Ageing in Coral Reef Fishes: Do we Need to Validate the Periodicity of Increment Formation for every species of Fish for which we collect age-based Demographic Data?

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AGEING IN CORAL REEF FISHES: DO WE NEED TO VALIDATE THE PERIODICITY OF INCREMENT FORMATION FOR EVERY SPECIES OF FISH FOR WHICH WE COLLECT AGE-BASED DEMOGRAPHIC DATA?

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1 Preamble

The purpose of this chapter is to consider the question "Is it necessary to validate the periodicity of increment formation in every species of fish for which we seek age-based demographic data"? The focus is on coral reef fishes. Four issues require consideration. Firstly, validation programs are expensive in terms of resources and time. This is especially important for coral reef fishes as resources available to tropical fisheries are often very limited. Secondly, many modern techniques used to validate the accuracy of age estimates require field and laboratory infrastructure that may not be available to fisheries laboratories serving coral reefs. Thirdly, the great majority of validation studies have confirmed the annual periodicity of increment formation. Fourthly, opportunities to study undisturbed populations of reef fishes from which reference age data can be derived are limited due to over-fishing and habitat alteration. We argue for a more strategic approach to age-based studies in coral reef fishes.

We firstly acknowledge the substantial effort and expertise devoted to ensuring appropriate standards of accuracy in the ageing of fishes. As a result of this effort, there are now numerous examples where the increments observed in sagittal otoliths have been demonstrated to form annually. At some stage we might assume that such increments are annual in nature without the requirement that the assumption of annual formation be validated in every species for which age data are published. We argue that the time to accept this assumption has now arrived. This does not imply that we should cease validation studies. We would make a distinction between studies of individual species of widespread commercial importance, especially if they are the targets of new fisheries, and those of species assemblages for which the focus is ecological and evolutionary processes. Demanding validation of age estimates for all species before publication in the latter type of study will distort the allocation of scarce resources and result in substantial delays in dissemination of age-based data.

2 The historical setting

Teleost fishes are the most readily aged of all vertebrates. This reflects the unique properties of their otoliths, including continuous patterns of growth and the absence of metabolic reworking of otolith material once deposited (Campana & Thorrold 2001). Age-based information is of crucial importance to the understanding of life history features of fishes (Beverton & Holt 1957), especially as they exhibit highly plastic patterns of growth (Gust et al. 2002, Swain et al. 2003). Research over the last two decades has demonstrated that thin sections of sagittal otoliths provide the most consistent and reliable records of age (Secor et al. 1995, Campana 2001, Begg et al. 2005), especially for fish with ages exceeding 20 years. The increasing availability of age-based information now makes it possible to develop comprehensive studies of life-histories within this most diverse and abundant group of all vertebrates.

Age-based data have been rapidly accumulating over the past two decades. The process has been highly uneven with respect to the lineages of fish that have been examined, however, as well as the environmental settings where the studies have been carried out. Teleost fishes, like most other groups of living organisms, show strong latitudinal gradients in species richness. Our ignorance is greatest for the diverse assemblages characteristic of low latitude shallow water environments.

History strongly influences the course of research enterprises, and the study of fish population dynamics is no exception. It is important to trace the course of fisheries science over the latter half of the last century in order to understand why we are ignorant about the demography of large groups of fishes. Pauly (1998a) identified the publication of the seminal study of Beverton and Holt (1957) as the genesis of modern fisheries science and noted the critical importance of age-based demographic information in this development. The dynamics of those fishes that supported extensive multi-national fisheries in northern temperate and boreal waters (mainly gadids, clupeoids and pleuronectids) became a research priority (Beverton 1992). The success of Beverton & Holt (1957) as a blue-print for fisheries science was due to two factors. Firstly, the existence of a substantial archive of fisheries data, scientific infrastructure and expertise developed in association with the industrial-scale fisheries of northern temperate and boreal waters. Secondly "coldwater fish could straightforwardly be aged by reading annuli on otoliths" (Pauly 1998a). In the same study, Pauly provided a comprehensive account of the difficulties faced by tropical fisheries biologists, including ageing studies, and advocated length-based approaches as an alternative. Pauley presented a convincing case for the difficulties associated with tropical fisheries biology, partly based on the argument that identification of growth increments in calcareous structures was easier in temperate than in tropical species (Munro 1983, Gjosaeter et al. 1984, Fowler 1995), a fact usually associated with the stronger seasonal cycling characteristic of higher latitudes. Subsequent research demonstrated, however, that tropical fish could be aged through the reading of annuli in otoliths.

A problem in fisheries biology has been the underestimation of age in many commercially important species (Campana 2001), especially those inhabiting deeper water (Berkeley et al. 2004, Cailliet et al. 2001, Munk 2001). Campana (2001) also emphasized the methodological issues where artefacts of otolith preparation frequently led to underestimation of ages and thus resulted in artificially high estimates of growth and mortality rates. Campana also summarized the protocols by which the frequency of growth increments and absolute ages in fishes were validated. The manifest impacts of fishing on long-lived species demanded greater accuracy in the assignment of ages to individuals and focused attention on the need to identify artefacts in otolith preparation, with particular emphasis on those that resulted in underestimation of ages.

Advances in the methods used in validating age estimates have resulted in greater accuracy in the interpretation of age, including for long-lived, deep water species. The most significant result of these advances has been provided by the opportunity to use combinations of methods (e.g., bomb radiocarbon, marginal increment analysis, chemical marking of otoliths) to confirm age estimations in a wide variety of species. Coupled with this has been the improvement of the preparation and optical resolution of otolith sections and the capacity to store and transmit high quality images of otolith preparations. The validation of different methods (Campana 2001) and the associated technical advances have resulted in increasing confidence that thin sections of otoliths are providing the basis for accurate age interpretation. These advances occurred in an environment dominated by extensive commercial fisheries supported by well developed sampling and laboratory infrastructure.

The most influential paper in the context of validation studies was that of Beamish & McFarlane (1983) who emphasized the importance of validation. They argued for a comprehensive protocol, including validation of all age classes for each species studied, and warned that extrapolation of the results from one population even to other populations of the same species was dangerous. The messages in this widely cited study (263 citations by July 2003) were reinforced by the comprehensive review of Campana (2001) who also prioritized different validation protocols.

The challenges of validation in most cases were successfully met during the two decades spanning the publication of these studies (Secor et al. 1995, Campana 1999, 2001). In almost every case, the results have confirmed the hypothesis that structures observed in sectioned sagittae represented annual increments, allowing estimates of age from direct counts. The support for annual periodicity of increments is very strong, even though there may be a bias due to the non-reporting of negative results. The most impressive evidence comes from two sources. Firstly, there have been multiple studies of widely distributed species in which controversies have been resolved via the application of independent methods (Baker & Wilson 2001, Kalish 2001, Cass-Calay & Bahnick 2002, Fischer et al. 2005). Secondly, with increases in the sample sizes of fish aged from sagittal otoliths, congruent demographic patterns are emerging among phylogenetically-related groups of species, including those of deep water (Cailliet et al. 2001, Munk 2001) and coral reef environments (Choat and Robertson 2002).

Access to large vessels, modern laboratory infrastructure and innovative research approaches based on the analysis of bomb radiocarbon and the use of radiochemical dating, (Kalish 1993, Campana 1999) have been crucial. The new methods demanded a high level of technical skill and expensive instrumentation, but they allowed fisheries scientists to validate a wide range of species including those from deep water environments (Cailliet et al. 2001). These studies resolved some controversial issues with respect to fish life spans and confirmed that the deep sea was dominated by populations of very long-lived fishes with slow growth and extended generation times.

A more strategic approach to the study of ageing in tropical teleost populations is now required. At present, ageing and demographic studies proceed on a case by case basis in which detailed investigations are carried out when the exploitation of a particular species becomes an issue. The logic and future directions for this type of research have been debated in only in a few instances. We pose two questions: 1) Do the benefits of validating the age of every species studied outweigh the need for a more comprehensive demographic picture based on the assumption that formation of growth increments in otoliths are annual?; and 2) How many more species must be validated before annual periodicity in increment formation is accepted as a credible assumption? The purpose of this chapter is to present the case that attention to single-species detail should be be traded off against studies aimed at providing broader perspectives on prevailing patterns of demography and age-structure among large groups of species, based on the assumption of annual periodicity in otolith increment formation.

There are two further issues that should be considered in the context of reef fish ageing. Firstly, molecular tools have allowed us to develop an evolutionary perspective on reef fish life histories and demography. The opportunities for evaluating ecological and evolutionary hypotheses in this diverse assemblage of vertebrates are exciting. Secondly, over-fishing and habitat destruction are increasingly impacting tropical fish assemblages (Jackson et al. 2001, Pauly et al. 1998). Both the opportunities for comprehensive ecological and evolutionary research and the urgency generated by increasing over-fishing suggest that delays in analyzing age-based dynamics of tropical fishes will be problematic. If, as suggested by Bell (2001), chronologies must be validated *before* "ecological and evolutionary studies *become* possible" then it is unlikely that comprehensive demographic studies will ever see the light of day. Time is short and resources limited, especially for tropical species. Understanding of reef fish demography lags behind that of temperate species. There is a lot of time to make up.

2.1 WHAT DID BEAMISH & MCFARLANE (1983) ACTUALLY SAY AND HOW DID IT IMPACT ON SUBSEQUENT STUDIES?

The core issues of Beamish & McFarlane (1983) were illustrated by two examples of the consequences of non-validation. One was a freshwater fish (*Catostomus*) and the second a deepwater marine fish (*Sebastes*). In both instances, initial ageing was based on the examination of growth increments in scales. Subsequent investigation of sectioned fin rays in *Catostomus* and sectioned sagittal otoliths in *Sebastes* showed that in each case the initial estimates of growth and mortality rates were significantly greater than the true rates. The assumption of rapid growth and high natural mortality rates had serious consequences when applied to long-lived species, especially for *Sebastes*.

Two primary messages emerged. Firstly, *underestimation* of true ages was the most serious problem facing fisheries biologists and, secondly, scales were an inappropriate structure for age estimation. The concerns of Beamish & McFarlane (1983) and Campana (2001) have been met over the past two decades, however, in that ageing studies recognize the reality of extended life spans in fishes and focus on sagittal otoliths to assess age. Long-lived fishes from a range of environments are being identified and reported with increasing frequency (Cailliet et al. 2001, Reznick et al. 2002). The literature has confirmed repeatedly that sectioned sagittal otoliths accurately record older ages in many species of teleosts (Table 1). Modern image-capture and analysis techniques have improved vastly the capacity to identify and measure increments in sectioned sagittae. Figure 1 illustrates the capacity to obtain consistent estimates of increment widths near the otolith margin in long-lived reef fish species. Otolith increments can be clearly identified and analyzed in tropical species, providing reliable estimates of growth processes. The assumption that increments identified in sectioned sagittae of long lived fish are annual is a realistic working hypothesis.

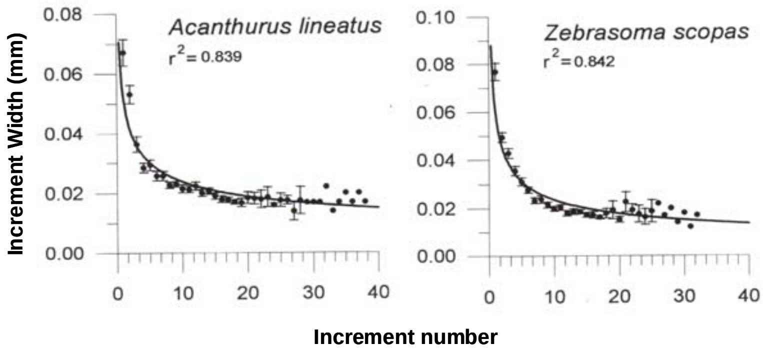

Figure 1. The relationship between increment width (mm) and increment number in two long-lived species of acanthurid fishes (Choat & Axe 1996). N=5 for each species.

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There remains the possibility, however, that the record of annual growth increments will not accurately reflect the true age of the fish. Why would this occur, and if so, how frequently? Firstly, rings may be deposited annually but may sometimes be difficult to detect. Secondly, the rings may be always detectable but deposited more frequently or less frequently than each year. For example, while the pattern of increment formation may be annual, there might be some years in which deposition does not occur. Individual increment formation may be modified or suppressed either in individuals or in populations, possibly in response to climatic forcing (Meekan et al. 1999). Moreover, there is no doubt that in some species growth increments are difficult to identify (Figure 2) and measure, and that there is a gradient in increment clarity from low to high latitudes (Figure 3). These alternatives cannot be distinguished (Francis 1995), but unless they occur consistently they are unlikely to have major effect on the estimation of life spans, especially in long-lived species.

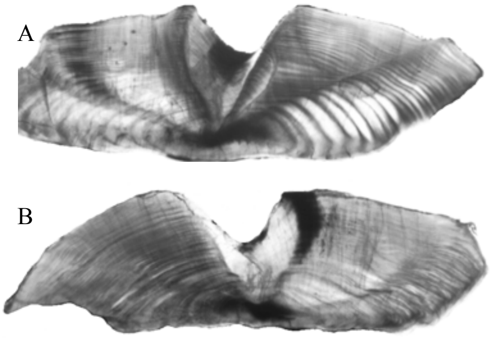

Figure 2. Transverse sections of sagittal otoliths of two species of serranid fishes A) *Epinephelus polyphokadian* and B) *Cephalopolis argus* sampled from the same latitude, 18° S on the Great Barrier Reef. *E. polyphokadian* consistently had clear annual growth increments whereas increments in *C.argus* where invariably difficult to read.

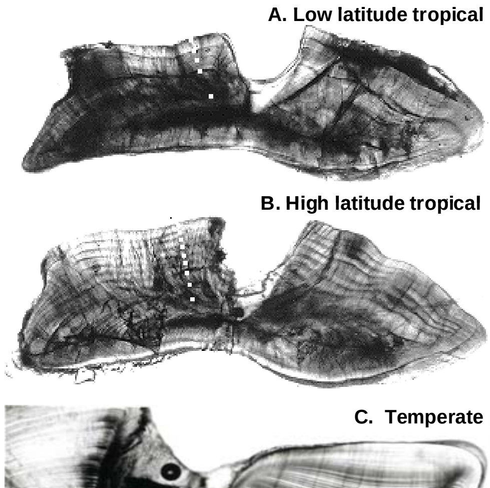

Figure 3. Gradient of clarity in the display of growth increments in sectioned sagittae from low to high latitudes. A. Sectioned sagitta from the tropical parrot fish *Sparisoma viride* from latitude 9° N and B, from 23 ° N. C is the sectioned sagitta of a temperate water reef fish *Girella tricuspidata* from 36 ° S.

A much greater problem arises in situations where increments are clearly displayed but do not reflect an annual signal. These will not simply truncate or extend age distributions, they will give an erroneous picture of population dynamics. Examples are the European hake *Merluccius merluccius* (Morales-Nin et al. 1998), *Pagrus pagrus* growing in culture (Machias et al. 1998) and the reported non-annual periodicity of increment formation in lutjanids (Milton et al. 1995) (see below).

Table 1 provides examples of three important groups of exploited reef fishes in which recent validations of the annual periodicity of increment formation have been completed. These are serranids (groupers), lutjanids (snappers) and sparids (porgies). The first two occur mainly in coral reef waters, while the third group also extends into temperate reef and estuarine environments. The majority of validations were accomplished using marginal increment analysis (MIA), a reflection of the logistic and infrastructure issues in tropical fisheries. The table identifies widely distributed species within each family that have been subject to at least two independent validation protocols. These are *Epinephelus flavolimbatus, Lutjanus campechanus, L. erythrograma, L. malabaricus, L. sebae, L. griseus* and *Pagrus auratus*. In each case, the validation of annual periodicity of increments visualized in sectioned sagittae was confirmed independently through bomb radiocarbon analysis.

Table 1. Species of the families Serranidae, Lutjanidae and Sparidae from tropical and warm temperate environments in which periodicity of increment formation has been validated recently. Shading indicates species in which annual periodicity has been confirmed independently by bomb radiocarbon analysis. Ages were derived from sectioned sagittae unless otherwise indicated with * following the method, in which case whole sagittae were used. ***Legend:*** MIA – Marginal increment analysis; OTC – Oxytetracycline injection; δ^{14} C – Bomb Radiocarbon.

Serranidae

Species	Method	Reference
Epinephelus adscensionis	MIA	Potts & Manooch 1995
Epinephelus cruentatus	MIA	Potts & Manooch 1999
Epinephelus flavolimbatus	MIA	Manickchand-Heileman & Phillip 2000
Epinephelus flavolimbatus	δ^{14} C	Cass-Calay & Bahnick 2002
Epinephelus fulvus	MIA	Potts & Manooch 1999
Epinephelus fuscoguttatus	OTC MIA	Pears et al 2005
Epinephelus guttatus	OTC	Sadovy et al 1992
Epinephelus guttatus	MIA	Potts & Manooch 1995
Epinephelus itajara	MIA	Bullock et al 1992
Epinephelus merra	OTC	Pothin et al 2004
Epinephelus niveatus	MIA	Wyanski et al 2000
Epinephelus octofasciatus	δ^{14} C	Kalish 2001
Epinephelus striatus	MIA	Bush et al 1996
Cephalopholis boenak	MIA	Chan & Sadovy 2002
Cephalopholis cyanostigma	OTC	Mosse 2001

Species	Method	Reference
Plectropomus maculatus	OTC	Ferreira & Russ 1992
Plectropomus leopardus	OTC	Ferreira & Russ 1994
Myctoperca microlepis	MIA*	McErlean 1963
Myctoperca microlepis	MIA	Hood & Schlieder 1992
Myctoperca bonaci	MIA	Crabtree & Bullock 1998
Myctoperca interstitialis	MIA	Manickchand-Heileman & Phillip 2000
Polyprion oxygeneios	OTC	Francis et al 1999
Polyprion americanus	MIA	Peres & Haimovici 2004
Serranus cabrilla	MIA	Tserpes & Tsimenides 2001
Centropristis striata	MIA	Hood et al 1994
Lutjanidae		
Lutjanus adetti	OTC	Newman et al 1996
Lutjanus analis	MIA	Mason & Manooch 1985
Lutjanus analis	MIA	Burton 2002
Lutjnaus argentimaculatus	OTC	Cappo et al 2000
Lutjnaus argentimaculatus	OTC	Russell et al 2003
Lutjanus bohar	OTC	Marriott & Mapstone 2006
Lutjanus campechanus	MIA	Patterson et al 2001
Lutjanus campechanus	MIA	Wilson & Nieland 2001
Lutjanus campechanus	δ^{14} C	Baker & Wilson 2001
Lutjanus campechanus	Radiometric	Baker et al 2001
Lutjanus campechanus	MIA	White & Palmer 2004
Lutjanus erythropterus	Radiometric*	Milton et al 1995
Lutjanus erythropterus	OTC	Cappo et al 2000
Lutjanus erythropterus	δ^{14} C	Kalish 2001
Lutjanus fulviflamma	MIA	Kamukuru et al 2005
Lutjanus griseus	MIA	Burton 2001
Lutjanus griseus	δ^{14} C	Fischer et al 2005
Lutjanus johnii	δ^{14} C	Kalish 2001
Lutjanus kasmira	Daily Rings	Morales-nin & Ralston 1990
Lutjanus malabaricus	Radiometric*	Milton et al 1995
Lutjanus malabaricus	OTC	Cappo et al 2000
Lutjanus malabaricus	δ^{14} C	Kalish 2001
Lutjanus malabaricus	MIA	Newman 2002
Lutjanus peru	MIA	Rocha-Olivares 1998
Lutjanus quinquilineatus	OTC	Newman et al 1996
Lutjanus sebae	Radiometric*	Milton et al 1995
Lutjanus sebae	OTC	Cappo et al 2000
Lutjanus sebae	C14	Kalish 2001

Species	Method	Reference
Lutjanus sebae	MIA	Newman & Dunk 2002
Lutjanus synagris	MIA	Manickchand-Dass 1987
Lutjanus synagris	MIA	Luckhurst et al 2000
Aprion virescens	MIA	Pilling et al 2000
Pristipomoides multidens	MIA	Newman & Dunk 2003
Rhomboplites aurorubens	MIA	Hood & Johnson 1999
Ocyurus chrysurus	MIA	Manooch & Drennon 1987
Sparidae		
Acanthopagrus berda	MIA	James et al 2003
Acanthopagrus bifasciatus	MIA	Grandcourt et al 2004
Acanthopagrus butcheri	MIA	Sarre & Potter 2000
Archosargus probatocephalus	MIA	Beckman et al 1991
Archosargus probatocephalus	MIA	Dutka-Gianelli & Murie 2001
Argyrops spinifer	MIA	Grandcourt et al 2004
Argyrozona argyrozona	OTC	Brouwer & Griffiths 2004
Dentex dentex	MIA	Machias et al 2002
Diplodus vulgaris	MIA*	Gonclaves et al 2003
Diplodus vulgaris	MIA*	Pajuelo & Lorenzo 2003
Diplodus sargus	MIA	Pajuelo & Lorenzo 2002a
Diplodus annularis	MIA*	Pajuelo & Lorenzo 2002b
Lithognathus aureti	M/Recap	Holtzhauzen & Kirchner 2001
Lithognathus mormyrus	MIA	Lorenzo et al 2002
Lithognathus mormyrus	MIA	Pajuelo et al 2002
Pagrus auratus	δ^{14} C	Kalish 2001
Pagrus auratus	OTC	Ferrell et al 1992
Pagrus auratus	OTC	Francis et al 1992
Pagrus pagrus	Culture	Machias et al 1998
Pagrus pagrus	MIA	Hood & Johnson 2000
Polysteganus undulosus	MIA	Chale-Matsau et al 2001
Rhabdosargus sarba	MIA/OTC	Radebe et al 2002
Sarpa salpa	MIA	van der Walt & Beckley 1997
Sarpa salpa	MIA	Villamil et al 2002
Sparodon durbanensis	MIA	Buxton & Clarke 1991

Lutjanus campechanus, important in the commercial and recreational fisheries of the south-eastern USA, was aged from sectioned sagittae and validated by MIA in three independent studies (Wilson & Nieland 2001, Patterson et al. 2001, White & Palmer 2004). The accuracy of annuli revealed in sectioned sagittae was confirmed by bomb radiocarbon analysis (Baker & Wilson 2001) and radiometric analyses (Baker et al.

2001). A similar confirmatory procedure was carried out for *E. flavolimbatus* with sagittal increments validated (MIA) by Manickchand-Heileman & Phillip (2000) later confirmed by bomb radiocarbon analysis (Cass-Calay & Bahnick 2002).

What are the challenges to studies that clearly confirm the one ring – one year hypothesis? One of the most explicit is provided by Milton et al. (1995). They found differences in counts of the increments observed in sectioned compared with whole otoliths of the tropical lutjanids *Lutjanus erythropterus, L. malabaricus,* and *L. sebae* from unexploited populations in the Gulf of Carpentaria, Australia. Increments in sectioned sagittae were 1.6 to 2.4 times the number found in whole otoliths. Pb-210/Ra-226 radioactive disequilibria of both whole and cored otoliths were measured to obtain independent estimates of age. The whole-otolith counts agreed better with the radiometric age in samples whose sectioned and whole-otolith ages differed by more than 4 years. The conclusions of this paper were particularly important as the species were subject to commercial exploitation elsewhere and independent studies based on sectioned sagittae indicated that each species (in contrast to the radiometric assessments) was long lived with a relatively slow growth rate.

A substantial amount of additional work on these species using both marginal increment analysis and oxytetracycline (OTC) marking (Newman et al. 2000, Cappo et al. 2000, Newman 2002, Newman & Dunk 2002) on both the east and west coasts of Australia confirmed that sectioned sagittae provided estimates of greater longevities and slower growth rates than those obtained from radiometric analyses and whole otoliths. Confirmation of the estimates of age structure and growth rates derived from MIA and OTC marking was provided by Kalish (2001), who validated the accuracy of these age estimates by analysis of bomb radiocarbon for all three species. This example demonstrates the benefits of using a combination of methods to resolve problems where artefacts of otolith analysis have resulted in discrepancies (in this case underestimation) of ages (Campana 2001). The value of bomb radiocarbon analysis has been confirmed clearly by Kalish (2001), who reported validation of the accuracy of annual increments in sagittae in 23 species from a wide range of environments including the deep sea, open ocean and temperate and tropical reefs. In addition, Cailliet et al. (2001) demonstrated that radiometric ageing confirmed the age estimates of four species of the genus *Sebastes* derived from sagittal growth increments.

The only problematic examples in the Kalish (2001) study concerned species from the open ocean and deeper waters. These included species in which the environment of juveniles was variable with respect to δ^{14} C (*Pristipomoides multidens),* otolith structure was difficult to interpret (*Hyperoglyphe antarctica)* and species in which non-otolith structures were used in ageing (*Xiphius gladius).* Although problems may arise in deep water groups (e.g., trachicthids, oreosomatids) with respect to the pattern of penetration of δ^{14} C by depth and with interpretation of otolith morphology, bomb radiocarbon analysis has confirmed longevity in many deep sea species.

2.2 WHY HAS THE AGE-BASED ANALYSIS OF TROPICAL FISH POPULATIONS MOVED RELATIVELY SLOWLY?

The life history features of stocks in shallow water tropical regions are poorly known compared to the temperate and deep water fishery stocks. This situation is being rectified through increasing studies of larger, commercially important species.

Demographic analysis of coral reef fishes has had a mixed history. Whilst Beamish & McFarlane's (1983) paper has received numerous citations, the FAO report on ageing tropical fish by Gjosaeter et al. (1984) largely has been forgotten. Gjosaeter and co-workers, however, made a pertinent point. They stressed that whilst the importance of considering the different validation methods should not be underrated, worthwhile studies can still be performed without rigorous validation. They claimed that even 'rather rough indications [of age] may be sufficient'. In fact, the record was more informative than suggested by Gjosaeter et al. (1984). McErlean (1963) showed clearly that tropical serranids could be aged through analysis of sagittal otoliths. Subsequent studies on the dynamics of tropical fish (e.g., Munro 1983) did not expand on these findings, mainly because otolith structure in tropical fishes is often difficult to interpret compared with that seen in high latitude fishes.

Age-based demographic studies of tropical fishes lag behind their temperate counterparts. This reflects to some extent the view that it is not possible reliably to age fishes from low latitudes except through daily increments (eg: Polunin & Roberts 1996). Examples to date, however, demonstrate that fish at low latitudes retain a reliable record of age in sagittal otoliths (Choat et al. 2003, Robertson et al. 2005). In addition, the view that tropical fishes have shorter life spans and higher growth and mortality rates than their temperate equivalents (Pauly 1994, 1998b) seems to have diverted attention from age-based to size-based models of reef fish demography. Surprisingly, the view that there are few examples of age based studies on tropical marine fishes and that tropical species generally have fast growth rates is still being promulgated (Henderson 2005). It is now clear, however, that the perciform assemblages that constitute reef fish fauna harbour a great deal of ecological diversity, including a wide range of life spans, growth rates and size structures — including long-lived and slow-growing species (Choat & Robertson 2002).

2.3 DO REEF FISHES PRESENT SPECIAL CHALLENGES TO AGE-BASED STUDIES AND VALIDATION?

The answer is yes, both in terms of their biological features and the nature of tropical fisheries biology. Local and regional diversity in reef fishes is greater than that encountered at higher latitudes (Helfmann et al. 1997). Reef fish assemblages are highly diverse at local scales and characterized by complexes of closely related species, though many species are rare at local scales (Figure 4). Consequently, most reef fisheries are usually multi-specific (Polunin et al. 1996). There is increasing evidence of demographic variation at a variety of scales over the geographic range of a species, reflecting the influence of habitats, environmental gradients and evolutionary history (Kritzer 2002, Williams et al. 2003, Robertson et al. 2005). Many tropical species are longer lived than anticipated, attaining ages in excess of 30 years or more (Choat &

Robertson 2002), although the majority of reef fishes alive today were recruited post-1970, after the cessation of nuclear atmospheric testing, so diminishing the utility of bomb radiocarbon methods for validation. Flat-topped growth curves, in which size and age are decoupled for the majority of the life span, characterize many lineages so that size-based estimates of population processes are not informative (Robertson et al. 2005, Marriott et al. 2007).

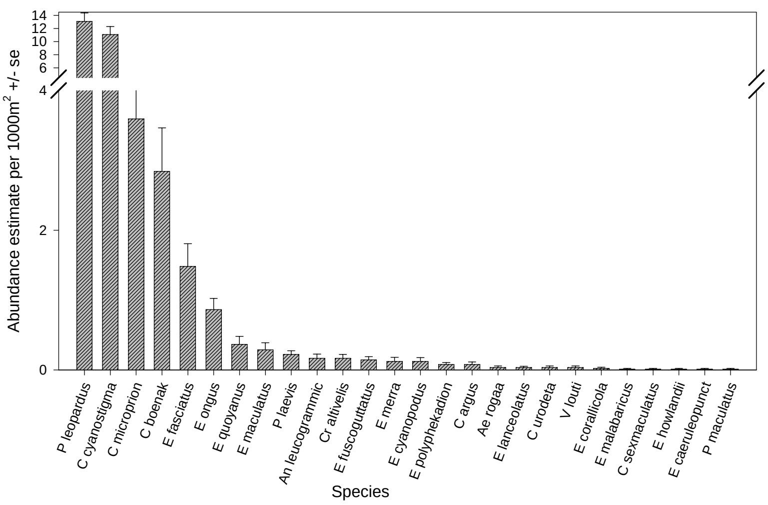

Figure 4. Abundance estimates of serranid fishes from northern midshelf reefs of the Great Barrier Reef Marine Park. With the exception of *Plectropomus leopardus* (highly characteristic of the GBR), larger commercially important species are rare with abundances of less than 1 individual per 1000 m^2 (Pears 2006).

The early life history of reef fishes provides a number of challenges for tropical fisheries biologists. Knowledge of gyres and other oceanographic features has provided a framework for understanding the pattern and magnitude of recruitment variation in commercially important species in temperate environments (Cushing 1975, Iles & Sinclair 1982, Sinclair 1988). The environment for pre-settlement reef fishes, however, is complex (Cowen 2002), with variable and relatively unpredictable movement of water masses. Different groups of fishes exhibit very different capacities for active movement and directional swimming during the “larval” phase (Stobutzki & Bellwood 1997, Jones et al. 1999). The result is that patterns of recruit variation are difficult to predict in coral reef systems.

Coral reef fishes have been exploited since prehistoric times (Wing & Wing 2001), but historically their fisheries have been subsistence or artisanal. The highly dispersed nature of coral reefs means that fisheries research in many localities has substantial logistical costs and is often expeditionary in nature. The recent development of industrial level coral reef fisheries (largely associated with the live reef fish trade) has been competitive, highly exploitative, and lacking a concomitant development of research infrastructure (Sadovy and Vincent 2002). The distribution of coral reef fisheries across broad, politically complex geographical regions means that they lack a shared information infrastructure. FISHBASE (Froese & Pauly 2000) is an exception.

3 Validation protocols and coral reef fishes

The most comprehensive listing of validation protocols is in Campana (2001) where 16 methods are listed ordered by scientific value. Not all of these are appropriate for reef fishes. We deal with the most realistic protocols below, and provide comments on the methodological issues that arise in each case.

Release of known age fish into the wild. The most effective method involves the release of hatchery reared chemically mass-marked fish into the natural environment. There have been no instances in which reef fish have been successfully established on reefs through the release of cultured juveniles of known age, however, despite the success of re-seeding sessile invertebrates on coral reefs. A key problem is the difficulty associated with closing the life-cycle via culture experiments with groups such as serranids, lutjanids, haemulids and labrids. The high mortality rates experienced by newly recruited reef fishes and the possibility that cultured fish released back into the environment would suffer enhanced mortalities (Carr et al. 2004, Fairchild & Howell 2004, Masuda et al. 2003) suggest that this will not be effective for reef fishes. It is no surprise that success has been primarily with fresh water species (Campana 2001).

Bomb radiocarbon. This method is unlikely to be effective for future work on reef fishes because the hatch dates of most reef fish alive today do not extend back to the 1960s, when nuclear tests provided signature isotopes that could be incorporated inot otoliths. Moreover, the costs of the method will be beyond research budgets of many tropical institutions and most workers dealing with tropical fish species. Archived otoliths might be used to obtain specimens with the correct temporal window for bomb radiocarbon dating, though very little archival material from the appropriate periods exists, because of the prevailing views during the 1970s and 1980s that otoliths would not provide an acceptable basis for ageing tropical fish. The method has been most valuable in confirming age estimates in long-lived commercially important species.

Mark-recapture of chemically-tagged wild fish. This has proved to be the most rigorous and cost-effective method for validating increment periodicity in reef fishes. Most examples are Australian (Ferreira & Russ 1992, 1994, Lou 1992, Choat & Axe 1996, Choat et al. 1996, Newman et al. 1996, Cappo et al. 2000, Hernaman et al. 2000) or from tropical Atlantic waters (Bullock et al. 1992, Sadovy et al. 1992, Crabtree et al. 1995, 2002, Crabtree & Bullock 1998, Luckhurst et al. 2000, Choat et al. 2003, Robertson et al. 2005). Drawbacks lie in the initial capture of fish in a condition that makes tagging worthwhile and the difficulty of securing adequate recaptures. The local rarity of many species (Figure 4) and the structural complexity of the reef environment means that initial tagging rates generally will be low. Coral reef fish cannot usually be caught alive in large numbers and must be handled with great care to avoid eye infections and skin lesions. Any injury to the fish associated with capture (by line fishing and traps especially) or tagging usually results in high initial mortalities after release through predation. Logistic difficulties associated with capture means that tagging rates are low (compared with temperate fishes), which influences recapture rates, although site-fidelity of many coral reef fishes may make recapture easier. It is desirable to leave tagged fish as long as possible in the field, but recapture rates even for long-lived species are usually very low, reflecting both mortality and tag loss. Moreover, tagging locations of reef fish are often widely dispersed and in remote locations. In many instances the cost-effectiveness of recaptures may be a significant problem. The primary method for recapture to date has been selective spearing following visual identification of tagged individuals. Difficulties with initial capture and subsequent recapture compound rapidly with increase in size of the fish. Despite these problems, there is an increasing number of successful validations of annual increment periodicity for coral reef fishes (Choat and Axe 1996, Cappo et al. 2000, Robertson et al. 2005, Marriott & Mapstone 2006). A further problem is not so much logistics, but the fact that researchers with access to reef environments seem disinclined to embark on tagging and recapture programs for the purpose of validation.

Radiochemical dating. This method may be used to effectively distinguish between divergent age-estimates, at a high cost per otolith. This is not a major issue in coral reef fish studies, however, given that perciform otoliths are relatively easily read.

Progression of length modes and length frequency analysis. This is not useful for coral reef fishes as many species have size and age decoupled and table-topped growth curves, with no evidence of length modes over the majority of the life cycle.

Capture of wild fish with natural date-specific markers. This is an underused resource. Such markers arise primarily through influences of temperature anomalies on fish growth patterns (Meekan et al. 1999). Strong possibilities exist for use with long-lived fish showing growth responses to known temperature anomalies (Nakano et al. 2004, Black et al. 2005).

Marginal increment analysis. This is the most commonly used protocol but there are potential problems associated with indistinct marginal conditions, especially for long-lived fishes in which growth increments may be compressed near the otolith margins. An additional problem is that sampling of specific age classes may be difficult in a number of reef fish taxa in which the relationship between size and age is so obscure that it is not possible to pre-select age classes for otolith processing. Most importantly, the protocol requires monthly samples, which may be difficult to obtain for many species in reef environments distant from transport or research hubs. Similar issues have been raised with respect to MIA in deep sea fishes (Cailliet et al. 2001).

Captive rearing of chemically tagged fishes. This method has been "generally discounted" as a reliable means for validating annulus formation but, with exceptions such as Machias et al. (1998), little evidence to support its dismissal has been provided. The important issue is to determine whether increment periodicity is modified in captivity, even though growth in captivity is likely to vary from growth in the wild. This remains the most realistic possibility for a wide range of tropical species as culture technologies improve, especially for those of large size (Cappo et al. 2000).

All validation protocols involve some expense. The least expensive are those based on the analysis of size structures, e.g., progression of length modes and length frequency analysis, but these are compromised due to the uncertainty of the relationship between size and age, or their complete decoupling, in many reef species. Other protocols such as the mark-recapture of chemically tagged fish must bear the cost of the tagging field work, which may be considerable as it involves not only the initial sampling but episodes aimed at recapture of tagged individuals. Given the complex nature of reef environments and the local rarity of many species, this usually involves dedicated sampling carried out at the expense of other activities. Furthermore, lessons from those studies that have successfully used this method of validation indicate that it is necessary to keep the number of species targeted for tagging to a minimum. Captive maintenance of chemically tagged fish offers a cost effective alternative provided suitable large scale aquaria or field enclosures are available. Bomb radiocarbon usually requires 10–15 otoliths for analysis with a cost in the order of US$1,000 per otolith. Although given a low priority by Campana (2001), marginal increment analysis remains the method of choice in most coral reef fisheries enterprises, as the major requirement is simply samples of a number of age-classes collected on a monthly basis.

A true analysis of costs highlights two major problems that inhibit the widespread application of age validation in coral reef fishes. Firstly, while many tropical maritime nations support excellent fisheries groups, they frequently lack the infrastructure of modern vessels and sophisticated laboratories found in temperate and boreal maritime nations. Secondly, research budgets are often not sufficient to cover the costs of novel analytical procedures.

4 What are the problems if we don't validate?

Analyses of otoliths for individuals and species of reef fishes are now routine. Given the difficulties of validation studies in coral reef environments, we must consider problems that may arise if we estimate and publish age-based demographic information without validation of the periodicity of increment formation in every species studied. The costs of validation of reef fishes become prohibitive when whole species assemblages are considered, because of the high diversity in tropical reef fish assemblages. It is unlikely that this will be accomplished in the more speciose lineages such as serranids, pomacentrids, labrids and acanthurids. Will this invalidate comparative studies on demography and life histories in such lineages? We argue that it will not. The major concern (underestimation of ages due to the use of inappropriate structures) of Beamish & McFarlane (1983) and Campana (2001) largely have been dealt with. Contrary examples to the one increment per year hypothesis are very rare. Bomb radiocarbon analysis, in providing estimates of age independent of our visualization of otolith increments, has overwhelmingly confirmed that counts of sagittal increments provide accurate estimates of age in long-lived species. Even in those taxa where accuracy is still questioned, extended life spans have been confirmed (Kalish 2001).

The issue driving the need for validation is not inaccuracies at the level of 12–13 as opposed to 14–15 increments. Reading errors will invariably introduce this level of variation into our estimates, regardless of whether a validation program has been undertaken or not. Miscounts of a small number of increments or occasional or localized disruptions to the cycle of increment formation due to climatic or metabolic variation are unlikely to influence demographic conclusions for species living in excess of 15 years. The critical issues are: i) is the level of underestimation likely to be sufficient to result in counts of approximately 15 as opposed to 40 increments? ii) Are schedules of increment formation as visualized in thin sagittal sections non-annual in nature? The published record strongly suggests that neither of these circumstances is likely in shallow water tropical species. Validated age estimates are more critical where estimates of biomass rely on age-length keys for fisheries stock assessments, where the key is used to convert lengths into age classes (Jones 1992). This emphasizes the distinction between the use of age data for fisheries estimates and for investigation of ecological and evolutionary processes.

It remains difficult to get demographic work on fishes published without validation procedures for each species, despite the consistent results from numerous studies over the last two decades. The philosophy that validation of ages in all species must be accomplished before general treatments of life histories can be developed is well established in the reviewing community. This has a particularly negative effect on the analysis of demographic and life-history trends for coral reef fishes. For reasons given above, this requiremtn is not only prohibitively time-consuming, but beyond the budgets of most tropical fisheries workers and biologists. Given the fact that we have an accessible protocol for estimating life spans (sectioning sagittal otoliths) for which accuracy has been confirmed in the majority of confirmatory studies, the question should be turned around. What problems will accrue if publication of age-based demographic work must await the validation of periodicity of increment formation in every species investigated?

Problems might occur in three areas of investigation.

A. **Fisheries management**. Although a large number of successful validations have occurred (primarily serranids, lutjanids and sparids), the number of species validated or even aged is trivial compared with the number of taxa harvested in tropical multi-species fisheries.

B. **Evaluating the efficacy of Marine Protected Areas**. Demographic information is fundamental to understanding responses of different groups of reef fishes to protective measures (Sale et al. 2005).

C. **The evolution of life histories in reef fishes.** The diversity of perciform reef fishes, coupled with the increasing availability of phylogenetic analyses, provides a significant opportunity to analyze contrasting patterns of size structure, longevity, growth rates and reproductive tactics manifested within and among different clades of reef fishes.

5 The consequences of miscounts of increments or an irregular pattern of increment formation

As a preliminary exploration of what can happen when the number of increments shown in the otolith (or counted by the researcher) differs from the true age of the fish, we compared true and estimated values for the von Bertalanffy growth coefficient, *K*, and mean asymptotic length, L_∞, and the total mortality rate, *Z*, from replicate samples of four hypothetical fish populations. Each population was generated to exhibit a different combination of either a short or long lifespan and either a steep or gradual growth trajectory (Figure. 5). The four populations capture much of the range of life history variation exhibited among coral reef fishes (Kritzer et al. 2001, Choat and Robertson 2002). Two general types of discrepancies between real and estimated age were considered – overestimation and underestimation – and three different degrees of error were considered for each (Appendix 1). Our simulations combined population- and individual-level error by using a common function for the degree of error for an entire population, but choosing the specific error for each specimen individually. See Appendix I for more detail on our simulation approach.

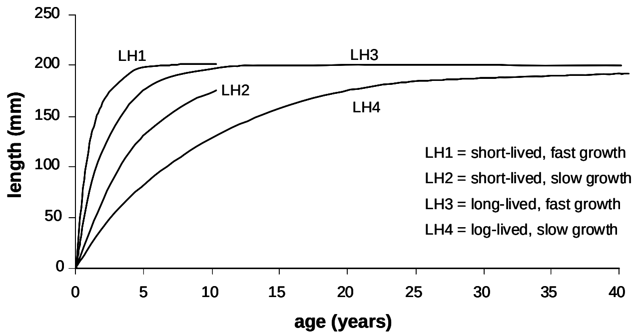

Figure 5. Four life history (LH) types considered in simulations to examine the effects of discrepancies in otolith increment periodicity on estimation of growth and mortality parameters. See Appendix I for descritions of the 4 LH tyems.

The simulations showed that age estimation error had little effect on values of L_∞ for any of the life history types considered. Percent differences in L_∞ between the true and estimated values were all on the order of 10^{-5} or 10^{-6}, and are therefore not shown. This suggests that L_∞ estimates are far more dependent upon length characteristics and are largely independent of age values. The result supports Pauly's (1984) approach to obtaining a preliminary estimate of L_∞ as the average of the 10 largest fish in a sample without reference to age.

Age error had greater effects on estimates of K when the growth trajectory was less steep (i.e., slower growth; Figure. 6A). This is to be expected. There is less scope for the ascending slope of the growth curve to vary when maximum body size is reached more quickly and fewer age classes will have an effect on the parameter value. In contrast, when growth continues for much of the life of the fish, there is considerable room for the curve to become more or less steep as size-age pairs move about within the plot by changing the age value. There is also evidence of an interaction between the growth trajectory and longevity (Figure. 6A). A general, though not consistent, trend was that age error had greater effects on the longer-lived species, presumably because common proportional errors are much larger in an absolute sense when fish get older.

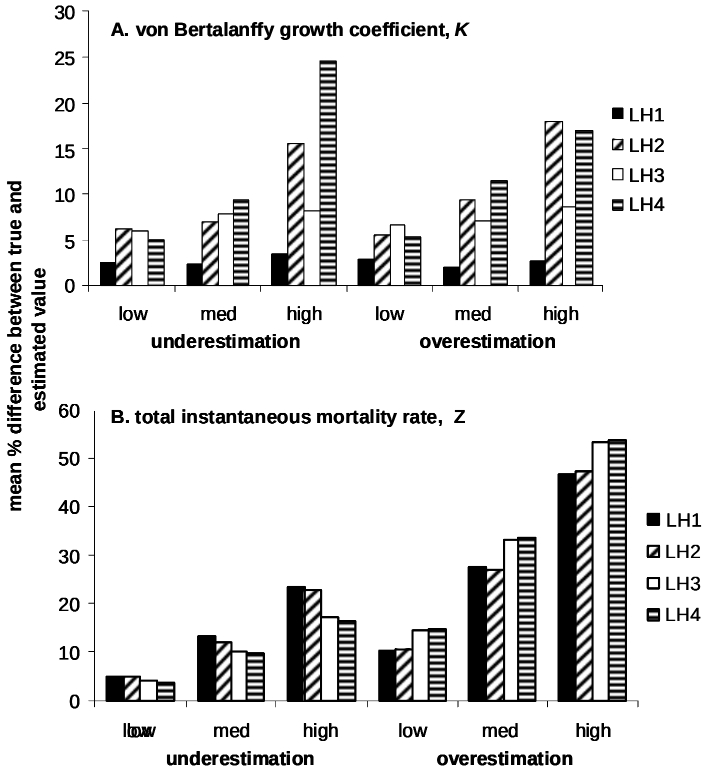

Figure 6. Mean difference between true and estimated values of two key demographic parameters, expressed as a percentage of the true value, due to different types and degrees of error in age estimation because of variation in increment periodicity (Appendix 1) for four life history (LH) types (Fig. 5, Appendix 1).

Estimation of mortality using an age-based catch curve is independent of length, so results for the species with common longevity were similar (Figure. 6B). The results showed that underestimation of age had greater effects on shorter-lived species, whereas overestimation had greater effects on longer-lived species. The pattern was not strong, however, and differences were similar for all species for a common pattern of age error. Overestimation of age seemed to have proportionally greater effects than underestimation. Potentially doubling the number of increments observed in an otolith (i.e., the high overestimation scenario) caused an approximately 50% difference in mortality estimates for all species but halving the number of increments observed only resulted in an approximately 20% difference (Figure. 6B). This result is due more to the fact that doubling the age estimate results in addition of more age classes than are lost by halving an age estimate. The low overestimation and medium underestimation used similar percentage changes (+20% and -25%, respectively; Figure. A1, Appendix I) and caused similar differences in parameter estimates (Figure. 6B).

The mean percent differences reported in Figure 6 are based on absolute values and therefore do not indicate the direction of parameter estimation error. Directionality was predictable, however, based upon the type of error introduced. Overestimation of age decreased values of both *K* and *Z*, while underestimation increased values of both.

These simulations can be expanded in a myriad of ways. Age errors can be size-specific, age-specific, or occur at specific times within a population (simulating environmental events that cause increment anomalies, and not affecting age classes born after the event). Marriott and Mapstone (2006) have recently explored the analogous question of what happens when different criteria for choosing an age estimate based upon multiple readings are applied. Their analysis likewise considered the effects of not getting the age of the fish right, although with a focus on observer error as opposed to biologically-induced discrepancies. Also, different demographic parameters (see Kritzer et al. 2001) or results of stock assessment models using the age and demographic information could be considered in future analyses.

Our initial results provide some important insights, despite the potential for extension of the study. Our scenarios were far from conservative even though we did not consider the cases where increment deposition was consistently different from annual (i.e., two increments per year or one increment per two years as the norm rather than the exception). We only considered errors in one direction in each scenario and did not allow some ages to be overestimated and others to be underestimated within a sample, which might have resulted in errors offsetting one another and therefore smaller relative differences from the true parameter values for the sample. Also, what we defined as "low", "medium" and "high" all entailed incidence of age discrepancies much greater than suggested by the consistency of the one increment — one year pattern reported in existing validation studies (Table 1), non-reporting of other patterns notwithstanding. For instance, our "medium" level of overestimation still allowed 25% of the population to show 38% more increments than the true age of the fish, likely closer to a "high" level of error. Despite this high level of error introduced, many estimates in our simulations were within approximately 10% of the true values (Figure. 6). This is comparable to the degree of error that can be introduced simply by effects of sample size typically used in many studies of reef fish (Kritzer et al. 2001).

Irregular deposition cannot be distinguished from miscounting or failing to detect increments (Francis 1995), as noted earlier, but the two scenarios have very different implications for future improvement of age estimation of tropical fishes. Counting errors can be corrected by continued refinement of the techniques by which otoliths are prepared and analyzed (e.g., microscope power, image analysis tools) and vigilant observer training and calibration. Biological anomalies, on the other hand, call for greater understanding of the mechanisms that cause deviations from the one increment — one year pattern. Given that parameter estimation seems robust to likely degrees of error, we argue that the burden of proof needs to be shifted not toward defending annual periodicity, but rather toward demonstrating where, why, and how frequently it does not occur. This will be a far more stimulating line of ecological and physiological research than repeated pedestrian age validation. Furthermore, we will learn more from a handful of studies describing mechanisms by which annual periodicity does not occur than we will from numerous studies for numerous species re-confirming the general annual pattern.

6 What is the way forward?

The literature on the age-based demography of fishes is focused mainly on temperate, boreal and deep sea fishes. Validation studies in these groups have been aided by access to sophisticated infrastructure and to extensive data bases including otolith archives. By comparison, research into the demography of coral reef fish is in its infancy and lacks the comparative data base that has guided the analysis of temperate and boreal fish populations over the last four – five decades. A more structured approach to reef fish demography is required which includes the establishment of otolith archives. The capacity of otoliths to record the influence of past climatic events and variations in ocean chemistry demonstrates that archives would have a critical role in predicting responses of fish populations to environmental change.

Reef fish demography is at an exciting stage, with the variety of life histories in perciform assemblages becoming apparent. A more coherent approach to population biology of tropical fish should occur in three phases: i) wide dissemination of otolith based analyses of growth and age structure in a broad range of species and populations of coral reef fishes, without the requirement to validate increment periodicity for every species; ii) validation procedures that confirm the temporal meaning of the increments and understanding of the mechanisms by which the timing of increment formation can be altered, especially in commercially important species; and iii) studies on selected species to provide quantitative estimates of accuracy (Francis 1995). This approach requires greater collaboration among tropical fish biologists.

The first of these is controversial due to the insistence that age information must be accompanied by validation of at least the temporal meaning of increments. Analysis of demography of tropical parrot fishes is a case in point. This group, comprising 80 species (Parenti & Randall 2000), is arguably one of the most ecologically important components of the reef fish fauna (Hughes 1994, Bellwood et al. 2003, Mumby et al. 2004) and is heavily over-fished at many localities (Jackson et al. 2001). It is unclear whether members of this group will respond rapidly to protective measures or whether it is one of those in which the recovery process will be prolonged (Russ & Alcala 2004). Demographic information is required to resolve this issue but, while age-based information may be readily obtained (Choat & Robertson 2002), to date annual increment formation has been validated for only six species. It is a moot point as to whether it is better to retain non-validated age data until we have confirmed the temporal meaning of increment formation or to publish the material acknowledging that the working hypothesis is that one ring is formed each year. We argue for the latter.

The case of the largest parrot fish *Bolbometopon muricatum* is instructive. This species is a critically important functional component of the reef fish fauna but is heavily over-fished over much of its range (Bellwood et al. 2003, Hamilton 2004). It is now considered to be threatened (Donaldson & Dulvy 2004) and issues such as growth and mortality rates and generation times are important in manageing existing populations through harvest regulation and the application of marine protected areas. Otoliths of this species show well defined increments. A large body of data on the age-based demography of this species now exists (Choat & Robertson 2002, Hamilton 2004). This information is of potential value to coral reef conservation and management enterprises. In addition, there is renewed interest in the demography and life history patterns of labroid fishes following analyses that provide a fresh perspective on evolutionary relationships within this group (Clements et al. 2004, Westneat & Alfaro 2005). Attempts to validate periodicity of increment formation in this very large, mobile and ecologically important reef fish, however, have failed. Tagged and tetracyclined individuals in the Solomons processed after night-time capture were killed and eaten by sharks the next day following release. Individuals maintained in external enclosures starved to death (Hamilton 2004), an indication of the lack of knowledge of their nutritional ecology (Choat & Clements 1998).

The problems encountered in validating age and growth rates in parrot fishes reflect four general problems. i) Individual species distributions extend over thousands of kilometers and a wide range of habitats. Population parameters are not informative if applied to whole species. ii) High local diversity is associated with the local rarity of many species. Obtaining sufficient individuals at a locality is frequently a problem. iii) Local fisheries are usually multi-specific, targeting complex assemblages of ecologically similar fish at a given site. iv) Many species are large and highly mobile or rare and cryptic.

The fact that such a small proportion of tropical fish species has been successfully validated confirms the importance of these issues but there have been few attempts to develop alternative approaches. We advocate the development of wide-scale multi-species marking programs using either natural or anthropogenic dated marks in otoliths. One approach is to analyze natural date specific markers such as temperature anomalies that influence short term growth and leave signals in otolith increments. Meekan et al. (1999) present a recent example where Galapagos pomacentrids displayed checks in their otoliths that corresponded to the timing of the 1982–1983 El Niño and suggested a reduction in growth over this period. Similar growth reductions corresponding with the same El Niño were observed in the otoliths of species of *Sebastes* (Woodbury 1999) and in the otoliths of Pacific pomacentrids that corresponded to the 1997–1998 El Niño (Nakano et al. 2004). The most promising approach is suggested by Black et al. (2005) where cross validation methods developed by dendrochronologists have been successfully applied to populations of long-lived fishes. In addition evidence is becoming stronger that other metrics of otoliths, such as sagitta weight – age relationships, can be used reliably as a proxy for direct estimates of age (Lou et al. 2005).

The possibility of marking egg clutches with chemical makers that will incorporate a date specific pre-dispersal mark into embryonic fish has been confirmed, providing a rigorous estimate of age that will be retained in the adult fish. The study of Jones et al. (1999), designed to assess the dispersal of larval pomacentrid fishes, is an additional example of mass chemical marking that may provide cost-effective age validation. In addition, an exploratory technique involving marking reproductive females with elemental markers that would be incorporated into eggs and subsequently larvae as a date-specific marker is also now available (Thorrold et al. 2006). These techniques hold promise for large scale, multispecies validation studies. Innovative funding proposals are required as many agencies are reluctant to fund what they see as confirmatory activities, such as OTC marking of yet another set of species.

Campana (2001) made the important point that validation of increment periodicity in very young and very old age classes was a priority. We believe that well prepared and analyzed sagittal otoliths of perciformes will allow identification of the oldest age-classes. Most somatic growth occurs within the first 15% of the life span in many species of reef fishes (Choat & Robertson 2002). Identifying the first growth increment becomes an important issue under these circumstances. Errors in identification of the first three annual increments can lead to substantial changes in growth parameters, especially the VBGF parameter *K*. Ideally, regular sampling of recruits over an annual interval with analysis of daily increments will allow the time of the first annual growth increment to be confirmed.

A difficulty in the ageing of coral reef fishes is that many workers have unduly optimistic expectations as to the clarity of growth increments visualized in sectioned sagittae. Perciformes sampled from high latitudes invariably display clearer growth increments than those from low latitudes (Figure 3). We are frequently approached by researchers commencing demographic studies on tropical reef fishes claiming that they are unable to detect recognizable growth increments in sectioned sagittae. In each instance, however, we have been able to detect increment structures that correspond to those in related and validated species. A useful approach is to examine populations along latitudinal gradients, determining the structure of increments in high latitude populations and using these as a template to help establish the usually problematic increments laid down at young ages (Roberson et al. 2005). Various forms of validation studies may be attempted then but it is unlikely that validation will be achieved in all populations and age classes along latitudinal gradients.

The bottom line in such studies is that there are no short cuts. It is likely that hundreds of otolith sections from a variety of habitats must be examined for each species before low latitude populations can be aged with confidence. We can understand why initial attempts to age low latitude reef fishes were discouraging and led to attempts to use size-based approaches. Both basic and applied studies are making assumptions about growth, mortality rates and longevity in reef fishes, however, and there is an increasing need for more age-based data to be widely disseminated to encourage further studies in age-based demography, including validation.

Unfortunately, demographic studies on reef fishes are increasingly unpopular, driven by the perception that most reef fishes are endangered or threatened. Analysis of otoliths means that fish must be killed, most effectively by selective spearing that can accommodate variation attributable to identity, size classes, habitats and location. Given the expeditionary nature of coral reef research, this can result in numbers of dead dissected fish that result from intensive episodes of sampling over short time periods. Research-driven mortality is usually trivial in terms of the numbers removed relative to the numbers present and the prevailing natural and fishing mortality rates. Sample sizes needed for demographic studies of reef fish can be and have been strategically selected by quantitative analysis of precision, reducing impacts and increasing cost-effectiveness (Kritzer et al. 2001). Still, demographic studies frequently get a hostile reception not only from management and conservation agencies but sometimes within the scientific community during the peer review process. A better understanding of the benefits of age-based analyses with respect to management and conservation will flow from a more comprehensive data base on fish life histories and population biology.

7 Conclusions

The concerns driving arguments for a comprehensive approach to age-validation in fishes have arisen historically from situations in which under-estimation of age has resulted in over-fishing (Beamish & McFarlane 1983, Campana 2001). The widespread use of sectioned sagittal otoliths as an ageing tool has shown that many species do have extended life spans and low natural mortality rates. Harvesting of such species should proceed only with precautionary safeguards.

Validation of the temporal pattern of increment formation and age structures of many species has strongly confirmed that the primary increments visualized in sectioned sagittae are indeed annual. Bomb radiocarbon analyses (Campana 2001, Kalish 2001) have been crucial in this process.

Coral reef fishes pose particular problems for the validation process. Evidence exists that otoliths from some coral reef fishes may have annual increments that are difficult to detect or may not be deposited every year (Fowler 1995), but there is little evidence that increment formation reflects a metabolic or environmental cycle that is not annual. If this was found to be a common situation then clearly the utility of otoliths as an ageing tool would be severely compromised. This has not been the case to date.

We argue that it is unrealistic to attempt validation of every species for which demographic information is sought, given the logistic difficulties associated with age-validation in reef fishes, their biological characteristics, and the record of validation studies to date. We contend that unvalidated otolith age information is more valuable if made available to the scientific community with the caveat that the temporal pattern of increment formation is only assumed to be annual. Retaining data until validation is achieved would serve little purpose. Hopefully, publication would encourage well-funded groups concerned with reef fish management and conservation to embark on their own validation studies in order to provide a stronger basis for remedial management. We agree with Fowler (1995), however, that the biological processes that underlie the formation of macrostructures in otoliths are still poorly understood and require additional experimentally-based research.

A more strategic approach is warranted for reef fish demographic research, regardless of the controversies that different approaches to validation may generate. As validation studies are logistically expensive, decisions must be made with respect to the effort devoted to validation as opposed to more general age-based demographic studies. Validating species simply because they happen to be a research target is not a good guide for deploying funds and effort. We do not not deny the importance of validation studies where the sustainability of commercially important fisheries is under consideration, but this involves only one component of the reef fish research agenda. Numerous studies focus on ecological and evolutionary processes for which demographic data are important. For these studies, many of which involve whole lineages and species assemblages of tropical fishes, the demands for comprehensive validation are unrealistic in terms of both deployment of resources and timely publication.

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Appendix I: Age error simulation method

Populations of four hypothetical species were established to compare effects of age errors on different life history (LH) types. Species differed in longevity and growth trajectory. Growth trajectories were varied by changing the growth coefficient, K, in the von Bertalanffy growth function (VBGF) while keeping the mean asymptotic length, L_∞, and x-intercept, t_0, constant. Total instantaneous mortality rate, Z, was calculated from the maximum age of each species using the equation of Hoenig (1983). Attributes of the four populations were as detailed in Table A1.

Table A1. Demographic attributes of the four hypothetical species modeled to asses the effects of age errors arising from violation of the assumption of annual increment formation in otoliths.

Species	Max. age	Mortality rate, Z	VBGF K	VBGF L_∞	VBGF t_0
LH1	10 yr	0.42 yr^{-1}	0.8 yr^{-1}	200 mm	-0.2 yr
LH2	10 yr	0.42 yr^{-1}	0.2 yr^{-1}	200 mm	-0.2 yr
LH3	40 yr	0.10 yr^{-1}	0.4 yr^{-1}	200 mm	-0.2 yr
LH4	40 yr	0.10 yr^{-1}	0.1 yr^{-1}	200 mm	-0.2 yr

Each population had a stable age distribution, with the frequency in each age class from 0 up to the maximum age determined by Z. Demographic parameters were estimated from replicate samples drawn from each population, the size of which was infinite (i.e., sampling was done with replacement). Each sample was 200 specimens for LH1 and LH2, and 400 specimens for LH3 and LH4. Sample sizes were chosen to be small enough to minimize computing time but large enough to minimize sample size effects on parameter estimates (Kritzer et al. 2001) and focus on effects of age errors.

A length was assigned to each specimen in each sample. The length was the mean length for that age class in that population, determined by the underlying VBGF for each life history type, modified by a random normal variate from a distribution with a mean of 1 and a CV of 0.15. Length was assumed to be measured without error.

The true age of each specimen was known. The estimated age was determined by selecting a random number, r, between 0 and 1 for each specimen, and entering it into the equation:

$$\text{estimated age} = \text{true age} + (\text{true age} \times r \times m),$$

where m is a slope parameter that scaled the degree of error in age estimation. Modified ages were rounded to the whole number, since age values are rarely assigned as fractions in actual studies. Values of m for different scenarios are provided in Table A2 and illustrated in Figure A1.

The extreme values for each type of error were selected to simulate the possibility of half and twice as many increments shown (or counted) as the true age of the fish. However, we did not apply those extreme degrees of error, or any degree of error, across the entire population, instead allowing for individual variation in age discrepancy under a population-wide function.

Table A2. Error scenarios modeled for each of the four populations and slope parameters for the assignment of variation to age estimates under each error scenario.

Type of Error	Degree of Error	*m*
Overestimation	Low	-0.1
Overestimation	Medium	-0.25
Overestimation	High	-0.5
Underestimation	Low	0.2
Underestimation	Medium	0.5
Underestimation	High	1.0

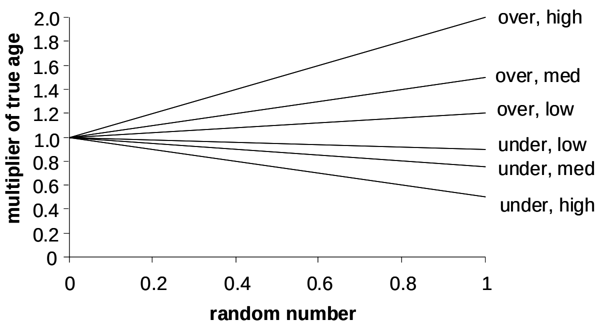

Figure A2. Functions used to modify true ages of fish to simulate deviations from annual deposition of otolith increments and examine effects on estimation of demographic parameters. Two general types of error were considered, overestimation and underestimation, with three degrees of error considered within each. Each function was used for a separate set of simulations.

For each sample, a VBGF was fitted using both the set of true ages and the set of estimated ages by non-linear least-squares regression of length on age. Total mortality rate was estimated by fitting an age-based catch curve to log-transformed age frequency data. Effects of age error were examined by calculating the difference between the value of each parameter for the set of true ages and the set of estimated ages, expressed as a percentage of the parameter value for the true ages. The percentage difference between the true ages and estimated ages for each sample was recorded as the absolute value and used to calculate the mean. The mean percentage difference was calculated for 100 replicate samples for each life history type under each type and degree of age discrepancy.

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