not think that otolith weight was a good predictor of age.

Ron Thresher queried whether the analysis would be affected by other metals in the otoliths. He felt that given the natural sources of metals around Tasmania, there was likely to be some incorporation of trace metals in otoliths. However, David Ritz was not aware of this being a problem. He pointed out that it was estimated that there were only in the order of 200 atoms of polonium in the otolith that counts are measured from anyway. Peter Young then questioned to what extent the theories of quantum mechanics are important if there are so few atoms, and he wondered whether probability levels come into the actual measurements. David Ritz did not think this was a problem because you are only counting atoms when they decay. It is not important to know *when* an atom decays, only that it does.

In response to a question from Rick Fletcher, *David Smith* advised that the change in the otolith weight curve did not occur at sexual maturity, but slightly after. The change occurs at lengths greater than 30 cm, while maturity is at about 30-32 cm. When asked how old he thought such fish were, David Smith replied that they were 20+ years old. David Ritz confirmed that their work suggested that orange roughy were 25-30 years old at maturity.

John Anderson was interested in the advantage of the anterior-posterior section over the transverse section and was advised by David Smith that with a transverse section of an orange roughy otolith, one was confronted with a lot of unresolved material.

Richard Beamish opened the *General Discussion*, following Bob Kearney's review of Session 2, by raising the issue of a common birthday. He realised that not everyone is convinced of the need for a common birthday and admitted that he had not always felt it necessary until he started looking at other people's data in the literature. He then discovered that it was extremely difficult to figure out what was going on because there was no common birthday. In response to a question from Mike Moran, Richard Beamish expressed the view that the main advantage of a common birthday was that it is like a common language - it allows people to talk about year classes and no-one gets the year classes mixed up.

David Smith was not convinced that there needs to be a common birthday for every species, but said that in his opinion if there is to be one it should be related to spawning time.

Peter Young felt it would be difficult to assign a common birthday for invertebrates. Some spawn more than once a year, and a given species may spawn in summer in one location and in winter in another.

Terry Walker pointed out that in the case of sharks it is easy to determine an actual birthday because you can look at the embryos as they develop.

David Smith thought that one problem may be in getting people to change what they are already doing. Richard Beamish agreed that one of the biggest obstacles is getting people to change, especially if they have been using the same method for 20 years. He recommended that if we are going to have a common birthday, the decision needs to be made as soon as possible because it will be harder and harder as data bases build up.

John Kalish advised that there is no common birthday in New Zealand. Chris Francis thought that as long as researchers clearly state what birthday they are using,there is no need for a common date.

Richard Beamish was still not convinced. He was afraid that people may state what they are doing at the time, but in 20 years time would it still be stated? His experience is that often there is no reference to the terminology that was used in the past. He believes that the main problems arise when trying to work out the age composition of a population where different workers have used different methods.

Kay Allen suggested that there may be advantages in having a common birthday for a particular species, but there was no real advantage in having the same birthday for all species.

Mike Moran asked Richard Beamish to clarify if a year class was all fish that were spawned in a given year. The answer was yes. Kay Allen then asked what happens if a species spawns over the months of December and January, and pointed out that there are such species. Richard Beamish's answer was that you may have a July 1 birthday.

Alex Schap expressed the view that one of the main advantages of having a common birthday is lost if there are species that spawn at all different times of the year. He saw one of the advantages of a common year class is that you can relate strong cohorts to some environmental factor. However environmental factors affecting fish spawning in winter are different to those affecting fish that spawn in summer. Richard Beamish agreed, but pointed out that in the northern hemisphere there is not a range of species spawning throughout the year. Many bottom dwelling fish spawn in January-February. Peter Young thought that this might be a very important point. There are relatively few important northern hemisphere species, and they are temperate and sub-arctic species that have very defined spawning periods. When there is a diverse number of species, many of which are sub-tropical, there will be problems with extended spawning periods and more than one spawning.

Keith Sainsbury ended this part of the discussion by supporting the concept of a standardised birthday, where it is possible. He agreed that there are problems with protracted spawning and more than one spawning, but he pointed out that there are problems with ageing these species anyway. There are still a number of advantages for some species in having a standardised system.

The Chairman then invited comment on the use of tagging data to validate ageing.

Chris Francis saw two problems with the idea that tagging data could validate ageing by looking at growth rates obtained from tagging experiments and comparing them with growth rates from age-length curves. Firstly there is the theoretical problem of what you are actually comparing - the question of length-based growth or age-based growth. Secondly, the important problem of tagging itself actually affecting the growth rates of the tagged animals. What may be done in some cases eg. snapper in NZ, is to get information from the tagged fish and also get the otoliths back when the fish is recaptured. You are then on more solid ground with validation.

Bob Kearney stated that it is not necessarily true that tagging affects growth. Chris Francis agreed but asked how do you know? Bob Kearney suggested that you can do tests with fish in an aquarium, as NSW are doing with snapper, but Chris Francis had difficulty in accepting that any information on growth obtained in an aquarium is representative of what happens in the wild, even comparisons in an aquarium between tagged and untagged fish. Bob Kearney conceded that there may be a problem, but not a serious one compared with the magnitude of some of the other problems we have to deal with. He considered that it was very useful to establish the relative growth rates between tagged and untagged fish in an aquarium, or to compare different tags, and that this information should be obtained where possible. Richard Beamish did not disagree with Bob Kearney, but said that in his experience what happens in aquaria is not what happens in the wild.

Peter Young made the point that most of the discussion had centred on using otoliths for ageing, although sectioned fin rays had been mentioned. If fin rays can be used it should be possible to take a sample at the time of release and again at the time of capture. He asked if this had been done? However, Richard Beamish had found that fin rays were much better than otoliths for ling cod, and that fin rays had been removed from fish without killing them. He made the point that one of the advantages of having an ageing facility was that there are a variety of skills in the unit and someone who can take the time to check out different methods. Richard Tilzey agreed that other non-terminal methods (for the fish) should be considered, and stated that scales had also proved very useful for young fish.

Bob Kearney raised the question of whether two different hard part analyses from the same fish could validate the age estimate. If a fin ray and an otolith from the same fish lead to similar age estimates should you feel happier? He did not think so. Richard Beamish agreed that this did not validate the method, although you should still feel happier.

John Anderson felt that the question of validation standards needed to be addressed. He thought that referees for journals were having trouble in knowing when you can regard a method of age determination as being valid. David Smith asked what was actually meant by validation? Do you have to validate every single ring on a 60 year old fish or do you just have to have additional information that suggests that the 60 rings are annuli? He considered that the latter was sufficient. Kay Allen thought that it all depended on what the results were going to be used for. You need to know this before deciding if the validation is good enough because different applications of the results may be affected in different ways.

David Smith considered that one of the main issues was whether or not a piece of work should be accepted for publication. Should a paper be rejected if all available methods of validation have been tried without success? The researcher may have a method that would be useful to others, that fits in with some broad picture of a certain type of fish, but just cannot be validated. John Kalish said that he would be reluctant to accept it. He pointed out that Richard Beamish had already raised the huge problem of a fish with an estimated age that is in reality very much older. Chris Francis considered that it was wrong to publish any work and claim it as "God's truth" if there has been no attempt at validation. However he would publish something that explains exactly what has been done so that others can make use of the work. David Smith agreed with this approach, but Peter Young thought it could be very dangerous. Keith Sainsbury suggested that if there had been no validation, graphs in papers should not be labelled as "age", but something else.

Richard Beamish stressed that people are obliged to talk about validation. It may be too expensive or too difficult to validate all ages, but it cannot be ignored because it hasn't been done. He pointed out that this does not mean that a paper must not be accepted; reviewers and the scientific community can see what has been done and make a judgement. However he favoured publishing papers that discuss validation, otherwise valuable information may be withheld. He expressed the view that fisheries science should not stand still while someone tries to validate everything. Just make it clear what you did!

Further discussion on the important question of validation was deferred until the final General Discussion when the Chairman, David Smith, promised to bring a summary statement for endorsement by the Workshop.

SESSION 3

Inferences about Growth and from Growth

Chairperson: K.J. Sainsbury

CHAIRPERSON'S INTRODUCTION

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This session deals with the analysis of growth and the uses made of these analyses in fisheries assessments. To a large extent the subject of this session can be summarised as 'what to do with age data once one has it'.

The session is divided into three sub-sessions:

(A) current usage of growth models and appropriate forms and limitations;
(B) estimation and comparison of model parameters; and
(C) uses of age and growth data in fishery assessments.

The first of the sub-sessions will take us through some contemporary case studies, highlighting the range of models used, the growth models identified as appropriate for the various types of animals studied, and the experiences researchers have had in using these models. It would also be useful to have the panellists comment on why the application of a growth model was seen as a worthwhile aim in the first place.

The second sub-session deals with estimating and comparing model parameters. This is a large and somewhat specialist subject area that we cannot do justice to in the time available. However, it is very important, and difference in opinion among researchers concerning the most appropriate way to compare growth (e.g. comparison of male and female growth, or growth at different locations) was one of the main reasons for this workshop. We should look to the panellists to tell us the methods they recommend. Besides the issues of estimation and comparison, there is also the more fundamental question of the appropriate model structure - are the commonly used model structures, such as the von Bertalanffy equation, the most appropriate for comparison and inference?

And finally the third sub-session will illustrate the use of age and growth information in fisheries assessment. Again this is a rather large topic to cover in the time available; the panellists will be describing a wide range of methods and applications. One of the important aims of this sub-session is to provide a broad coverage of the topic before the more detailed examination of the use of legal size limits tomorrow.

All in all a busy program, so we had best get into it.

Sub-session A

Current Usage of Growth Models. Appropriate Forms and Limitations

Panellists:	W.J. Nash B.F. Phillips K.R. Rowling D.J. Die I.F. Somers
Rapporteur:	I.W. Brown

GROWTH OF BLACKLIP ABALONE (*HALIOTIS RUBRA*) IN TASMANIA

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Summary

Samples of blacklip abalone (*Haliotis rubra*) have been collected from 25 sites around Tasmania for population analysis. The age of individual abalone has been determined by counting the growth lines in the shell, and the age-length relationship for each of these samples has been determined.

There is considerable individual variation in growth of *H. rubra* within populations. Although there is some variation between populations only one to a few kilometres apart, there is a latitudinal trend, with both growth rates and maximum size attained increasing from north to south.

The age-length relationship at all sites is sigmoidal; hence, growth is better described by the Gompertz growth function than the more commonly used von Bertalanffy growth function.

The Gompertz growth function provides a far more realistic estimate of L_∞ from the age-length data of heavily fished populations (where older year classes are absent) than does the von Bertalanffy growth function.

Introduction

As outlined in a previous session (Nash, these proceedings), caution must be exercised when applying the growth ring-age relationship determined by Prince *et al.* (1988) to localities beyond that at which Prince's study was conducted. Although Prince *et al.* (1988) reasoned that the growth checks in the shell were most likely related to seasonal changes in water temperature, it is not known whether this is the cause of shell layer formation elsewhere in Tasmania, or whether, in fact, other factors (such as reproduction) are also important.

Whatever the factors determining growth check formation it is probable that there is less variation in these factors within individual sites than between sites. With that cautionary note, the patterns of growth of *Haliotis rubra* in Tasmania are described below.

Patterns of growth

If it is assumed that there is one growth check per year for *Haliotis rubra* populations at the sites listed here, as found by Prince *et al.* (1988) at one site in south-east Tasmania, then the growth patterns with these populations are as follows.

Four sites were chosen to illustrate growth of *Haliotis rubra* in Tasmania (Figure 1). The patterns of growth observed at these sites are shown in Figure 2. Points to note are: (i) high individual variation in length-at-age occurs within sites; (ii) there is a general latitudinal trend in growth rates and maximum size attained, increasing from north to south; (iii) the age-length growth curve is sigmoid; and (iv) maximum age in unfished populations is about 25 years.

(iv) maximum age in unfished populations is about 25 years.

When the age-length data are fitted to the von Bertalanffy and Gompertz growth functions, there is similar fit over most of the range of the data (Figure 3). For those populations which are heavily fished, however, and therefore for which the older age classes are not represented, the two growth functions differ greatly in their estimate of L_∞: the von Bertalanffy estimate often greatly exceeds the maximum size attained by *Haliotis rubra*, whereas the Gompertz estimate is probably close to the true value of L_∞. This is illustrated in Figure 3, where the von Bertalanffy and Gompertz curves for the more heavily-fished Binalong Bay population deviate markedly beyond the upper limit of the data set. The estimates of L_∞ derived by the von Bertalanffy and Gompertz methods for the Binalong Bay sample were 242 mm and 153 mm respectively. The greater accuracy of the Gompertz-derived L_∞ value beyond the range of the data was confirmed by fitting the Gompertz growth function to experimentally truncated age-length data sets, and comparing the estimates of L_∞ so obtained with those of the entire data sets. It was found (although not shown here) that the L_∞ estimates for the truncated and complete data sets were very similar.

The highly erroneous estimates of L_∞ obtained by the von Bertalanffy growth function for heavily-fished populations (that is, with the older age classes missing) implies that analytical studies that require estimates of L_∞ as input, such as yield-per-recruit, can only be applied with confidence to heavily-fished populations in the size and age range bounded by the population. A limitation of this is that yield may in fact be maximised at a size and age greater than that of the population. There are two alternative approaches that may be taken to apply yield-per-recruit analyses beyond the size/age range of the population. Firstly, obtain an estimate of L_∞ by the Gompertz method; or secondly, establish marine reserves within which abalone may grow to their maximum longevity. The true age-length relationship may then be determined from a population with similar growth characteristics to the fished one, and yield-per-recruit analyses can then be conducted with confidence beyond the age and length limit of this fished population.

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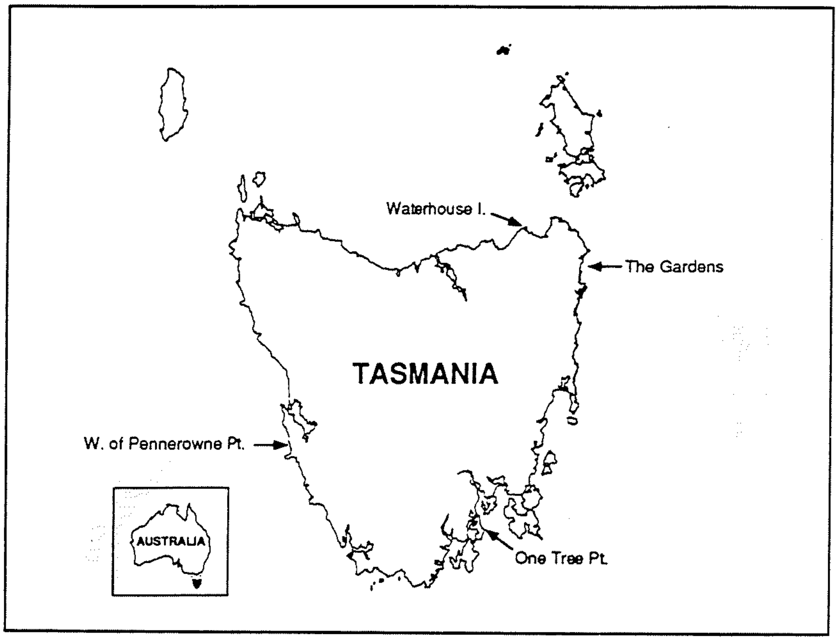

Figure 1. Blacklip abalone (*Haliotis rubra*) sampling sites.

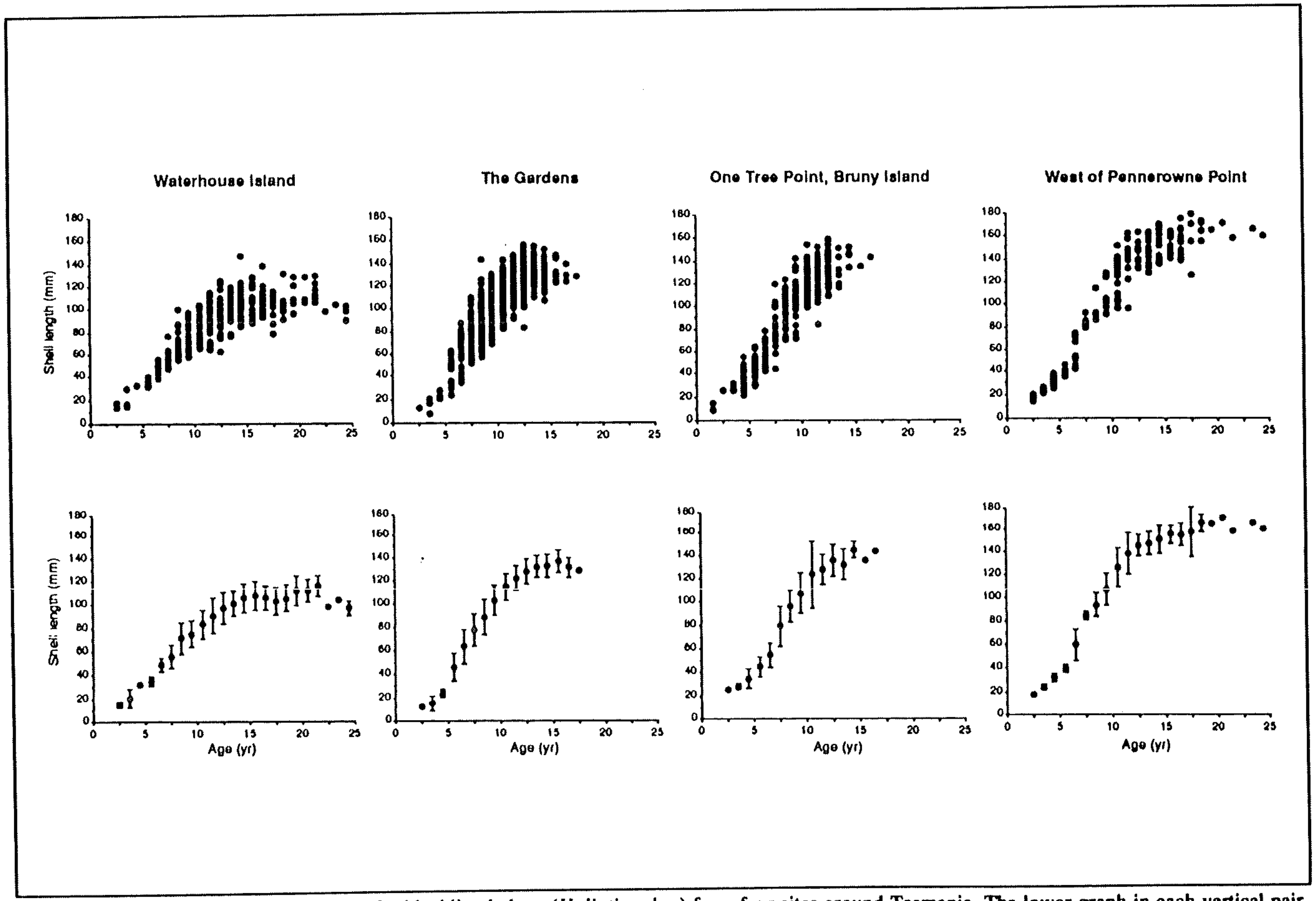

Figure 2. Age-shell length relationships for blacklip abalone (*Haliotis rubra*) from four sites around Tasmania. The lower graph in each vertical pair shows the mean length at age (± 1 s.d.) of the graph above it.

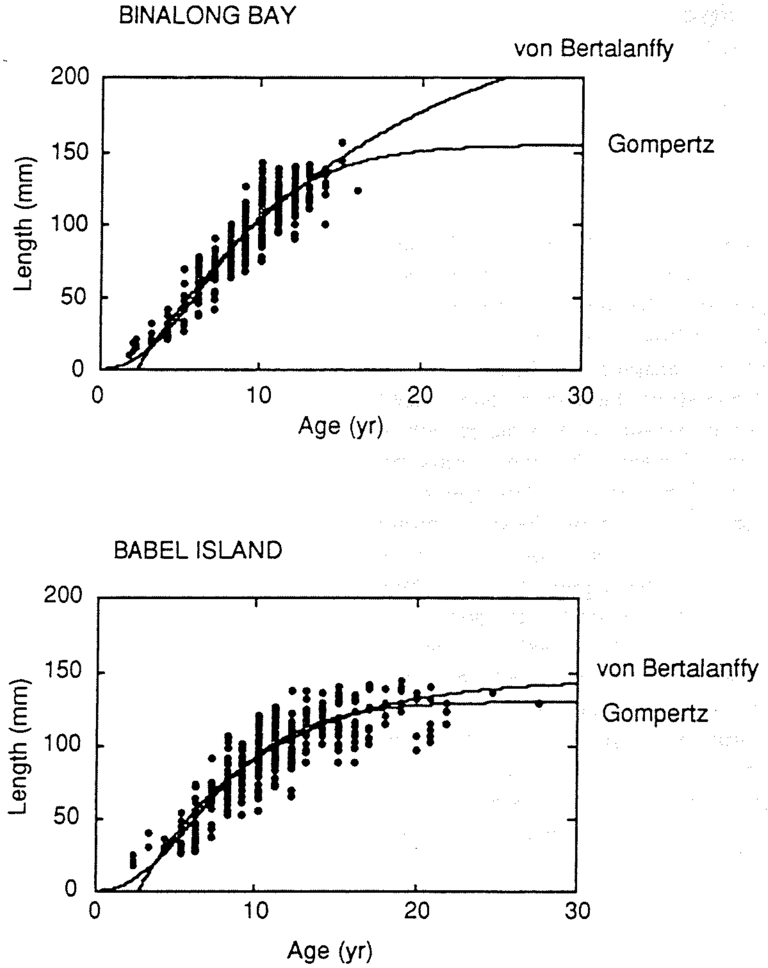

Figure 3. Age-shell length data of blacklip abalone (*Haliotis rubra*) fitted to the von Bertalanffy and Gompertz growth functions at two sites. At both sites, the fitted curves are similar over the range of the samples; however, at the more heavily fished site (Binalong Bay), the two curves diverge markedly between the maximum sample age (16 years) and the approximate maximum age attained (25 years).

MODELLING GROWTH OF SPINY LOBSTERS

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Abstract

Accurate assessments of growth of spiny (rock) lobsters have been attempted on many species, primarily because of the need to understand recruitment to the stocks as a background to managing the fisheries. The problem of modelling the data is compounded by the moult increment cycle of the growth of these animals. However, the von Bertalanffy growth curve, often used on finfish species, is also commonly used to model the spiny lobster data. Although it is not completely satisfactory, it provides a general model which can be easily incorporated into population dynamics models. Unfortunately its use has tended to become standard, and this may unintentionally result in the failure to identify the high variation in growth of individuals, which seems to be a feature of spiny lobsters. The application of non-linear random coefficient models to the analysis of growth data is a new approach which may offer a solution.

VARIATION IN GROWTH PARAMETER ESTIMATES FOR GEMFISH *REXEA SOLANDRI* - DEPENDENCE ON AGE STRUCTURE OF THE POPULATION SAMPLED

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The fishery for gemfish *Rexea solandri* developed off central New South Wales about fifteen years ago, following the discovery of winter pre-spawning aggregations of mature fish at depths of 300-400 metres along the edge of the continental shelf. Although the fish could only be caught during a short season of 2-3 months, landings increased rapidly and peaked at over 5,000 tonnes in 1980. Landings, and catch per unit effort, declined in subsequent years (Rowling 1990). Fortunately, a dedicated biological research program was established for the N.S.W. trawl fishery in the mid 1970's, and data collected during this study has been used to assess the impact of exploitation on the gemfish stock.

As part of this research program, gemfish catches were sampled biennially for age determination (using otoliths) between 1980 and 1986. During the period sampled there were substantial changes in the size composition of fish in the catch, involving an increase in the proportion of smaller fish and a corresponding decrease in the proportion of larger (and therefore older) fish. The age data collected therefore afforded an opportunity to investigate how such changes in the size composition of fish sampled affected the estimates of growth made from these samples.

The samples for each year were quite large (see Rowling 1990, Table 4). Whole otoliths were used for age determination. The only treatment of the otoliths prior to their examination under a low power binocular microscope consisted of soaking in freshwater for 1-2 hours. Ages of fish in the spawning run catch ranged from 2 to 11 years for males, and from 3 to 16 years for females; however there were only small numbers of males less than 4 years of age and females less than 5 years of age. Some otoliths were also collected during the winter season from juvenile fish that were not part of the spawning run. The ages of these juvenile fish (1 to 3 years old) have been well validated by modal analysis of monthly length frequency data.

The von Bertalanffy growth function was fitted to the length and age data for each year and sex, by means of a least squares fitting procedure, program VBLA, which uses Kirkwood's (1983) technique with iterative minimisation performed by subroutine LMM (Miller 1981). The resulting von Bertalanffy parameters for each year/sex calculation are shown in Table 1. Also shown are the parameters which result if data for the juvenile fish are included in the calculation of the growth curve.

As can be seen from the results, there are large variations between years in all the parameters calculated from the age/length data for the spawning run fish. These variations are largely attributable to changes in the size composition of the samples, especially the proportion of larger fish in the sample, and the consequent distribution of lengths for the older age classes. The degree of variation is considerably reduced if the data for juvenile fish are included in the calculations. If data for the spawning run fish for all years are pooled

(Table 1), then inclusion of the juvenile fish has much less impact (in fact the resulting curves for male fish are almost identical). The results for female fish still show some variation, especially for estimates of L_∞ and t_0. It is considered that the results for all years combined, including the data for juvenile fish, represent the best estimates of the von Bertalanffy growth parameters for male and female gemfish.

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Table 1. Von Bertalanffy growth parameters for gemfish calculated for each sex for each year sampled, and for all years combined
L_∞ - asymptopic length (cm); K - growth constant (yr^{-1}); t_0 - hypothetical age at length zero (yr)

	1980			1982			1984			1986			All years combined		
	L_∞	K	t_0	L_∞	K	t_0	L_∞	K	t_0	L_∞	K	t_0	L_∞	K	t_0
Males															
spawners only	129.8	0.09	-3.7	95.5	0.22	-0.06	86.8	0.31	0.25	91.2	0.22	-0.8	98.5	0.20	-0.7
incl. juveniles	97.6	0.22	-0.4	94.7	0.23	-0.4	93.6	0.23	-0.5	88.6	0.25	-0.4	97.5	0.21	-0.52
Females															
spawners only	134.1	0.09	-3.6	112.9	0.15	-1.6	127.8	0.10	-2.7	112.7	0.15	-1.2	119.7	0.13	-1.97
incl. juveniles	111.2	0.17	-0.6	105.5	0.20	-0.5	109.2	0.18	-0.5	106.1	0.19	-0.5	109.4	0.18	-0.61

TAGGING DATA DISTRIBUTIONS AND THE ESTIMATION OF GROWTH PARAMETERS IN PENAEIDS

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Abstract

Distributions of length at release and days at sea were analysed from experiments conducted on Australian penaeid stocks. These distributions were fitted to a range of probability density functions and their corresponding parameters were estimated. Distributions of length at release were found to be either uni or bimodal and a multinomial normal distribution fitted all cases studied. Observed distributions of days at sea fitted either a truncated exponential or a Weibull distribution. Some of the problems in fitting growth models such as von Bertalanffy's to this type of data are discussed. Preliminary simulation results show that a continuous growth model such as Fabens' (1965) may not be a good approximation of the stepwise process of size increases that characterises penaeid growth.

Introduction

Estimation of growth in penaeids and other small crustaceans is a difficult task because after moulting these animals do not retain any hard structures suitable for ageing. As a result tagging and length frequency analysis are the two most common methods used to estimate growth in crustaceans. Tagging is more widely applicable to penaeids than length frequency analysis because many species of penaeids have recruitment patterns that do not produce readily distinguishable cohorts (an essential requirement for length frequency analysis).

Growth may be modelled in several ways for penaeids. For an individual, increase in size is a stepwise process where length only increases at moulting time. For a population or cohort, growth in length may be represented by a smooth curve that represents the average size for all individuals. It is the average growth curve of a cohort that is of foremost interest for fishery stock assessment. Herein the relation between individual and average growth is discussed in the context of penaeid growth estimation through tagging.

The von Bertalanffy growth equation is commonly used to represent average growth for penaeids,

$$L_t = L_\infty[1-e^{-K(t-t_o)}] \qquad (1)$$

where L_∞, K and t_0 are population growth parameters, L_t is length at age t. In fact using computer simulation, Restrepo (1989) showed that average cohort growth in crustaceans may be approximated well enough by a continuous growth model, even if individual growth is a stepwise process.

Unfortunately tagging data can not be fitted to such age and population based models and a length and individual based growth model, such as the one proposed by Fabens (1965), is required. The most suitable form of Fabens's (1965) model for parameter estimation (Sundberg 1984) is,

$$\Delta L = (L_\infty - L_r)(1-e^{-Kd}) \qquad (2)$$

where ΔL is the length increment between release and recapture, L_r is the length at release and *d* the time between release and recapture (time at sea). Unfortunately L_∞ and K estimates from equation (2) are not comparable to parameter estimates from equation (1) because: a) they are derived from data that has no information on age (Francis 1988a, 1988b), and b) model (2) assumes all individuals have the same L_∞ and K (Sainsbury 1980).

Fitting equation (2) to penaeid tagging data assumes that all prawns grow continuously and all individuals have the same growth parameters. In reality individual prawns grow incrementally at each moult, therefore the first assumption is not correct. However, equation (2) may still be a worthwhile approximation of individual stepwise growth.

Simulation can help to evaluate the effects of failures of model assumptions. For instance Hearn (1986) showed that the presence of individual variability in growth will generate biased estimates of average growth parameters when equation (2) is fitted to tagging data. Furthermore in the presence of individual growth variability the characteristics of the distributions of time at sea also determine the amount of bias in parameter estimates.

Equation (2) is not linear, therefore regression or maximum likelihood estimates of its parameters will be dependent on the range of observations obtained for the two independent variables *d* and L_r. The distribution of lengths at release L_r for a tagged sample is determined by the population's length distribution, and the sampling design. In penaeids the population's length distribution may be uni or multimodal, reflecting the presence of one or more yearly or seasonal cohorts. Tagging of such populations is often designed to maximise the numbers of returns and is usually constrained by the smallest-sized prawn that can be tagged. For growth analysis it is not the distribution of lengths at release *per se* that is relevant, but the distribution of length at release of the recaptured animals. If the probability of recapture is independent of the length at release, these two distributions should not be statistically different.

Tagging and handling can reduce survival of the smallest animals, whereas fishing may be more selective towards the large animals. Therefore, for some experiments, length at release and probability of recapture may be correlated. Penn (1975), Glaister *et al.* (1987) and Kirkwood and Somers (1984) have demonstrated that good experimental design can ensure such independence.

In this paper the assumptions about the appropriateness of equation (2) are evaluated for penaeid growth analysis. Several tagging data sets from penaeid stocks around Australia are used to decribe the characteristics of the distributions of length at release and days at sea.

Methods

To investigate the characteristics of the distributions of length at release, length at recapture and days at sea, five data sets corresponding to different stocks of four penaeid species from Australia were used. These data, separated by sexes were from (1) the Gulf of Carpentaria stock of *P. semisulcatus* (Somers this meeting), (2) Gulf of Carpentaria stock of *P. esculentus* (Kirkwood and Somers 1984), (3) Torres Strait stock of *P. esculentus* (Derbyshire *et al.* 1990), (4) the Great Barrier Reef stock of *P. longistylus* (Dredge 1990) and (5) the Eastern Australian stock of *P. plebejus* (Glaister *et al.* 1987).

The distribution of length at release and days at sea were fitted to various probability distributions and descriptive statistics were computed for all five data sets. Four probability distribution functions (uniform, exponential, lognormal and Weibull) were fitted to each of the observed distributions of days at sea. In addition a truncated exponential probability distribution was fitted by disregarding all data from prawns that had been at sea for less than one lunar month (28 days). Kolmogorov-Smirnov statistics (Sokal and Rohlf 1981) were used as measures of goodness of fit.

The distributions of length at release were fitted to several mixtures of normal distributions and the F test used to determine the significance of adding extra components to the multinomial distribution (Die 1989). The fit of the multinomial was carried out by the method of Macdonald (1969).

To describe the range of sizes used to estimate the parameters of the growth equations, the distributions of length at release and length at recapture were pooled into a single distribution. The resulting length frequency should represent the range of sizes for which growth information from tagging exists. The characteristics of such pooled distributions of lengths were analysed and related to the estimated growth parameters for each data set.

Results

The distribution of days at sea (Figure 1) for most data sets tends to be highly skewed. The average number of days at sea ranged from 41 to 95 days, and the median of the distribution from 26 to 76 days (Table 1). The upper quartile of the same distributions ranged from 59 to 134 days, but in most cases very few recaptures occurred after three months of release. At the 5 percent level of significance the fit of a uniform distribution was rejected for all data sets (Table 2). The exponential distribution was rejected for all cases except for female *P. plebejus*, and the lognormal distribution only fitted the data for *P. longistylus*. In contrast, the Weibull distribution fitted all cases except the data corresponding to *P. esculentus* in Torres Strait. The truncated exponential distribution fitted most data sets except those corresponding to *P. longistylus* and females of *P. esculentus* from the Gulf of Carpentaria.

The distribution of length at release observed appeared to be unimodal for three of the five data sets (Figure 2) and bimodal for the other two. Length frequency analysis confirmed this, separating a single significant component in the data sets of *P. esculentus* and *P. longystilus*, and two significant components in the data sets of *P. plebejus* and *P. semisulcatus*. The estimated mean length at release of the normal components ranged from 27.8 mm, for the first component observed in males of *P. semisulcatus*, to 49.0 mm, for the second component of the females of *P. plebejus* (Table 3). The standard deviation of each normal component was not correlated with its mean length and ranged from 2.32 to 4.40.

The pooled distribution of lengths at release and recapture shows a small range of sizes compared to the total average range of sizes of each species (as defined by the L_∞ parameter). The maximum range of lengths observed in all data sets never exceeds 75 percent of L_∞. On the average for all data sets the maximum range is only about 56 percent (Table 4). Moreover, the middle interquartile range (25-75 percentiles) covers only 13 percent (on average) of the total size distribution (Figure 3).

Discussion

The short lifespan of most penaeids precludes the existence of more than two yearly cohorts in length frequency samples. However, several seasonal cohorts (those recruited in the same year) have been identified in length frequencies of some penaeid species. Thus for some penaeids a length frequency sample may have either one or two yearly components as well as several (most commonly two) seasonal cohorts. The fact that any of these components can be identified in a sample of length frequencies will depend on growth variability, recruitment pattern, mortality and sampling time. In addition to this, length frequency samples obtained during the course of tagging experiments will be affected by the minimum size at which an animal can be tagged successfully. The five data sets studied here show that only one or two components can be identified in these samples. Most estimated values of the standard deviation of the components were between 2 and 3 mm. Assuming that the variance of length for a cohort does not change with age, this result suggests that the analysis did not miss any components. For those data sets where two components were identified, the differences between the means of the two components were larger for females than for males (Table 3). However, the relative age difference (Die this meeting) between the two components is almost the same for males and females, about 115 days for *P. plebejus*, and 150 days for *P. semisulcatus* (assuming $t_0 = 0$ and according to Glaister *et al.* 1987 and Kirkwood and Somers 1984 growth parameters for the two species).

The relative age difference between these components would indicate that they were seasonal cohorts, recruited with 3.5 to 5 months difference. In fact, although some penaeids may spawn and recruit during the whole year, most have two recruitment pulses (Garcia 1985).

Given some knowledge on recruitment patterns, examination of the length at release distribution may help to determine how likely it is that all animals have the same L_∞ and K. In the case of the species of penaeids analysed here, it is difficult to draw any conclusion of that sort because recruitment patterns alone could explain most variability in length at tagging time. Kirkwood and Somers (1984) fitted penaeid tagging data to a model similar to (2) which incorporated individual variability in L_∞. The estimates of the coefficient of variations for L_∞ obtained by Kirkwood and Somers (1984) ranged from 4 to 13 percent, indicating there may be significant variability in individual penaeid growth.

The distributions of days spent at sea are the result of three principal factors: the mortality rate, the emigration rate and the distribution of sampling effort directed towards recapturing animals. The higher the mortality or emigration out of the sampled area, the faster the exponential decrease in the number of recaptures per unit time. If the sampling effort for recaptures relies mainly on the commercial fishery, it will be largely determined by the distribution of fishing effort. The high rate of exponential decline over time in the numbers recaptured, is a reflection of the high mortality rates of penaeid stocks.

The lower number of recaptures inmediately after tagging, which results in the better fit of the truncated exponential probability and Weibull distribution, may be attributed to a decreased catchability of prawns following trawling and tagging (Wassenberg and Hill 1989). Distributions of days at sea that do not fit the truncated exponential distribution are likely to be the result of uneven fishing effort distribution after the tagging experiment (this could apply to the data set from *P. longystilus* herein reviewed, M. Dredge, pers. comm.).

The assumption about equation (2) being a good approximation of stepwise growth can only be tested if the true form of the stepwise model of penaeid growth is known beforehand. However simulation can be used to assess how equation (2) would fit data generated from a hypothetical "true model". Several authors have developed stepwise growth models for crustaceans (Mauchline 1977, Restrepo 1989), which are based on the relationships between intermoult period and size, and moult increment and size. Fitting procedures have also been developed to estimate either one (Munro 1974; Restrepo and Hoenig 1988; Hoenig and Restrepo 1989; Mohr and Hankin 1989) or both of these relationships (McCaughran and Powell 1977; Conan and Gundersen 1979) from tagging data. Unfortunately nobody has developed an appropriate model to estimate the two relationships in asynchronous moulters such as penaeids.

Whether such a model needs to be developed or not partially depends on how well equation (2) approximates stepwise growth in penaeids. If the lack of fit is not too large it would be better to keep using model (2) for analysis of penaeid tagging experiments, because its parameters are easily incorporated in other traditional stock assessment methods. However if lack of fit is substantial, it may be appropriate to start developing more appropriate models for penaeid stepwise growth. In fact disregarding tagging data for growth analysis corresponding to the first three or four weeks after release is a way of acknowledging the failure of model (2) in explaining observations with zero growth (those prawns which have not had a chance to moult).

Preliminary work seems to indicate that if a stepwise growth function with asynchronous moulting is used to generate simulated tagging data sets, equation (2) yields different parameter estimates depending on the range of sizes tagged and on the exponential recapture rates (even ignoring data from the first four weeks). This can be interpreted as an effect analogous to that reported by Hearn (1986). Asynchronous moulting will effectively work as a source of individual variability in growth (prawns of equal size may have a different moult stage at tagging and therefore increase size at different times). It remains to be seen whether the instability in L_∞ and K represent significant lack of fit. However this preliminary work does highlight the fact that comparisons between growth curves should not be carried out on the sole basis of parameter contrasts. This is specially true in cases where the range of sizes tagged or the average days at sea are significantly different between data sets. Penaeid tagging data sets are likely to fall into this category because they often only produce information about a very restricted range of lengths. This is due to both the difficulty of tagging small penaeids and the high mortality rate among prawn stocks.

Future research should evaluate whether alternative continuous-growth models to equation (2) would be less sensitive to such variations in input data. Models that could be explored include those proposed by Schnute and Fournier (1980), Ratkowski (1986) and Francis (1988a). The present study suggests that serious consideration should be given to stepwise growth models for crustaceans rather than to continuous models, especially when growth is estimated by tagging.

Acknowledgements

This study would not have been possible without the cooperation of Ian Somers from CSIRO, and John Glaister, Mike Dredge and Kurt Derbyshire from QDPI who provided the raw tagging data analysed here. Comments by Keith Sainsbury and Chris Francis helped in the interpretation of the preliminary simulation results.

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Table 1. Descriptive statistics for the distributions of days at sea and length at release for the recaptures from tagging experiments in five Australian stocks of penaeid prawns

Sources (1) - (5) as in text)(s. = semisulcatus, e. = esculentus, l. = longistylus, p. = plebejus, GC = Gulf of Carpentaria, TS = Torres Strait, GBR = Great Barrier Reef, QN = Queensland-New South Wales, n = Number of observations, M = mean, m = median, q = lower quartile, Q = upper quartile and i = interquartile range

Sps	Area	Source	Sex	n	Days at Sea			Length at release (mm)		
					M	m	Q	M	i	q
s.	GC	(1)	♂	397	47	26	63	33	6	30
			♀	549	41	28	59	40	10	35
e.	GC	(2)	♂	225	95	76	134	28	3	27
			♀	155	79	73	112	30	5	28
	TS	(3)	♂	868	53	40	77	29	2	28
			♀	861	51	39	71	34	4	32
l.	GBR	(4)	♂	134	63	59	84	36	2	34
			♀	123	64	59	88	41	4	39
p.	QN	(5)	♂	109	44	32	59	38	10	30
			♀	123	45	41	59	38	16	32

Table 2. Results from fitting the observed distributions of days at sea to five different probability distribution functions

Significance probabilities from Kolmogorov-Smirnov test, and parameters estimated for those cases where the fit was significant: means for the exponential, lognormal and truncated exponential, variance of the lognormal and alpha and beta parameters for the Weibull, (e. = esculentus, s. = semisulcatus, l. = longistylus, p. = plebejus, GC = Gulf of Carpentaria, TS = Torres Strait, GBR = Great Barrier Reef, QN = Queensland-New South Wales). (Sources (1) - (5) as in text)

Sps	Area	Source	Sex	Significance probability (p) Probability distribution function				
				Unif	Expo.	Logn.	Weib.	T. Ex.
s.	GC	(1)	♂	0.000	0.000	0.000	0.070	0.384
							0.85	88.68
							43.22	
			♀	0.000	0.000	0.000	0.068	0.059
							0.86	73.30
							37.98	
e.	GC	(2)	♂	0.000	0.000	0.020	0.330	0.084
							1.29	109.0
							103.3	
			♀	0.000	0.019	0.009	0.170	0.012
							1.31	
							85.08	
	TS	(3)	♂	0.000	0.000	0.000	0.000	0.127
								75.14
			♀	0.000	0.000	0.000	0.000	0.095
								72.18
l.	GBR	(4)	♂	0.000	0.000	0.067	0.056	0.000
						63.11	2.31	
						31.17	70.93	
			♀	0.000	0.000	0.077	0.186	0.000
						63.23	2.51	
						32.25	71.97	
p.	QN	(5)	♂	0.000	0.116	0.014	0.354	0.375
					49.76		1.11	69.23
							51.76	
			♀	0.000	0.007	0.022	0.236	0.059
							1.36	64.92
							53.24	

Table 3. Results from fitting the observed distributions of length at release to a mixture of normal components with program MIX

Mean length and standard deviation (Std) of each of the significant normal components separated in the analysis, (s. = semisulcatus, e. = esculentus, l. = longistylus, p. = plebejus, GC = Gulf of Carpentaria, TS = Torres Strait, GBR = Great Barrier Reef, QN = Queensland-New South Wales). (Sources (1) - (5) as in text)

Sps	Area	Source	Sex	First component		Second component	
				Mean	Std	Mean	Std
s.	GC	(1)	♂	27.82	2.93	35.23	1.62
			♀	29.98	4.40	43.73	3.12
e.	GC	(2)	♂	28.13	2.32	-	-
			♀	30.47	4.15	-	-
	TS	(3)	♂	29.69	2.41	-	-
			♀	34.12	3.42	-	-
l.	GBR	(4)	♂	35.99	2.27	-	-
			♀	41.44	3.79	-	-
p.	QN	(5)	♂	29.17	2.96	38.68	1.97
			♀	32.50	4.02	48.97	2.35

Table 4. Relation between the estimated L_∞ and the range of sizes used to estimate it

Ranges correspond to the pooled distributions of length at release and length at recapture and are represented as percentages of the value of L . Maximum = difference between the largest animal recaptured and the smallest tagged, (s. = semisulcatus, e. = esculentus, l. = longistylus, p. = plebejus, GC = Gulf of Carpentaria, TS = Torres Strait, GBR = Great Barrier Reef, QN = Queensland-New South Wales). (Sources (1) - (5) as in text)

Sps	Area	Source	Sex	Ranges as a percentage of L_∞		
				Maximum	5 - 95 %	25 - 75 %
s.	GC	(1)	♂	57.54	42.45	18.40
			♀	45.33	25.60	10.67
e.	GC	(2)	♂	53.42	22.62	8.17
			♀	63.24	23.24	7.83
	TS	(3)	♂	73.80	45.34	13.28
			♀	58.58	33.99	10.50
l.	GBR	(4)	♂	48.13	26.11	7.99
			♀	34.54	16.43	6.43
p.	QN	(5)	♂	68.90	42.01	25.21
			♀	52.86	33.03	19.82
Average				55.63	31.09	12.83
Std. Dev.				10.93	9.93	5.95

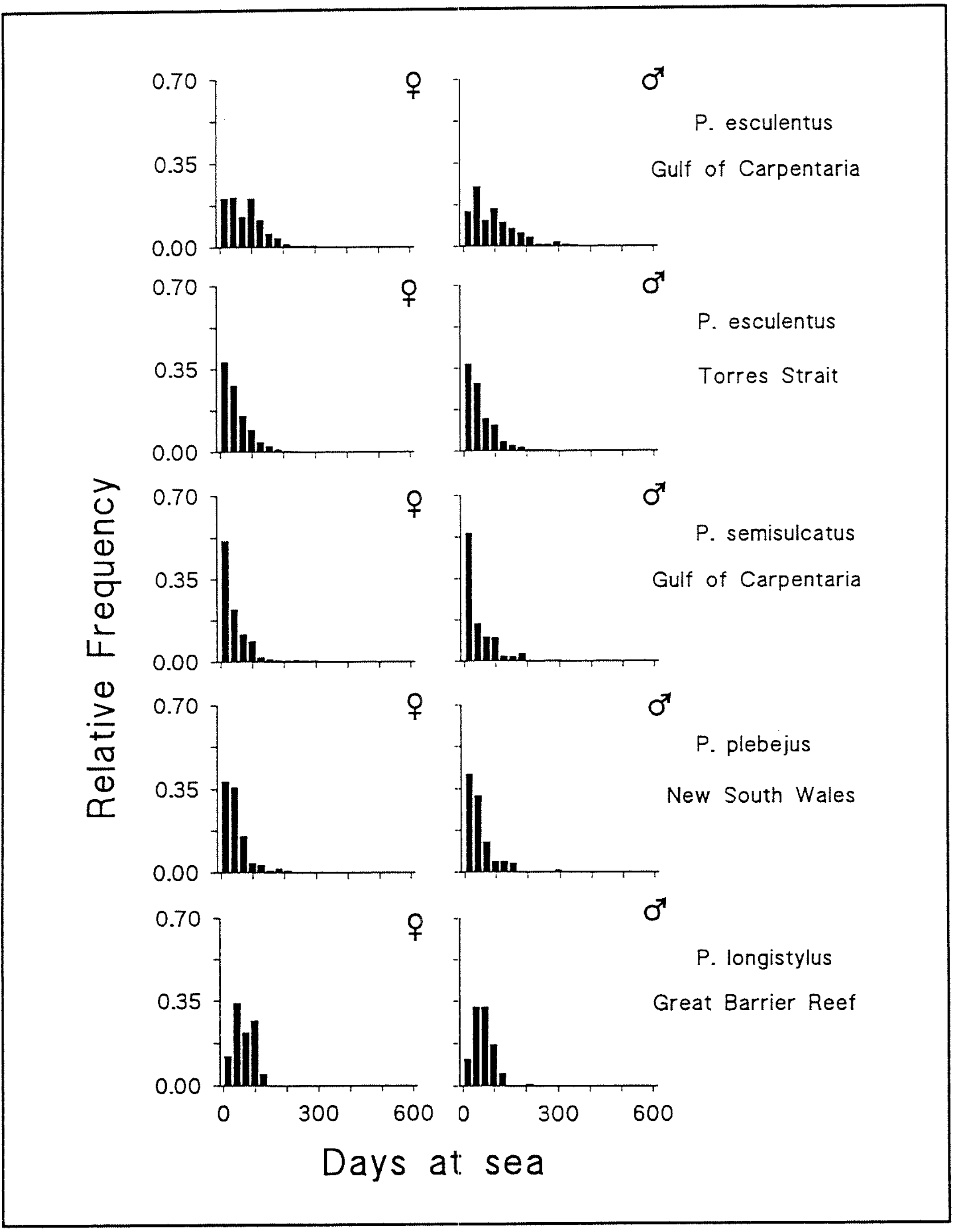

Figure 1. Relative frequency distribution of days at sea for five sets of penaeid tagging experiments.

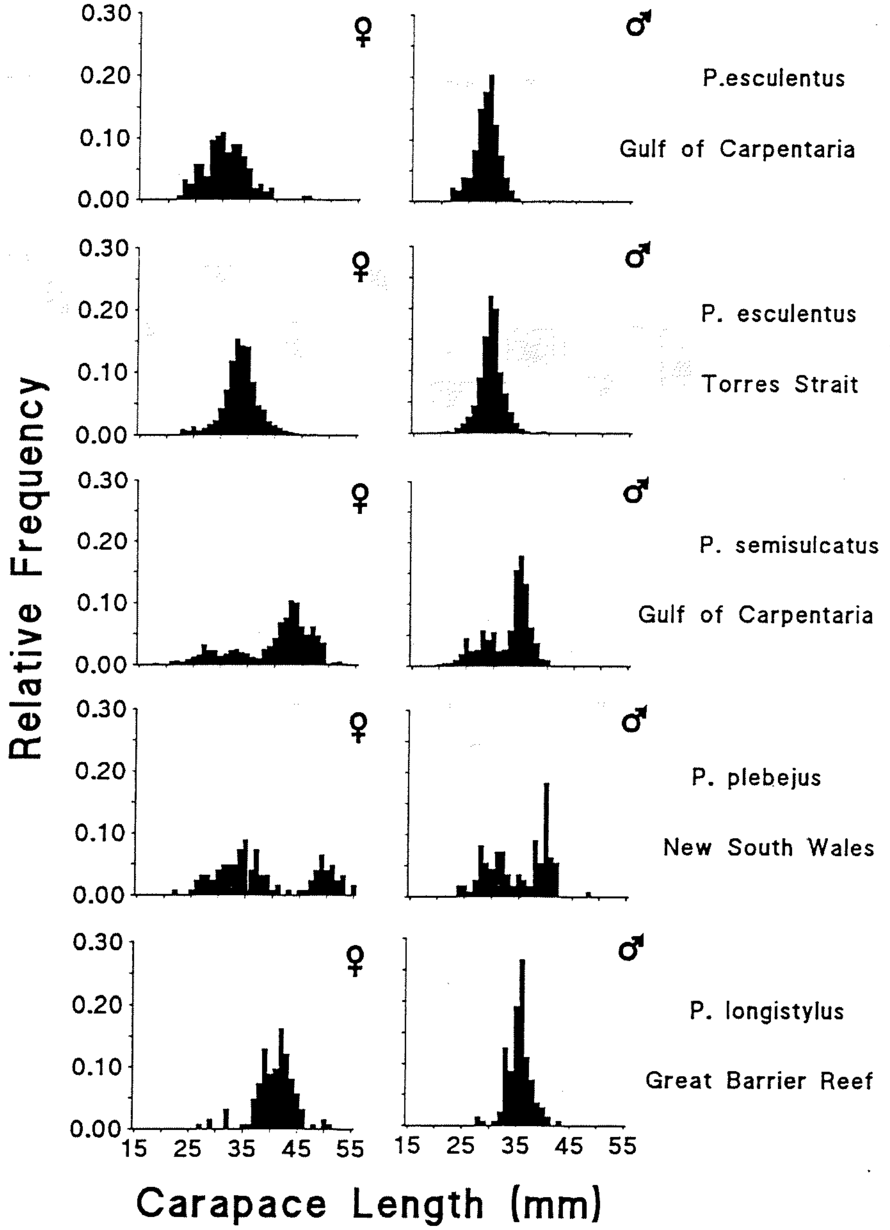

Figure 2. Relative frequency distribution of length at release (mm) for five sets of penaeid tagging experiments.

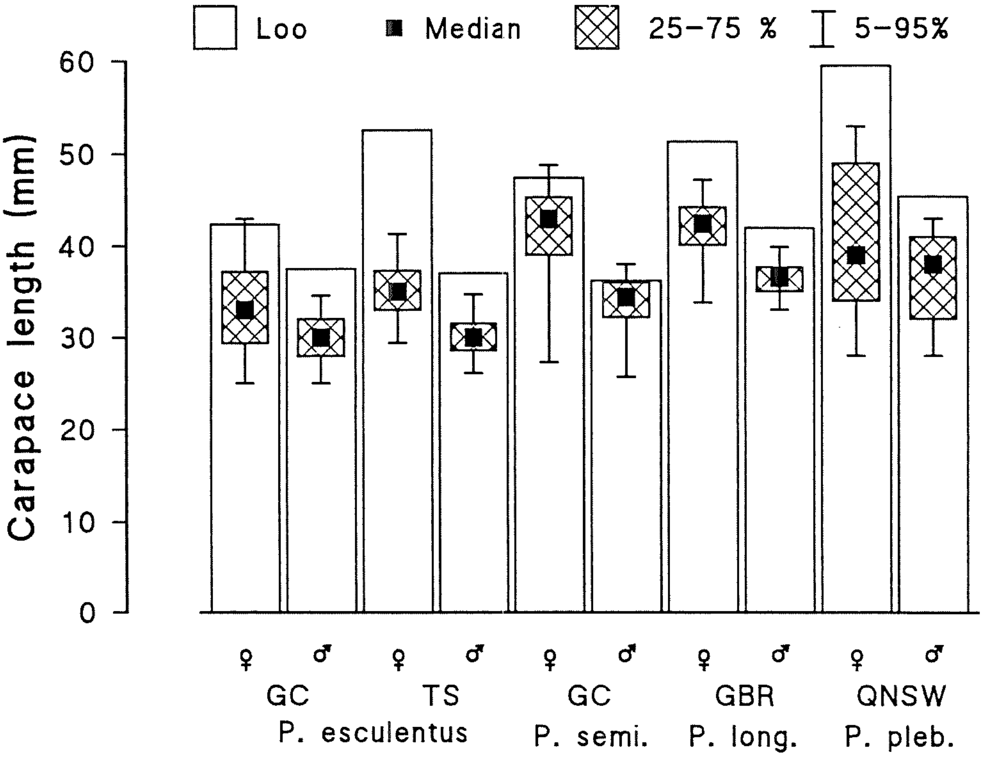

Figure 3. Relation between size distributions from which growth information was obtained for five sets of penaeid tagging experiments and the estimated $L\infty$. Size distributions correspond to the pooled distributions of length at release and length at recapture (GC = Gulf of Carpentaria, TS = Torres Strait, GBR = Great Barrier Reef, QN = Queensland-New South Wales).

USING A GROWTH MODEL TO DEFINE YEAR CLASSES IN THE TIGER PRAWN *PENAEUS SEMISULCATUS*

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Background

One objective of a major CSIRO prawn research project in the western Gulf of Carpentaria was to study the fate of an individual year class of the tiger prawn *Penaeus semisulcatus*. To encompass the approximate life span of this species, 21 trawl surveys were carried out at lunar monthly intervals between August 1983 and March 1985. Each survey was conducted over an area that extended beyond the main fishing grounds in order that the length-frequency data collected would be representative of the population as a whole. Because prawns cannot be aged directly, supplementary growth information was collected through concurrent tag-recapture studies to help determine the population age structure.

To identify and separate the individual year classes, two very different approaches were attempted. The first was to use the information contained within the length-frequency data and fit a growth-constrained model of distribution mixtures modified from Schnute and Fournier (1980). The second approach was to fit a modified von Bertalanffy growth model to tag-recapture data and to use growth projections in conjunction with population recruitment patterns to interpret the length-frequency data.

Method 1 - Multiple Length-Frequency Analysis

Schnute and Fournier (1980) described a method of simultaneously separating year classes and estimating von Bertalanffy growth parameters from a population containing a mixture of year classes. In fitting a model to the observed frequencies $\hat{f_j}$, they defined a separation statistic A :

$$A = 2\sum_{j=1}^{N} \hat{f}_j \log(\frac{\hat{f}_j}{f_j}) \qquad (1)$$

where N is the number of length intervals and f_j are the expected frequencies. To constrain the relationship between mean lengths of the year classes, they used a transformation of the von Bertalanffy model of the form:

$$\mu_i = l + (L - l)\frac{(1 - k^{i-1})}{(1 - k^{M-1})}; i = 1,\ldots,M \qquad (2)$$

where μ_i is the mean length of fish of a certain age class i, M is the number of age classes, l and L are the mean lengths of the youngest (but fully recruited) and oldest year classes respectively, and k is the fraction to which the difference in the lengths of successive year classes shrinks each year. The parameters (l, L, k) can easily be transformed back to those of the standard von Bertalanffy model (L_∞, K, t_o).

To apply this model to the *P. semisulcatus* data, age was defined in terms of lunar months relative to the time of the first trawl survey (August 1983). Then the only modification to the Schnute and Fournier (Appendix D, 1980) algorithm for fitting the growth model was the addition of a second dimension i representing the ith time period in the term denoting the sample frequencies (f_{ij}). The separation statistic thus becomes:

$$A = 2\sum_{i=1}^{M}\sum_{j=1}^{N}\hat{f}_{ij}\log\left(\frac{\hat{f}_{ij}}{f_{ij}}\right) \qquad (3)$$

where M is now defined as the number of time periods in which length-frequency samples are obtained. Carapace length (CL) boundaries between adjacent year classes were determined by the point of intersection of fitted normal distributions (Figure 1).

Method 2 - Tag-recapture model with variable L_∞

This method involves using fast and slow growth curves calculated from tag-recapture data to loosely define the upper and lower carapace lengths of a recruiting year class as it ages; fast and slow growth is simulated by high and low values of L_∞. A suitable growth model for this purpose was described by Kirkwood and Somers (1984) which was of the form:

$$I = (L_\infty - L_r)(1-e^{-KT}) \qquad (4)$$

where I is the growth increment between release and recapture, L_r is the length at release, T is the time at liberty, and L_∞ has a normal distribution $N(\mu,\sigma^2)$ distribution with mean μ and variance σ^2. Somers and Kirkwood (in prep) have further modified this model following Hampton (1989) to incorporate a model error term E which has an independent $N(\mu,\varepsilon^2)$ distribution. The model thus becomes:

$$I = (L_\infty - L_r)(1-e^{-KT}) + E \qquad (5)$$

As a guide to the upper and lower carapace length boundaries for a year class, growth curves were projected from 20 mm CL at the start (solid curve Figure 2) and end (dashed curve Figure 2) of the main annual recruitment period, using fixed values of L_∞ equal to $\mu+2\sigma$ and $\mu-2\sigma$ respectively. For those months where the population was clearly made up of two year classes, the point of separation between the two was defined to be midway between the lower boundary of the first year class and the upper boundary of the later year class.

Conclusions

Although the multiple length-frequency model may be more mathematically elegant, the method was not very robust. In fact, there were 24 parameters that had to estimated and although L_∞ was relatively insensitive to the model assumptions, K was very dependent on when recruitment was assumed to be complete. The year class boundaries determined by this method were not as credible as those based on growth curves from tag-recapture data; in general, the intersection of the fitted distributions appeared to be biased towards the most abundant year class. Although the second method was eventually adopted, estimates of relative abundance of the various year class components were insensitive to the differences in year class boundaries obtained from the two methods.

More recently, Fournier *et al.* (1990) have further developed the original Schnute and Fournier (1980) method to analyse multiple length frequencies with multiple age classes (MULTIFAN).Furthermore, they have attempted to account for cohorts that are incompletely recruited and have successfully applied their method to estimating growth of southern bluefin tuna (*Thunnus maccoyii*). We intend to evaluate this new methodology in relation to the *P. semisulcatus* data in the near future.

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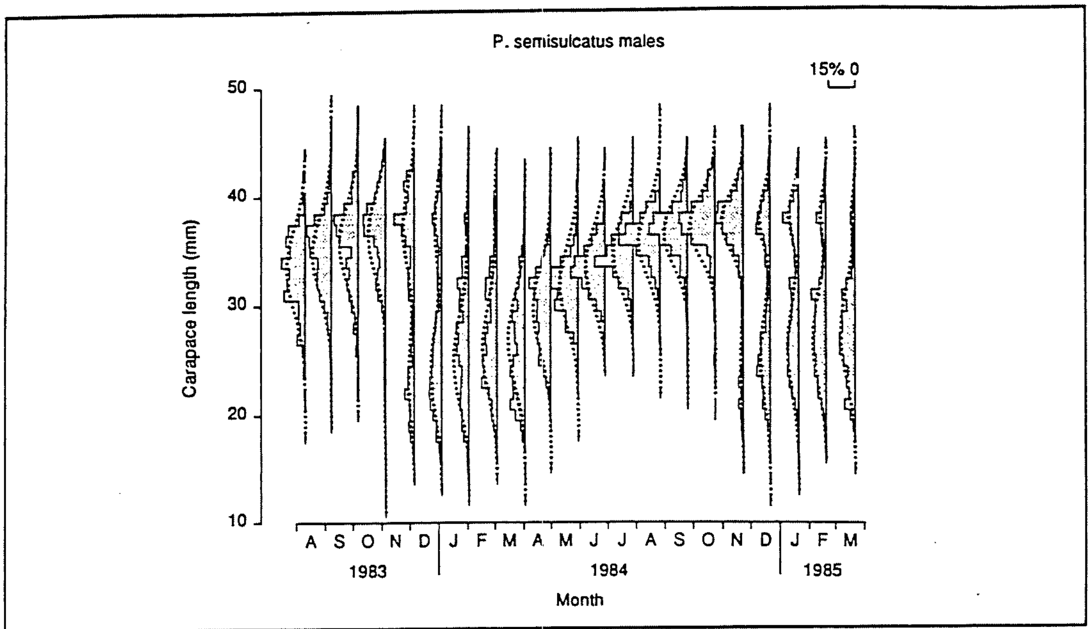

Figure 1. Percent length-frequency histograms for male *Penaeus semisulcatus* from trawl surveys carried out between August 1983 and March 1985. Dashed curves indicate the fitted model of a progression of normal distribution mixtures with the growth constraint.

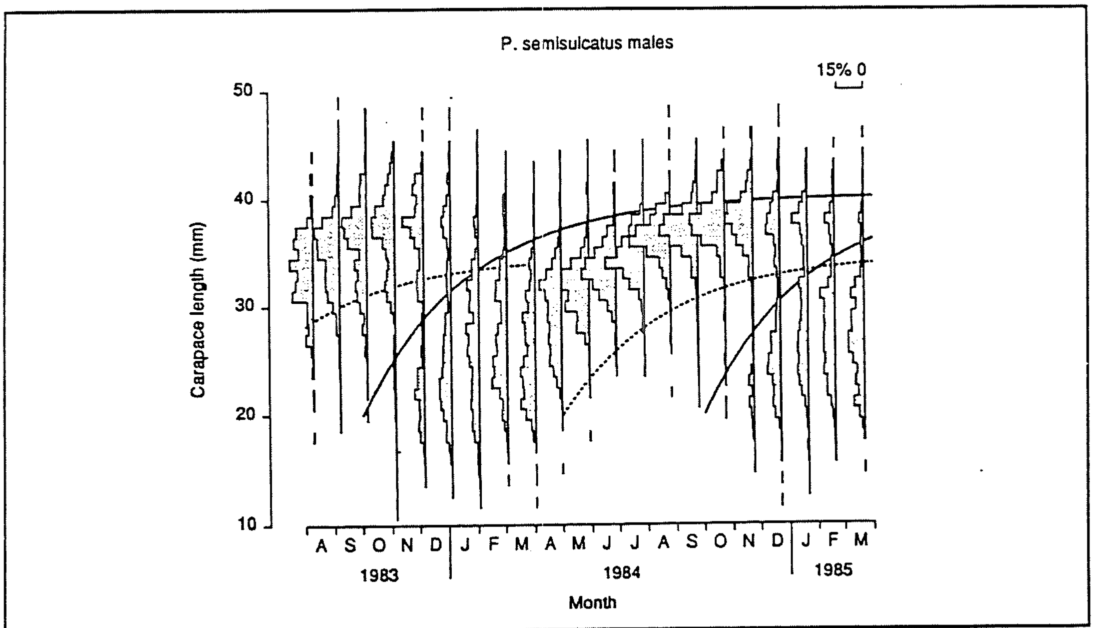

Figure 2. Percent length-frequency histograms for male *Penaeus semisulcatus* from trawl surveys carried out between August 1983 and March 1985. Solid curves indicate approximate maximum growth rates for prawns recruiting at 20 mm CL on 1 October, while the dashed curves indicate approximate minimum growth for prawns recruiting at 20 mm CL on 1 May. Growth rates are calculated from tag-recapture data.

DISCUSSION OF SESSION 3, SUB-SESSION A

Recorded by I.W. Brown

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The Chairman invited comments at the end of each panel contribution, following which the meeting was opened for more general discussion.

Chris Francis referred the first speaker, *Warwick Nash*, to his statement that variability in length at age started low, increased, then decreased again. However, the variability among older animals may only *appear* to decrease, because there are fewer animals. There may be a need to calculate and compare standard deviations.

Warwick Nash agreed, saying he had looked at standard deviations, and they vary between sites but generally decrease markedly in the large size classes.

Chris Francis then spoke about the information on length at age, and suggested that a yield per recruit (YPR) analysis could not be undertaken because of the lack of data for the older age groups.

Warwick Nash responded that the Gompertz curve may be close to reality. No animals reached 230 mm, and the estimate of L_∞ from the Gompertz curve was close to what would be expected for this species. Overall, then, the description of the growth of older animals seemed reasonable.

Philip Sluczanowski stressed the importance of realising what is meant by a 'model'. Is it a representation of a real underlying process, or the description of a line that fits a set of data points? Gompertz and von Bertalanffy models fit into the latter category, and you can't place much confidence in what happens outside the range of the data. It may be worthwhile to carry out a YPR using both, and see what difference there is. Mortality might make the differences irrelevant.

Rob Day suggested there was a serious issue here: i.e. trying to model YPR where data are missing. This highlights the need for having closed sites in representative areas of the fishery for such analyses, so that it is possible to study age classes that are rare or absent in fished populations.

Paul Breen questioned *Bruce Phillips* about the changes in carapace length plotted against days from settlement in trapped animals. How did he know the number of days after settlement in these cases?

Bruce Phillips responded that the only accurate information was from t_0 into the fishery from animals that were micro-tagged. Otherwise the initial age is unknown, but is estimated by the methods to be described later by modeller Mark Palmer.

David Smith asked *Kevin Rowling* whether he was saying that growth of gemfish changes from ages 4 to 5? - to which the author replied that it was the proportions of age 4 fish in the spawning stock which changed, and that there's probably some behavioural mechanism at work.

David Smith then asked what impact the decrease in K and L_∞ over the four year samples would have on a yield per recruit analysis, to be told that the estimates of K are not very different, although the L_∞s do change. Since a yield per recruit analysis had not yet been undertaken, the possible effect was not known. Keith Sainsbury thought it would be surprising if it made much difference.

David Die wanted to know whether the decline in size at maturity over the last few years, suggested by the data, was the result of exploitation? Kevin Rowling agreed that it was. Age at maturity in males had certainly dropped (males are precocious anyway), but age at maturity in females hadn't changed much.

Rob Day was not clear on how the four years of data were combined - were they pooled or run through one of Fournier's programs? He was told that the whole data set was combined and run.

Keith Sainsbury told *David Die* he had provided another example of the effect of variability on estimates. Possible re-parameterisation may be useful, but the reason why the model is being used needs to be kept in mind. David Die responded that even if re-parameterisation is used, estimates of *K* and L_∞ can still be retrieved. However, when testing differences between stocks it is dangerous to use parameters outside the range of the data.

Keith Sainsbury went on to say that testing differences between growth of males and females, for example, is straightforward, but care is needed when drawing inferences about underlying growth processes.

John Glaister expected that, in a practical sense, you would try for the widest possible size range, but there's a limit to the smallest size you can tag. Did the author have any feeling about how to tackle the lower end of the size-range? David Die wasn't aiming to tag the very small animals, but to cover the whole size range from the minimum taggable size. It might be useful to consider some way of weighting the data.

Ian Somers commented that problems with tagging animals approaching L_∞ include the truncation effect. An alternative approach he had adopted was to tag small animals and reduce recapture rate by doing it in a closed season to get sufficient contrast. David Die agreed with this and suggested you could also incorporate growth variability into the model.

Iain Suthers wondered if the meeting had forgotten comments of the previous day on the effect of tagging on growth rates? David Die had not, but referred to work by CSIRO which has shown that tagging affects growth in penaeids for the first month when moulting gets out of phase, but not later. He suggested not using data for that month during which growth is affected and recapture probability is reduced.

Ian Somers said they had worked on this at Cleveland. Moult frequency is increased over the first 4 months, but increments are reduced, so that overall differences in growth between tagged and non-tagged prawns were non-significant.

Following *Ian Somers'* panel contribution, Keith Sainsbury asked him about the instability in estimates he had mentioned? Was it in parameter values or demarcation between modes? Ian Somers answered that maximum length was not sensitive, only the K value. There are problems in using models with so many parameters; the models give slightly different answers depending on the starting values. He was interested in Fournier's 'Multifan', but it wouldn't fit his data to account for what he calls 'first length bias' satisfactorily. However, it could still be quite a useful tool.

Mike Moran pointed to a mesh selection effect at the lower end. Could a mesh-selection ogive be built into the model? Ian Somers replied that it did actually include this, but did not include a smooth recruitment ogive, since there were two recruitment pulses during the summer period.

Peter Young asked if there is any interest now in the use of 'day-degrees' in this sort of temperature-related growth problem, but Ian Somers was not aware of any. Elfan and Multifan only need another two parameters to account for seasonality and this is quite straightforward.

David Die mentioned another problem with penaeids - they only go through one cycle of fast growth, so it is difficult to model seasonality. Ian Somers, said he, had looked at putting a seasonal growth component in with the tagging data. There was some suggestion of seasonality, related more to spawning than a reduction in growth in winter.

Chris Francis asked if he could get a monthly index of recruitment to overcome the recruitment problem, to which Ian Somers replied that he had an index for small prawns. However, the problem is that the prawns are not always recruiting at the same size (<20 mm, 25 or 30 mm). Thus size is not a good indication of recruitment.

Terry Walker started off the *General Discussion* in this sub-session by referring to comments of the previous day about the increased survival of runts. This would have the effect of pulling L_∞ down and flatten the von Bertalanffy curve.

Ian Somers had found no evidence for size-dependent mortality in prawns. There was virtually no net selection above 30 mm, and most of the commercial catch was 30 mm and above.

Mike Moran's experience from Shark Bay was that tagging and scale studies on growth of pink snapper gave the same L_∞, but tagging gave lower K values. He wondered if there was any other evidence that K is influenced by tagging?

Keith Sainsbury expected some bias in these estimates because of differences in the age distribution of the animals and the effect of the initial size distribution and times at liberty on tagging results. He wondered if there would be any general comments about whether or not we are able to develop compatible ageing and tagging studies in view of the close interaction of the processes of growth, mortality, recruitment, fishing mortality etc?

Mike Moran wanted to know if he was saying that tagging had no value in this situation. Keith Sainsbury replied that he was not, but there are difficulties in estimating growth parameters without good knowledge of the other processes occurring simultaneously in the population. We are safe so long as we do not infer beyond the range of the data. However, we do need to extrapolate - as in the case of the abalone fishery where we are constrained about what we can say about growth in the large animals.

John Glaister commented that from the fisheries viewpoint, growth data are used either in yield models or in simple comparisons of growth parameters. He would be interested to hear of any recent developments in techniques for comparing growth.

Tony Smith replied that there were two issues - to decide what the analysis is to be used for, and the confounding effects. In Ian Somers' data there was confounding because the animals cannot be directly aged. For example, the existence of size-selective mortality makes the situation much worse.

Dave Smith asked how sensitive yield per recruit analyses are to errors in parameters such as L_∞ and K?

Keith Sainsbury did not believe there is a general answer to that. However he would try not to use L_∞ and K in a yield per recruit analysis. Rather he would try to remain as close as possible to the original data and use mean weight-at-age. This goes back to the question of what are we trying to do, and for yield per recruit a formal growth model is not necessary if extrapolations are not required. There's a fundamental problem when growth increment data are used to infer statements about age, for use in something like a yield per recruit analysis. Often (as in Ian Somers' data) the L_∞ and K estimates are quite unstable even when the length frequency modes are well separated and identifiable. Care is needed in drawing inferences when dealing with a mixture of length-dependent and age-dependent data and processes.

Peter Young believed that what we are really trying to do is to get a mathematical function to describe a set of points on a graph. It is dangerous to extrapolate beyond the data range unless there is an underlying biological or physiological mechanism which can be relied upon. Perhaps the comparisons should be made between the new data sets rather than the parameters.

In Chris Francis's view you do not need to compare the new data. Re-parameterisation can give you a better representation of the data you have got.

Terry Walker commented about the dynamic pool model. From experience with shark, if you push the growth curve around it doesn't make much difference. However, changes in mortality certainly do. It is probably better to put effort into estimating mortality accurately than into growth.

Rob Day was concerned whether enough emphasis had been given to size-dependent mortality. Size-selective mortality will change or bias estimates when smaller or larger individuals are involved in the 'gauntlet' case. The issue should be assessed when doing the growth study.

Terry Walker commented that if fish are going to be caught in the 'gauntlet' the fast growers will get there first. When the slow growers get into the 'gauntlet' they will be there for a longer period, so there will be all sorts of selection problems occurring.

Scoresby Shepherd, speaking on the question of bias, asked what is the best way assess the extent of bias, as a result, for example, of size-related fishing mortality?

Keith Sainsbury responded that the best way he could think of to get some indication of this sort of bias is to simulate the situation as you believe it to exist, then look at the bias and other problems (or lack of problem) that situation creates.

Don Hancock took up John Glaister's point, that biologists need to be innovative. Some time ago he and Eric Edwards were looking at a mass of moult increment data on crabs from tagging in the U.K., to try to obtain estimates of annual growth and moult frequency. They analysed the data by selecting only those crabs which had been returned one year after tagging. The 'birthday' period could be widened on the basis of knowing when moulting took place. The analysis not only provided the necessary estimates of annual growth but moult frequency information 'fell out' of the analysis. The estimates of annual growth at size could then be used in Kay Allen's technique to make predictions about the effect of changing minimum size. Thereafter, the 'anniversary' method involved instructing the fishermen not to return tags until they had been at liberty for a year.

Sub-session B

Estimation and Comparison of Model Parameters from Age, Length - Frequency and Growth Increment Data

Panellists:	R.L. Sandland M.J. Palmer K.A. Haskard R.I.C.C. Francis N. Dow
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COMPARISON OF GROWTH PROCESSES

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What does it mean when we say we want to model a growth process?

It usually means that we have some *data* and we want to make a prediction from the data about some important aspect of the growth process. For example: what is the expected growth between ages t_1, and t_2? How long does it take for the animal to grow from size W_1 to size W_2? What is the expected age of an animal of size W? What is expected difference in relative growth rates for different growth regimes between ages t_1, and t_2?

If the growth trajectory is of the form:

$W = f(\alpha, t)$

where α is known, then these quantities can be estimated as follows:

$$f(\alpha, t_2) - f(\alpha, t_1)$$

$$f^{-1}(W_2;\alpha) - f^{-1}(W_1;\alpha)$$

$$f^{-1}(W;\alpha)$$

$$\int_{t_1}^{t_2}\left[\frac{1}{f_2}\frac{df_2}{dt} - \frac{1}{f_1}\frac{df_1}{dt}\right]dt$$
$$= \log f_2(t_2) - \log f_2(t_1)$$
$$- \log f_1(t_2) + \log f_1(t_1)$$

Often what is required is an estimate of some functional of a growth process.

The question of how to model the growth process depends quite strongly on the answers one expects from the model.

One of the issues I was asked to address is how does one compare growth curves. At the outset I want to make the following comment. Straight comparison of growth curves is usually not an interesting exercise; what is usually required is an estimate of some biologically important growth characteristic which may well be a functional of the growth process. The comparison question usually boils down to the existence or otherwise of a statistically significant difference between the parameters of two or more growth curves. This is a reasonable starting point, because if the parameters do not differ between regimes there is little point estimating functionals predicated on the assumption of non zero differences.

My argument for the need to build *stochastic* models of growth processes is based on the need to properly estimate the model parameters; what is usually required is an estimate of parameters. Even in the case of the simple linear model with correlated errors, while the regression parameters are estimated without bias by ordinary least squares procedures (i.e. ignoring correlation) the estimated covariance matrix is inappropriate. In other words, we can estimate the parameters *accurately* but we don't know how *precisely*.

Methods of Comparison

Multivariate Methods

Let X_{ij} be a vector of observations of length p made on the *i*th individual from the *j*th treatment group,

$i = 1,\ldots,N_j\, j = 1,\ldots,g, \Sigma N_j = N$

Let B be a matrix of rank q

$$\underset{p\times 1}{E(X_{ij})} = \underset{p\times q}{B}\ \underset{q\times 1}{\xi_j}$$

Overall

$$\underset{p\times N}{E(X)} = B\ \underset{q\times g}{\xi}\ \underset{g\times N}{A} + E$$

B contains polynomial terms
ξ contains regression parameters
A is a design matrix

The columns of E are independently, identically distributed(0,Σ).

Examples of this structure are:

$$B = \begin{bmatrix} 1 & t_1 & t_1^2 \\ 1 & t_2 & t_2^2 \\ \vdots & & \\ \vdots & & \\ \vdots & & \\ 1 & t_p & t_p^2 \end{bmatrix}$$

$$\xi = \begin{bmatrix} \xi_{10} & \xi_{20} & \ldots\ldots & \xi_{g0} \\ \xi_{11} & \xi_{21} & & \xi_{g1} \\ \xi_{12} & \xi_{22} & \ldots\ldots & \xi_{g2} \end{bmatrix}$$

$$A = \begin{bmatrix} 11110\ldots\ldots\ldots\ 0 \\ 00001110\ldots.\ 0 \\ \vdots \\ \vdots \\ \vdots \\ 0\ldots\ldots\ldots\ldots\ldots\ 011 \end{bmatrix}$$

Thus each group is measured on ρ occasions, a quadratic polynomial is fitted to each group with different parameters, A indicates the first four 'animals' belong to group 1, the next 3 to group 2, etc.

Features of this analysis are:

(i) generality of the within individuals covariance matrix; no model is assumed;

(ii) *linear* regression model, same (up to parameter values) for all individuals;

(iii) all individuals must be measured at the same time points.

The analysis yields
(i) estimation of the parameters ξ;
(ii) test of model fit;
(iii) tests of linear hypotheses concerning ξ.

Reference

Grizzle, J. E. and D.M. Allen (1969). Analysis of growth and close response curves. *biometrics* **25**, 357-381.

Non-parametric comparison

Zerbe and Walker (1977) introduced a non-parametric method for the comparison of growth curves.

The underlying model for the analysis is

$$y_{ij}(t) = \mu_j(t) + E_{ij}(t)$$

where $y_{ij}(t)$ is the size at time t of the i^{th} organism in the j^{th} treatment group, $\mu_j(t)$ is the underlying (smooth) trend for the j^{th} treatment group and $E_{ij}(t)$ is an error process with expectation zero and unspecified correlation structure.

The comparison is based on an analysis of variance of these smooth curves between times *a* and *b*.

ANOVA

Source	S.S.	d.f.	EMS
Between Groups B	$\sum n_j \int_a^b (\bar{y}_{.j}(t) - \bar{y}_{..}(t))^2 dt$	$g-1$	$\int_a^b \sigma^2(t)dt$
Within Groups W	$\sum_i \sum_j \int_a^b (y_{ij} - \bar{y}_{.j})^2 dt$	$n-g$	$+(g-1)^{-1}\int_a^b (\mu(t))^2 dt$
Total T	$\sum_i \sum_j \int_a^b (y_{ij} - \bar{y}_{..})^2 dt$	$n-1.$	$\int_a^b \sigma^2(t)dt$

Note the potential generality of $\mu_j(t)$. Although polynomials were used by Zerbe and Walker, $\mu_j(t)$ can be a spline or other smooth of the data.

Test statistic: compute B*/W* for the experimental configuration.

Make all $(N!/\Pi N_j!)$ possible assignments of individuals to treatment groups.

Compute B/W for each such assignment.

Is the value B*/W* unusually large in the distribution of values of B/W? This provides a test of significance. The choice of a and b is under user control providing additional flexibility. If the number of possible assignments is too large, a smaller number should be selected at random.

Reference

Zerbe, G.O. and S.M. Walker (1977). A randomisation test for comparison of groups of growth curves with different polynomial design matrices. *Biometrics* 33, 653-657.

Stochastic Growth Models

There are three basic types of models which give rise to stochastic elements:

(i) Linear or non-linear models with correlated errors.

$$\omega = f(\alpha, t) + \varepsilon(t)$$

where $\varepsilon(t)$ is a stochastic process of errors with a specific correlation structure, e.g.

$$\begin{aligned}\operatorname{cov}(\varepsilon(t), \varepsilon(t')) &= \sigma^2 \exp(-\beta|t - t'|)\\ &= \operatorname{cov}(w(t), w(t'))\end{aligned}$$

(ii) Random coefficients models

$$\omega = f(\alpha, t) + \varepsilon(t)$$

α is a random vector, $\varepsilon(t)$ is a sequence of measurement errors.

$$\begin{aligned}\operatorname{cov}(w(t), w(t')) &= E_\alpha(f(\alpha, t'))\\ &= E_\alpha(f(\alpha, t))E_\alpha(f(\alpha, t'))\end{aligned}$$

Measurement errors may be assumed independent or correlated as in (i).

(iii) Stochastic differential equation models.

In this case the stochastic component is built directly into the generating differential equation, for example:

$$\frac{dw}{dt} = kw\left[(A/w)^{1-m} - 1\right]/(1-m)$$

is the deterministic differential equation which generates the Richard's curve, a generalisation of the von Bertalanffy growth equation.

The stochastic version is modelled via

$$dw = \{W\left[(A/w)^{1-m} - 1\right]/(1-m)\}\{kdt + \sigma d\varepsilon(t)\}$$

$d\varepsilon(t)$ is the increment of a Wiener process with zero drift, infinitesimal variance 1.

This leads to a direct enumeration of the statistical properties and a likelihood approach for estimation and inference.

It may be simpler and preferable to build empirical models, given the tenuous basis of the growth model.

$$\frac{1}{w}dw = f(\alpha, t)dt + h(\beta, t)\sigma d\varepsilon(t)$$

which leads to the solution (under certain mathematical assumptions in stochastic calculus):

$$\begin{aligned}\log w(t_2) - \log w(t_1) &= \int_{t_1}^{t_2} f(\alpha,u)du + \int_{t_1}^{t_2} h(\beta,u)\varepsilon(u)du \\ &= R(t_1,t_2) + E(t_1,t_2).\end{aligned}$$

This is a simple regression model. Under certain assumptions $E(t_1,t_2)$ and $E(t_3,t_4)$ are *uncorrelated* for non-overlapping intervals and simple linear regression approaches are available. This class of models offers considerable flexibility in describing the non-stationary nature of growth processes and facilitates simple methods of comparison and inference as described earlier.

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The notes given above are not intended to be exhaustive but merely to indicate some of the current major methods for comparing growth curves and stochastic modelling of growth processes.

NONLINEAR RANDOM COEFFICIENT MODELS FOR CAPTURE-RECAPTURE DATA

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Abstract

A nonlinear random coefficient approach to modelling growth is described. Maximum likelihood is used to estimate the population parameters. Extensions to capture-recapture data are discussed.

Introduction

The analysis of repeated measures or growth curve data can be greatly facilitated if they can be modelled parametrically. For example, either the response can be assumed to follow some function of time, such as a logistic curve, or the growth can be modelled by differential equations. This allows a large collection of data to be parsimoniously summarised by a few parameters, the coefficients of a curve.

The fitting of functions to individual animals and the analysis of the coefficients of these functions (generally known as the random coefficient approach) was apparently begun by Wishart (1938) and has been the object of continued research (Rao 1965; Fearn 1977; Laird and Ware 1982). A recent reference with particular regard to linear models is by Laird, Lange and Stram (1987). Racine, Grieve and Fluhler (1986) discuss a Bayesian approach to nonlinear random effects models.

A concurrent development was the use of differential equations to model changes in an individual with time and thus give more than an empirical justification to the curves (Richards 1959). Sandland and McGilchrist (1979) generalised this approach by the use of stochastic differential equations, which were subsequently used by Garcia (1983) for the analysis of tree growth data. Garcia's (1983) approach suffered from the presence of nuisance parameters that rendered the properties of his estimates, based on maximum likelihood, "uncertain".

Random Coefficient Model

In this paper we present a unified approach, based on random coefficients, for the analysis of growth curve data. General functions are considered and there is no requirement that the individuals be measured at the same times. The approach is also applicable when growth is modelled by stochastic differential equations.

Our approach is to model the variation between individuals' growth. The basic assumption is that although the growth of the individuals differ they can all be described by the same functional form; the differences between individuals are then contained in the coefficients.

These coefficients have a p-variate normal distribution with mean unknown and dispersion matrix. The animals' unexplained variation about the growth curve, is normally distributed with mean zero and unknown variance. In general the individuals' coefficients will not be available, and to remove the problem of nuisance parameters (leading to possibly inconsistent estimators) we integrate them out.

The likelihood for all the m observations made on an animal is then the product of the likelihood for each time, the whole expression being integrated with respect to the coefficients.

Maximising the likelihood over all individuals appears daunting; however this model fits naturally within the conceptual framework of the EM algorithm (Dempster, Laird and Rubin 1977), where the "missing" data are the individuals' coefficients.

Berkey (1982) estimates individual growth curves in a random coefficient model, but uses least squares estimates of the population parameters based on large samples. Berkey and Laird (1986) develop several approaches based on approximations to the mean and dispersion matrix of the individual coefficients and derive several weighted least squares solutions to the problem of estimating the population parameters.

Auto-correlation

A complication with growth curve data is the suspected presence of serial correlation between the measurements on an individual. A way of modelling one type of auto-correlation is outlined by Glaseby (1979) and this can be easily incorporated into our model.

Maximum Likelihood Estimation

Estimation of the population parameters requires maximisation of the likelihood, which is computationally difficult. However, when growth can be represented by a linear (in the parameters) model and the animals have all been measured at the same time, the maximum likelihood estimates can be calculated explicitly. In most cases, iterative procedures will have to be employed. The most natural algorithm is the EM algorithm (Dempster, Laird and Rubin 1977); its implementation and application to linear models is described by Laird, Lange and Stram (1987), and to non-linear models in Palmer, Phillips and Smith (in press).

Capture - Recapture Data

Capture-recapture, or mark-recapture, data are characterised by the lack of knowledge of an animal's age at first capture. However the time between the subsequent recaptures is known.

A difficult problem occurs when the population parameters are unknown and they have to be estimated from capture-recapture data. Placing the problem in the EM context again, we can consider the unknown initial age to be additional "missing" data and assume a non-parametric distribution for the initial ages. Details are given in Palmer, Phillips and Smith (in press).

The choice of distribution of t_1, $p(t_1)$, depends upon knowledge of the age distribution. Several approaches are possible, ranging from a position of complete ignorance and using a uniform distribution, to a non-parametric approach (Laird 1978).

There are several advantages that this approach has over the traditional Fabens (1965) approach. It is based on maximum likelihood and thus has proven theoretical properties relating to efficiency and optimality. It is applicable to any growth curve, not just the von Bertalanffy, it models individual growth and allows for any number of recaptures of an animal.

Bacon-Shone (1988) developed a Bayesian approach to this problem, but his model is not as general. He only allows the asymptotic size of an individual to vary and does not model the variation in other growth parameters nor the correlation between them.

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SIMPLE AND ROBUST COMPARISON OF GROWTH IN DIFFERENT POPULATIONS, USING ANOVA

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Abstract

Given lengths of animals in several age classes in each of two (or more) populations, a simple analysis of variance model can be used to compare the growth patterns of animals from the different populations. A difference between populations will generally produce a significant age by population interaction, which can be partitioned into linear, quadratic and higher order components to indicate the shape of the differences. Multiple comparison procedures can also be used.

This approach has the advantages of simplicity, clearly stated and checkable assumptions, robustness to moderate departures from assumptions, and utilisation of readily available standard statistical software. Transformations (such as log or square root) to stabilise variance will often be necessary, but should not hinder interpretation. Care must be taken with unbalanced data. The method compares populations directly, without estimating growth curve parameters. It potentially lacks power by neglecting knowledge about the shape of growth curves, but avoids the complications and sensitivity of non-linear estimation approaches.

Introduction

This paper demonstrates the use of analysis of variance (ANOVA) to compare the growth curves for two populations, given length at age data for several distinct ages. This method assumes no particular shapes (such as von Bertalanffy curves) for the growth curves, and thereby avoids the difficulties of non-linear estimation and insufficient data to estimate the parameters required (in particular length at age infinity in the case of the von Bertalanffy curve).

Form of Data Required

To apply ANOVA, we need a sample of lengths of fish at each of several distinct ages, rather than a continuum of ages. These may arise naturally, or be obtained by grouping ages in some sensible way. They need not be equally spaced, nor for whole year classes.

Table 1 shows means from a sample data set. ANOVA can tell us whether the population means represented by these sample means are significantly different, or whether the pattern of means across the age groups is the same for both populations.

Assumptions of ANOVA

Analysis of variance is described in many basic statistics books, for example Snedecor and Cochran (1980), and done by most statistical computer packages. Several theoretical assumptions must be met for ANOVA to be valid:

(1) Correct Model. The statistical model assumed is that all fish in a given age group and population have some true (but unknown) mean or average length, with individuals having some random variability about this mean. The difference between an individual and the mean is

termed the 'error'. Different age groups and different populations may have different means.
(2) Errors are normally distributed with mean zero.
(3) Errors have constant variance.
(4) Observations are independent.

ANOVA is moderately robust to non-normality, more so with large samples. It is more important that the error distribution be symmetric and have constant variance. If sample sizes are roughly equal, ANOVA is robust to unequal variances. Transformations may help symmetrise the error distribution, as well as stabilise variance.

Assumptions (2) and (3) can be roughly checked with a plot of residuals against fitted values after doing the ANOVA. This should be done as a matter of course, and is very quick and easy with computer packages. If the plot shows variance increasing with larger fitted values (evidenced by a widening band - as for example in Figure 1) a logarithmic or (less severe) square root transformation of the lengths may help. Simply calculate the log (either base 10 or natural logarithms - they have exactly the same effect) of the lengths and repeat the analysis on these transformed values.

Sample Analysis

For the sample data, an initial analysis produced the residual plot shown in Figure 1 (a), suggesting the need for a log transformation to stabilise variance. The analysis of variance was repeated on log(length), producing the ANOVA table shown in Table 2, with the corresponding residual plot in Figure 1 (b). The significant age group main effect is expected and is of no interest. We are primarily interested in the population effect and especially the population by age group interaction. The significant interaction tells us that our two populations have significantly different patterns across the age groups.

Special Attention to Unbalanced Data

With unbalanced data (i.e. unequal numbers in the cells), great care must be taken in interpreting the main effect F tests. They are not in general testing the 'obvious' hypothesis of equal means. Milliken and Johnson (1984) are very helpful on this subject. The so-called Type III sums of squares approach (SAS terminology) is recommended. Minitab (glm command) and Systat (MGLH) give these automatically, but many packages do not. The appropriate sums of squares and mean squares are labelled "adjusted" in Table 2.

A safe and simple alternative procedure is to treat our 2 x 5 combinations as 10 levels of a single factor and do a simple one-way analysis of variance. See Table 3.

To compare the two populations at each age, we can use multiple comparisons procedures, for example Fisher's least significant difference (LSD), perhaps with a Bonferroni adjustment (if making 5 comparisons, for an overall significance level of .05 or less, declare a difference significant only if its p-value is .05/5 = .01 or smaller), or Tukey's or Scheffe's methods. All must use the means of the log transformed data (Table 4). See a statistics book such as Milliken and Johnson (1984) for details.

For the sample data, we find that the mean lengths in the two populations are not significantly different at ages 1 to 4, but are different at age 5.

Polynomial Components

The multiple comparisons approach may be insensitive to a gradual increase in differences between populations if the effect is slight. A more sophisticated and possibly more enlightening method for comparing the two populations is to partition the interaction sum of squares in the two-way ANOVA into polynomial components, corresponding to linear, quadratic, ... changes over age.

Calculate:

x = age - 3 gives values -2, -1, 0, 1, 2
for age = 1, 2, 3, 4, 5 for the linear component of age
x2 = x^2 quadratic component
x3 = x^3 cubic component
x4 = x^4 quartic component

(The standardisation by subtracting a central value of age helps avoid high correlation of x, x squared, x cubed etc.) A factor (AGE) with 5 levels will have 4 degrees of freedom and 4 polynomials can be calculated. If the age groups are not evenly spaced, different x values may be chosen to reflect this.

The two-way ANOVA model

POP + AGE + POP.AGE

is exactly equivalent to fitting

POP+AGE+POP.x +POP.x2+POP.x3+POP.x4

but now we can test whether the population differences indicated by the interaction can be described with less than four parameters (corresponding to the 4 degrees of freedom).

Using a regression approach (e.g. glm in Minitab, MGLH in Systat, or by using dummy variables in any linear regression routine) we fit models

POP + AGE + x.AGE + x2.AGE + x3.AGE

POP + AGE + x.AGE + x2.AGE
POP + AGE + x.AGE

By comparing these models we may find that the higher order polynomials are not significant, and thereby have a simpler way of describing the population differences.

If a linear component is all that is needed to account for the interaction, we can say that the population differences are increasing (or decreasing) linearly with age.

If linear and quadratic components are needed, the differences change over time in a quadratic manner - perhaps they start off small, increase and then flatten off, or become small again.

A look at the means, or better, a plot of them, shows us the shape of the pattern.

In the example, only the linear component is significant (Table 5). With the aid of a plot, or table of means (Table 4), we can say that the differences increase linearly with age, and that there is little difference at early ages but as age increases, fish from population B have increasingly greater mean lengths relative to those from population A.

One catch in this example is that because we have used the log transform, a linear increase translates to an exponential increase in the ratio of the back-transformed means with an increase in age:

logmeanB - logmeanA = a + b.AGE

$$\Leftrightarrow \frac{\text{(geometric)mean B}}{\text{(geometric) mean A}} = e^{(a+b.\ \mathrm{AGE})}$$

An increase of 1 in age corresponds to multiplying the ratio of geometrical means by e^b. For example, if the geometric means are equal at age 2, then at age 3 the geometric mean for the population B is e^b times the geometric mean for population A, and at age 3, the geometric mean for population B is e^{2b} times the geometric mean for population A.

Comparisons with Differences in von Bertalanffy Curve Parameters

Several common patterns can be described in terms of the linear and quadratic components. In particular, population differences often expressed in terms of the von Bertalanffy curve parameters L_∞ and K may be detected by the polynomial breakdown and multiple comparisons as follows.

Same K but different L_∞: linear term significant, with little difference at early ages and then an increasing difference. If the oldest two or three age groups are near L_∞, the quadratic term may also be significant as the differences flatten off to a constant.

Different K but same L_∞: Linear and quadratic terms significant as the difference begins small and increases, then decreases to zero. With several large groups, the cubic term may appear significant, because differences flatten off at zero.

One population with greater K and greater L_∞: Linear (and, if more than one age group near L_∞ present, quadratic) components significant.

One population with greater K but lesser L_∞ (growth curves cross): linear, quadratic and, provided enough large fish (near L_∞), cubic components significant.

Another Example - Comparing Male and Female *Lutjanus vittus*

Table 6 shows mean lengths for 926 *Lutjanus vittus*, males and females separately. In this example a transformation proved unnecessary. Table 7 shows the ANOVA with the significant interaction sum of squares partitioned into polynomial components. A plot of differences (males minus females, Figure 2) against age shows why the cubic is highly significant. Apart from a perturbation at age 1, the difference increases notably with age, and this is brought out in the plot of mean lengths against age for the two sexes (Figure 3). At the younger ages males and females have similar mean lengths, but males subsequently grow larger than females. We cannot be confident from these data that males remain larger than females at greater ages, no matter what method we use to test this.

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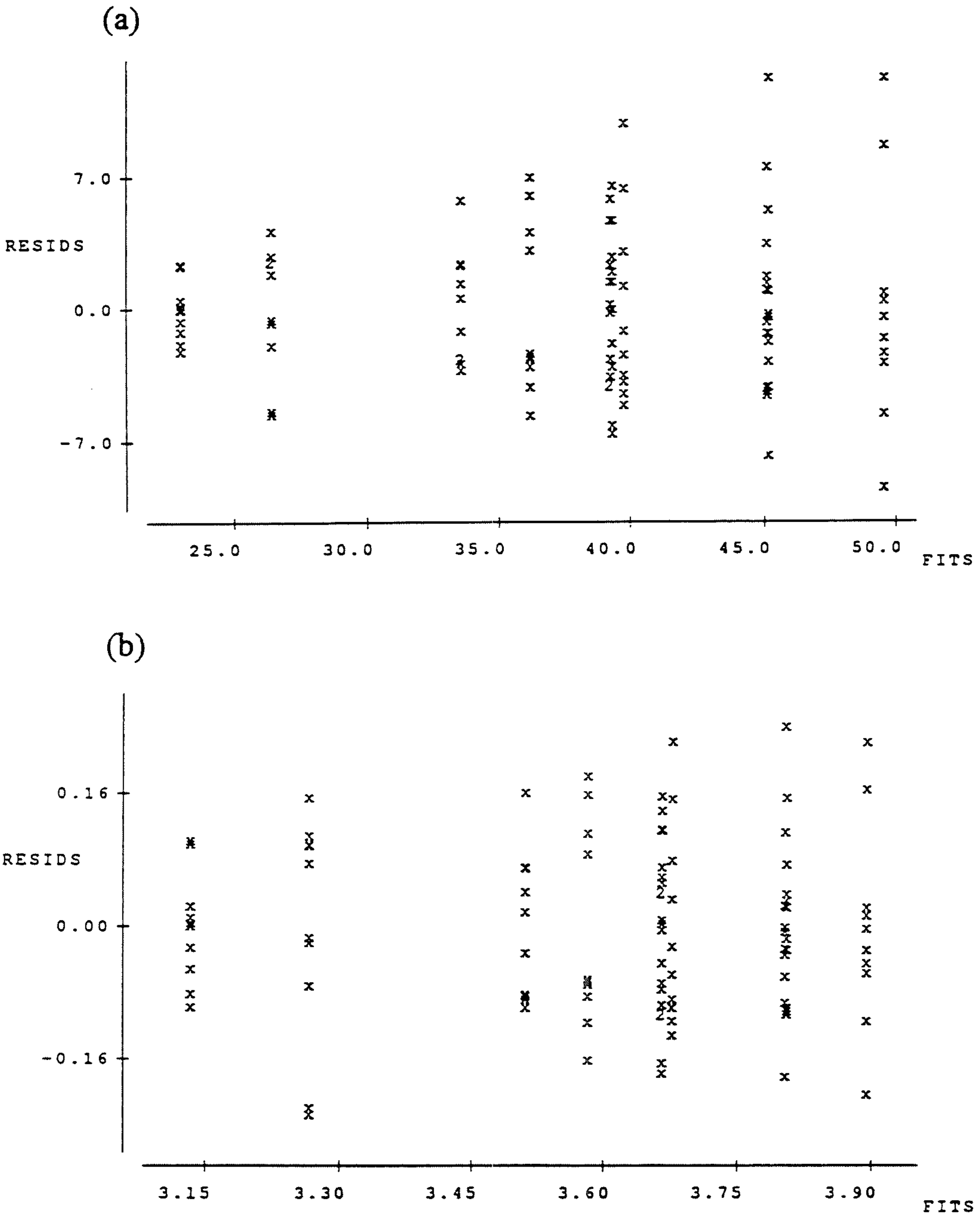

Figure 1. Plots of residuals against fitted values to check (a) raw data, (b) logarithmic transformation. A number "2" in the plot indicates two coincident points.

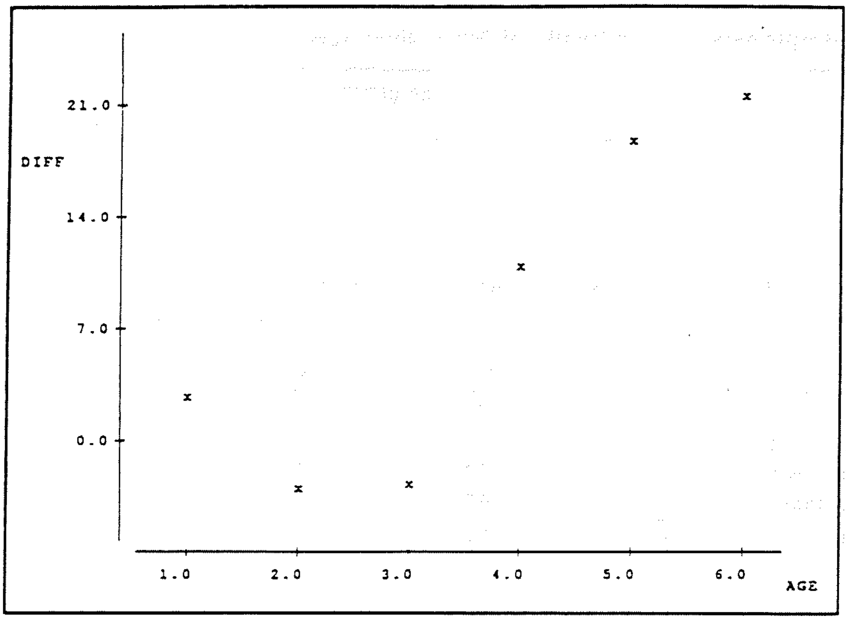

Figure 2. Differences (males minus females) in mean lengths at different ages for *Lutjanus vittus* data.

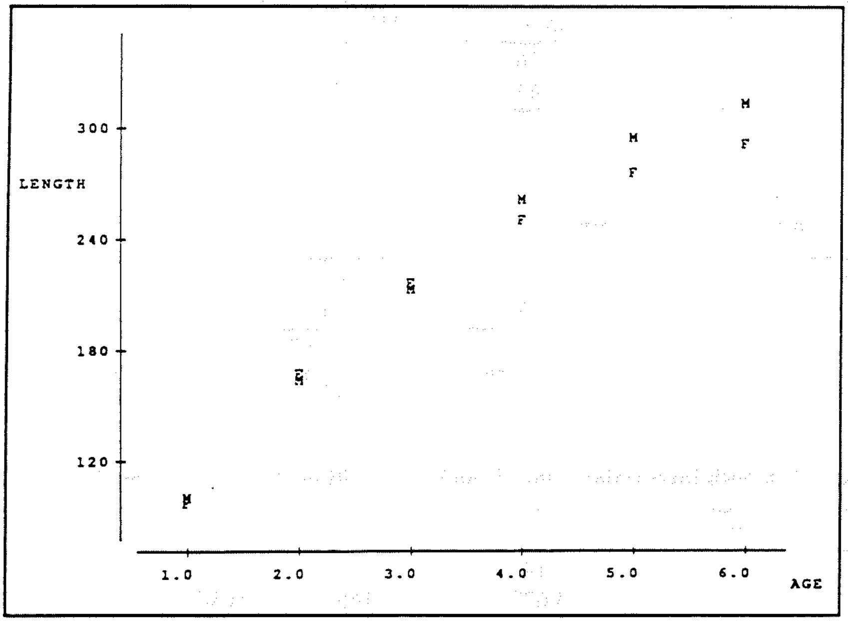

Figure 3. Mean lengths of male (M) and female (F) *Lutjanus vittus* of different ages.

Table 1. Sample data - mean lengths of fish at given ages

Population	Age group				
	1	2	3	4	5
A	26.4	33.6	39.3	39.8	39.3
B	23.0	36.2	45.0	45.1	49.5

Table 2. Analysis of variance on log(length) for sample data

Source			Adjusted		
	df	SS	MS	F	p
Population	1	0.187	0.187	15.81	0.000
Age group	4	4.677	1.169	98.86	0.000
Pop x age	4	0.362	0.0905	7.65	0.000
Residual	90	1.065	0.0118		
Total	99	6.291			

Table 3. One-way ANOVA with 10 classes for sample data

Source	df	SS	MS	F	p
Factor	9	5.226	0.581	49.1	0.000
Residual	90	1.065	0.0118		
Total	99	6.291			

Table 4. Cell means for log(length)

Population	Age group				
	1	2	3	4	5
A	3.27	3.51	3.67	3.68	3.67
B	3.13	3.58	3.80	3.80	3.89

Table 5. ANOVA with interaction sum of squares partitioned into polynomial components

Source	df	SS	MS	F	p
Population	1	0.187	0.187	15.81	0.000
Age group	4	4.677	1.169	98.86	0.000
Pop x age	4	0.362	0.0905	7.65	0.000
linear	1	0.301	0.3013	25.47	0.000
quadratic	1	0.029	0.0286	2.42	0.124
cubic	1	0.031	0.0308	2.60	0.110
quartic	1	0.001	0.0013	0.11	0.897
Residual	90	1.065	0.0118		
Total	99	6.291			

Table 6. Mean lengths for 926 *Lutjanus vittus*

Sex	Age: 1	2	3	4	5	6
M	100.58	163.94	213.68	261.43	294.95	312.90
F	97.79	166.94	216.39	250.51	276.05	291.20

Table 7. ANOVA table for *Lutjanus vittus* data

Source	df	Adjusted SS	MS	F	p
Sex	1	9419	9419	26.48	0.000
Age group	5	2699914	539983	1517.78	0.000
Sex x age	5	16408	3282	9.22	0.000
linear	1	15	15	0.04	0.837
quadratic	1	3846	3846	10.81	0.001
cubic	1	11055	11055	31.07	0.000
quartic	1	1438	1438	4.04	0.045
quintic	1	54	54	0.15	0.697
Residual	914	325176	356		
Total	925	3086479			

L_{∞} HAS NO MEANING FOR TAGGING DATA SETS

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Elsewhere, I have shown that growth parameters estimated from tagging are not directly comparable to those from age–length data (Francis 1988b). This is because the former describe growth as a function of fish length, and the latter as a function of age (Francis 1988b; Figure 1). In particular the von Bertalanffy parameter, L_{∞}, when estimated from tagging data, does not have its usual meaning of the asymptotic mean length. In this paper I show, with two tagging data sets, that it has no biological meaning.

The usual form of the von Bertalanffy equation when used with tagging data is:

$$\Delta L = (L_{\infty} - L_1)*(1 - \exp(-K\Delta T)) \text{ .... (1),}$$

where L_1 = fish length at tagging (cm, say),
ΔT = time at liberty (years),
ΔL = length increment (cm), and
L_{∞} and K are the von Bertalanffy parameters (Fabens 1965).

The geometric form of this equation is simplest in the case where ΔT is held constant ($\Delta T = 1$, say): here it forms a straight line that intersects the x–axis at $L_1 = L_{\infty}$.

I believe this equation does not describe fish growth well, and that this lack of fit will be seen for any data set with a wide enough range of lengths at tagging (e.g. Figure 1). As length at tagging increases, the expected growth decreases asymptotically to zero, not linearly, as equation (1) predicts.

For data sets with a relatively narrow range of lengths at tagging, equation (1) is probably adequate to describe the expected growth. However, an alternative form of the equation should be used – one in which the parameters have biological meaning. This is well illustrated by a data set for New Zealand rig, *Mustelus lenticulatus* (Figure 2).

Estimates of the usual von Bertalanffy parameters for these data are:

females: L_{∞}= 122.6 cm, K = 0.118 y^{-1}
males: L_{∞}= 126.9 cm, K = 0.067 y^{-1}.

If L_{∞} has any meaning in the tagging context it is something like the 'maximum length', so the implication here is that males have a higher 'maximum length'. This is counter–intuitive in that the tagging data show faster growth for females over the observed range of lengths (Figure 2). It is also contrary to the observation that large specimens are usually female. The problem arises because the L_{∞} estimates are clearly (poor) extrapolations from the data.

More sensible results are obtained using the parameters suggested by Francis (1988a):
females: g_{70} = 5.9, g_{100} = 2.5
males: g_{70} = 3.7, g_{100} = 1.7
(g_{70} is the expected annual growth (cm) for a fish with initial length 70 cm). These parameters have direct biological meaning and do not involve extrapolation. They show clearly that (at least for the range of initial lengths observed) females grow 50 - 60% faster than males. It is reasonable to suppose

that this superiority of growth rate continues for larger fish (as shown by the broken lines in Figure 2).

Acknowledgements

I am grateful to John McKoy (scallops) and Malcolm Francis (rig) for permission to use their data.

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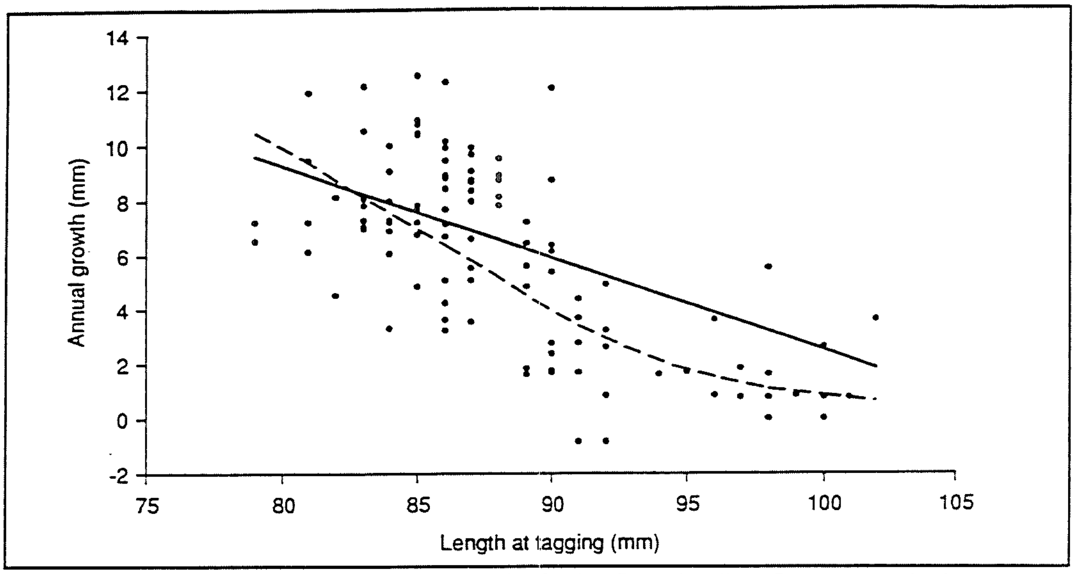

Figure 1. Observed annual growth rate vs length at tagging for New Zealand scallops, *Pecten novaezelandiae*. The solid line is the mean annual growth estimated using equation (1); the broken line shows the probable form of the true relationship between mean annual growth and length. All data (n = 146) were used to fit the line; only those with times at liberty close to one year (n = 109) are plotted.

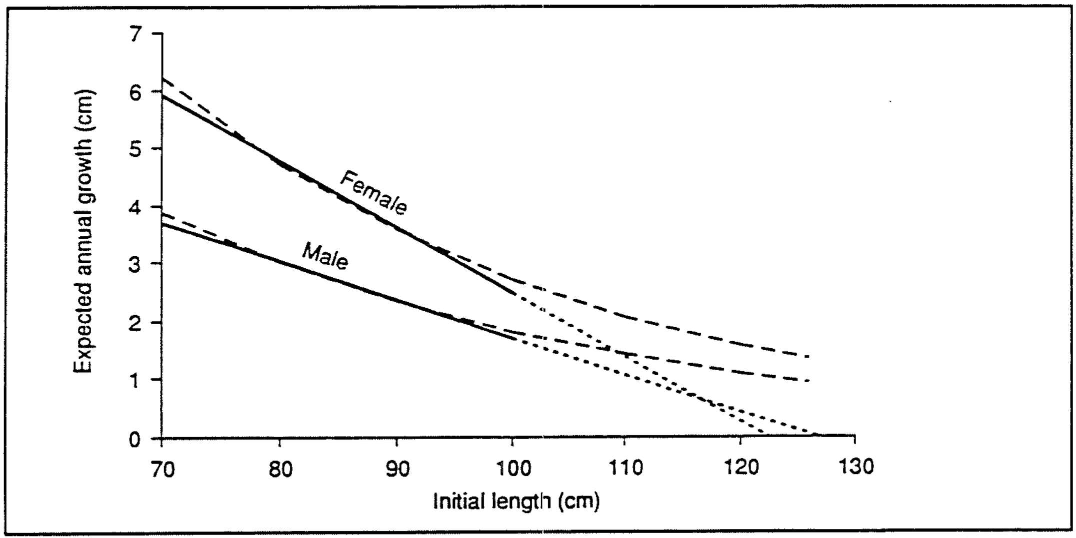

Figure 2. Expected annual growth vs initial length as derived from tagged New Zealand rig, *Mustelus lenticulatus* (females, n = 44; males, n = 86).The solid lines show the estimated relationships (with extrapolations beyond the range of the data shown as dotted lines).The broken lines show the probable form of the true relationships.

GROWTH PARAMETER ESTIMATION FROM TAGGING AND AGEING DATA

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Abstract

Two models are derived which take into account the size-specific selectivity of fishing gear when the models are used to estimate the growth of fish from their release and recapture lengths or from ageing data. The important innovation is the derivation of a posterior probability density function for lengths obtained by conditioning on recapture with selective gear. The prior distribution can be any existing model such as Fabens' (1965) standard model for tag data. In addition to the data normally required the selectivity function for the gear involved in each recapture must be known. The likelihood equation is developed leading to estimation theory and a computationally simple algorithm. Non-selective gear and different types of length-selective gear can be combined in one analysis, and the effect of different assumptions regarding recapture gear on the parameter estimates can be examined.

An additional model is proposed, but not developed, which can simultaneously utilise tagging and ageing data.

Introduction

There are two main techniques for obtaining information on the growth of fish. The most direct is to obtain both the age and the length of a sample of fish and perform a non-linear regression of length against age. This approach results in an estimate of the mean length-at-age of the population. The second technique is to tag fish and to measure their length at release and at recapture and the time at liberty. Francis (1988b) discusses the difference in the curves resulting from these two types of data and we will not consider it here.

Fabens' (1965) model has long been the standard method of estimating a von Bertalanffy growth curve from tag-recapture data. In statistical terms the likelihood is developed by conditioning on the release length and on time at liberty, although random occurrences are considered fixed and attention is focussed on the length increment during the liberty period, which is considered random. The distribution of length increments is what gives the information used to estimate the parameters of the growth curve. In the same way, when age-length data are used, the age of each fish, which is random, is considered fixed (and assumed to be measured without error) and attention focussed on the length.

In each case the random quantity, length increment or length, must be assumed to be sampled randomly from the population, (of tagged fish in the case of length increment data). That is to say that all fish alive at the time of any sampling event must have equal probability of capture. The purpose of the present paper is to examine the effect of departures from this condition which are caused by the use of fishing gear which is length-selective and to propose a method of correcting for the bias introduced thereby.

The reason the use of length-selective gear introduces a bias into growth parameter estimation can be understood by considering the distribution of the random quantities (length or length increment) before sampling (i.e. in the population) and after sampling. The former distribution will be called the prior distribution and the latter the posterior distribution. When captures are effected with length- selective gear the length distribution is altered; for example consider the length of all fish of a given age. If length- selective gear is used there is greater fishing power at some lengths than at others. Fish at these lengths will thus be over-represented in the catch relative to their abundance in the population. The posterior distribution of lengths, in other words, differs from the prior. As will be seen from the examples presented below, the effect on the estimates of growth parameters can be large.

We show here how by making assumptions regarding the prior distribution, and by knowledge of the selectivity of the gear, the posterior distribution can be inferred. Parameter estimation then follows through the use of the maximum likelihood technique, for which the likelihoods are given by the posterior distribution. The selectivity of the gear used in each recapture must be known and be expressed as a function of the length of the fish. Where the gear type, or its selectivity, is unknown, the observation can be omitted from the model without any bias resulting, so that data sets in which only some recaptures are fully documented may still be used.

Tag Data

Fabens' model predicts the length of recaptured fish from the von Bertalanffy growth law and assumes the recapture length is normally distributed and that its variance is uniform across all recaptures. This assumption regarding variance is hardly satisfactory, as Francis (1988a) points out and can be replaced by a more realistic model in which variance of recapture length depends on predicted length increment. This allows the variance of recapture length to vary between individuals, for example, so that the length of individuals recaptured soon after release has less variability than those with longer liberty periods. This formulation also allows measurement error to be estimated separately from individual growth variability. These model choices affect the prior distribution only and can thus be incorporated into the method presented here without modification if desired.

Francis (1988b) also suggests two alternative parameterisations of the von Bertalanffy model, one for tag data, the other for ageing data. For tag data the parameters L_∞ and K are replaced by g_λ and g_μ - the mean annual growth increments of fish arbitrary lengths λ and μ where λ and μ are chosen to represent the range of lengths in the data. This alternative parameterisation is more suitable for tag data both because the estimators have better statistical properties and because they are easier to interpret. Because they directly describe the data they are easy to roughly estimate from it by eye, which is useful in providing starting estimates for the parameter estimation algorithm. Although in the example presented below the traditional parameters are also shown the reader is encouraged to work with the new parameters which are not (unlike L_∞) extrapolations from the data and (unlike K) have an immediate biological interpretation. Francis shows that the new parameters are related to the usual ones by the transformation.

$$\mathrm{L}_\infty = (\mu g_\lambda - \lambda g_\mu)(g_\lambda - g_\mu) \text{ and}$$
$$e^{-K} = 1+(g_\lambda - g_\mu)(\lambda - \mu)$$

Ageing Data

In the case of ageing data the three parameters required to replace L_∞, K and t_0 are l_ϕ, l_χ and l_ψ which are the mean lengths at the arbitrary ages ϕ, χ and ψ, where $\chi = (\phi+\psi)/2$ and ϕ and ψ are chosen to be representative of the range of ages in the data. These mean lengths should not be confused with the mean lengths of any particular group of fish. They are the mean lengths predicted by the growth model and are unlikely to be exactly equalled by the mean length of, say, a sample of ϕ -year old fish, or indeed, of the whole population of ϕ -year old fish.

Likelihood

In his paper, Fabens (1965) develops a least squares algorithm which is a maximum likelihood estimation based on the assumption of normally distributed recapture lengths. The mean recapture length is determined by the von Bertalanffy growth curve, so that if l_1 is the released length of a tagged fish and l_2 its recapture length after a liberty period ΔT,the expected recapture length is given by

$$E(l_2) = l_1 + \left[\frac{\mu g_\lambda - \lambda g_\mu}{g_\lambda - g_\mu} - l_1\right]\left\{1 - \left[1 + \frac{g_\lambda - g_\mu}{\lambda - \mu}\right]^{\Delta T}\right\} \qquad (1)$$

The variance of l_2 is a parameter (σ^2) of Fabens' model and is there considered uniform. for all recaptures. The likelihood implicit in Fabens' model is thus $\phi(E(l_2),\sigma^2)$ where $\phi(.,.)$ is the Normal probability density function with given mean and variance. Alternatively we can write the likelihood, as $\phi(x \mid \Delta T, l_1)$ which expresses the dependence of the likelihood on the release length and period at liberty.

If we take this likelihood as prior we can easily obtain the posterior likelihood, that is the likelihood conditional on the length selectivity of the recapture gear. The posterior likelihood will be proportional to the product of the selectivity function $S(x)$ and the prior likelihood, or

$$S(x)\phi(x \mid \Delta T, l_1) \qquad (2)$$

In the case of ageing data the prior likelihood is $\phi(x \mid T)$ and so the posterior likelihood is $S(x)\phi(x \mid T)$

An Application to a Gill Mesh Net Fishery

We now discuss an application to tagging data from the southern Australian Shark Fishery.

Kirkwood and Walker (1986) have used the pdf of the gamma distribution, appropriately normalised, in order to model gill mesh net selectivity. The selectivity curve is bell shaped. We assume a gamma distribution of length increments or of lengths, rather than a normal distribution, so that the prior distributions $\phi(x \mid \Delta T, l_1)$, and $\phi(x \mid T)$of lengths become $\gamma(x \mid \Delta T, l_1)$ and $\gamma(x \mid T)$, the density function of the gamma distribution, which is given by

$$\frac{x^{\alpha} e^{-x/\beta}}{\Gamma(\alpha+1)\beta^{a+1}}$$

The mean and variance of this gamma distribution are to be determined as before and it is unlikely that any practical difference would be introduced by the change. The reason for proposing the gamma distribution is that when gear selectivity is modelled on the density function of the gamma distribution, (2) becomes the product of two gamma densities which can be shown to be also a gamma density.

We allow the mean of the prior distribution to be determined by (1) as previously, but make its variance proportional to its mean. The gamma distribution has mean $(\alpha+1)\beta$ and variance $(\alpha+1)\beta^2$ and the log likelihood is

$$\alpha \log(x) - x/\beta - \log[\Gamma(\alpha+1)] - (\alpha+1)\log\beta. \qquad (3)$$

The prior distribution will be specified by setting the expected value of l_2 given in (1) to

$(\alpha+1)\beta$ and its variance, which is $\theta E(l_2)$ equal to $(\alpha+1)\beta$. Solving for α and β we obtain

$$\alpha = E(l_2)/\theta - 1 \qquad (4)$$
$$\beta = \theta$$

Thus Fabens' assumption of uniform variance expressed as σ^2 is replaced by a proportional variance equal to $\theta E(l_2)$. If a variance model of the type of Francis' (1988a) is required any other relationship could be used here to determine the variance.

If we represent the gamma distribution parameters of the selectivity function by *a* and *b* then the posterior distribution has a gamma distribution with parameters $\alpha' = \alpha + a$ and $\beta' = \beta b/(\beta + b)$. The log-likelihood of the sample is thus

$$\sum_{\text{recaptures}} \alpha' \log(l_2) - l_2/\beta' - \log[\Gamma(\alpha'+1)] - (\alpha'+1)\log(\beta') \qquad (5)$$

where α' and β' are calculated for each recapture depending on the selectivity parameters of the gear used to recapture each tagged fish and depending on the predicted mean length increment for each fish also.

If a fish was recaptured with non-selective gear, α' and β' are simply set equal to α and β, the parameters of the prior distribution given in (4).

The computational algorithm is thus to maximise (5) with respect to g_λ, g_μ and θ.

Fitting to Data

The model was fitted to tag release-recapture data taken from school shark (*Galeus galeorhinus*) and gummy shark (*Mustelus antarcticus*) (Walker 1984). The fishery employs two main gear types, gill mesh nets and hooks on baited long lines; the latter is not length-selective (Walker 1984). The mesh selectivity parameters for gill net were calculated according to the method given in Kirkwood and Walker (1986) who calculated the parameters for gummy shark. We have also fitted school shark data to the same model to obtain a selectivity function for that species and below give results for both species. We used Francis' reparameterisation of the von Bertalanffy model with λ=800 mm and μ =1200 mm so that, for example, g_λ is the mean annual length increment of 800 mm fish.

Table 1 shows parameter estimates and likelihoods with and without the selectivity correction for both school and gummy shark. The differences are more marked for gummy shark than for school shark. Two possible reasons are that gummy shark grow to greater lengths than do school shark, so that the selective gear does not catch the larger gummy shark, whereas the older school shark do not outgrow the nets to as great an extent. The second reason is that the selectivity curve for school shark is flatter than for gummy shark; that is the gear is more selective in the case of gummy shark.

The discrepancies in parameter estimates show that length-selective gear can introduce a bias to growth curve estimates if not corrected for, and so lead to further errors when the estimates are used to predict aspects of fish stock behaviour.

Table 1. Growth model estimates for school and gummy shark, with and without selectivity
Parameter standard errors given in parenthesis

Species and Sex	g_λ	g_μ	θ	Log-likelihood
School shark				
males (n=24)				
with selectivity	126(8)	70(9)	2.6(0.7)	-132.029
without selectivity	116(8)	57(8)	2.8(0.8)	-130.367
females (n=14)				
with selectivity	133(10)	44(7)	1.6(0.6)	-75.0736
without selectivity	125(10)	37(7)	1.8(0.7)	-73.1681
sexes combined (n=38)				
with selectivity	129(7)	57(6)	2.4(0.5)	-210.507
without selectivity	119(7)	46(6)	2.7(0.6)	-206.027
Gummy shark				
males (n=101)				
with selectivity	122(8)	59(7)	3.8(0.5)	-580.935
without selectivity	108(8)	32(7)	4.6(0.6)	-573.321
females (n=74)				
with selectivity	107(7)	84(7)	3.3(0.5)	-424.848
without selectivity	94(7)	63(8)	3.9(0.6)	-414.772
sexes combined (n=175)				
with selectivity	116(5)	70(5)	3.7(0.3)	-1011.04
without selectivity	102(5)	43(5)	4.5(0.5)	-992.227

A COMBINED MODEL FOR FISH GROWTH

Introduction

Two methods have traditionally been used in fisheries science to obtain information on growth. The first involves age-length data, typically obtained from ring counts, resulting in a predictive relationship of the form

$$l(t,\varepsilon) = f(t) + \varepsilon \qquad (1)$$

where
t is age
f(t) is length as a function of age and
ε is normally distributed with expectation zero.

Estimation has been a straightforward application of non-linear regression techniques resulting in a predictive regression of length from age.

The usual form of f(t) has been the von Bertalanffy growth equation:

$$f(t) = vB(t) = L_\infty\,[1\text{-}\exp\,\{K(t\text{-}t_0)\}] \qquad (2)$$

However, in what follows any growth relationship can be substituted.

The second method of obtaining information on growth uses length-increment data obtained from tagging experiments. The earliest model for length-increment data is that of Fabens (1965). Fabens' model predicts length increment from release length and liberty period and locates all error in the second measurement of length. A generalisation of Fabens' method was introduced by Francis (1988a) who suggested partitioning the error into measurement error and individual growth variability and showed how to introduce seasonality.

Francis (*ibid*) made the point that although age-length and length-increment data may both be used to estimate a growth curve, the curve estimated does not have quite the same meaning in each case. In the former case, length is predicted from age, so that length increment depends only on age, whereas in the latter case length increment depends on starting or release length. In other words, where data on both types are available for one species, the expectation of the von Bertalanffy parameters estimated may differ even if all the model assumptions are met. This possibility was raised by Kirkwood (1983) in discussing a proposed model to combine data of both types available for the Australian bluefin tuna fishery. The model proposed here combines either type of data, allowing simultaneous or separate estimation and comparison of the two types through likelihood ratio tests.

A New Model

All the above models treat variability as additive to the growth equation, so that individual variability or measurement error is regarded as a "deviation" from the curve, which is in turn regarded as an "average" for the population. In a break with this view, we assume all fish follow the growth curve, but at stochastically varying rates.

We first introduce the concept of apparent age, a function of observed length and defined as

$$A = vB^{-1}(l)$$

where
vB^{-1} is the inverse of vB(t) and
A has units of time.

The length of an individual is thus given by vB(A) and individual growth variability is expressed by making A a stochastic function of time, using a type of Brownian motion.

Brownian motion is derived by postulating a particle which moves under the impact of many small shocks. In one dimension the shocks are modelled as Bernoulli trials, with a probability p of movement in one direction and (1-p) in the other. In the limit, as the shocks are made smaller and more frequent, the position of the particle is shown to be normally distributed, in an application of the central limit theorem (Feller 1968). Thus each shock is of equal size and drift occurs via imbalance in the probabilities p and (1-p). Brownian motion has the property of independence of non-overlapping time intervals so that movement, or in our case ageing over successive periods is described by independent normal variables whose variance is proportional to the length of the period.

Brownian motion of the above type has the drawback for our purposes of allowing a positive probability of decrease in A over any time interval, corresponding to negative growth, although the expected growth will always be positive. An alternative type of Brownian motion is derived by considering the small shocks to be all in the positive direction, but having a gamma distribution. The gamma distribution has the probability density function

$$G(x \mid \alpha, p) = \alpha^p e^{-\alpha x} x^{p-1} / \Gamma(p), \ \alpha>0, \ p>0, \ 0<x<\infty$$

with mean $E(x) = p/\alpha$ and variance $V(x) = p/\alpha$ (Rao 1973).

If we consider time divided into intervals δt so that the apparent age at time T is the sum of $T/\delta t$ shocks and let $\alpha = 1/\sigma^2$ and $p = \delta t/\sigma^2$ then A will have a gamma distribution with parameters $\alpha = 1/\sigma^2$ and $p = T/\sigma^2$ and

$$E(A) = T \text{ and } V(A) = \sigma^2.$$

By allowing $\delta t \rightarrow 0$ we obtain a new type of uni-directional Brownian motion with independence properties as before and a zero probability of negative growth. The increment in apparent age over any time period T has a gamma distribution with parameters $\alpha = 1/\sigma^2$ and $p = T/\sigma^2$ and is independent of any non-overlapping time period.

Structural Consequences

The above model of growth results in certain structural consequences which may or may not be considered desirable. One prediction is that an individual with a positive residual ε at time t_1 (i.e. large for its age) will tend to retain an advantage, because at any subsequent time t_2 the expected apparent age is $t_2 + \varepsilon$. In length terms, with the asymptotic von Bertalanffy growth equation the expected length advantage diminishes over time to zero as expected apparent age reaches the asymptotic plateau in growth.

The model correctly captures the fact that a tagged fish recaptured soon after release should show a similar residual for both length measurements. Indeed the correlation between the two apparent ages is

$$\sqrt{[(t_2 - t_1)/t_1]}$$

where

t_1 is time of release and
t_2 is time of recapture.

An immediate consequence of the model is that no fish can grow larger than the asymptote and any who do will always be regarded as outliers unless measurement error is incorporated into the model. This is not necessarily a disadvantage since outliers can be well modelled by a method such as that used by Francis (1988a) and although they are usually regarded as arising from measurement error, they can also usefully be modelled as "freak" fish which possess a genuinely atypical phenotype.

Another structural consequence, at least when the growth equation is asymptotic, is that length-increment variance first increases with liberty period then decreases as growth reaches the asymptote. This will apply to all species whose growth slows sufficiently with age, since the variance in apparent age increases with time but the slope of the growth curve decreases, and since to a first order approximation

$$V(l) = vB'(A)^2 . V(A)$$

where

$V(l)$ is variance in length, and

$vB'(A)$ is the derivative (slope) of $vB(a)$.

This behaviour is appropriate when individuals of a species grow to a fixed size with individual variation only in the rate of approach. It will not describe species whose members stop growing at different lengths. In any case the behaviour will not be marked in cases where growth slows only moderately over the life span.

Seasonality

The method of Pitcher and MacDonald (1973) is easily adapted here since they introduce seasonality by adding a sine function to the time in (2) above. We introduce the sinusoidal variation at the level of the Brownian motion, so that the small shocks (occurring at intervals δt) have a gamma distribution with parameters $\alpha = 1/\sigma^2$ and $p = [\delta t + C\delta \sin\{2\pi(t-t_0)\}]/\sigma^2$

where

$\delta \sin(t) = \sin(t+\delta t) - \sin(t)$,

C is the amplitude of seasonality and

t_0 is a location parameter giving the start of the growth season.

In the passage to the limit, we obtain a non-stationary stochastic ageing process such that increment in apparent age A between t_1 and t_2 is gamma distributed with parameters

$\alpha = 1/\sigma^2$ and

$p = [(t_2-t_1)C[\sin\{2\pi(t_2-t_o)\} - \sin\{2\pi(t_1-t_o)\}]/\sigma^2]$.

The desirable property that negative growth has probability zero for any individual is retained, but the parameter p must be non-negative, which constrains $C < 1/2\pi$. In the case of very marked seasonality when this is violated (in Pitcher and MacDonald's paper this results in negative mean growth) the alternative switched growth model suggested by them will be appropriate.

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DISCUSSION OF SESSION 3, SUB-SESSION B

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The Chairperson once again invited comments at the end of each panel presentation, followed finally by more general discussion.

Keith Sainsbury asked *Ron Sandland* whether there was any practical application of the non-parametric bootstrapping *he had* technique described? Ron Sandland responded that the technique had been used in laboratory studies of sheep exposed to a hormonal regime. In that case the functions were modelled by splines. He suggested that more emphasis should be placed on seeing what the data say and less on trying to fit particular models.

Terry Walker asked *Mark Palmer* whether, of those animals that had been measured repeatedly, did the ones that grew quickly early in the study continue to do so later? The author had not, however, looked at that aspect of the data.

Chris Francis wanted to know how well Mark Palmer thought the model estimated the age at capture which was used in the plots shown of growth vs age. Mark Palmer could not supply a general answer. Likelihood bands could be put around the ages; he suspected they would probably be large, but this had not really been examined.

Ron Sandland suggested that if the model specification were incorrect, then there would be two kinds of error involved and both would need to be considered. Mark Palmer agreed, and considered that the data actually illustrated this: the aquarium data did not fit a von Bertalanffy curve very well.

Keith Sainsbury returned to Ron Sandland's point, with the thought that one has to be suspicious or sceptical of likelihood ratio methods in this context - they are efficient but if the model and the errors are not both specified correctly, the answers aren't robust. For example his experience with the Kimura (1979, *Fish. Bull.* **77**: 765-776) tests suggested that they are very sensitive.

Mark Palmer responded that his method, given the right model, did not appear to be highly sensitive. When autocorrelation was modelled in other data it appeared to have little effect on the results.

Keith Sainsbury then asked how the model would behave with just one observation of release and recapture? The answer given was that was what had been demonstrated in the talk. Chris Francis disagreed, saying that the only way to test that is with simulated growth data, not real data.

Ron Sandland objected to such a procedure; it assumes the growth model is known perfectly. Chris Francis agreed, but insisted that such a procedure is still useful in answering the question "how well does the procedure do, given that the growth model is correct?". The other question "how well does the growth model fit the data?" can't be answered.

Following *Kathy Haskard's* presentation Nik Dow asked whether conducting a 1-way ANOVA, as described, doesn't always result in significant F-tests because the mean lengths-at-age are different within one population? Kathy Haskard agreed, but then one would always go in with specific comparison tests such as LSD to find the means that differ and compare them.

Rob Day commented that the problem of unequal variances becomes worse when the sample sets are unequal, so one has to be cautious if there are not equal data sizes from the two populations. Variances often are unequal in biological data sets, so this is a real problem, and it isn't fixed by the transform procedure.

Kathy Haskard replied that the ANOVA is reasonably robust to heteroscedasticity when sample sizes are equal. Problems occur when the smaller sample has the bigger variance, so if possible one should try to have the larger variance contained in the larger sample.

Rob Day asked whether, when looking at the orthogonal polynomials, the method is powerful enough to detect differences in K? Kathy Haskard believed that the method to be powerful enough, provided that the data represented a sufficient part of the growth curve.

Tony Smith, in opening the discussion of *Chris Francis's* contribution asked what effect was caused by tagging large fish. If they were above the average L, and if they grow, then that might cause the effect seen (curvilinearity in the plot of growth increment against initial length).

Chris Francis agreed that was precisely what was going on. Big fish, above L, had to get there somehow. Either they were still growing or they just stopped growing.

Kathy Haskard thought the method presented in *Nik Dow's* paper would not work for species where individuals do not all follow exactly the same growth curve, and they actually stop growing at very different final sizes. Nik Dow agreed that the model wouldn't work for all species, humans being an obvious example where the method wouldn't work. Kathy Haskard asked whether most species aren't like humans in this respect, but Nik Dow disagreed.

Chris Francis thought that in this example, there would be no problem - apparent age would simply stand still at the point where growth stopped and the model would work fine. Nik Dow agreed. The school shark is a good example of a fish in which all individuals appear to have the same L. However, the method does have a statistical problem, which was discovered by Geoff Kirkwood. The method requires that apparent age moves only in one direction, and never decreases. The random walk used in the method is based on the gamma distribution, and this creates the theoretical problem that "sample paths", the realised lengths of the fish, aren't continuous but have jumps.

Laurie Laurenson asked what happens if the original growth curve is incorrect for the species being studied? Nik Dow suggested trying different curves and picking a curve that looked about right. The curve is just an organising tool: there is no "correct" curve except in simulated data.

Chris Francis led off the *General Discussion* on the sub-session with the comment that we are always making statistical inferences from the sample to the population. But in fisheries there are always reasons why the sample is usually somehow not a random sample, representative of the population as a whole. So if one has large enough samples and looks for statistical differences s/he will almost always find them. So people should always ask whether differences are biologically significant as well as statistically significant.

Kathy Haskard suggested that biologists should always present confidence intervals because of this problem.

Keith Sainsbury endorsed the ANOVA method suggested by Kathy Haskard, because of the simplicity with respect to assumptions about the data.

Ron Sandland commented that the assumptions for simple ANOVA (such as normality; see the list Kathy Haskard gave) are quite stringent, such as independence of samples. So the approach is not suitable for repeated measurements on the same animals. Keith Sainsbury agreed that ANOVA would not be appropriate for that case, but still saw ANOVA as a good method for doing most of the comparisons of growth that biologists are interested in.

Peter Young was concerned that Kathy Haskard's ANOVA technique discards structure that must be there, such as the increase in mean length with increasing age. Kathy Haskard, however, did not see this as a problem: the method looks at the errors and what accounts for them.

Murray MacDonald asked Chris Francis whether the curvilinear effect seen in plots of increment vs initial length could be explained by the differential effects of tagging on different sized fish. Chris Francis said he would be very surprised if that were the explanation for curvilinearity. Tagging effects might move the curves up and down, but probably do not induce the effect seen.

Rob Day wondered whether the curvilinear effect discussed by Chris Francis might be caused, not by changing growth patterns of an individual fish as it grows large, but by the truncation of normally distributed increment error as mean increments became small (one doesn't see many negative growth increments). Chris Francis agreed that some problems might come from this effect, but did not consider it to be the major effect.

Keith Sainsbury reminded the meeting of the ancient work on the idea that each fish grows to its own final size, so that large animals are more likely to be the ones with a large L, so causing the curvilinearity seen (Sainsbury 1980, *Can. J. Fish. Aq. Sci.* **37**, 241-247).

Chris Francis agreed that was the explanation for the curves he observed. Large animals must have a growth of either zero or some positive value, so the mean growth increment for a given length, if there are any animals of that length to tag, is always positive.

Mike Moran asked Chris Francis whether one could just truncate the data to avoid the curvilinearity towards the right-hand end. Chris Francis agreed that one could, but then L would have no meaning. In itself that's not a problem, but people always want to compare one data set with another.

Keith Sainsbury warned that if one truncated the data set, she would then have to be very careful not to extrapolate beyond the range of data used to develop the relationship.

Mike Moran asked whether, if the aim is to estimate fish age from length, then is Nik Dow's approach, based on age-at-length rather than length-at-age, more appropriate than others?

Keith Sainsbury found a fundamental problem in mixing length and age-based data. To date we don't have an appropriate technique because we don't yet have a consistent model for the length and age cases. Nik Dow's method is an attempt to collapse some of the differences between the two models, but at the expense of some questionable assumptions.

Rick Fletcher commented that mean age-at-length and mean length-at-age give quite different growth curves.

Rob Day wondered if it would be possible to sort out the problems raised in Chris Francis' talk if we had enough individual age and length data. The problem seems to lie in being able to describe how individuals vary rather than focusing on one overall growth rate.

Keith Sainsbury replied that one needs both age and increment data, which are very hard to get for most species.

Ian Somers thought the problem is in assigning an age to the length at which an animal is released. He suggested tagging small animals, where there is little uncertainty about age, and leaving them at liberty for a long time to generate length-at-age data.

Chris Francis believed that this would solve only part of the problem because growth is like a response surface with the axes initial length and time at liberty. The Fabens approach has a surface height of zero at a place called L in the right-hand corner. What Ian Somers suggested would generate data only along the left-hand edge of the surface, but would provide no information about the growth of large fish.

Sub-session C

Use of Age and Growth Information in Fisheries Assessment

Panellists:	K.J. Sainsbury W.J. Nash A.D.M. Smith K.R. Allen
Rapporteur:	D. Williams

YIELD PER RECRUIT BASED ASSESSMENT METHODS. YIELD, VALUE, BIOMASS AND EGGS PER RECRUIT - THE $F_{0.1}$ MANAGEMENT STRATEGY

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Introduction

A major goal of fisheries assessment is prediction of the effects of different levels of fishing mortality and different age/size specific vulnerabilities to fishing on the weight of catch, value of catch, and size of the population. The fishing regime is usually specified by the combination of a fishing mortality and the age at which fish become susceptible to that fishing mortality (the 'age at first capture'). Prediction of how the catch quantity and value changes with the age at first capture is the usual scientific basis for the minimum legal size in fisheries.

A common method of making these predictions is based on calculating how much of the relevant quantity is produced per recruit entering the population. This production per recruit is the expected quantity produced per recruit over the entire lifetime of the recruit, from a defined age at recruitment, under the specified fishing regime.

The calculated 'per recruit' values are determined by the interaction of mortality and production of the quantity of interest. Since most of the quantities of interest relate to size or body weight, the 'per recruit' values are primarily determined by interaction of growth and mortality. Most applications assume steady state conditions, and so do not consider time dependent changes in the biological or fishing regime parameters, but the basic method is easily modified to account for transient features if necessary (see Beverton and Holt 1957; Ricker 1958).

Some advantages and disadvantages

The major advantage of the 'per recruit' calculations is that the relative effects of different fishing regimes can be calculated and compared without the need to specify the level of recruitment in the fishery. The major disadvantage is that it does not allow calculation of the effects of the fishing regime on the level of recruitment itself. A fishing regime giving the maximum yield per recruit will provide the greatest absolute yield available from whatever number of recruits enter the population, but that absolute yield will be small if the number of recruits is small. Obtaining the globally maximum yield also requires that the number of recruits be maintained at a high level. A fishing regime that provides less than the maximum yield per recruit, because fishing mortality is too high and/or age at first capture is too low, causes 'growth overfishing'. A fishing regime that reduces the recruitment below that giving the globally maximum yield causes 'recruitment overfishing'. 'Per recruit' methods are best suited to the examination of growth overfishing, although they can provide some insight into recruitment overfishing. Examination of the effect of a fishing regime on recruitment requires calculation of the number of recruits per recruit (ie. the expected number of recruits that a recruit will ultimately produce over its lifetime) and hence specification of the stock - recruitment relationship.

Another limitation of the 'per recruit' approach is that it is not strictly applicable to the aggregate yield or value in multispecies fisheries, although some progress can be made if the relative recruitment to the component species can be specified (Sainsbury 1984; Pikitch 1987).

Applications

The earliest and most common application of the approach is in the calculation of the yield per recruit; the yield to the fishery from a recruit under a particular fishing regime (Beverton and Holt 1957; Ricker 1958). However the same method is easily modified for calculation of the economic value (or other utility) per recruit (Beverton and Holt 1957, pp. 383-386), the eggs produced per recruit (Beverton and Holt 1957, pp. 44-54), the population biomass produced per recruit, or the spawning biomass produced per recruit (e.g. Beddington and Cook 1983; Gabriel *et al.* 1989).

There are two common applications of the yield per recruit in fishery assessment, and the economic value per recruit can be used in much the same way. These are:

(1) Calculation of the minimum legal size from the size/age at first capture that maximises the yield per recruit under the current fishing mortality.

(2) Calculation of the 'best' fishing mortality for a given age/size at first capture. This is usually of interest as a step in calculating a Total Allowable Catch (TAC) for a fishery, with the TAC being approximately the chosen F multiplied by the present population biomass. One definition of the 'best' F is that which gives the maximum yield per recruit (F_{max}). However the use of F_{max} sometimes results in difficulties. F_{max} is sometimes infinite, is commonly much higher than the economic optimum fishing mortality, and is often large enough to cause a reduction in recruitment (ie. recruitment overfishing). The $F_{0.1}$ fishing mortality was defined to help overcome these difficulties (see Deriso 1987). $F_{0.1}$ is defined in terms of the rate of change in the yield per recruit with increasing F, and is the F value at which this rate is 0.1 of the theoretical rate at F=0. The use of the 0.1 level is arbitrary, but provides reasonable protection against recruitment overfishing for many stock-recruitment relations and often gives economically reasonable results. An $F_{0.1}$ management strategy is one that sets catch quotas from $F_{0.1}$ and an estimate of the biomass present at the beginning of the fishing period.

The eggs per recruit is used to examine the implications of a given fishing regime to lifetime fecundity, and consequently the change in egg-to-recruit survival that would have to occur to maintain the recruitment at the unfished level.

The biomass per recruit is used to determine the relative change in population biomass that would occur under the given fishing regime if there was no reduction in recruitment. For constant recruitment and constant catchability, the biomass per recruit is proportional to the catch rate in the fishery.

Calculation of Per-Recruit Quantities

It is not necessary to assume any particular growth form or relation between length and weight for the calculation of per recruit quantities. The commonly used yield per recruit analysis developed by Beverton and Holt (1957) does assume such relations to allow a closed form integration and an explicit solution, but more generally a summation that effectively provides a numerical integration can be used. The numerical integration also allows inclusion of complex relationships to describe the selectivity of fishing gear, and hence the size or age dependence of vulnerability to fishing mortality, whereas the closed form integration usually assumes knife-edge selection for simplicity.

The yield per recruit is obtained from a summation of the product of four terms across a number of age intervals. The four terms are: number surviving to enter the age interval, the mean weight of an individual at the midpoint of the age interval, the number of deaths occurring during that age interval and the proportion of the deaths that are due to fishing. Specifically, this is

$$Y/R = \sum_{T=0}^{T=\infty} N_T W_T [1 - \exp(-(M + P_T F)t)] \frac{P_T F}{M + P_T F}$$

T = age interval, such that chronological age at T=0 is the age at recruitment,
W_T = weight per individual at the midpoint of age interval T,
t = width of age intervals,
M = natural mortality,
F = fishing mortality for fully vulnerable age classes,
P_T = relative vulnerability to fishing mortality at the midpoint of age interval T (knife-edge selection at age a would have $P_T=0$ for T<a and $P_T=1$ for T>a), and
N_T = number surviving at beginning of age interval T, from

$$N_T = \exp(tTM + t \sum_{j=0}^{j=T} P_j)$$

The value per recruit can be obtained simply by including an extra variable, V_T (the value per unit weight at age T), within the yield per recruit summation.

The eggs per recruit are given by

$$E/R = \sum_{T=0}^{T=\infty} N_T E_T$$

where E_T is the egg output during the age interval T (which can be a relative index, because it is only relative changes in egg per recruit that are usually of interest), and the biomass per recruit by

$$B/R = t \sum_{T=0}^{T=\infty} N_T W_T P_T$$

The biomass as calculated above refers to that part of the population that is available to the fishery. Other reference ages could be used; in particular (i) the spawning biomass per recruit could be calculated by excluding P_T from the above summation and taking the summation from the age at maturity instead of T=0, and (ii) the biomass of fish older than the age at recruitment could be calculated by excluding P_T from the above summation.

All of these calculations are easily modified to account for incidental mortality to animals that are affected by the gear but are not captured and/or retained (e.g. Walters and Huntsman 1986).

As with any numerical integration, some care must be taken to ensure that the summation interval used, t, is small enough to give a good estimate of the area under the curve. The appropriate size of the time step is determined by the relationships and processes that change rapidly with age. Usually the critical processes are the change in vulnerability to fishing gear with fish age and seasonal spawning patterns (in the case of eggs per recruit). When an appropriate time step is used the per recruit quantity will be stable to small changes in the time step, and usually a few trial values will quickly establish what is reasonable. It should be noted that if age steps are used that differ from the age steps for which weight and fecundity at age data are available, then some interpolation will be necessary. This interpolation is usually achieved most easily by fitting a summary growth curve to the data.

Example

Table 1 provides the age-length-weight-gonad weight schedule for *Lutjanus malabaricus*, an important target of many of the trawl fisheries in northern Australia. In this example it is the minimum mesh size, rather than the minimum legal age directly, that is of interest. From the data in Table 1 the von Bertalanffy parameters for length at age were calculated to be $t_0=-0.08y$, $K=0.25y^{-1}$ and L_∞ =86.1 cm, and the weight in g is $0.025L^{2.9}$ where L is the length in cm. A natural mortality of 0.4 is considered reasonable for this species. The relative vulnerability at age T (P_T) is given by a logistic selectivity ogive, so that

$P_T=1/(1+\exp(a-b\,l_T)$

where l_T is the length at age T and a and b relate to the selectivity parameters of the fish and gear (in this example a=2.05 D, where D is the mesh size in cm, and b=0.732). The gonad biomass was used as an index of the eggs produced at each age, and spawning occurs annually in this species. The use of gonad weight instead of egg output is probably reasonable, particularly because it is only relative changes in eggs per recruit that are of interest in this application.

The yield per recruit, eggs per recruit, biomass per recruit and $F_{0.1}$ are given in Table 2. The points of interest are:

- For any mesh size (age at first capture) $F_{0.1}$ is considerably smaller than F_{max}. F_{max} becomes extremely large for mesh sizes larger than 20 cm.

- The optimal $F_{0.1}$ strategy has F=0.43 with a mesh size of 17 cm. The optimal F_{max} strategy in not defined because F_{max} becomes infinite for large mesh sizes. However for the purposes of comparison, here it is taken that the optimal F_{max} strategy is F=8.0 with a mesh size of 20 cm.

- The optimal $F_{0.1}$ gives a yield per recruit that is 457/556=0.82 of the yield per recruit at optimal F_{max}. Thus, if recruitment is constant, the optimal $F_{0.1}$ results in a yield that is only about 20% lower than that obtained from F_{max}, despite the fact that the fishing mortality under F_{max} is over 10 times that under $F_{0.1}$.

- The eggs per recruit monotonically decreases with increasing F for any given mesh size, and increases with increasing mesh size for any given F level. Consequently the eggs per recruit is large both for small mesh sizes with a small F and for large mesh sizes with a large F, but eggs per recruit is low at intermediate values of mesh size and F. At high mesh sizes the eggs per recruit is large and insensitive to F; the spawning stock is protected no matter how large a fishing mortality is applied.

- The $F_{0.1}$ strategy is expected to reduce the eggs per recruit to 47/115= 0.41 of the unfished level. The corresponding reduction for the F_{max} strategy is 25/115=0.22.

- If recruitment remains constant then the $F_{0.1}$ strategy is expected to reduce the biomass to 1015/3756= 0.27 of the unfished biomass. The corresponding reduction for the F_{max} policy is 1095/3756=0.29. Under the assumptions of constant recruitment and catchability the catch rate in the fishery will show the same reduction upon application of each management strategy.

- The maintenance of the eggs per recruit and biomass per recruit under the $F_{0.1}$ strategy depends critically upon maintaining the appropriate, low, F value in the fishery. For the optimal mesh size of 17 cm under the $F_{0.1}$ strategy, the yield per recruit continues to increase with increasing F from F=0.43 (the optimal $F_{0.1}$ value) right up to F=1.74 (F_{max} for this mesh size). So if the recruitment remains constant the total yield will increase with increasing F up to F=1.74. However the eggs per recruit and biomass per recruit decrease greatly with this increase in F. At F=1.74 the eggs per recruit is 15/115= 0.13 of the unfished level, and the biomass per recruit is 273/3756= 0.07 of the unfished level.

- Whether or not recruitment can be maintained with the reductions in lifetime fecundity implied by the optimal $F_{0.1}$ or F_{max} fishing strategies cannot be answered without further information or assumptions about the relationship between the number of eggs and the number of resulting recruits. However some general comments can be made about the form of the stock and recruitment relationship that is necessary if the unfished level of recruitment is to be maintained; the range of population biomass over which recruitment is assumed to be constant and the level of density dependent compensation in egg to recruit survival that is required to maintain that constant recruitment can both be calculated. For the optimal $F_{0.1}$ strategy in this example it is assumed that (1) recruitment is constant for population biomasses between the unfished level and 0.27 times the unfished level, and (2) that density dependent processes will, on average, about triple the egg to recruit survival at the optimal $F_{0.1}$ compared to the survival in the unfished situation (ie. 3711 units of egg output give replacement in the unfished population, and this replacement must be achieved with 1015 at the optimal $F_{0.1}$).

Whether or not these assumptions are met, and recruitment maintained, can only be determined empirically. The management regime defines the experimental design, and the data collected from the fishery and by researchers provide the observations in this learning process. Together they will determine how quickly learning occurs, whether learning about these matters occurs at all, and the risks to the stock during the period of ignorance.

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Table 1. The age, length, body weight and ovary weight for *Lutjanus malabaricus*

Age (y)	Length (cm)	Weight (g)	Gonad (g)
1	21.1	137	0
2	36.3	663	0
3	47.8	1473	30
4	55.4	2143	130
5	61.8	3103	165
6	66.7	3871	190
7	70.4	4527	220
8	73.3	5090	220

Table 2. The yield per recruit (y/r), 'eggs' per recruit (e/r), biomass per recruit (b/r), F_{max} and $F_{0.1}$ for *Lutjanus malabaricus*

e/r gives a measure of the life-time egg output of an individual under the specified fishing regime. b/r is proportional to the population biomass under the specified fishing regime if recruitment remains constant. unfished e/r = 115; unfished b/r = 3756

Mesh (cm)	F_{max}	y/r	e/r	b/r	$F_{0.1}$	y/r	e/r	b/r
7.0	0.36	359	24	998	0.23	341	40	1483
8.0	0.40	376	22	914	0.24	354	40	1449
9.0	0.44	394	21	873	0.26	370	39	1404
10.0	0.49	412	19	854	0.27	383	39	1432
11.0	0.55	431	18	835	0.29	399	39	1425
12.0	0.62	450	17	761	0.31	413	39	1368
13.0	0.72	469	16	602	0.33	426	40	1242
14.0	0.85	488	15	533	0.35	437	40	1215
15.0	1.04	505	14	515	0.38	449	42	1224
16.0	1.34	521	14	458	0.41	457	43	1167
17.0	1.74	534	15	273	0.43	458	47	1015
18.0	2.58	545	16	166	0.46	457	50	972
19.0	4.39	552	18	150	0.49	451	55	969
20.0	>8.00	>556	>25	<188	0.53	441	59	812

THE UTILITY OF YIELD-PER-RECRUIT AND EGG-PER-RECRUIT ANALYSES FOR DETERMINING SIZE LIMITS FOR BLACKLIP ABALONE (*HALIOTIS RUBRA*) IN TASMANIA

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Taroona TAS 7053

Summary

The validity of managing Tasmanian abalone fisheries using the egg-per-recruit approach to conserving egg production is evaluated. Shortcomings of the approach are (i) it was not possible to obtain accurate estimates of natural mortality (*M*) for fished populations; and (ii) the regional variability in survival rates between the egg stage and recruitment to the fishery indicate that there is no single, widely applicable egg production level appropriate for the conservation of sustainable stock levels at any given level of fishing mortality.

Managing a fishery to maximise yield, without regard to the conservation of egg production, can only be sensibly advocated for species with no relationship between stock abundance and recruitment over the range of fishing mortality to which the species would be subjected. An important use of yield-per-recruit analysis is to demonstrate that the reduction in yield caused by a size limit increase is minor, and is more than offset by the advantages of allowing individuals more time to spawn before entering the fishery.

The Egg-per-recruit Approach

Several characteristics of blacklip abalone (*Haliotis rubra*) stocks in Tasmania suggest a means by which egg-per-recruit analysis may be used to determine size limits appropriate for sustainable fishing (Nash in press). These are:

1. Blacklip abalone in Tasmania exhibit variable growth, with a latitudinal trend in growth rates: abalone in the south grow faster, and to a larger size, than those in the north. Despite localised exceptions, this trend is fairly continuous.

2. Sexual maturity is attained at a given age, not a given size (Nash 1990a). The slower growing northern stocks therefore reach sexual maturity at a smaller size than their southern counterparts.

3. Until very recently, there was a single Tasmania-wide minimum legal size for abalone. Hence, the slow-growing northern stocks were able to breed for a greater number of years before attaining catchable size than the southern stocks. There is therefore greatest protection of the egg production in the northern stocks, and least protection in the southern stocks.

4. Since the northern stocks are underexploited at this size limit and the southern stocks are vulnerable to overfishing, it is likely that some geographically intermediate stocks, with intermediate growth rates, are receiving an optimal level of protection by the current size limit. If these "ideally-fished" stocks

can be identified, the "ideal" level of protection of the egg production can be determined by egg-per-recruit analysis.

5 Egg-per-recruit analysis can then be used to determine, for other areas, the size limit which provides the same level of protection of egg production as in the "ideally-fished" area.

The validity of this approach relies on (i) being able to identify "ideally-fished" stocks, and (ii) being able to estimate M for fished stocks. The method for determining M in fished stocks was to (i) calculate M of unfished abalone stocks by catch curve analysis (hence, $Z = M$); (ii) calculate Z for fished stocks, then, assuming the estimate of M obtained for the unfished stocks was approximately the same as that of the fished stocks, determine F as $Z - M$.

It was found, however, that neither of these requirements could be met: no satisfactory method for identifying "ideally-fished" stocks was found, and the intended method of determining M for fished stocks was shown to be invalid, because Z for some of the fished abalone populations (Top Rocks, Ketchem Bay: Table 1) was not more than, and in some cases less than the value of M obtained for the stunted unfished populations (Babel Island, Hogan Island and the Kent Island) (Nash in press). Most notably, the abalone populations sampled from west and south-west Tasmania (Figure 1) exhibited low values of Z, and therefore M.

Another major limitation of egg-per-recruit analysis in assessing size limits is that it does not take into consideration the variation in recruitment rates (that is, survival between the egg stage and recruitment to the fishery) that may occur between populations (Nash in press). Populations with high recruitment rates will be able to sustain higher levels of fishing mortality than populations with low recruitment rates. Thus, for example, the fishery in a high-recruitment rate area may be sustained with only 20 percent of egg production conserved, whereas a lower-recruitment rate site may require 50 percent of the egg production to be conserved.

There is strong evidence that large variation in recruitment rates between populations of *Haliotis rubra* in Tasmania does in fact occur. As described elsewhere (Nash 1990c), large differences in the abundance of pre-recruits (abalone smaller than the minimum legal size) were found to occur between two adjacent sites that were virtually identical in their growth, fecundity, maturation and mortality rates (Figure 2), as well as the abundance of abalone of legal size. The most likely reason for this is between-site variation in recruitment rates.

The Yield-per-recruit Approach

Managing a fishery to maximum yield is wise only if there is no stock-recruitment relationship over the range of fishing mortality that the stock would be subjected to. The history of severe stock declines in abalone fisheries elsewhere (Mexico: Guzmán del Próo (1989); California: Tegner *et al.* (1989); and British Columbia: Breen (1986), suggests that such an assumption would be ill-advised. Since it is likely that size limits are an effective means of maintaining adequate egg production and recruitment rates, an important use of yield-per-recruit analysis is to consider the effect that an increase in the minimum legal size would have on the yield from the fishery. If yield is not greatly reduced, then the increased protection of egg production provided by such a size limit increase would likely outweigh the adverse effects that a slight reduction in yield would incur.

This is exemplified by a consideration of the effect on both yield- and eggs-per-recruit of increasing the minimum legal size for blacklip abalone (*Haliotis rubra*) on the west and south coasts of Tasmania from 132 to 140 mm maximum shell diameter.This size limit increase was introduced because the fast-growing abalone in that region were particularly prone to overfishing because they were entering the fishery at a younger age, and therefore at an earlier state of maturation (since onset of sexual maturity is primarily related to age rather than size: Nash 1990a). Besides increased protection of egg production, it was argued that the size limit increase would actually increase the yield from these stocks. This is shown in Table 2: using a range of *M* values derived by catch curve analysis, it was argued that the size limit increase to 140 mm increased the yield-per-recruit , in addition to conserving a greater proportion of the egg production.

This example illustrates the use of yield-per-recruit analysis to refute arguments that an increasing proportion of the population would be lost to the fishery, through natural mortality, by this increase (Nash 1990b); in the example just cited, it can be used to demonstrate that increasing the size limit would actually increase the yield-per-recruit.

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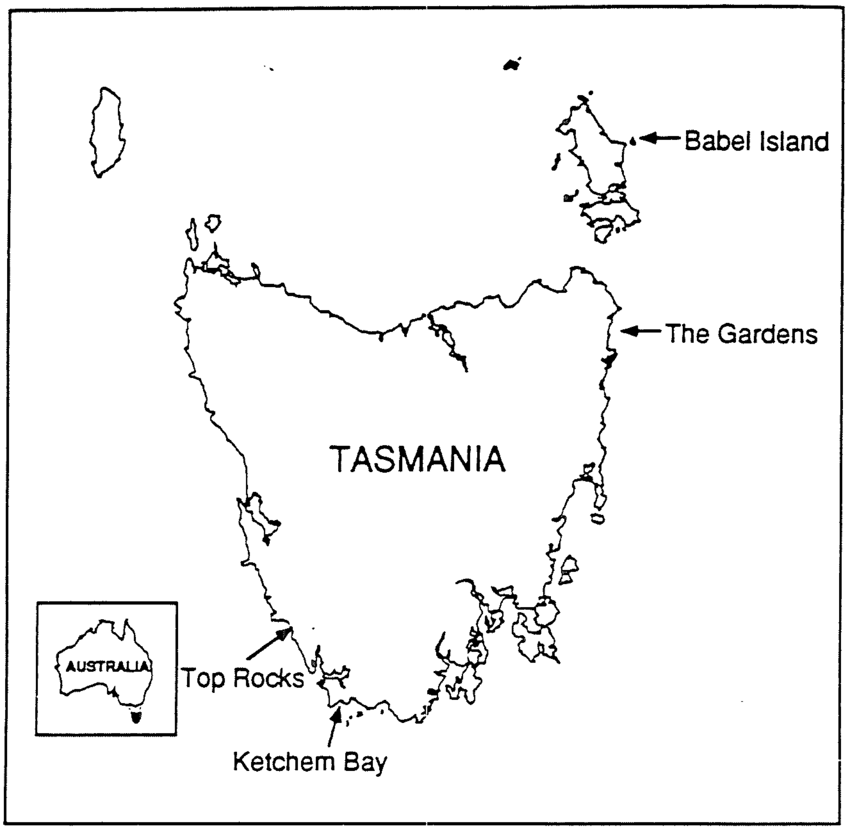

Figure 1. Blacklip abalone (*Haliotis rubra*) sampling sites.

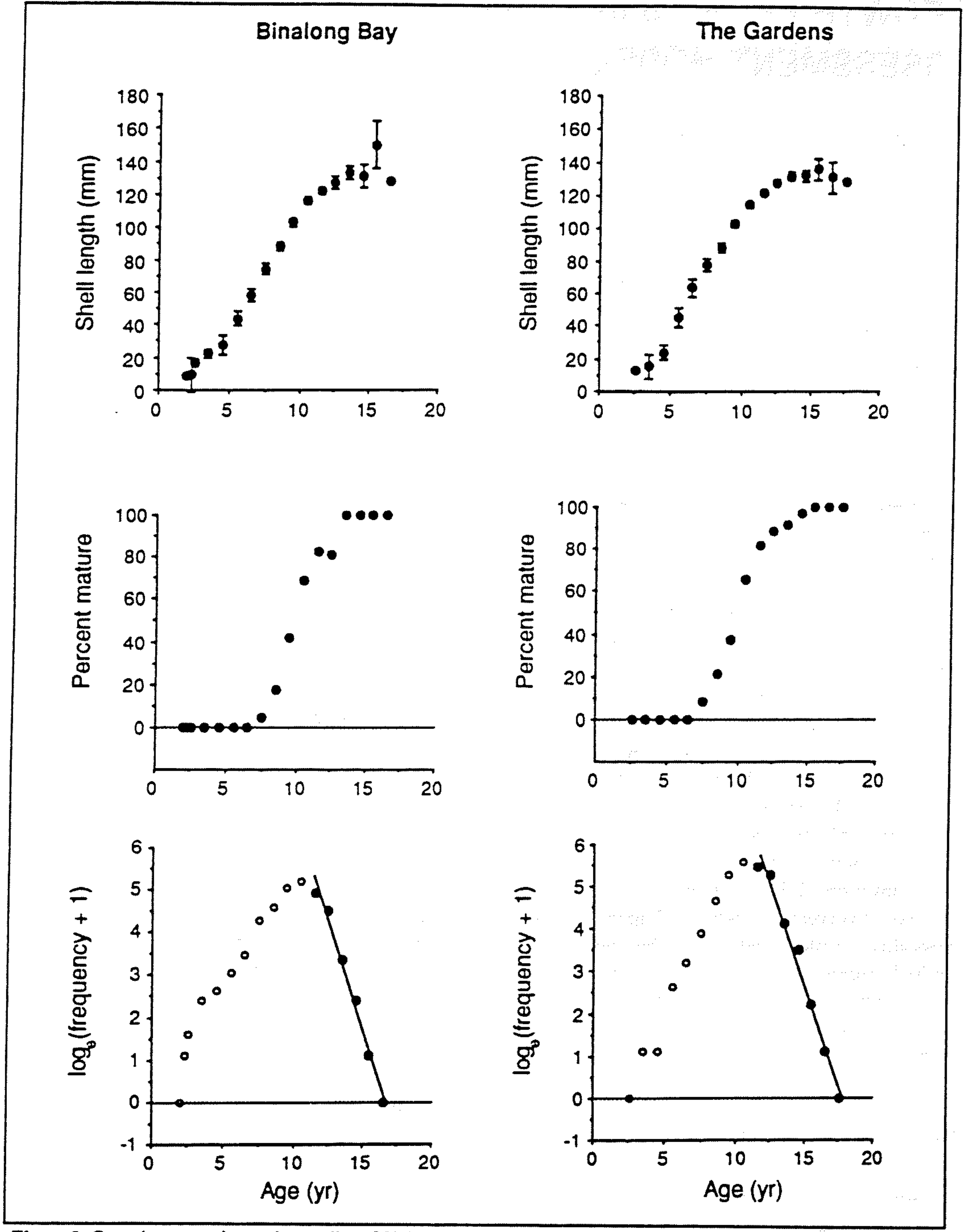

Figure 2. Growth, maturation and mortality of *Haliotis rubra* from Binalong Bay and The Gardens.
Total mortality (Z) was calculated as -(slope of the regression line fitted to the solid data points (•)) in the lower pair of graphs. Error bars in the age-length plots are the 95% confidence limits about the mean.

GROWTH EFFECTS IN A SIZE STRUCTURED STOCK ASSESSMENT MODEL

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The aim of this note is to draw to the attention of the audience a 1987 paper by Jon Schnute entitled "A general fishery model for a size-structured fish population" (Schnute 1987) and to use some results from it to explore the way in which fish growth affects yield estimates and biomass predictions.

To summarise Schnute's approach very briefly, he develops a population model based on size rather than age, where, in addition, size is measured as weight rather than length. The model comprises a recruitment function, a growth model (described in more detail below), and an equation for the change over time in the numbers by weight in the population. In common with most fishery models which assume *age* independence in both natural and fishing mortality rates, Schnute's model assumes that these rates are independent of the *size* of the fish for those fish which have recruited to the stock. Given this assumption, Schnute then shows that the full size structured model collapses to a remarkably simple equation for the change in recruited biomass from one year to the next. It is this equation which makes explicit the way in which growth affects both biomass dynamics and yield estimates derived from the model.

The Growth Model

The growth model used by Schnute is the Ford-Brody equation for change in weight over one year's growth:

$$w' = W + \rho w \qquad (1)$$

where a fish starting at weight w grows to weight w' in one year, and W and ρ are parameters of the model. Although equation (1) does not depend on age, it can be related to the parameters W_∞ and K of the (modified) von Bertalanffy equation for weight at age:

$w_a = W_\infty(1 - e^{-K(a-a_0)})$ by setting

$\rho = e^{-K}$ and $W = W_\infty(1 - \rho)$.

Note that K is a weight dependent rather than the usual length dependent parameter, and that for the more general case of a time step T, $\rho = e^{-KT}$.

Biomass Dynamics

Schnute shows that the dynamics of the full size structured model collapses to the simple first-order difference equation

$$B_{t+1} = R_{t+1} + \tau_t\,(X'_t / X_t)\,B_t \qquad (2)$$

where B_t is biomass (of the recruited population) in year t, R_t is recruitment (in biomass units) in year t, τ_t is survival of fish in year t (from the combined effects of fishing and natural mortality), and X_t is the average weight of fish in year t. X'_t is the projected weight at time t+1 of a fish of average weight at time t and is given by equation (1). Thus (X'_t / X_t) is a "growth factor" (call it "g"), greater than one, which will be higher for fish with higher growth rates at the average size in the recruited population. The growth factor is given by

$$g = (W + \rho X_t) / X_t .$$

Equation (2) is intuitively very sensible. It says that biomass next year will comprise newly recruited biomass plus whatever survives of biomass this year, but with a factor ("g") accounting for the increase in biomass due to growth of surviving fish. The nice feature of equation (2) is that g is such a simple function of average weight.

Yield Predictions

To make further use of equation (2), it is necessary to specify R and t , the recruitment and survival functions. For illustrative purposes, let us assume a Beverton-Holt recruitment function

$$R_t = a\,B_{t-k} / (1 + b\,B_{t-k}) \qquad (3)$$

where k is the age at recruitment and a and b are parameters of the model. Let us also assume separable fishing and natural mortality such that equation (2) can be written as

$$B_{t+1} = R_{t+1} + s * g * B_t - C_t \qquad (4)$$

where R_{t+1} is given by equation (3), C_t is the catch (weight) in year t, and s is a survival term. (Note that $s = e^{-M}$ where M is the usual "instantaneous" natural mortality rate. For the more general case of a time step T other than one, $s = e^{-MT}$). Further, define

$$m = (1 - s * g) \qquad (5)$$

to be a new "mortality" parameter.

Equations (3) and (4) and definition (5) combine to give a biomass dynamic model with three parameters: a, b, and m. Provided a>m, the model predicts a sustainable catch for stock sizes up to an unfished (virgin) biomass B_0 (where $B_0 = (a-m) / mb$). It can be shown that maximum sustainable yield C_{MSY} for this model is given by

$$C_{MSY} = (\sqrt{a} - \sqrt{m})^2 / b \qquad (6)$$

and hence that, given a and b constant, an increase in m will result in a decrease in sustainable yield and conversely, a decrease in m will increase yields. Since from equation (5), m and g are inversely related, this implies that an increase in growth rate will generally serve to increase sustainable catches, as would be expected. The above formulation provides a theoretical framework for predicting the likely size of the effect, given a specific growth model.

Comments

As noted in the introduction, Schnute's model provides a useful framework for thinking about how variability in growth might affect yields and biomass estimates. One of the virtues of the model is that it is derived directly from numbers at weight and avoids the necessity of considering more indirect quantities such as numbers at age, length at age, and the like. However like most fishery models it assumes that density dependent effects are limited to the stock-recruitment relationship, and does not consider the possibility of density related changes in growth rate.

Another advantage of the model is that the data requirements are modest. In relation to growth in particular, the minimum requirement is for an estimate of growth at average size, which might be obtained for example from quite limited tagging data (without the necessity of being able to age the fish). Average weights are easily measured (total weight of a representative sample divided by numbers of fish). Schnute shows how a time series of means and variances in weight, together with catch data and indices of relative abundance, can be sufficient to estimate all the parameters of the growth and dynamic models. This suggests that the regular collection of weight data may be very useful for fish which can not be readily aged.

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PROBLEMS IN COHORT ANALYSIS
THE GEMFISH EXAMPLE

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Cohort analysis has become one of the most widely used methods of fish stock assessment. Its basic data requirement is a time series of the number of fish of each age caught in each year. It is therefore dependent upon our ability to determine the age of individual fish, and it is thus an appropriate subject to include in this symposium.

Essentially the method is very simple. It involves the calculation of the number of fish of each age at the beginning of a year from the number at the beginning of the preceding year and the number of that age caught during the year. The reverse or "backward" calculation is perhaps even more widely used and is the subject of this paper.

The forward calculation requires the solution for F and P_t of the two equations, both derived from the Beverton and Holt population model:

$$P_{t+1} = P_t(1-\exp(-F-M)) \qquad (1)$$

and

$$C_t = P_t F(1-\exp(-F-M))/(F+M) \qquad (2)$$

using the standard symbols.

These equations can only be solved by iterative techniques and in practice the approximation

$$P_{t+1} = P_t\exp(-m) - C_t\exp(-AM) \qquad (3)$$

is commonly used. In the original form, due to Pope (1972), A was given the value 0.5 and this is generally satisfactory if F and M are not too large.

In the simple method (3) is used sequentially, either forward or backward, to give a series of deterministic estimates of P_t and F_t for each cohort in each year. To do this an estimate of M has to be supplied for each cell.

Allen and Hearn (1989) have described methods of determining a value of A which will give a better approximation. For the present study A was set at 0.55; this value gives an error of less than 0.2% for a continuous fishery with a value of F + M less than about 0.9. It is also the exact value for an instantaneous fishery taking place at a point in time 0.55 through the year. The main gemfish fishery lasts for about two months, centred on July, and lies therefore somewhere between these two conditions.

More recently several methods have been developed which combine the data for the various cohorts to obtain overall estimates of F for each cell on the assumption that these values are the sum, or some other function, of an age component and a year component, these components being defined by functions whose parameters are the primary estimates. These methods have been reviewed by Megrey (1989).

While there are some obvious advantages in using methods which pool data to give estimates with determined confidence limits, there are also advantages in initially performing a simple cohort analysis to examine any patterns which may be shown.

The purpose of this paper is to consider some of the assumptions that are involved in applying cohort analysis, using as an example a recent study of the gemfish population (Allen 1989). A number of specific problems are discussed in the following paragraphs.

Is the stock subject to a single fishery?

For gemfish the answer is "No". The main fishery extends usually over two or three months in mid-winter and is concentrated on mature fish, but there is also a smaller summer catch, comprised mainly of younger fish, taken largely as a by-catch of fishing targeted at other species. To meet this situation, equation (1) is modified to

$$P_t = P_{t+1}\exp(M) + C_{s,t+1} + C_{w,t+1}\exp(1-AM) \qquad (4)$$

where C_s and C_w are the summer and winter catches respectively.

Is the stock homogeneous?

Again for gemfish the answer is "No". The catch curves show that in the youngest recruited age groups of the spawning-run fishery there are many more males than females and that at older ages the numbers of males fall off more rapidly with age than the numbers of females. One interpretation of this situation would be that M or F or both are larger for males than for females at least at older ages and also that there is a difference in age-specific vulnerability between the sexes in the youngest fish. An alternative explanation would be that a sex-change takes place with all or most of the fish being initially male but with an increasing proportion becoming females at later ages. The cohort analysis can be modified to meet either of these situations by performing the calculations for each sex separately. If there is not a sex-change the estimates for the sexes are quite independent; the relative abundance of the sexes in the estimates then becomes a factor which can be considered in assessing the validity of the analysis.

If a sex-change is included in the model it is necessary to assume a value for the proportion of males becoming females at each age and then to carry out the calculations for the males first so as to have an estimate of the number to be added to the females in each cell.

What is the appropriate value of terminal F for the oldest age group?

The chief problem here is to avoid using a value which is too low because this leads to high estimates of the number of fish in the oldest age group in the cohort, and this carries through to cause large over-estimates of the size of the cohort at earlier ages. The under-estimates caused by setting the terminal F too high are, on the other hand, relatively minor. In the gemfish analysis an iterative procedure was used by which the terminal F was made equal to the overall value of F in the same year for the other fully recruited age groups; this estimate converges very rapidly and only a few iterations are needed.

What is the appropriate value of terminal F in the final year?

A rather similar procedure to that above was employed to obtain these values, but it was necessary to allow for the fact that the younger age groups are only partially recruited. In this study iteration was used to make the value of q for each age group equal to that of the same age group in the following year. This takes into account age-variation in vulnerability and therefore provides a rational estimate for the younger, partially recruited age groups. However, because the terminal age group makes a relatively large contribution to the initial cohort size the results for the last few years are very sensitive to errors in terminal F.

Variation of M and F with age and year

The catch curves for male gemfish are generally rather convex upwards in the right hand limb, and the same effect is shown to a lesser extent in the curves for females (Rowling 1987). This suggests that the mortality rates (M or F or both) tend to increase with age in the fully recruited age groups. It is not surprising therefore that if the cohort analyses are run with M independent of age the resulting estimates of F generally show an increasing tendency with age, particularly in the males. Running with M increasing with age tends to reduce the extent to which F is age-dependent (Allen 1989). The younger partially recruited age groups of both sexes (3 and 4 for males and 3,4 and 5 for females) show decreasing values of F compared to the older age groups. Further, the relative increase in the frequency of the younger age groups in the catches of recent years noted by Rowling (1987) is reflected by higher values of F for these age groups compared to those fully recruited. The value of F for 5 year old females for example rose after 1983 from about 10% to 25% of that for fully recruited age groups, and the corresponding change for 4 year old males was from about 6% to 12%.

Selection of M and validity testing

These subjects are closely inter-related, since M is the main variable which has to be introduced into the model from an external source. In the modifications of cohort analysis where the values of P and F are fitted to the data as a whole the resulting measures of goodness of fit can be used to find the M values which give the best results. In the most developed techniques, such as CAGEAN (Deriso *et al.* 1985), M is included in the fitting procedure. If, as in the present study, only the basic cohort analysis is employed, several criteria can be used, provided effort data are available, to examine the compatibility of the results with other aspects of the stock. Three of these have been used in the gemfish analysis and are discussed here.

Comparison with changes in CPUE

Given data on growth in weight the population estimates from the cohort analysis can be converted to biomass. An estimate of exploitable biomass can then be obtained by multiplying the estimates for the younger age groups by their annual value of F relative to that for the age groups assumed to be fully recruited. Figure 1 compares the annual estimates of recruited biomass obtained from a separate sex model and from a sex-change model with the observed catches per unit effort in the winter fishery. The separate sex model shows relative changes in biomass throughout the period which closely parallel those in the CPUE; the sex-change model fits almost as well from 1979 onwards although it diverges substantially in the earlier years.

Comparison of actual and expected catches

A logarithmic multiple regression was used to fit the winter catches in each year to the associated effort and the estimated mid-season recruited biomass to an expression of the form

$$C=qE^{l}B^{m} \qquad (5)$$

where q, l and m are constants and E and B are effort and biomass. Analysis of variance shows that this regression would account for about 96% of the variation for both models when M was about 0.2-0.3. Figure 2 compares the actual catches with those expected from the regression.

The stock-recruitment relationship

From the results of a cohort analysis covering a sufficient period it is possible to compare the size of the recruitment with that of the parent stock. For the gemfish analysis these have been defined as the number of three year olds and the biomass of mature females three years earlier respectively. For some models these show a relationship which is not consistent with the forms of stock-recruitment usually expected, e.g. they are concave upward or show a continuing increase over all population sizes. Where however the points lie close to a domed or asymptotic curve they are at least not inconsistent with a normal relation. For high values of M the gemfish analyses generally gave unacceptable curves, but when M was about 0.2-0.3 the points fitted reasonably to a domed curve. Such results are shown in Figure 3, the superimposed curves being Ricker curves fitted to the points.

All of these tests lead to the conclusion that, for gemfish, the value of M for the recruited age groups is in the range 0.2-0.3. Increasing M with age has little effect on the consistency of the comparisons. Balancing the separate sex model, at the recruit stage, requires M to be about 50%. greater for males than for females.

Calculation of Yield Curves

If a stock-recruitment curve can reasonably be fitted to the results it is then possible to use the data to set up a population model which can be used for forecasting purposes. Such a model can be used in various ways; it can be used to estimate expected future catches under specified management regimes or to give an estimate of the maximum sustainable yield. This has been done for the gemfish model (Figure 4). Some other functions could probably have been equally well fitted to the points in this Figure. However, since the points appear to lie in the region of the peak of the stock-recruitment curve other functions fitted to them would be likely to give rather similar forecasts of the maximum yield the stock could produce. Thus, there is no information about the way in which the curve descends towards zero recruitment and therefore no conclusions can be drawn from it as to the extent of the risks of a population collapse under heavier exploitation.

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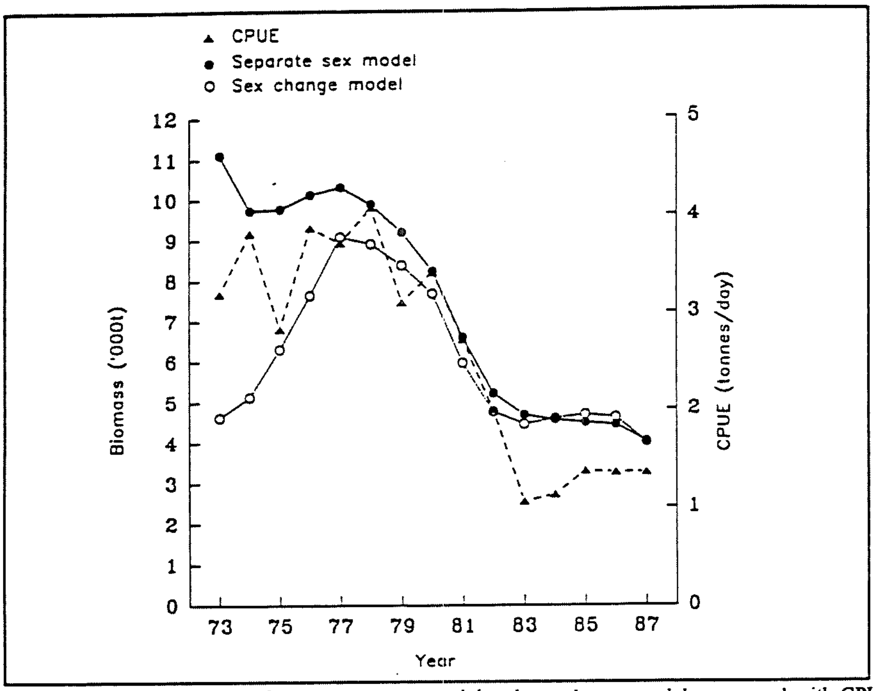

Figure 1. Estimated recruited biomass from separate sex model and sex change model, compared with CPUE for the winter fishery.

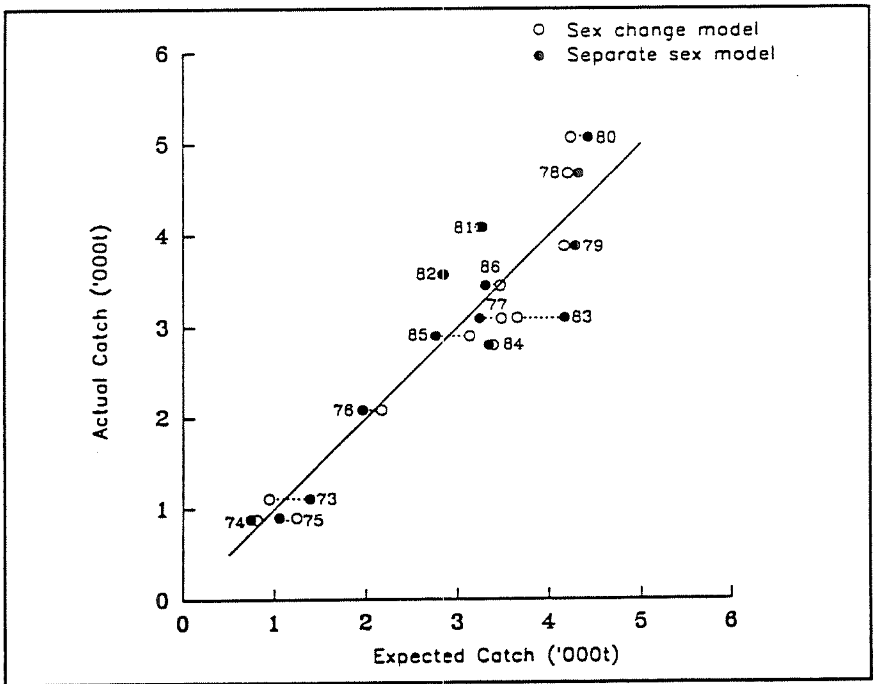

Figure 2. Actual and expected catches compared for the sex change and separate sex models.

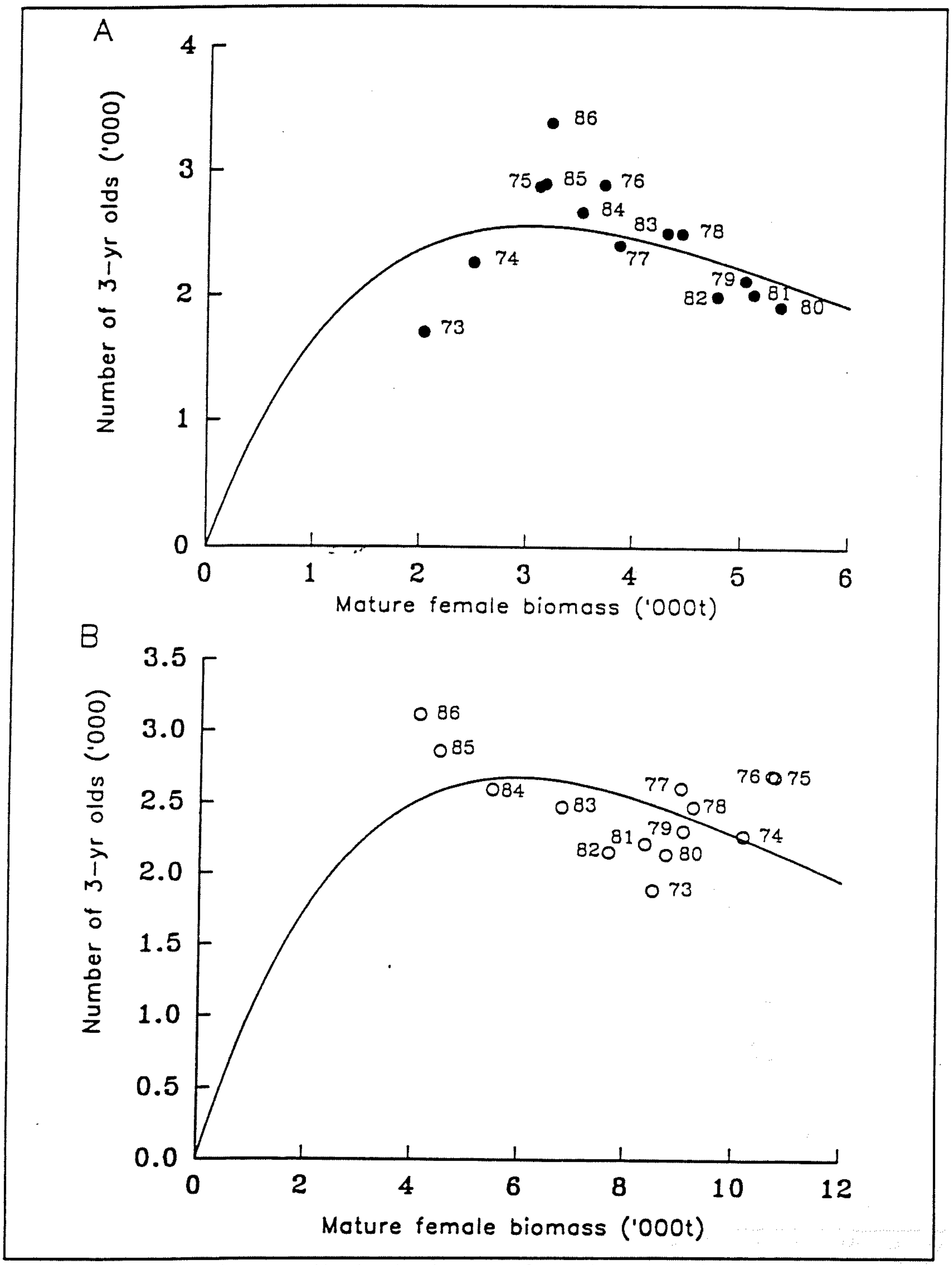

Figure 3. Number of recruits (3-year olds) plotted against mature female biomass for separate sex (A) and sex change (B) models.

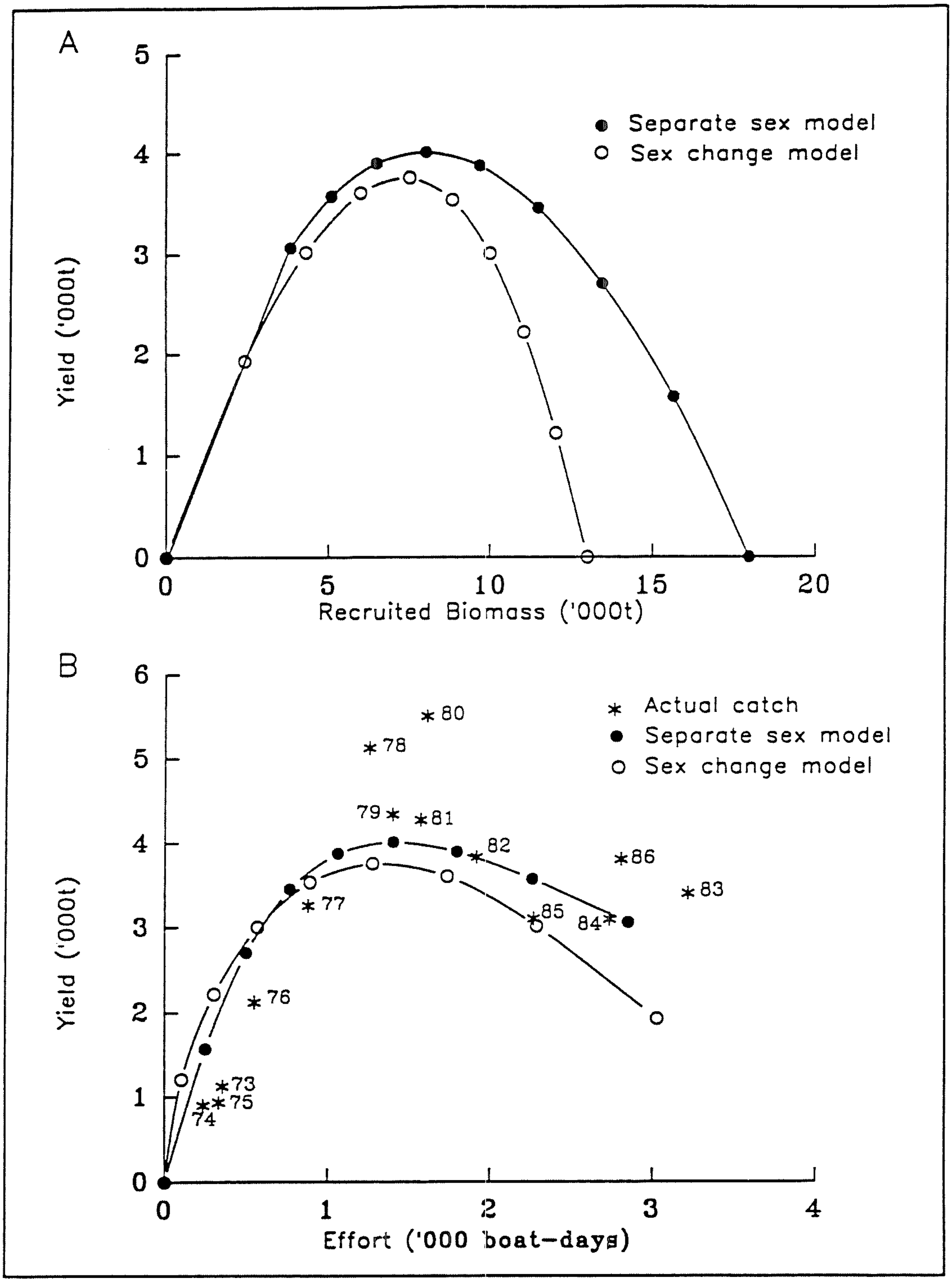

Figure 4. Yield curves under stable conditions.
(A) Yield versus total recruited biomass.
(B) Yield versus estimated required effort with annual catches and efforts superimposed.

DISCUSSION OF SESSION 3, SUB-SESSION C

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The Chairperson invited comments at the end of each panel contribution, following which the meeting was opened for more general discussion.

Scoresby Shepherd commenced the discussion on *Warwick Nash's* contribution with the comment that in the absence of any stock-recruitment relationship for abalone, it seems that the best that can be done is to set a size limit that gives say 40% or 50% of the unfished eggs/recruit. As suggested by the author, this does have some limitations, but a lot of different sites are needed to try and get egg-production percentage values under which the fishery has persisted in the past and get a feeling for what is the optimum level. He had analysed the mid-zone in the Mexican abalone fishery and it looks as if egg per recruit levels were between 6 and 17% of the unfished levels, and of course that fishery collapsed.

Warwick Nash agreed on the need to conserve egg production, and the fact that there have been collapses of abalone fisheries all around the world shows how important this is. However in his opinion one can't use an egg per recruit approach to determine a size limit giving an appropriate level of egg production without having some appreciation of what's affecting recruitment rates in different regions (other than egg output) and what the different ranges of recruitment rates are.

Phillip Sluczanowski promised to enlarge on Scoresby Sheperd's comment on the following day. However he would take issue with Warwick Nash's comment that the approach isn't appropriate because of differing growth and mortality rates. The fact is that there are differential growth and mortality rates and, like it or not, they have to be coped with. This approach gives you perhaps some way of understanding what you're doing; something that is optimal for one area may compromise another, but that's life. Maybe more imaginative management strategies will be needed to deal with that but, as far as tools go, this is the best tool we have got.

Warwick Nash could see that it is a very good way to get an insight into what is happening in terms of the levels of egg-production that are being protected. Indeed, it was through the egg production/egg per recruit approach, and looking at it in relation to differences in growth and mortality rates, that it became clear there *were* differences in recruitment rates between areas. There are differences in recruitment rates as well as growth and mortality rates all around the state. This causes difficulties in the practical management of the fishery.

Rick Fletcher suggested that what is needed is to go one step further with the isopleths that Keith Sainsbury showed, i.e. knowing the variability around them, to work out what is the optimal approach for all of Tasmania given all the variation you have. Warwick Nash agreed that was about the best that could be done. So far, Tasmania has been divided into two size-limit zones based on the variation in growth rate around the state. But within these zones there is still great variability, and within those zones management has to be based on some sort of average. His concern was that the stocks in the less productive areas may end up collapsing. But if they are collapsing, unless the quota is adjusted downwards, then the quota is increasingly concentrated on the more productive stocks.

David Die was not familiar with the life histories of abalone. What evidence is there that each of those sites is self-sustaining? Warwick Nash responded that this was based on the work of Jeremy Prince, who did some removal experiments on a scale of about 60 m. He obtained significantly reduced recruitment in the areas from which he had removed adult abalone (sub-adult abalone were not removed). He concluded that recruitment was on the scale of 10s or 100s of metres.

Phillip Sluczanowski wanted to raise an important issue with regard to per-recruit models. As minimum legal length is increased, more and more of the stock becomes what is defined as "stunted" stock; in other words it's alienated from the fishery. All those animals below the minimum legal length are no longer accessible, but the fishermen want to catch the same number of fish, so the fishing mortality on what's still accessible in fact increases. Traditional per-recruit analysis has never taken this into account, though he had seen mention of it in a couple of papers. It seems that there is a need to build this into the theory. With models which provide the ability for such manipulation it is quite often the case that, by raising the minimum length, egg production is actually compromised even more. So the answer is not always obvious and it is also not obvious how to deal with this empirically.

Warwick Nash gave an example of this. The size limit on the west coast of Tasmania was increased from 130 to 140 mm, and now some of the divers are saying that it is shifting their effort to the east coast areas. This would increase fishing effort on those areas, which is not the desired effect.

Phillip Sluczanowski added to what probably happens. The theory says the large abalone are often in areas where there is abundant food, therefore they grow quicker, therefore they spawn quicker, and they are also the ones that are more likely to be recruitment overfished. The slow growers have plenty of time to spawn before they reach the minimum length. So, by raising the minimum legal length the fastest growing stocks on which the fishery relies, may in fact be destroyed.

Warwick Nash asked if Phillip Sluczanowski was suggesting that we tend to protect our more stunted stocks when we increase the size limit. In the fast-growth west coast area of Tasmania there is a relatively stunted stock, and he thought that ultimately Tasmania would be taking the same approach as Victoria, with localised fish-downs on the appropriate size group for a short period.

Keith Sainsbury did not think it would be very difficult to incorporate the first problem mentioned by Phillip Sluczanowski into the models. A simple approach is to change the F axis into an Effort axis and redistribute the effort onto the available animals. That wouldn't deal, however, with the second problem of a spatial shift in effort.

Phillip Sluczanowski agreed that theoretically it is quite simple to construct a way of dealing with it, but the fact is that the advice given to managers for years assumes that F doesn't change. Almost everything he saw supported the reality of this change, and that as we move size limits we shift egg per recruit or yield per recruit by 'this' unaccounted-for amount. Managers should be warned that fishing mortality may increase or decrease as a result of the size limit changes, and be aware that the changes may be compromising the management objectives.

Keith Sainsbury agreed that advice has not directly taken account of that. But that touched on another important area; we have not been giving managers and researchers measurable quantities to go along with our predictions. It is common that suggested changes in management, as for example in mesh size, are introduced, and the fishery continues for years without any check on whether yield per recruit has been improved as predicted. Failures in the model of the type suggested should result in the failure of other predictions of the model. It is the responsibility of researchers, when giving options, to also indicate measurable quantities that can be used to determine whether the option is working as predicted.

Keith Sainsbury questioned *Tony Smith* on his apparent suggestion that very little growth information is needed for the assessments based on the method he had described.

Tony Smith responded that all that is really needed is an estimate of the annual growth of an average fish in the population. This information could come from sources that did not rely on the ageing of individuals (e.g. they could come from tagging). The method does not necessarily require a detailed description of a growth curve (i.e. the length at age).

Keith Sainsbury expected that this statement by Tony Smith would provoke some comments from the 'defenders of age determination' but it failed to produce a response until general discussion.

Following the contribution on gemfish by *Kay Allen*, John Glaister asked whether there is any biological evidence to support the hypothesis of a sex change in gemfish. Kay Allen replied that it is under investigation. It was an obvious alternative way to model the observed data. But it doesn't make much difference, from a management point of view, to the results.

Peter Millington wondered whether the differential abundance in sexes in the fished stock could simply be due to the males being in a different place? Kay Allen could not dismiss the possibility, but these are spawning aggregations. The fishermen are fishing them pretty hard, and if the males were there they'd probably get them. What he hadn't mentioned was that there have been apparent changes in the way males enter the spawning aggregations. In recent years there have been more of the young males; three and four year olds. Something is happening down there but what, we don't know.

Keith Sainsbury asked how big a difference did uncertainty in growth estimates make in the gemfish VPA (virtual population analysis)? Kay Allen replied that growth, as such, is only used in converting numbers into biomass. Uncertainty in the age estimates with respect to the length frequency structure would be a much more serious source of bias in the VPA than uncertainty in growth.

Tony Smith commented that the gemfish yield curve suggests a very productive, but not very large, resource, and asked if that high productivity is the result of fast growth rates in the recruited population or a function of the derived stock-recruitment curve? Kay Allen said it is a function of the growth of the population. The height of the yield curve is unlikely to be affected by the nature of the stock-recruitment relationship. It will, however, be affected by mortality rates and number of recruits.

Rob Day made the first comment after the Chairman had opened the Sub-session for *General Discussion*. He had some reservations concerning the concept that "Growth doesn't matter", the proposition fielded by the Chairperson following Tony Smith's presentation. Models have only concerned post-recruitment growth. But growth *before* recruitment affects the very stock-recruitment relationships used in the models. The stock-recruitment relationship may be very sensitive to growth because pre-recruit growth determines the period over which mortality reduces the number of eggs produced to the number of subsequent recruits entering the fishery. Growth may also affect the S-R relationship during this period if it is density-dependent.

Tony Smith, however, said he wasn't claiming that growth in itself doesn't matter, because it clearly does in the way Rob Day had indicated. But knowledge about the whole growth process isn't a pre-requisite for doing sensible stock assessment. Rob Day replied that this was providing a stock-recruitment relationship can be established. When Tony Smith agreed, Rob Day continued that is not easy to do.

Tony Smith's response was that knowledge about growth of juveniles isn't going to help much in establishing the stock-recruitment relationship.

Rob Day emphasised that the number of cases in which stock-recruitment relationships can usefully be used as a tool for an understanding of what is going on is very limited.

Tony Smith concluded that most approaches assume some kind of stock-recruitment relationship and often there isn't any information about them. On the other hand, totally ignoring stock recruitment relationships is equivalent to ignoring possible problems with recruitment overfishing.

Rob Day then wondered whether egg per recruit relationships can be taken to a level where they help with the understanding of stock-recruitment relationships.

Terry Walker reminded the meeting of the dependence of per-recruit models on knowledge of M. Total mortality can be determined relatively easily but M cannot.

Keith Sainsbury advised of the need to look at a range of M's in any model and be beware of the sensitivity of the output from the models.

Don Hancock asked if anyone would like to make a comment on Lee's Phenomenon? Or is it something that went out with herring in the North Sea?

Phillip Sluczanowski commented that there are two major papers, one by Rodney Jones and one by Bill Ricker. The Ricker paper is a very long one - about 50 pages. He tried to understand it but did not get past page 10. So he gave up on the whole subject.

Don Hancock believed Lee's Phenomenon to be a fairly simple concept. If you back-measured the otoliths of your fish, and compared the average size of each age with the average size of age groups in the population, you found that the growth rate expressed by your otolith, or in Lee's case the scales, could be considerably less than that which was experienced by the population. Rosa Lee attributed it to scale shrinkage but there was also the possibility of gear selection coming into it. Don found the phenomenon in measurements of the shells of cockles so that certainly wasn't scale shrinkage. He could only come to the conclusion it was mesh selection through repeatedly sieving the cockles during fishing.

Keith Sainsbury cited this as another manifestation of what had been talked about earlier; that whenever you have a combination of length-based and age-based processes, interpretation becomes really difficult. This difficulty was what Ricker was trying to deal with.

Phillip Sluczanowski thought it was that faster growing fish are more susceptible to being caught earlier, and that was supposed to give the bias. However none of the calculations by Ricker seem to explain the *degree* of Lee's Phenomenon. So the phenomenon *does* exist and maybe someone should try to tackle it, but it's very difficult.

Chris Francis said that using the wrong back-calculation formula can also contribute to Lee's phenomenon. He did not think any analysis that he had seen put one in the position of being able to determine which one of the various things that could contribute to this apparent change in growth rate is responsible, whether it's differential mortality, the wrong back-calculation formula, whatever it is. He thought it to be almost an insoluble problem with the kinds of data it is possible to gather.

Geoff McPherson claimed that one of the reasons it doesn't appear very often, at least in the Australian literature, is that it's being deliberately avoided. You can see the difference from the American literature where it does appear a bit. It's primarily because they are back-calculating to previous age-classes. He guessed that the gospel, at least according to Keith Sainsbury, is that you only back-calculate to the last annuli, and that's becoming more and more common here in Australia.

Keith Sainsbury responded that back-calculation of fish length at the time of the latest annulus formation makes some analysis and the presentation of length-at-age data easier. However, he did not see much value in back-calculation beyond that. It seemed to him that if length-at-age of young animals is required, then the most direct and reliable approach is to age small fish, rather than involve all the assumptions and uncertainties associated with inferring these lengths-at-age from back-calculation on old fish.

Chris Francis offered a good reason for back-calculation. What it gives, at least notionally, is a growth history of an individual fish. What Keith Sainsbury was saying before about the importance of devising integrated growth models that give length-based growth and age-based growth is relevant here. If you can convince yourself you have reasonably reliable back-calculations, that is the data set that will help you formulate the model. Chris Francis *has* the data set, and now he is working on the model.

Phillip Sluczanowski said in a sense he had taken the same approach as Keith Sainsbury, that it is too difficult. But it's almost unique in that it's something that is empirically shown to contradict everything we understand. That's usually where major advances in science happen. So he thought it important that it be explained because it's empirically true, which means at least one of our assumptions is wrong.

Rick Fletcher advised that there is a paper on this phenomenon in Australian salmon (Stanley, 1980, *Aust. J. Mar. Freshwater Res.* **31**: 13-19).

Keith Sainsbury agreed that Stanley's paper gave another example of the interactions between age-related and size-related phenomena as discussed in Ricker's paper.

Rob Day was of the view that we need a lot more work to focus on whether important population processes are age- or size-related.

Tony Smith, in following up that comment, concluded the discussion by expressing interest that so many of the models that we have used in stock assessment have been related to things like age, rather than length and weight of the catch which are the variables often of more interest to the fishermen. Just from that point of view it makes a lot of sense to adopt the sort of approach that Schnute, and others have taken: to use size-based, rather than age-based, models. It also makes a lot of biological sense because many of the major population processes with which we are concerned should be size-related rather than age-related.

SESSION 4

General Discussion and Summary

Chairperson:	P.C. Young
Panellists:	P.C. Young K.R. Allen
Rapporteur:	B.F. Phillips

GENERAL DISCUSSION

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Introductory Remarks by Chairperson

I will give a quick rundown, as I saw it, of the major topics that have come up over the last couple of days.

Going right back to the start of proceedings, one of the obvious problems that has been regularly identified is the difficulty of ageing individual animals by the use of hard parts. A major problem raised is the presence of false marks, what causes them and what can we do about it. Solutions to errors of reading include suggestions for intercalibration workshops and also perhaps to look for other ways of either staining or examining hard parts. Sources of variation in growth estimates may be either due to errors of reading, or to true inter-individual variation. This latter derives from a number of sources, including variation due to genetics or natural environment, it may be a function of particular populations, and/or it could be due to effects of fishing. These sources of variation were not examined in detail.

In the case of gemfish we had a series of growth curves derived from sequential catch sampling. It is worth emphasising that this sort of work should be repeated, and repeated regularly, for commercial species as the populations get fished down.

To aid in methods of ageing there are now methods, which need not be necessarily optical, to detect periodic episodes in an animal's life. Such methods include the analysis of isotope ratios, microchemical constituents and histochemical analysis. Other methods for ageing use analyses of whole animals or tissues, such as the radioactive decay methods, and chemical approaches, such as the use of lipofuscins. There has recently been discussion elsewhere on the use of microstructure of the eye lens.

Intercalibration to improve our methodology may well be very important in species which occur either at opposite ends of Australia, or in New Zealand as well as in Australia, and consideration should be given to exchanging on a regular basis, the hard parts that are being used for ageing in these species. Of course the methodology itself could be much better refined by the use and development of new technology such as image processing, to try to make this labour-intensive job quicker, easier, and more accurate.

Now we have heard some talk today about the models used to describe growth. Apart from problems associated with getting the models running, the effects of variability will influence the output of the model. I do not know if it is possible to run sensitivity analyses on the models to include these sorts of variation, but I guess one of the things that came up right at the end of the proceedings emphasised the use to which we want to put a knowledge of age, and whether a knowledge of size would be sufficient. So I raise here the suggestion that perhaps we should be looking at the physical linkage of metabolic processes such as maturity and growth, to the condition and size of the animal rather than to its absolute age, for when one examines the effects of population density on physiological processes, strong interactions have been recorded. The development of maturity at a younger age as stocks are fished down is frequently reported and maybe we should be trying to decide what effect the size of animals has on, for instance, the stock - recruitment relationship, by changes in fecundity with size, rather than estimating this by developing series of time - varying growth rates to relate variability in fecundity to age as growth rates speed up and maturity commences earlier.

General Discussion

The Chairman then opened the meetings for General Discussion commencing with David Smith who had been asked earlier during the workshop to prepare a statement on validation. He offered the following summary to the meeting:

> *"The lack of validation need not necessarily preclude publication, provided the authors state why they have not completely or thoroughly validated the work, and can demonstrate that they have done all they can, have looked at the techniques that are appropriate, and state clearly the reasons why validation has not been undertaken completely or thoroughly."*

Mike Moran agreed with David Smith's proposal. Publication of some work that is not perfect can act as a stimulus and cause work to be done. This will come closer to the ideal situation than maybe would have eventuated if the imperfect work had not been published.

Rick Fletcher suggested that the other thing it would do is to stop people using the same methods that have already been tried and which didn't work. If sectioning otoliths has been tried and found not to work, or scales found to be useless or something like that, publication of the results would stop somebody else possibly spending time and finding the same problems.

Bob Kearney definitely believed results should be published. He felt strongly that the peer review process will determine whether as good a job as is possible to do, has been done, and that is really all you can expect from any scientist. You cannot expect miracles. If somebody has done what is scientifically possible to do and done it well, and appears to believe so, then it warrants publication. If it is not published, then look at it from the other end from the Manager's perspective. He is going to use the information anyway, and say "this was not published but this is the information that I based my decision on" because the Manager is still going to be in the position of being forced to make a decision based on the best available information. If that happens to be unpublished that won't worry him about using it, and because of this it is going to find its way inadvertently into the literature anyway.

Richard Beamish agreed with the previous speakers. However, basic determination studies sometimes use material that is collected by someone else and it looks as if they have been pressed to do something with the material. This can lead to authors writing a paper that is trying to make the best use of the existing material when for instance, they could have looked at sections from better material. He thought it legitimate to request, if necessary, that the authors go back and look at some other structures or to get larger samples. Frequently in the papers he reviewed the problem is not necessarily validation, it is just that the authors have not done everything they should have.

To carry on from that, in most cases people validate young species. For ages less than five years a list of what he regarded as appropriate validation methods for young fish generally would include age frequencies, strong year classes coming through, and marks.

Rob Day indicated the possibilities for using aquarium results for crayfish but these would probably be in the same category as tagging.

Kay Allen felt that there was a little bit of a distinction arising there. Validation should be a process in which we show that the age determination can be directly related to a time scale.

Richard Beamish referred to what some people call natural tags e.g. a poor growth year, and did not think that enough of these are used. There are only one or two examples, but more might be used if people will look for them. He believed they happen more with freshwater fish than with marine.

Keith Sainsbury agreed that the term validation should be applied only to exercises that get you back to an absolute time scale. The use of the term age class only applies in cases where that is done, otherwise you need to use some other description, like ring class.

Richard Beamish noted that very often validation is made only for the young age classes and not carried through to some of the older age classes. Typical examples come from length frequencies where year classes can be followed through time but as soon as growth slows they reach a size where the length frequencies cannot be decomposed and used to validate age classes.

Chris Francis suggested that talking about ageing being validated or not validated is not fruitful; rather it is a question of how *well* ages are validated. As you get more and more information you either have more and more confidence about your ageing method or it falls over. The existence of shades of grey in the results should provide the basis for improvement. There is no black and white.

Ron Thresher was in agreement that this is so for some validation methods, but for scale age determination methods, it *is* black and white. The method may work to age of say 5, 6, or 7 years and then break down totally. Even where you have got data that proves it does not happen in your case most people won't believe you. They will assume you have done something wrong, and you probably won't get it published. What we are doing is solving all these things and hoping they will add up to a near certainty.

The North West Pacific species we had heard about are a classical example. He was sure all of these were examined at the early ages we have been talking about, all of the inferences were there, but they were all dead wrong. We are very much in the same situation. The sort of ages we saw on the screen the other day look suspiciously like the ones he used to think were right for NW Pacific species.

Peter Young asked what effect these dramatic changes in the estimates of age will have on the models.

Richard Beamish replied that accurate ages give you the information about the biology of the animal. In his opinion, and at least in North America, that information has not yet been translated to the models. In fact it has made its way to the management strategists faster than it has made its way to the scientists. For at least three species, management on the basis of strong year classes had begun with a sort of a perception that a minimal stock size is important. He didn't know of a stock assessment method yet, that has incorporated this into the management strategy for a specific area.

Kay Allen commented that where variable recruitment occurs in the first few years, then it will be correctly determined. In the older groups, methods which are based on lumping all of the older age groups together, may not be affected. For instance gemfish analysis was based on pooling all the age groups over 6 or 4. If the 8, 9 and 10 were actually 20 or 30 would not have made any difference because the analysis was based on the whole group.

Rick Fletcher believed that whether or not you have a constant level of recruitment or whether you have spikes is probably the fundamental problem. If the resolution of ageing was a little bit larger than the difference between recruitment spikes and troughs, and age classes were being lumped in 5 year groups, then all that recruitment variation would have been squashed out of the data.

Richard Beamish considered this to be a really interesting area in fisheries science and a real opportunity for people to make a fundamental contribution. It really indicates that the environment is very important, and it is interesting that in all of the day's procedures he hadn't heard of anyone talk about the environment. It really is important , it is open to change, and has to be thought about.

Mike Moran expected that quite a lot of people would have started work on a species and found definite marks in structures that have usually been used for ageing. Consequently they could not definitely say that a species could not be aged. But when they actually try to use the marks for ageing there may be all sorts of problems; for instance, suspected missing rings or false checks, and generally a lot of noise. So when you get more than one person doing the ageing, there might be 10,20,30% disagreement between them.

Peter Young asked whether there is an accepted way or a good way of using the uncertainty between estimates to give confidence ranges in the results? For instance the level of difference between two readers; is there a useful way of using that in your models?

Richard Beamish did not think that you can relate the variability in structures processed to the measurement of accuracy. What is needed is an assessment of the error associated with accuracy. This can only be obtained for known - age fish. There very few cases with known - age fish. There were some data from one particular area where 50,000 fish had been marked. After 10 years only 15 or 20 fish were being returned.

Keith Sainsbury suggested that there are ways of answering the question and it all comes down to the hazard. The criteria you are looking for are determined by the hazards that are attached to making certain kinds of mistakes. If you are wondering about how precise you have to be in ageing you could certainly go through how to do it properly. You should also have a look at effects on differences in yields for different mistakes. It could be done and he suspected it probably should be done more than it is. This would allow more of an all-encompassing view in the process.

Peter Young raised the question of calibration. Certainly in other fields where we are measuring minute amounts of chemicals in sea water, inter-laboratory calibration exercises are used to eliminate operator error and there is quite a lot of emphasis put on these calibration studies. Should we initiate the keeping of hard parts for data banks, transfer between NZ and Australia and vice versa etc. One of the immediate problems of course, is that we don't have centres where there is an exchange of material, particularly for the species which are in some dispute.

In response to a question by Tony Fowler concerning future plans for an ageing facility David Smith replied that the objective has been to get some sort of centralised agency in which the main aim would be to do "routine" and ongoing ageing. Problems with the existing system are that work is usually short term. Four different institutions are all undertaking ageing and the problem of a central agency is trying to obtain the money for setting up the hardware, videos, etc. The final decision will hopefully be within the next month.

Richard Beamish's laboratory was set up 12 years ago, but they had never used the word "routine". Rather it was referred to as an experimental service. Also some type of archiving facility is really important. Even where the material cannot be aged it can be collected and stored and be available for use some time in the future.

After the laboratory had been set up there were debates between the Americans and Canadians about the ages of fish. These were resolved with frequent exchanges of material and an annual meeting at which the people involved in age determination discussed problems.

Bob Kearney commented that one of the reasons why the term "routine" ageing came into this subject was because of the argument in Australia that things that were a prerequisite for management, and not necessarily a requirement for research, were leviable under some of the Commonwealth levy arrangements. It was therefore more likely to be funded as a requirement for management than if it was for pure research and that is why the term routine was used.

John Kalish told the meeting about the setting up of an Ageing Laboratory in New Zealand which will perform a combination of routine ageing and validation. The Laboratory is really set up to carry out age validation research and to investigate new methods to age, validate and investigate deep-water species.

The Chairman closed the discussion by introducing Dr K Radway Allen whose role it was to sum up the proceedings of the past two days.

MEASUREMENT OF AGE AND GROWTH - WHAT IS IT ALL FOR?

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Introduction

This workshop was made possible by financial support from the Federal government. Also, most of the contributions have come from people who are paid by governments to do the work they have talked about. This support is forthcoming because someone has the hope that the work will advance the economic well-being of the country by assisting in the effective management of our fisheries. In this talk I want to examine some of the ways in which studies of fish age and growth are used in the development of management regimes. As a guide to identifying the processes involved I have drawn up the schema shown in Figure 1.

Determination of Age

Current Usage

This first day of the workshop dealt with the top line of figure 1; ways of determining the ages of individual fish and invertebrates and the use of the results to determine how the animals grow. I believe that we got a good picture of the present state of this work in Australia and to some extent also in New Zealand. Most of it was, inevitably, along traditional lines, seeking to identify and count structures laid down annually on various hard parts. Otoliths have been most commonly used, although vertebral centra, scales and dorsal spines were also mentioned. The species discussed included gemfish, orange roughy, hoki or blue grenadier, sharks, *Pomacentrus* and various freshwater fish. Where lamellibranch molluscs show on their shells zonation which can be accepted as annual, the nature of the data, the opportunities for their use and the associated problems are essentially the same as for fish. One point which was emphasised in this discussion was the need, when starting work on a new species, to make a preliminary examination of as many structures and methods of examination as possible.

Although marks laid down annually still dominate ageing studies, the increasing interest in marks laid down at shorter intervals, particularly daily, was also evident. Ron Thresher gave a general review of progress in this direction, especially with "daily" marks on otoliths; John Anderson spoke of such work on a variety of Australian freshwater fishes, and Peter Young described fine markings on scallop shells which are likely to correspond to daily or tidal periods.

Bruce Phillips and David Die introduced us to the problems in determining absolute age in animals like rock lobsters and prawns which do not have permanent hard parts. In general the most useful approaches seem to involve making direct observations of some aspect of growth and working back from this to a time scale, and hence to age.

Validation

It was apparent, particularly in the general discussion, that there is a general appreciation of the importance of seeking ways of validating estimates of age. Most of the well-established methods were mentioned, including seasonal changes at the edge, marking with dyes like tetracycline, and comparison with growth estimates obtained from tagging data. It was pleasing to observe that there was little or no tendency to confuse accuracy, or validation against absolute time scales, with precision or reproducibility in ageing studies.

It seemed to be generally accepted that, in publishing the results of ageing studies, an adequate account of the steps that had been taken to validate the results should be included. This was however seen as leading on to a need for editorial consistency in deciding what constitutes an adequate level of validation, although there were indications that this need may not always be met. Discussion on what constitutes adequate validation showed a tendency to overlook the fact that the level of adequacy may depend upon the way in which the results are to be used. It is, for example, common to find that in representative samples of catches or populations, the precision or reproducibility of the estimates of age decreases as the animals become older, while at the same time the difficulties of validating that estimate increase. However, if the results are being used to develop management recommendations by means of the usual population dynamics procedures, uncertainties or even inaccuracies in the ageing of a small proportion of the population comprised of the oldest individuals may have little or no significant effect on the practical implications. Sensitivity testing by means of simulations could often be used to examine the appropriate level of validation; in some cases it might reveal that efforts to extend validation over a full range of ages were wasteful of time and effort which could be better spent on improving the data regarding the more abundant age groups.

Such a concept does not however detract from the importance of the idea, introduced by Dick Beamish in his opening address, that the range of ages in some populations, particularly of deep-water commercial species, is much greater than has been commonly accepted in the past. This seems to be likely, for example, in a number of North Pacific species; in our region evidence is accumulating that the orange roughy has a very low natural mortality rate and may survive to well over 50 years. The Canadian results suggest that this species is possibly not as unusual in this respect as we have been inclined to think. If some commercially important species do, in fact, survive to much greater ages than has been previously believed, there are important implications for the management of the fisheries based on such species. In the first place, if these high ages exist in long-established fisheries, then not only the natural but also the fishing mortality rate must have been low. This would suggest very substantial underestimates of the size of the exploited stock. Secondly, as Dick Beamish pointed out, it could well be that some of these stocks are maintained not by fairly regular recruitment, year by year, but by occasional very strong year classes at long intervals. The appropriate strategies for managing fisheries on stocks of this kind require much further study. Such strategy might be based on fishing each recruitment pulse down to a safe minimum level. It would still be necessary to maintain an adequate spawning stock that could take advantage of favourable conditions when they occurred. Establishing a basis for a stock-recruitment relationship under such conditions would be even more difficult than it is with regular recruitment.

Future Developments

The final part of yesterday's session dealt with future developments in the techniques of ageing. These fell into two distinct categories. The first was comprised of improvements in the methods of observing and recording the structures which form the basis of ageing studies, e.g. rings on otoliths. Such methods include the automation and digitising of measurements of the observed structures (Greg Jenkins) and also image processing to make selected structures more clearly and sharply visible (Ron Thresher). Developments on these lines seem to offer great possibilities of increasing the speed and the reproducibility or precision of the observations. In addition, image processing may make it possible to base ageing on structures which cannot be observed effectively without enhancement. However, validation or confirmation of the accuracy of results will still depend on other means of verifying the time scales ascribed to the observed structures.

The second category relates more directly to the problems of validation since it is concerned with techniques which can be used to relate observable structures to absolute time scales. Craig Proctor described work on the relation of cyclic patterns in the deposition of elements such as strontium and calcium to events in real time. David Ritz discussed methods based on radionuclide analysis. These may make it possible to determine the time which has elapsed since a particular piece of material was incorporated in the scale or otolith and thus provide a means of relating even more directly to absolute time scales.

Inferences from Age And Growth

Construction and Use of Growth Curves

On the second day discussion centred on ways in which age data can be used in developing fisheries management strategies. Two main processes are involved here. These are the construction of growth curves and the analysis of the age composition of exploited populations; jointly, these provide the information needed for most of the established techniques of stock assessment.

The von Bertalanffy curve continues to be the growth model most frequently used. Kevin Rowling and Bruce Phillips discussed some of the problems encountered in using age data to construct these curves for gemfish and rock lobsters respectively. Warwick Nash pointed out that where the growth is sigmoid, as in abalone, the Gompertz curve can provide a better fit. In discussion the point emerged that the most useful curve to choose may depend upon the size or age range of the recruited part of the population. If this range is dominantly beyond the point of the inflection of the curve, the von Bertalanffy curve may provide a statistical fit over the range of interest which is as good as that of a sigmoid function, and can be used more easily in the common population models. Ian Somers presented the reverse of the usual problem; he described the use of growth curves to determine the age of juvenile prawns and the application of the results to track their wanderings.

The rest of the morning dealt with more mathematical aspects of the problems of quantifying growth. Both of the main kinds of data which can be used in such studies; observations on the changes in size of individuals over a period (e.g. tagging data), and size-age matrices for populations, figured in the discussion. David Die described the use of Monte Carlo methods in examining biases in estimates of growth parameters from tagging data, while Mark Palmer showed that where repeated measurements of individual animals were available - tagging data are a special case of this - random coefficient models can be used to get more powerful estimates of the error structure of the growth parameters. Chris Francis pointed out that when a von Bertalanffy curve is fitted to tagging data it is dangerous to attach any biological meaning to the estimate of L_∞; this is because growth is being described in this case as a function of size rather than of time.

Kathy Haskard took us back to the value of applying basic statistical techniques, such as ANOVA, to the original size and age data, and showed how these analyses can be used effectively to compare populations without necessarily making any assumptions as to the nature of the growth function. This approach should be very relevant to comparisons of differences from year to year, as described by Kevin Rowling for gemfish, or for local variations, as in the abalone of Warwick Nash. Nik Dow discussed ways of attacking the problems which arise in trying to fit growth functions to either size/age or tag-recapture data when size-selection has operated in the catching process, illustrating them by reference to Southern shark data. Finally Ron Sandland's general discussion of the problems of choosing and fitting growth functions must have convinced every biologist present of the vital need to talk to a real mathematician before deciding how to tackle his statistical problems.

This completed consideration of the questions of age and growth represented by the top right block of Figure 1. It was noticeable that the questions involved in getting from individual or sample age compositions to estimation of population age structures received relatively little attention. It was not clear how much this was due to the constraints of time and how much it reflected the kinds of age and growth work being done in Australia at present. Two important aspects of these problems are:

First, the extent to which the age or length samples are representative of the population from which they are taken, and -

Secondly, the validity of obtaining age structure estimates for one period or area by combining the size distribution data for that period or area with size/age data for another.

Applications to Management

In the last afternoon we moved down into the bottom part of Figure 1 and considered some of the ways in which the results of age and growth studies can be applied in developing management recommendations, particularly as to levels of catch and/or effort and minimum size limits. Age-structured models are still the mainstay of stock assessment. Surplus yield models have largely receded into history, and length-structured models are still in the process of development although great progress has been made in this direction in recent years.

The simplest age-structured models which can be made to yield conclusions relevant to management are yield-per-recruit models. These need estimates of growth parameters and of natural mortality rate, while they become more useful if estimates of fishing mortality rate are also available. The workshop has dealt at length with the estimation of growth. Mortality rate estimates also are generally founded upon growth data using techniques such as the analysis of catch curves, but this bridge from age data to estimation of mortality rates was passed over in silence in the workshop. The use of yield-per-recruit models was introduced by Keith Sainsbury, who rightly reminded us that the yield in such models does not have to be the weight of the catch, but may be almost any quantity which is of interest. Examples are the value of the catch, the biomass of the recruited population (relevant to economic analyses requiring forecast of catch per unit effort), or,if fecundity-at-age data were available, the egg production per recruit. The last leads into consideration of recruitment effects in determining optimum catches or effort levels, but, because mortality between egg and recruitment is unknown and potentially density-dependent, yield-per-recruit analysis cannot alone lead directly to estimates of optimal catch or fishing mortality levels. Keith Sainsbury's paper also introduced the currently fashionable rule of thumb for obtaining an estimate of the optimal value of F, i.e. $F_{0.1}$; this can be calculated from yield-per-recruit analysis. Simulations suggest that values of F set equal to $F_{0.1}$ may give a good chance of avoiding recruitment over-exploitation, and may also be reasonably near to economically optimal levels.

Warwick Nash described an attempt to use estimation of egg production per recruit to determine appropriate size limits for a set of abalone populations. The results were instructive in indicating that even within one species there may be differences between stocks, in the recruitment and mortality rates, which can make it inappropriate to use the stocks as a comparable series from which to draw conclusions about the optimal management regimes.

The workshop concluded appropriately, with two papers describing ways in which age and growth data can be used in assessments based on fully structured models which include mortality and recruitment processes. Tony Smith drew attention to the work which is being done, for example, by Jon Schnute, on the development of size-structured models, which enable populations to be simulated on the basis of weight data. These models, which require provision of a growth function but not of detailed age data, have been reduced to remarkably simple mathematical forms incorporating relatively few assumptions. I believe that further work along these lines constitutes one of the most promising directions in which the techniques of fish stock assessment for management purposes are likely to develop in the coming years.

A more traditional approach was presented in my paper (Allen this meeting) on the cohort analysis of the gemfish stock. This illustrated the way in which this kind of analysis, which makes use of age distribution, growth and catch-effort data, can be used to obtain estimates of the parameters of a recruitment function. This function can then be combined with yield-per-recruit analysis to develop yield curves which may be tested by simulation of past events and then used to explore the possible effects of future exploitation regimes.

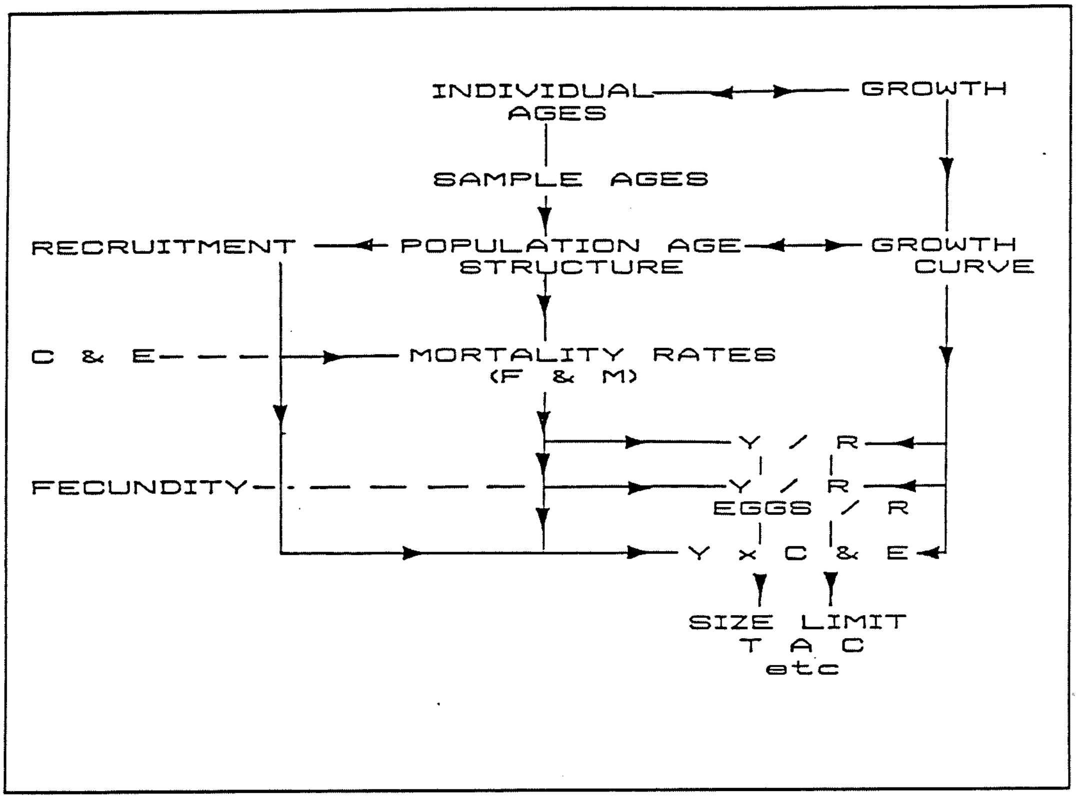

Figure 1. The relation of age and growth studies to management problems.

GLOSSARY

GLOSSARY OF TERMS FOR AGE DETERMINATION METHODS

During the workshop the need for standard terms for age determination methods was stressed. The reasons should be apparent from the proceedings of the Workshop. Many terms are used to describe the same features, e.g. growth rings, increments, checks or annuli. This leads to confusion and in some cases errors in interpretation particularly when methods are compared and terms are inadequately defined. It was argued that to improve scientific communication in general and scientific writing in particular, an attempt at defining terms was urgently needed.

This has been widely realised in the fisheries literature and a number of glossaries have already been produced (see for example Prince and Pulos 1983; Summerfelt and Hall 1987). It was suggested at the workshop that previous glossaries be used as a starting point and a revised version circulated to fish societies and editors of journals. A competing set of terms in different international journals that are mutually incompatible should be avoided at all costs.

Following discussions amongst participants after the workshop, it became clear that what was needed was more than another list of terms. Published glossaries are inconsistent and there is little discussion of why one term is preferred to another. It was decided that the most useful approach would be to prepare a paper, separately from the workshop, in which the range of terms used for the major features can be discussed and reasons for preferred names given.

David Smith
Chairperson Session 2

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POSTER DISPLAYS

POSTER DISPLAYS

Growth Model for Spencer Gulf Prawns

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Mark-recapture data were used to develop a harmonic growth model which was combined with real-time sampling information to determine optimum fishing periods for prawns in Spencer Gulf.

Age, Growth and Structure of the Vertebra in the School Shark *Galeorhinus galeus* (Linnaeus, 1758) from Southern Brazil [A]

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The age and growth of the Brazilian school shark *Galeorhinus galeus* was studied from rings in the vertebra and length frequency data. The samples were collected by trawling off the southern Brazilian coast from June 1980 to September 1986. Standard histological techniques and microradiography were used to determine the pattern of vertebral calcification. The vertebra presents a pattern of alternating heavily and less heavily mineralised zones, narrow and wide, respectively. The narrow zones were named rings, which are translucent under transmitted light and white to the microradiograph. These rings are probably laid down yearly in a slow growing phase extending throughout the four winter months of June to September. The largest number of rings observed was 41. Lengths at age were back-calculated and the von Bertalanffy growth parameters estimated. ELEFAN software was used to determine the growth curve best fitted to length-frequency data.

[A] This research was conducted at Fundacao Universidade do Rio Grande, Departamento de Oceanografia, Rio Grande, RS, 96200, Brazil.

Growth and Mesh Selection in the Edible Cockle *(Cerastoderma edule)*

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Poster based on a paper by the author (J. Appl. Ecol. 4, 137-157, 1967) describing the use of validated annual rings on the shell to describe variations in growth and shell dimensions within year-classes, and the resultant selective action of sieves during harvesting.

A Preliminary Study of Age and Growth of a Tropical Damselfish *(Stegistes apicalis)*

Dongchun Lou
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By assuming that the fine increments on otoliths of *Stegistes apicalis* from the northern Great Barrier Reef were deposited on a daily basis, annual bands on the otoliths can be validated by counting daily increments. There was no significant difference in the relationships between body length and weight and sex. Age and growth structures were investigated using aging methods of otolith with preliminary results that the maximum attainable size (L_∞) of the von Bertalanffy equation was 154.6 mm whilst the growth coefficient (K) was 0.148.

A New Approach to Ageing Gummy Shark, *Mustelus antarcticus*, and School Shark, *Galeorhinus galeus*

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[c]Southern Shark Assessment Group, Marine Science Laboratories, Queenscliff VIC 3225

Previous methods of ageing commercial sharks in Australia have relied on histological stains applied to whole vertebrae. By scoring the articular face along the stained lines and filling the groove with radio-opaque paste, it was possible to correlate the lines visible under the light microscope on the surface with those seen within the vertebrae using x-rays. Microradiographs of longitudinal and oblique sections through vertebrae provided a much clearer image of incremental lines than was visible using traditional methods. These techniques combined with tetracycline marking, photometry and scanning electron microscopy provide a new and potentially highly accurate method of validating the age of two species of commercial sharks.

SURVEY

NATIONAL SURVEY OF AGE DETERMINATION STUDIES

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Introduction

This survey is the second of its type to be jointly conducted by the Australian Society for Fish Biology (ASFB) and the Bureau of Rural Resources (BRR), the first being a survey of the use of (fish) tagging in Australia (Stoddart 1989). The earlier survey preceded the ASFB Workshop on Tagging (Hancock 1989) and formed the basis for the National Tagging Register held by BRR.

The rapid growth of fisheries biology in Australia, together with the increasing number of agencies involved in fisheries research, are such that available information is widely scattered and often in unpublished form. A prerequisite to accessing such data is obviously a knowledge of their existence /availability. Whereas periodic ASFB Conferences and Workshops fulfil the vital function of keeping researchers up to date with work in progress, a centralised data repository is the most effective means of facilitating access to pertinent information at any time. The returns from this survey constitute the nucleus of a fish age/growth database to be held at BRR. One of BRR's major roles in fisheries research is to promote and maintain databases which relate to issues of national significance.

The vital importance of age/length data to fish stock assessments and consequent fisheries management strategies has recently been acknowledged by the Commonwealth, via the establishment of a Central Ageing Facility (CAF) based at the Marine Science Laboratories, Queenscliff, Victoria. The main function of the CAF will be to provide periodic age/length keys for commercially important fish species for which a validated ageing method has been established. Such keys, together with the necessary catch composition data, will constitute a much firmer foundation for stock assessments than has usually been the case in the past, and will eventually enable cohort analyses to be undertaken once adequate time series are available. It is also hoped that the CAF will serve as a central repository for the otoliths, bony parts, etc, used for ageing.

This survey is by no means exhaustive. Although questionnaires were sent to all organisations listed as conducting fisheries research in the 1988 edition of Australian Marine Research in Progress and to known Australian freshwater fisheries research centres, the actual coverage achieved of potential respondents is not known, nor is their response rate. Some potential respondents are known to have been overseas, others are known to have failed to respond. These comments notwithstanding, this survey constitutes a useful start to a central, Australian (fish) age/growth database and a current guide to Australian-based researchers with experience in this field.

The questionnaire consisted of 3 pages and a bibliographic request (Appendix A).

The respondents are listed in alphabetical order of surname, followed by organisation, subject-species and reference number in Appendix B.

Results

A total of 74 ageing projects were reported (Appendix B). The great majority (92%) of these studies centred on teleost fishes (Figure 1). The "ecosystem types" in which most such studies took place were as follows; marine pelagic (24%), marine shelf (22%) and running freshwater (19%) (Figure 2). Comparison between the time periods in which these studies were conducted implied a 400% increase in the number of projects from the 1970's to the 1980's (Figure 3), with the number of 1990's projects under way suggesting that a further increase will occur during the present decade. However, the incomplete coverage achieved by this survey should be borne in mind, with the apparent absence of ageing studies conducted prior to 1960 (Figure 3) being almost certainly more a function of the ageing process on respondents, rather than the total lack of such work !

Many studies attempted more than one ageing method and/or technique. The methods /techniques used are summarised in Table 1. Otolith-based methods/techniques comprised over half (56%) of the 330 listed. Where a technique other than those listed in Table 1 was used, the project number (Appendix B) is also listed. Although the methods used were summarised in tabular form by "status" (see questionnaire), there is little value in showing all such tables, excepting the important "validation" summaries (Tables 2 & 3). The use of scales with a light microscope had by far the highest rejection rate of 73% (16/22), whereas that for otoliths was extremely low (2%).

Of the methods/techniques used, 27% were partially validated (Table 2) and a further 27% were fully validated by the authors (Table 3).

All the Von Bertalanffy growth parameters supplied by respondents are summarised in Table 4. These are listed by project number to facilitate cross-referencing with the pertinent researchers (Appendix B).

Discussion

The fact that only 27% of the methods /techniques described in the survey were fully validated, highlights the need for increased validation of ageing studies, particularly where age/length data are to be used for stock assessment purposes.

As stated above, this survey only achieved a partial coverage. Whereas a greater coverage could certainly have been achieved by directly contacting known researchers who did not respond to the questionnaire, resources were not available for this time-consuming process. The effectiveness of questionnaire-based surveys should therefore be measured against other methods of accruing information before proceeding with future ASFB surveys. In the interim, BRR is compiling additional, published age/size/growth information with the eventual aim of producing a summary of known parameters for commercially /recreationally important Australian fish species.

References

Hancock, D. A. (1989). Editor: Australian Society for Fish Biology Tagging Workshop. Sydney 21-22 July 1988. BRR Proc. No. 5. Australian Gov. Pub. Service, Canberra. 208 pp.

Stoddart, J. A. (1989). The National Tagging Register. *In* Hancock, D. A. (Ed.) Australian Society for Fish Biology Tagging Workshop. Sydney 21-22 July 1988. BRR Proc. No. 5. Australian Gov. Pub. Service, Canberra. 23-32.

Table 1. Summary of methods/techniques listed by respondents

METHODS/TECHNIQUES	LENGTH FREQUENCY	SCALES	OTOLITHS	FIN SPINES	VERTEBRAE	CHEEK BONES	STATOLITH GASTROLITHS	SHELL	EYE LENS	TEETH	EARPLUGS	OTHER
OPTICAL												
Visual	25	3	7	-	2	-	1	-	-	-	-	-
Light Microscope	8	22	52	6	9	2	1	-	2	-	-	1 AD29
Electron Microscope	-	-	10	-	-	-	1	-	-	-	-	-
Projection	-	8	-	-	-	-	-	-	-	-	-	-
PROCESSING												
Staining	-	-	5	-	4	-	-	-	-	-	-	-
Burning	-	-	12	-	-	-	-	-	-	-	-	-
Grinding	-	-	23	2	2	-	1	-	-	-	-	-
Mould/Impression	-	-	-	-	-	-	-	-	-	-	-	-
Chemical/Etching	-	-	2	-	-	-	-	-	-	-	-	-
INTERVALS												
Tagging	-	9	4	1	4	-	-	-	-	-	-	-
Oxytetracycline	-	1	22	-	2	-	-	-	-	-	-	-
Daily Rings	-	-	22	1	-	-	-	-	-	-	-	-
Annual Rings	1	16	24	2	4	1	1	-	-	-	-	1 AD29
MICROANALYSIS												
X-ray microchemistry	-	-	1	-	-	-	-	-	-	-	-	-
Radionuclide	-	-	-	-	-	-	-	-	-	-	-	-
OTHER	-	-	1 AD35	-	-	-	-	-	-	-	-	1 AD46

Table 2. Summary of partial validations achieved by respondents

METHODS/TECHNIQUES	LENGTH FREQUENCY	SCALES	OTOLITHS	FIN SPINES	VERTEBRAE	CHEEK BONES	STATOLITH GASTROLITHS	SHELL	EYE LENS	TEETH	EAR PLUGS	OTHER
OPTICAL												
Visual	6	-	1	-	-	-	-	-	-	-	-	
Light Microscope	1	2	18	-	2	1	-	-	-	-	-	
Electron Microscope	-	-	4	-	-	-	-	-	-	-	-	
Projection	-	2	-	-	-	-	-	-	-	-	-	
PROCESSING												
Staining	-	-	1	-	2	-	-	-	-	-	-	
Burning	-	-	3	-	-	-	-	-	-	-	-	
Grinding	-	-	6	-	-	-	-	-	-	-	-	
Mould/Impression	-	-	-	-	-	-	-	-	-	-	-	
Chemical/Etching	-	-	-	-	-	-	-	-	-	-	-	
INTERVALS												
Tagging	-	1	-	-	4	-	-	-	-	-	-	
Oxytetracycline	-	-	5	-	2	-	-	-	-	-	-	
Daily Rings	-	-	6	-	-	-	-	-	-	-	-	
Annual Rings	1	3	12	-	4	1	-	-	-	-	-	
MICROANALYSIS												
X-ray microchemistry	-	-	-	-	-	-	-	-	-	-	-	
Radionuclide	-	-	-	-	-	-	-	-	-	-	-	

Table 3. Summary of full validations achieved by respondents

METHODS/TECHNIQUES	LENGTH FREQUENCY	SCALES	OTOLITHS	FIN SPINES	VERTEBRAE	CHEEK BONES	STATOLITH GASTROLITHS	SHELL	EYE LENS	TEETH	EAR PLUGS	OTHER
OPTICAL												
Visual	3	-	3	-	2	-	-	-	-	-	-	
Light Microscope	-	-	18	1	2	-	-	-	-	-	-	
Electron Microscope	-	-	3	-	-	-	-	-	-	-	-	
Projection	-	6	-	-	-	-	-	-	-	-	-	
PROCESSING												
Staining	-	-	1	-	2	-	-	-	-	-	-	
Burning	-	-	3	-	-	-	-	-	-	-	-	
Grinding	-	-	8	-	-	-	-	-	-	-	-	
Mould/Impression	-	-	-	-	-	-	-	-	-	-	-	
Chemical/Etching	-	-	-	-	-	-	-	-	-	-	-	
INTERVALS												
Tagging	-	7	-	1	-	-	-	-	-	-	-	
Oxytetracycline	-	-	6	-	-	-	-	-	-	-	-	
Daily Rings	-	-	5	-	-	-	-	-	-	-	-	
Annual Rings	-	10	8	1	-	-	-	-	-	-	-	
MICROANALYSIS												
X-ray microchemistry	-	-	-	-	-	-	-	-	-	-	-	
Radionuclide	-	-	-	-	-	-	-	-	-	-	-	

Table 4. Summary of von Bertalanffy parameters recorded by respondents

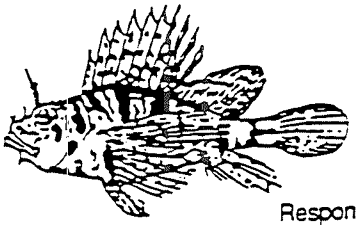
NUMBER	SCIENTIFIC NAME	LOCATION	SEX*	K	L_∞	T_0	AGE UNITS	LENGTH UNITS
AD01	*Saurida undosquamis*	NW shelf	U	0.4359	63.50	0.90	years	cm
AD02	*Nemipterus furcosus*	NW shelf	U	0.2500	41.90	-0.74	years	cm
AD03	*Abalistes stellatus*	NW shelf	U	0.1900	55.20	-0.33	years	cm
AD13	*Lampanyctodes hectoris*	Tasmania	U	0.0062	70.09	0.92	months	cm
AD19	*Trachurus declivis*	Tasmania	U	0.1700	48.80	-0.33	years	cm
AD20	*Emmelichthys nitidus*	Tasmania	U	0.1480	38.90	-2.83	years	cm
AD21	*Trachurus declivis*	S.E. Australia	U	0.2000	46.40	-0.87	years	cm
AD21	*Trachurus declivis*	Great Australian Bight	U	0.1900	41.70	-2.08	years	cm
AD22	*Macruronus novaezelandiae*	West coast Tasmania	M	0.1960	93.00	-2.48	years	cm
AD22	*Macruronus novaezelandiae*	West coast Tasmania	F	0.1810	101.20	-1.71	years	cm
AD22	*Macruronus novaezelandiae*	East coast Tasmania	M	0.2760	89.50	-1.03	years	cm
AD22	*Macruronus novaezelandiae*	East coast Tasmania	F	0.2680	93.50	-0.93	years	cm
AD23	*Arripis trutta marginata*	N.S.W.	U	0.2965	58.72	-0.17	years	cm
AD23	*Arripis trutta marginata*	Victoria	U	0.3782	49.50	-0.07	years	cm
AD23	*Arripis trutta marginata*	Tasmania	U	0.2909	57.71	-0.11	years	cm
AD25	*Arripis trutta esper*	W.A.	U	0.2994	75.63	-0.01	years	cm
AD25	*Arripis trutta esper*	S.A.	U	0.2609	68.91	-0.24	years	cm
AD25	*Arripis trutta esper*	Victoria	U	0.2751	62.93	-0.23	years	cm
AD26	*Scomber australasicus*	Great Australian Bight	U	0.2400	44.10	-1.79	years	cm
AD27	*Carcharhinus sorrah*	Northern Australia	F	0.3400	123.90	-1.90	years	cm
AD27	*Carcharhinus sorrah*	Northern Australia	M	1.1700	98.40	-0.60	years	cm
AD28	*Carcharhinus tilstoni*	Northern Australia	F	0.1400	194.20	-2.80	years	cm
AD28	*Carcharhinus tilstoni*	Northern Australia	M	0.1900	165.40	-2.60	years	cm
AD28	*Carcharhinus tilstoni*	Northern Australia	F	0.1900	181.40	-2.10	years	cm
AD28	*Carcharhinus tilstoni*	Northern Australia	M	0.2500	156.80	-1.90	years	cm
AD29	*Lutjanus vittus*	N.W. Shelf	M	0.2650	40.10	0.06	years	cm
AD29	*Lutjanus vittus*	N.W. Shelf	F	0.4010	32.20	0.21	years	cm
AD30	*Lates calcarifer*	Mary River, N.T.	U	0.1250	142.50	-1.26	years	cm
AD30	*Lates calcarifer*	West Alligator River, N.T.	U	0.2960	86.80	-0.53	years	cm
AD30	*Lates calcarifer*	East Alligator River, N.T.	U	0.0850	177.50	-1.76	years	cm
AD30	*Lates calcarifer*	Norman River, N.T.	U	0.1250	144.90	-1.27	years	cm
AD30	*Lates calcarifer*	N.E. Gulf of Carpentaria	U	0.1790	74.00	-1.10	years	cm
AD31	*Tandanus tandanus*	Gwydir River, N.S.W.	U	0.3130	613.00	0.53	years	mm

Table 4. (Continued)

NUMBER	SCIENTIFIC NAME	LOCATION	SEX*	K	L_∞	T_0	AGE UNITS	LENGTH UNITS
AD35	*Sardinops neopilchardus*	Albany, W.A.	F	0.2090	205.00	-3.40	years	mm
AD35	*Sardinops neopilchardus*	Albany, W.A.	M	0.6020	170.00	-0.09	years	mm
AD35	*Sardinops neopilchardus*	Albany, W.A.	U	0.5790	175.00	-0.07	years	mm
AD36	*Cnidoglanus macrocephalus*	Wilsons Inlet, W.A.	U	0.2800	788.10	0.01	years	mm
AD37	*Platycephalus speculator*	Wilsons Inlet, W.A.	F	0.3090	601.00	-0.42	years	mm
AD37	*Platycephalus speculator*	Wilsons Inlet, W.A.	M	0.4080	477.00	-0.33	years	mm
AD39	*Galaxiella munda*	S.W. Australia	M	4.2170	44.30	-0.01	years	mm
AD39	*Galaxiella munda*	S.W. Australia	F	3.7020	48.60	-0.01	years	mm
AD40	*Edelia vittata*	S.W. Australia	M	1.1780	54.90	-0.21	years	mm
AD40	*Edelia vittata*	S.W. Australia	F	1.1240	57.90	-0.20	years	mm
AD41	*Bostockia porosa*	S.W. Australia	M	0.8180	92.00	-0.15	years	mm
AD41	*Bostockia porosa*	S.W. Australia	F	0.6690	104.00	-0.18	years	mm
AD42	*Galaxias occidentalis*	S.W. Australia	M	0.7580	109.00	-0.34	years	mm
AD42	*Galaxias occidentalis*	S.W. Australia	F	0.7620	124.00	-0.22	years	mm
AD43	*Torquigener pleurogramma*	Swan Estuary, W.A.	U	0.2400	255.00	-0.56	years	mm
AD44	*Cnidoglanis macrocephalus*	Swan Estuary, W.A.	U	0.2000	917.00	-0.11	years	mm
AD52	*Chrysophrys auratus*	Outside Shark Bay, WA	U	0.1200	80.00	-0.40	years	cm
AD55	*Chelidonichthys kumu*	Canterbury, NZ	U	0.4060	52.00	0.29	years	cm
AD56	*Maccullochella peeli*	Murray-Darling river system	U	0.0600	136.90	-5.20	years	cm
AD57	*Pomacentrus mollucensis*	John Brewer Reef	U	0.6000	45.60	-1.37	years	mm
AD58	*Macquaria novemaculeata*	Sydney basin (gorge)	F	0.2148	329.00	-0.97	years	mm
AD58	*Macquaria novemaculeata*	Sydney basin (gorge)	M	0.1777	396.00	-2.09	years	mm
AD58	*Macquaria novemaculeata*	Sydney basin (tidal)	F	0.1203	368.00	-2.57	years	mm
AD58	*Macquaria novemaculeata*	Sydney basin (tidal)	M	0.2004	271.00	-0.95	years	mm
AD72	*Mustelus antarcticus*	Bass Strait	M	0.1240	149.50	-3.41	years	cm
AD72	*Mustelus antarcticus*	Bass Strait	F	0.0470	277.80	-4.29	years	cm
AD72	*Mustelus antarcticus*	South Australia	M	0.3040	127.50	-0.85	years	cm
AD72	*Mustelus antarcticus*	South Australia	F	0.0640	218.80	-4.99	years	cm
AD73	*Galeorhinus galeus*	Bass Strait	U	0.0840	215.80	-2.17	years	cm
AD73	*Galeorhinus galeus*	South Australia	U	0.1440	173.70	-0.92	years	cm

* M = male, F = female, U = unspecified

AUSTRALIAN SOCIETY FOR FISH BIOLOGY



Response No:
[_[_[_[_[_[_] Page 1
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GPO Box 858
CANBERRA A.C.T. 2601

NATIONAL REVIEW OF AGE DETERMINATION STUDIES

(Please provide a set of forms for each species; photocopy if necessary)

- -

Today's Date: [_[_[_[_[_[_] e.g. 900526

Full Name & Address of Responder ______________________________
____
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Telephone No: ______________________________

- -

Species

(office use only)

Scientific Name: ______________________________ [_[_[_[_[_[_]··[_[_]

Common Name: ______________________________

(Please photocopy additional sets of forms to provide details for more than one species)

- -

(Please circle one choice in each section below)

Taxonomic Category

Crustacean	1
Mollusc	2
Echinoderm	3
Elasmobranch	4
Teleost	5
Amphibian	6
Reptile	7
Mammal	8
Other (Specify...............................)	9

Main Ecosystem Type

Freshwater (still)	1
Freshwater (running)	2
Estuarine	3
Marine & Freshwater	4
Marine Reef	5
Marine Shelf	6
Marine Slope	7
Marine Pelagic	8

Main Period of Work (circle one)

Pre 1950	1	1970's	4
1950's	2	1980's	5
1960's	3	1990's	6

DETAILS OF METHODOLOGY AND STATUS

Use the following codes to indicate status of the approach used for each structure/characteristic; leave blank where the approach is not relevant:

Structure collected (**C**), Examined (**E**), Examined and Rejected (**R**), Examined and Deferred (**D**), Examined and Partially Validated (**P**), Examined and Fully Validated (**V**), Used and Replicable but not Validated (**U**).

Structure or Characteristic

Approach	Length Frequency	Scales	Otoliths	Fin Spines	Vertebrae	Cheek Bones	Statoliths/Gastroliths	Shell	Eye Lens	Teeth	Ear Plugs	Other (specify)
"Optical"												
visual												
light microscope												
electron microscope												
projection												
"Processing"												
staining												
burning												
grinding												
mould/impression												
chemical/etching												
"Intervals"												
tagging												
oxytetracycline												
daily rings												
annual rings												
"Microanalysis"												
X-ray microchemistry												
radionuclide												
Other (specify)												

....

RESPONSE No: [_[_[_[_[_[_](office use only) Page 3

AGE/SIZE TABLES

SPECIES: (office use only)
Scientific Name: ______________________________ [_[_[_[_[_[_]..[_[_]
Geographic location: ______________________________
Ageing Method: ______________________________
(photocopy more pages to provide tables for different areas or aging methods for this species)

AGE	"LENGTH"	"WEIGHT"	SIZE (other)
	*..........................	*..........................	*..........................
	....	....	....
(unit#..................)	(unit#..................)	(unit#..................)	(unit#..................)
1			
2			
3			
4			
5			
6			
7			
8			
9			
10			
11			
12			
13			
14			
15			
16			
17			
18			
19			
20			

* specify which size dimensions are involved, e.g. length to caudal fork, carapace length, shell diameter, processed weight, etc.

indicate whether age is in years, months, weeks, etc.; give units for size, e.g. "cm", "kg", etc.

Von Bertalanffy Growth Parameters

K
L_∞
t_0
Notes/Reference:

Response No:
[[[[[[ ] Page 4(....)
(Office use only)

PUBLICATIONS FROM THE PROJECT

(Please use a new page for each reference)

Author(s) ....
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Title ....
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Journal Title or Publishing Organisation ....
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Year of Publication ....

Report No. or Journal Vol. .... Page Numbers ....

(Location : ....)

Copy Enclosed? Yes .... No ....

Appendix B: National review of age determination studies - list of projects

NO.	CONTACT	ORGANISATION	SCIENTIFIC NAME	COMMON NAME
AD01	A.W. WHITELAW	CSIRO	*Saurida undosquamis*	Brush toothed lizard fish
AD02	A.W. WHITELAW	CSIRO	*Nemipterus furcosus*	Peron's threadfin bream
AD03	A.W. WHITELAW	CSIRO	*Abalistes stellatus*	Starry trigger fish
AD04	S.J.M. BLABER	CSIRO	*Spratelloides delicatus*	Blue sprat
AD05	S.J.M. BLABER	CSIRO	*Caranx bucculentus*	Blue-spot trevally
AD06	S.J.M. BLABER	CSIRO	*Macruronus novaezelandiae*	Blue grenadier
AD07	S.J.M. BLABER	CSIRO	*Archamia zosterophora*	Black sash cardinal
AD08	S.J.M. BLABER	CSIRO	*Amblygaster sirm*	Spotted pilchard
AD09	S.J.M. BLABER	CSIRO	*Herklotsichthys quadrimaculatus*	Gold spot herring
AD10	S.J.M. BLABER	CSIRO	*Stolephorus heterolobus*	Blue anchovy
AD11	S.J.M. BLABER	CSIRO	*Stolephorus devisi*	Gold anchovy
AD12	S.J.M. BLABER	CSIRO	*Spratelloides gracilis*	Silver sprat
AD13	J.W. YOUNG	CSIRO	*Lampanyctodes hectoris*	Lanternfish
AD14	P.E. DAVIES	IFC (TAS)	*Onchorhyncus mykiss*	Rainbow trout
AD15	P.E. DAVIES	IFC (TAS)	*Onchorhyncus mykiss*	Rainbow trout
AD16	P.E. DAVIES	IFC (TAS)	*Salmo trutta*	Brown trout
AD17	R.D. SLOANE		*Anguilla reinhardtii*	Long-finned eel
AD18	A. JORDAN	DPI (TAS)	*Trachurus declivis*	Jack mackerel
AD19	G. PULLEN	DPI (TAS)	*Trachurus declivis*	Jack mackerel
AD20	G. PULLEN	DPI (TAS)	*Emmelichthys nitidus*	Redbait
AD21	C.A. STANLEY	CSIRO	*Trachurus declivis*	Jack mackerel
AD22	C.A. STANLEY	CSIRO	*Macruronus novaezelandiae*	Blue grenadier
AD23	C.A. STANLEY	CSIRO	*Arripis trutta marginata*	Australian salmon (East. ssp.)
AD24	C.A. STANLEY	CSIRO	*Sardinops neopilchardus*	Pilchard
AD25	C.A. STANLEY	CSIRO	*Arripis trutta esper*	Australian salmon (West. ssp.)
AD26	C.A. STANLEY	CSIRO	*Scomber australasicus*	Blue mackerel
AD27	J.D. STEVENS	CSIRO	*Carcharhinus sorrah*	Black tip shark
AD28	J.D. STEVENS	CSIRO	*Carcharhinus tilstoni*	Black tip shark

Appendix B: Continued

NO.	CONTACT	ORGANISATION	SCIENTIFIC NAME	COMMON NAME
AD29	T.L.O. DAVIS	CSIRO	*Lutjanus vittus*	One-band sea perch
AD30	T.L.O. DAVIS	CSIRO	*Lates calcarifer*	Barramundi
AD31	T.L.O. DAVIS	CSIRO	*Tandanus tandanus*	Eel-tailed catfish
AD33	V. WADLEY	CSIRO	*Nototodarus hawaiiensis*	Hawaiian squid
AD34	R.K. GRIFFIN	NTDPIF	*Lates calcarifer*	Barramundi
AD35	W.J. FLETCHER	W.A. FISHERIES DEPT	*Sardinops neopilchardus*	Pilchard
AD36	L. LAURENSON	MURDOCH UNIVERSITY	*Cnidoglanis macrocephalus*	Cobbler
AD37	G.A. HYNDES	MURDOCH UNIVERSITY	*Platycephalus speculator*	Southern blue-spotted flathead
AD38	M.J. KINGSFORD	UNIVERSITY OF SYDNEY	*Plectropomus leopardus*	Coral trout
AD39	L.J. PEN & I.C.POTTER	MURDOCH UNIVERSITY	*Galaxiella munda*	Western mud minnow
AD40	L.J. PEN & I.C. POTTER	MURDOCH UNIVERSITY	*Edelia vittata*	Western pygmy perch
AD41	L.J.PEN	MURDOCH UNIVERSITY	*Bostockia porosa*	Nightfish
AD42	L.J. PEN	MURDOCH UNIVERSITY	*Galaxias occidentalis*	Western minnow
AD43	I.C. POTTER	MURDOCH UNIVERSITY	*Torquigener pleurogramma*	Banded toadfish
AD44	I.C. POTTER	MURDOCH UNIVERSTY	*Cnidoglanus macrocephalus*	Cobbler
AD45	J. PUCKRIDGE	UNIVERSITY OF ADELAIDE	*Nematalosa erebi*	Bony bream
AD46	J. PEPPERELL	FRI (NSW)	*Makaira indica*	Black marlin
AD47	T. PARK	FRI (NSW)	*Helicolenus percoides*	Ocean perch
AD48	G. HENRY	SPCC	*Pagrus auratus*	Snapper
AD49	G. THORNCRAFT	FRI (NSW)	*Macquaria ambigua*	Golden perch
AD50	J.D. BELL & D.J. FERRELL	FRI (NSW)	*Pagrus auratus*	Snapper
AD51	D. FARRELL	FRI (NSW)	*Pseudochromis novaehollandiae*	Basslet
AD52	M. MORAN	MRL (WA)	*Pagrus auratus*	Snapper
AD53A	R.D.J. TILZEY	BRR	*Salmo trutta*	Brown trout
AD53B	R.D.J. TILZEY	BRR	*Salmo trutta*	Brown trout
AD54A	R.D.J. TILZEY	BRR	*Oncorhynchus mykiss*	Rainbow trout
AD54B	R.D.J. TILZEY	BRR	*Oncorhynchus mykiss*	Rainbow trout
AD55	D.K. STAPLES	BRR	*Chelidonichthys kumu*	Red gurnard

Appendix B: Continued

NO.	CONTACT	ORGANISATION	SCIENTIFIC NAME	COMMON NAME
AD56	S.J. ROWLAND	DEPT AG. & FISHERIES (NSW)	*Maccullochella peeli*	Murray cod
AD57	A. FOWLER	AIMS	*Pomacentrus moluccensis*	Lemon damselfish
AD58	J.H. HARRIS	FRI (NSW)	*Macquaria novemaculeata*	Australian bass
AD59	M. LINTERMANS	ACT PARKS	*Gadopsis bispinosus*	Two-spined blackfish
AD60	D.M. WILLIAMS	AIMS	*Escualosa thoracata*	White herring
AD61	D.M. WILLIAMS	AIMS	*Herklotsichthys* species	Spotted herring
AD62	D.M. WILLIAMS	AIMS	*Herklotsichthys koningsbergeri*	Koningsberger's herring
AD63	D.M. WILLIAMS	AIMS	*Sardinella brachysoma*	Deep-bodied sardinella
AD64	D.M. WILLIAMS	AIMS	*Sardinella albella*	White sardinella
AD65	D.M. WILLIAMS	AIMS	*Sardinella gibbosa*	Gold-stripe sardinella
AD66	D.M. WILLIAMS	AIMS	*Amblygaster sirm*	Spotted sardinella
AD67	M. CAPPO	AIMS	*Istiophorus platypterus*	Pacific sailfish
AD68	M. CAPPO	AIMS	*Herklotsichthys castelnaui*	Castelnau's herring
AD69	M. CAPPO	AIMS	*Makaira indica*	Black marlin
AD70	M. CAPPO	AIMS	*Lutjanus argentimaculatus*	Mangrove jack
AD71	M. CAPPO	AIMS	*Lutjanus johni*	Fingermark
AD72	T.I. WALKER	VIC. MARINE SCIENCE LABS	*Mustelus antarcticus*	Gummy shark
AD73	T.I. WALKER	VIC. MARINE SCIENCE LABS	*Galeorhinus galeus*	School shark

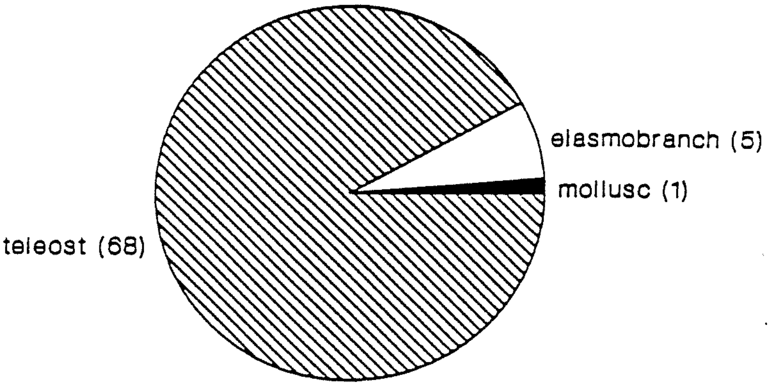

Figure 1. Number of projects by taxonomic category.

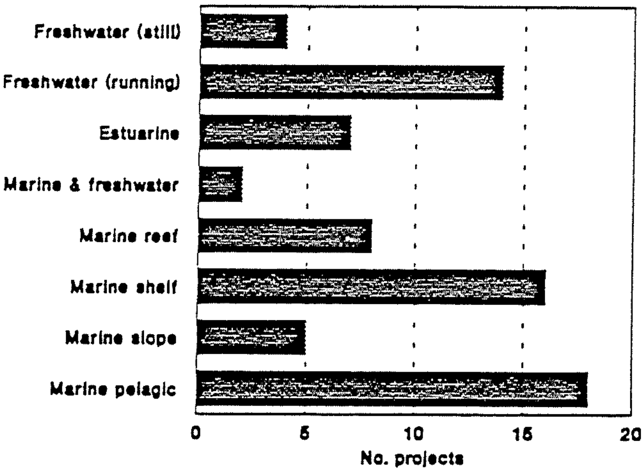

Figure 2. Number of projects by main ecosystem type.

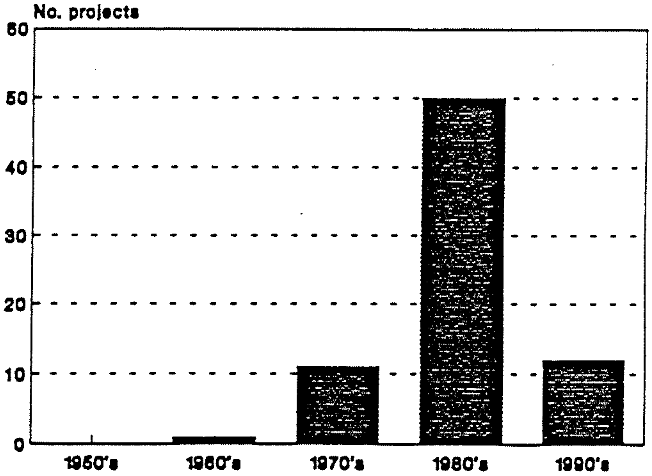

Figure 3. Number of projects by main period of work.

USEFUL REFERENCES

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This reference list contains the references cited in the survey questionnaire, those from the workshop papers and those generated from a single literature search (Compact Cambridge: ASFA 1982 to 1989). Given the multitude of published age and/or growth studies, or studies involving age/growth parameters, the list is not likely to be complete. However, emphasis is given to Australian studies (which are marked with an asterisk *) and it is hoped that "local" coverage is much more extensive. Contributions to this Workshop have not been included.

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ABSTRACTS

ABSTRACTS OF AGE AND GROWTH PAPERS GIVEN AT THE AUSTRALIAN SOCIETY FOR FISH BIOLOGY SEVENTEENTH ANNUAL CONFERENCE

Tropical Fish in Sub-tropical Waters: Some Problems Encountered in Scale Analysis of *Oreochromis mossambicus* (Pisces: Cichlidae)

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and Angela H Arthington
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Traditional methods of ageing fishes are based on Northern hemisphere temperate species and these methods are often inappropriate for tropical species. *Oreochromis mossambicus* is a tropical species which has established a feral population inhabiting North Pine Dam in southern Queensland.

Petersen's method was found to be inappropriate because of the extended breeding season of this population (6 to 8 months) which does not produce identifiable yearly cohorts.

Scale analysis was undertaken, which raised some interesting problems. The annual nature of ring deposition needed to be proven, and the causes and effects of scale resorption had to be taken into account. The results of this analysis showed, amongst other things, that the growth (size at age) curve was not of the von Bertalanffy type, and the actual shape of the curve varied with time of spawning. Thus growth estimates based on the von Bertalanffy growth function may not be accurate for this species.

The implications of these findings are discussed, as is the need for appropriate data collection and analysis.

Age and Growth of King George Whiting Larvae

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The age and growth of King George whiting larvae have been examined in both field-collected and laboratory-reared material. Validation of daily increment formation in otoliths from larvae of known age has been undertaken. In addition trial tetracycline marking of newly recruited post-larvae has been undertaken in cages in nursery areas.

King George whiting eggs hatch after 48-60 h at 16.5-18.7°C. The larval phase is protracted, with larvae remaining planktonic for some 60-80 days prior to recruitment to nursery habitats at 15-18 mm. Growth of whiting larvae in the laboratory was similar to estimated growth rates of field collected fish. Otolith micro-structure was less well defined in reared larvae although daily increment formation was observed.

The Movement and Growth of Tagged Blue Endeavour Prawns, *Metapenaeus endeavouri* (Schmitt) in the Western Gulf of Carpentaria

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Mark-recapture experiments were used to define movements and growth of *Metapenaeus endeavouri* in the western Gulf of Carpentaria fishery. Releases of 4765 streamer-tagged prawns were made in summer 1984, and 8798 in winter.

The overall recapture rate was 2.3%. Patterns of recaptures reflected logbook fishing effort data. There were no preferred directions or depths, nor were there sex or size differences in movements. A slow dispersal after release was indicated.

The fit of the von Bertalanffy model to summer data was satisfactory but limited by the small number of recaptures. Parameter estimates from winter data were stable after removal of early recaptures. L_{inf} differed significantly between sexes but not between seasons and K differed only between sexes in winter. A seasonally oscillating model did not generally improve fit. It was suggested that, in adverse conditions, the male prawns reduced growth rates, while females may reduce reproductive output.

Growth of *Haliotis rubra*: Effects of Food Supply and Competition between Abalone

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Juvenile *Haliotis rubra* (+/-35 mm) from Port Phillip Bay were placed in small cages in a flow-through seawater system to investigate whether individuals affect each other's growth. They were kept alone in cages, accompanied by a 60-65 mm abalone, or in groups of four of the same size, and were fed weekly or fortnightly, on a mixture of red and green algae, or *Ulva* alone. In each case the remaining algae were removed after a week. Growth was variable over time and between individuals, and some apparently eroded their shells against the substratum. Nevertheless juveniles grew significantly faster when alone than with other abalone. The larger abalone, similar in wet weight to three small juveniles, had similar effects on growth. Juveniles grew less when food was supplied less often, and the effects of competition were more pronounced. Growth was also reduced on *Ulva* as compared to the mixed algae. These results suggest that growth rates in the field may be density dependent.

A Study of Shell Deposition and Growth in *Haliotis rubra*

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The growth of *Haliotis rubra* is being studied in Port Phillip Bay, Victoria using a number of methods. The pattern of nacre deposition in the shell is mapped to determine whether the sequence of layers at the growing edge of the shell corresponds to the sequence of layers underneath the spire. Shells from four sites will be aged by counting the number of rings in the spire using the method of Munoz-Lopez (1976), and the growth of individual shells will be followed by determining the sizes of the shell when each layer was laid down. These results will allow a graph of shell length versus apparent age to be drawn up for individuals within a population. A short-term tag-recapture study will provide some results on the growth, especially of juveniles, in the different populations. A transplant study of abalone from a slow growing site to a fast growing site will show whether layer deposition is different between the two sites by comparing the transplanted abalone shells with those of the parent population. Finally, the possibility that fluorescent dyes can be used as markers of shell deposition in live abalone is being investigated in order to determine how regularly shell layers are deposited.

Use of Otolith Weight to Age in Pilchards (*Sardinops neopilichardus*) and Australian Salmon (*Arripus truttaceus*)

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The lengths and otolith weight of pilchards which had been aged using counts of rings on both otoliths and scales were examined using an analysis of co-variance, which showed that the otolith weight of an individual was a better predictor of age than was its length. Size frequency distributions of otolith weights sampled at this time had modes with means that were similar to the mean otolith weights of the different age classes. These modes persisted even when a sub-sample of fish was used which had a uniform distribution of lengths. Further evidence that otolith weight is a good predictor of age for pilchards was provided by the examination of size-frequency of otolith weights over a yearly period. The modes increased through time in agreement with the hypothesis that they represented different year classes.

An additional test of the relationship between age and otolith weight was made for Australian salmon. This species was also found to have a multimodal structure for its otolith weight size-frequency distribution. These modes generally corresponded to different ages as ascribed by scale readings. The implications of these results for studies requiring long-term evaluation of age structures are discussed in relation to the precision of the ageing method, the numbers of individuals that can be aged and the cost in time.

Comparisons between the Ages Estimated for the Flathead, *Platycephalus speculator*, Using Whole and Sectioned Otoliths

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Sagittal otoliths have been used to determine the age and growth of the southern blue-spotted flathead, *Platycephalus speculator*, in Wilson Inlet, a seasonally closed estuary on the south coast of south-western Australia. The clear seasonal and annual trends shown by the growth of the opaque (summer growth) zone on the periphery of otoliths (marginal increment) after sectioning, irrespective of the number of translucent (winter growth) zones, demonstrates that these latter zones correspond to annuli. Although the relative size of the marginal increment in whole otoliths with one translucent zone followed similar seasonal trends to those in sectioned otoliths, such marked seasonality was not observed in whole otoliths showing two or more translucent zones. This implies that the sectioning of otoliths with multiple translucent zones enhances the ability to differentiate between the outer opaque and translucent zones. This would account for the observation that 23, 37 and 57% of the otoliths which, after sectioning exhibited two, three and four translucent zones, each showed one less translucent zone prior to sectioning. Underestimates of the age increased with the number of translucent zones. Thus, the number of translucent zones was frequently two less in whole otoliths than in those of corresponding sectioned otoliths which possessed five to ten annuli. Underestimates of age by as much as five or six years were found in the oldest fish which were estimated as eleven and twelve years of age. Many of the underestimates in the otoliths with two to four annuli could be attributed to the fact that the outer translucent zone became visible later in whole than in sectioned otoliths (December vs October). The respective parameters L_{inf}, K and t_o of the von Bertalanffy growth curves were 477, 0.408 and -0.332 for males and 601, 0.309 and -0.423 for females.

Density-Dependence of Larval Growth of a Marine Fish, the Southern Bluefin Tuna, *Thunnus maccoyii*

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The role of density dependent factors in the mortality of larval fishes is a poorly understood but potentially very significant area of research into fish population dynamics. Growth of larvae of southern bluefin tuna, *Thunnus maccoyii*, in the East Indian Ocean was significantly different among stations sampled randomly within a 20 km radius. Growth rate was correlated with feeding rate but not with temperature, indicating that, on a fine-to coarse-scale, larvae were food limited to a varying degree. A negative correlation between growth rate and abundance suggested that food limitation was density dependent. We conclude that in areas of high abundance, larvae were competing for food, leading to a density dependent reduction in growth rate. Growth rate was depressed up to 25% in areas of maximum larval abundance. Because the larval stage is prolonged, cumulative mortality of slow growing larvae over this period will be greater, even if the mortality rate is constant. The implications for southern bluefin tuna population dynamics are discussed.

Fish Otolith Micro-Chemistry: Validation of the Effects of Physiology, Environment and Life History on Otolith Chemistry

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The effects of temperature, somatic growth, otolith growth, condition factor, RNA/DNA ratio, age and season on the incorporation of Sr, Na, K and S into the sagittal otoliths of Australian salmon and blue grenadier were investigated by a combination of laboratory rearing experiments and monthly collections of wild fish. Micro-chemical analyses of otolith chemistry were carried out with a wavelength dispersive electron micro-probe. There were significant differences in otolith Sr/Ca ratios among Australian salmon maintained in the laboratory at different temperatures and a slight positive correlation with temperature, but there was no evidence for a linear relationship between Sr/Ca ratio and temperature. Biologically significant relationships between other factors were not evident in laboratory-maintained fish. Furthermore, the variability of elemental ratios within temperature treatments and within individual otoliths was very significant. It is hypothesised that seasonal variations in otolith chemistry in both wild blue grenadier and Australian salmon are partly due to seasonal changes in growth rates and/or reproductive investment. There were highly significant correlations between otolith chemistry and fish age in wild blue grenadier and these were largely explained using a similar rationale regarding growth rates and reproduction. It is hypothesised that the seasonal and age-related variation in otolith Sr content is largely the result of changes in the proportions of free and bound Ca and Sr present in the blood plasma and that this is in turn a function of the quantity and type of proteins present in the plasma. Data on the level of Sr present in the saccular endolymph and the sagittae of 12 fish species showed that there was a very strong relationship between the composition of the endolymph and the otoliths. Because of their variability, otolith micro-chemistry data indicate the need for large sample sizes, validation experiments and extreme caution when investigating the relationship between otolith micro-chemistry and physiology, life-history stage and environment.

The Age and Growth of *Cnidoglanis macrocephalus* (Plotosidae) in Western Australia

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The age and growth of *Cnidoglanis macrocephalus* has been determined for populations in Wilson Inlet, Princess Royal Harbour, Irwin Inlet, Peel-Harvey Estuary and the Swan Estuary. Validation of ages was determined using translucent zones on sagittal otoliths and was carried out separately for each age group. Back calculated data were compared with length at age data to determine the accuracy of back calculation methods. Ages estimated using the lapillus were lower than those obtained with the sagittal otoliths. Length at age data have been fitted to both the von Bertalanffy growth model and a seasonal growth model.

Age, Growth and Reproduction of the Three *Lutjanus* Species in the Great Barrier Reef Inter-Reef Handline Fishery

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The age, growth and reproduction of three species of the Great Barrier Reef inter-reef handline fishery were investigated. Selected von Bertalanffy growth parameters (L_{inf} and K) of *Lutjanus sebae*, *L. malabaricus*, and *L. erythropterus* for males are 103 cm and 0.15, 99 cm and 0.18, and 60 cm and 0.44 respectively, and for females 89 cm and 0.18, 84 cm and 0.23, and 60 cm and 0.44 respectively. The estimates of age were only partially validated by marginal increment analyses, possibly due to the prolonged spawning seasons for the three species.

Differential growth between the sexes was evident in older age classes of *L. sebae* and *L. malabaricus*, males being larger. Estimates of 50% length at first maturity of females for all three species ranged between 49 and 58 cm.

Different von Bertalanffy growth parameters between the sexes of *L. sebae* and *L. malabaricus*, the species that dominate this fishery, indicate that sex should be considered in mortality assessments for these species.

Comparisons between Growth Rates, Size and Age at Maturity and Spawning Modes of Four Small South-western Australian Freshwater Fish

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Ten principal species of principle freshwater fish are found in south-western Australia, of which eight are endemic to that region. Data on growth and age (using otolith annuli) and on the reproductive biology (using gonadosomatic indices, ovarian staging and histology of the oocytes) have been obtained for the four most abundant endemic species. *Galaxias occidentalis* and *Bostockia porosa*, which can reach 5-6 years of age, and spawn only once in a breeding season. The first species attains sexual maturity at the end of its first year when the females have reached a length and weight of *circa* 75 mm and 2.3 g. By contrast, the second species, which reached only 56 mm and 1.8 g at the end of its first year, does not breed for the first time until the end of a further year when the females are *circa* 79 mm and 5.1 g. *Edelia vittata* and *Galaxiella munda* are both multiple spawners, i.e., their females produce batches of eggs at intervals in a breeding season, and reach sexual maturity at the end of the first year of life. *E. vittata* can live for up to 5 years, whereas *G. munda* does not survive to spawn in a second year. Although *G. occidentalis, B. porosa, E. vittata* and *G. munda* each spawn at some stage between mid-winter and late spring, the time of peak spawning activity and the duration of the spawning period differ amongst these species. The significance of differences in the reproductive biology of these species is discussed.

Population Ecology of the Grooved Tiger Prawn *Penaeus semisulcatus* in the North-western Gulf of Carpentaria, Australia; I: Growth, Movement, Population Age Structure, and Infestation by the Bopyrid Parasite *Epipenaeon ingens*

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Concurrent trawl survey and tag-recapture studies carried out in the north-western Gulf of Carpentaria between August 1983 and March 1985 provided a reliable and detailed description of the growth, movement and population age structure of the grooved tiger prawn, *Penaeus semisulcatus*. Growth curves based on the tag-recapture data were used to interpret the length-frequency data collected from the trawl surveys and determine the number of year classes present. The length-frequency data pertaining to the 1984 year class were identified and separated from the adjacent year classes and provided the basis for a description of the longevity of the species and its off-shore movement patterns. The effect of infestation by the bopyrid parasite *Epipenaeon ingens* on growth and movement was also examined.

Longevity of the species is about two years but, in the north-western Gulf of Carpentaria, very few survive beyond 18 months of age. Subadults recruited to the off-shore fishing grounds during summer and autumn (November to March) at sizes of between 20 and 25 mm carapace length (CL), corresponding to approximate ages of between 4 and 6 months. By 18 months of age, males reached a size of about 39 mm CL and females about 50 mm CL. Growth rates of both sexes were affected by the presence of *E. ingens*. Infested males and females grew at about the same rate and to the same size; for males this was faster and larger, but for females slower and smaller. The population rapidly dispersed off-shore during the autumn and winter months (from December to July) with highest abundance in depths of 35 to 40 m, but it also extended well beyond the commercial fishery into depths greater than 50 m. However, in late Winter and Spring (August to November), the population contracted shorewards and was concentrated in depths of 25 to 35 m, with very few in depths greater than 45 m. Although prawns infested with *E. ingens* showed a similar off-shore movement followed by a shore-ward contraction, the movement was less than the uninfested population. The sex ratio within the year class remained at around 1:1 from the time of recruitment to about one year of age. Thereafter, the percentage of females declined steadily, reaching 25% by about 18 months of age. The percentage of females showed no similar decline for prawns infested with *E. ingens*.

A Preliminary Study of Age and Growth of a Tropical Damselfish (*Stegistes apicalis*)

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By assuming that the fine increments on otoliths of *Stegistes apicalis* from the northern Great Barrier Reef were deposited on a daily base, annual bands on the otoliths can be validated by counting daily increments. There was no significant difference on the relationships between body length and weight in both sexes. Age and growth structures were investigated using ageing methods of otolith with preliminary results that the maximum attainable size (L_{inf}) of Von Bertalanffy equation was 154.6 mm whilst the growth coefficient (K) was 0.148.

Age, Growth and Structure of the Vertebra in the School Shark *Galeorhinus galeus* (Linnaeus, 1758) from Southern Brazil[A]

Beatrice Padovani Ferreira
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The age and growth of the Brazilian school shark *Galeorhinus galeus* was studied from rings in the vertebra and length frequency data. The samples were collected by trawling off the southern Brazilian coast from June 1980 to September 1986. Standard histological techniques and micro-radiography were used to determine the pattern of vertebral calcification. The vertebra presents a pattern of alternating heavily and less heavily mineralised zones, narrow and wide, respectively. The narrow zones were named rings, which are translucent under transmitted light and white to the micro-radiograph. These rings are probably laid down yearly in a slow growing phase extending throughout the four winter months of June to September. The largest number of rings observed was 41. Lengths at age were back-calculated and the von Bertalanffy growth parameters estimated. ELEFAN software was used to determine the growth curve best fitted to length-frequency data.

[A] This research was conducted at Fundacao Universidade do Rio Grande, Departamento de Oceanografia, Rio Grande, RS, 96200, Brazil.

WORKSHOP PROGRAM

WORKSHOP PROGRAM

The Measurement Of Age And Growth in Fish and Shellfish

Day 1 (Wednesday 22 August)

0900 - 0915 Introduction: Dr John Glaister, President ASFB

Session 1

0915 - 1030 Keynote Address: Dr Richard Beamish, Director,
Biological Sciences Branch,
Pacific Biological Station,
Nanaimo, Canada.

1030 - 1100 MORNING TEA

Session 2

Determination of Age

1100 - 1245 Session Chairman: Dr David Smith

(a) *Current Usage and Validation - Fish and Sharks*

Panellists:
Kevin Rowling
Tony Fowler
John Anderson
Terry Walker
Ron Thresher
John Kalish

1245 - 1345 LUNCH

1345 - 1500 (b) *Current Usange and Validation - Commercial Invertebrates*

Panellists:
Bruce Phillips
David Die
Warwick Nash
Peter Young

1500 - 1530 AFTERNOON TEA

1530 - 1715 (c) *Future Directions and Problems Encountered*

Panellists:
Greg Jenkins, VIMS
Ron Thresher
Craig Proctor
David Ritz
David Smith
Bob Kearney

Day 2 (Thursday 23 August)

Session 3

Inferences about growth and from growth

Session Chairman: Dr Keith Sainsbury

0900 - 1030 (a) *Current usage of growth models. Appropriate forms and limitations.*

Panellists:
Warwick Nash
Bruce Phillips
Kevin Rowling
David Die
Ian Somers

1030 - 1100 MORNING TEA

1100 - 1230 (b) *Estimation and comparison of model parameters from age, length frequency and growth increment data.*

Panellists:
Ron Sandland
Mark Palmer
Kathy Haskard
Chris Francis
Nik Dow

1230 - 1330 LUNCH

1330 - 1500 (c) *Use of age and growth information in fisheries assessment.*

Panellists:
Keith Sainsbury
Warwick Nash
Tony Smith
Kay Radway Allen

Session 4

General discussion and summing up

Chairman: Dr Peter Young

1500 - 1545 *General Discussion: Age and Growth*

Panellists:
Keynote speaker
Session Chairmen

1545 - 1615 AFTERNOON TEA

1615 - 1715 *Synthesis and Applications* - Dr Kay Radway Allen

Concluding Discussion

Poster Session: J. Anderson
Agreed Glossary of Terms: D. Smith
Bibliography of Australian Publications: R. Tilzey
National Review of Age Determination Studies: BRR

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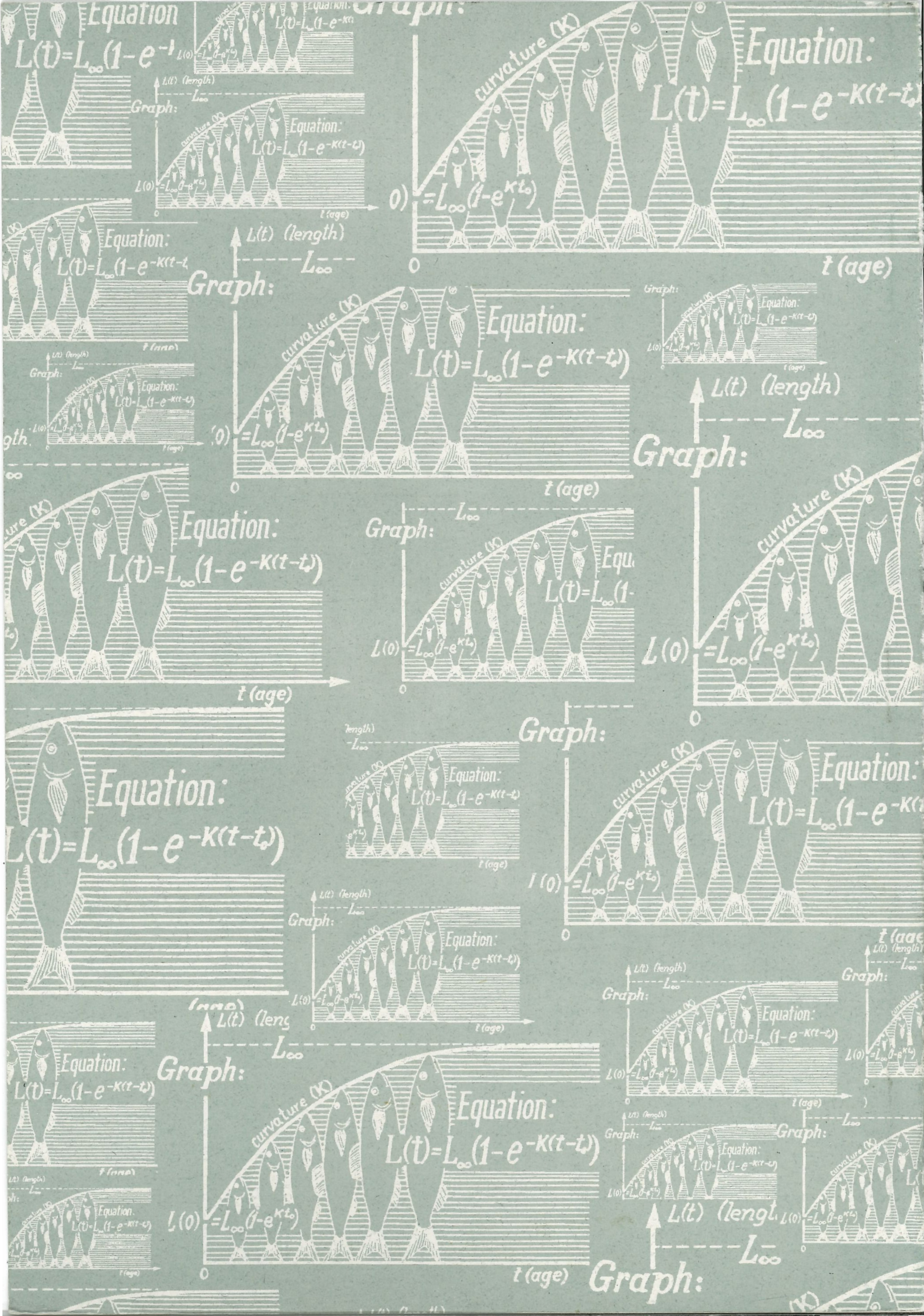
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L(t) (length)
L∞
curvature (K)
Equation:
L(t)=L∞(1-e^{-K(t-t0)})
L(0)=L∞(1-e^{Kt0})
0
t (age)