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Review

Age validation in the Lutjanidae: A review

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ABSTRACT

The Lutjanidae (tropical snappers) are important to fisheries throughout the tropics and subtropics. Reliable age-based demographic data are essential for the sustainable management of lutjanid fisheries, and are underpinned by the selection of appropriate ageing structures and validation of increment periodicity within these. Lutjanid age validation has attracted considerable research attention over the past three decades, but lacks a recent synthesis. This paper reviews the four main approaches used in lutjanid age validation; bomb radiocarbon dating, radiometry (lead-radium dating), chemical tagging and marginal increment analysis (MIA). Bomb radiocarbon and lead-radium dating provide absolute age estimates, which can validate increment counts in calcified structures. However, bomb radiocarbon dating cannot accurately age fish older than ∼55 years, an age that some lutjanids may meet or exceed. The development of $\Delta^{14}C$ reference curves for the postbomb decline period offers potential to accurately age fish only a few years old. Technical advances and empirical verification of key assumptions over the last two decades have established the accuracy and validity of lead-radium dating. However, this approach is not uniformly applicable to all study species or areas. Mark-recapture studies using fluorochromes clarify changes in increment appearance and periodicity as fish age, but lutjanid recapture rates are often poor. Marginal increment analysis (MIA) is susceptible to bias and misinterpretation if not rigorously applied. While no single validation approach offers a complete solution, almost all studies support annual increment formation in lutjanid otoliths. Future validation studies would benefit from the development of otolith reference collections and cross-institutional collaboration. Because MIA is inexpensive and logistically simple, its use on lutjanids will inevitably continue, and we therefore provide guidelines for its rigorous application.

Contents

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1. Introduction

In fisheries science, age is "the most influential of biological variables" (Campana, 2001). Accurate and reliable age data are essential for the derivation of growth and mortality rates, and also enable the estimation of production from a fished stock (Beverton and Holt, 1957; Campana, 2001). Age estimation in fish uses a variety of techniques, but most commonly involves counting growth rings in a variety of calcified structures (CS), including bones, scales, fin spines and otoliths (Davis and West, 1992; Campana, 2001; Newman and Dunk, 2002). Correct choice of ageing structure and validation of a regular (generally annual) cycle of growth increment deposition underpin the usefulness of these data (Beamish and McFarlane, 1983, 2000). As with age estimation more generally, consistent interpretation criteria and objective measures of precision are vital in age validation studies, particularly those reliant on visual interpretation of growth increments (Morales-Nin and Panfili, 2002; Wright et al., 2002).

The importance of validating the frequency of increment deposition in calcified structures was recognised early in the 20th century, but was largely neglected until the early 1980s, when it became apparent that ages derived without validation from scales and whole otoliths had underestimated age for the Pacific ocean perch (*Sebastes alutus*) (Beamish and McFarlane, 1983). Consequent overestimation of natural mortality rates and sustainable yields resulted in costly overexploitation, prompting Beamish and McFarlane (1983) to publish their influential paper calling for age validation as a fundamental precursor to the use of age data. Subsequent age validation studies established sectioned otoliths as the most suitable ageing structure for many temperate and boreal marine fish and demonstrated the generally annual nature of growth increments observed in sectioned otoliths (e.g. Leaman and Nagtegaal, 1987; de Pontual et al., 2006; Ross and Hüssy, 2013). In particular, extensive mark-recapture programs using chemically-tagged fish contributed to a substantial body of knowledge on the preparation and interpretation of otolith sections (Beamish and McFarlane, 2000; de Pontual et al., 2006).

Age validation in tropical reef fish proceeded more slowly, reflecting the rarity of comprehensive assessment and monitoring programs at low latitudes (e.g. Mees and Rousseau, 1997; Pilling et al., 2000; Fry et al., 2006; Grandcourt et al., 2006, 2008, 2011; Williams et al., 2013) and the perception that tropical fish otoliths did not form sufficiently clear growth increments to enable their routine use for age estimation (Choat et al., 2009). Difficulties in the interpretation of tropical fish otoliths, while real (e.g. Pilling et al., 2000; Marriott and Mapstone, 2006), rarely prove insuperable, and annual increment formation has now been demonstrated for many tropical marine fishes (Newman and Dunk, 2002; Choat et al., 2009). Age validation in the tropics was further advanced by bomb radiocarbon and radiometric dating of otoliths, since these techniques enabled independent confirmation of age estimates from sectioned otolith ring counts (e.g. Kalish, 1993; Fischer et al., 2005; Andrews et al., 2011, 2012).

The apparent ubiquity of annual increment formation raises the question of whether validation should still be considered a mandatory precursor to any age-based demographic study on a new species or in a new study area (c.f. Beamish and McFarlane, 1983). Choat et al. (2009) argued that annual increment formation should now be accepted as a reasonable working assumption for most tropical marine fish species, particularly where the focus is on ecological or evolutionary processes rather than stock assessment. Similarly, Newman and Dunk (2002) considered annual increment formation to have been adequately demonstrated in Indo-Pacific lutjanids following a series of age validation studies on 14 species from the group.

Here, we assess these claims using the Lutjanidae as a case study. While many of the points we address are applicable to fish in general, there are two primary reasons for our focus on lutjanids. First, although the last two decades have seen considerable research effort devoted to age validation in this family (e.g. Newman et al., 1996; Cappo et al., 2000; Szedlmayer and Beyer, 2011), a synthesis is required to identify research gaps and suggest strategic approaches to future age-based work. Second, lutjanids possess biological, ecological and anatomical characteristics that make them particularly suited to illustrating some important points regarding age validation generally. Specifically, these traits are:

(1) An almost ubiquitous tendency towards ontogenetic migration, with consequent exposure to varying physico-chemical conditions that can create ambiguous banding patterns in otoliths (Milton et al., 1995).
(2) The long life spans of many lutjanids create challenges in the interpretation of otolith sections and validation of increment periodicity at older ages (e.g. Andrews et al., 2012). The life spans of some species may also test the temporal limits of the bomb radiocarbon chronometer (Andrews et al., 2013). Lutjanids therefore exemplify many of the issues associated with validating total lifespan and increment periodicity in long-lived tropical fishes.

A final reason for choosing lutjanids as an example is their importance in fisheries. Lutjanids are sought by artisanal and subsistence fishers throughout the tropics and subtropics (Kamukuru et al., 2005; Amezcua et al., 2006; Grandcourt et al., 2008; Previero et al., 2011). Some species, most notably the red snapper (*Lutjanus campechanus*), also support large commercial fisheries (Cowan et al., 2011), while many others are valued by recreational fishers (Russell et al., 2003) or in aquaculture (Muhlia-Melo et al., 2003; Sanil et al., 2011). Many lutjanids exhibit slow growth, substantial longevities (exceeding fifty years for some species), late maturity and low natural mortality rates, predisposing them to overexploitation (Newman, 2002; Newman and Dunk, 2002, 2003; Marriott et al., 2007; Williams et al., 2013; Piddocke et al., in press). Lutjanid biology, assessment and management are therefore of primary importance in many tropical and subtropical fisheries.