Age, Growth and Early Life History of Carp (*Cyprinus carpio* L.) in the River Murray, South Australia

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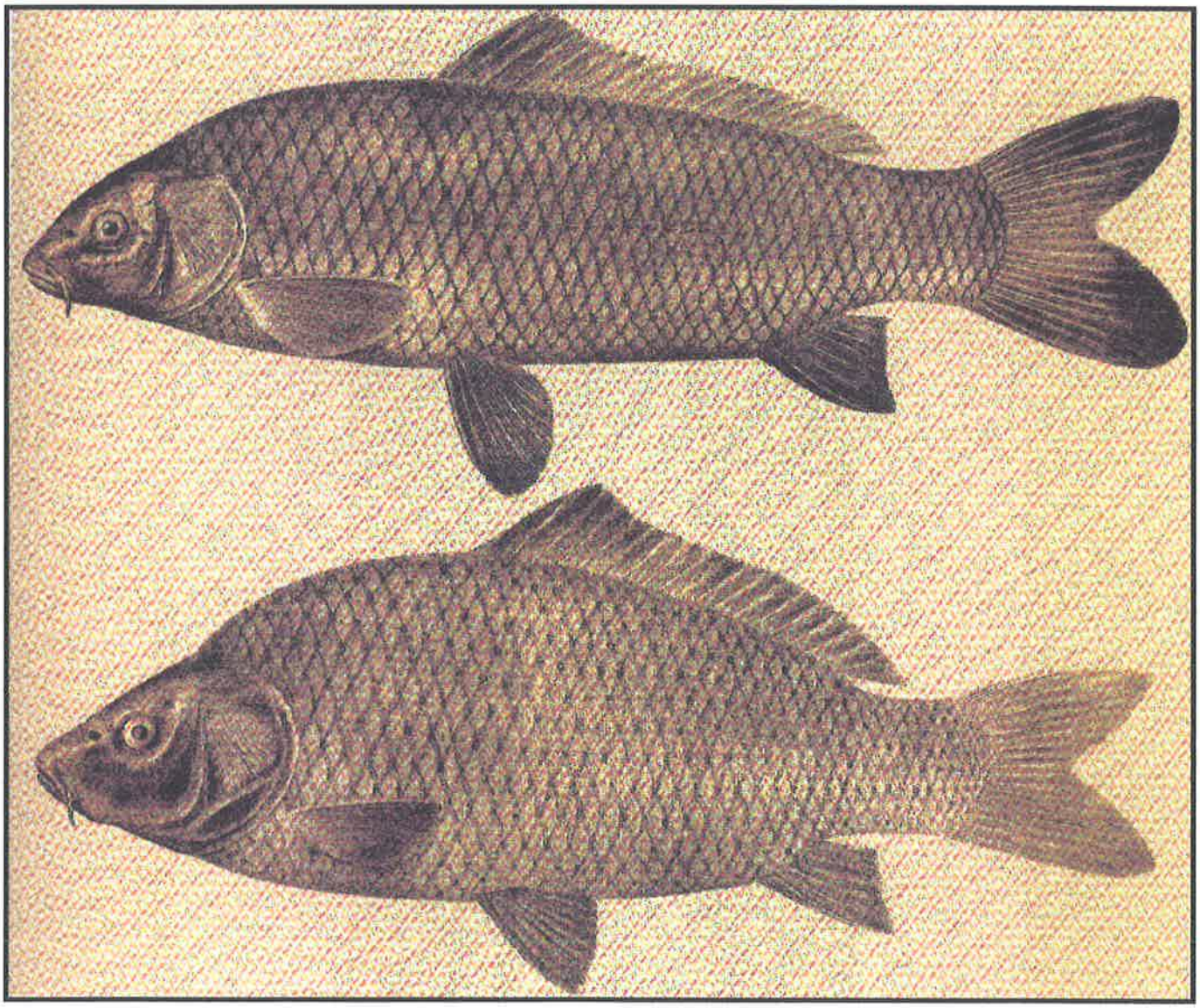
Angell went on to suggest a fascinating and plausible explanation for the origin of the fox terrier simile (no excuse, of course, for its cloning). Fox terriers were bred "to dig out foxes from their burrows, when a fox had gone to earth during a traditional British hunt". Apparently, generations of fox-hunting gentlemen selected fox terriers not only for their functional role in the hunt but also under a breeder's advice to make them look as much like horses as possible. Angell continues, "The dogs rode up on the saddle during the hunt, and it was a pretty conceit for the owner-horseman to appear to put down a little simulacrum of a horse when the pack of hounds and the pink-coated throng had arrived at an earth where the animal was to do his work". He also pointed out that fox terriers tend to develop varied patches of color on a basically white coat and that a "saddle" along the back is "considered desirable and handsome". Thus, Angell proposed his solution: "Wouldn't it seem possible that some early horse geologist, in casting about for the right size animal to fit his cliché-to-be, might have settled, quite unconsciously, on a breed of dog that fitted the specifications in looks as well as size?".

S. J. Gould (1988)

To my beloved wire-haired fox terrier Blichi



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SYNOPSIS

Since their escape into the Murray-Darling Basin (MDB) in the mid-1960s carp (*Cyprinus carpio* L.) have attained high densities and are now widely held responsible for detrimental effects on freshwater communities. Given the extensive literature from other countries little is known of the basic biology of this exotic invasive species in Australia. In particular, the ability to assess the age profiles of wild populations and a better knowledge of early life history events are fundamental for studies on population dynamics, particularly recruitment and Year-Class-Strength (YCS), and for the evaluation of control methods like intensive fishing, water drawdown and immunocontraception. The objectives of this research project were therefore (1) to determine a reliable method of age determination, (2) to evaluate models of growth in wild populations, (3) to assess and speculate on growth patterns, (4) to describe the onset of the juvenile period, (5) to monitor the early life history of a wild population, and (6) to review the literature on carp ecology.

Interpreting the ages of individual carp is difficult, but possible, as a comparative analysis of the relative value of scales, opercular bones and otoliths (asterisci) from 603 specimens caught in the lower Murray in 1994–95 and an evaluation study of the bias and reproducibility of age interpretations have demonstrated. Validation of age estimates by marginal increment analysis has been achieved for carp 1–7 years old, although there is evidence that annulus patterns in opercular bones and otoliths can be used to interpret the age of fish up to 15 years old.

Six models, including the Von Bertalanffy Growth Function (VBGF) and polynomial curves with combinations of log-transformed and decimal variables, were used to describe growth in length and weight of lower Murray carp. A log-linear quadratic function, by virtue of its precision, and the VBGF, with wider applicability and more biological realism, were chosen to describe growth in length, which was found to differ significantly between males and females; similar results were obtained upon comparison of growth in weight between the sexes. Otolith growth was also modelled, although the weight of these calcified structures could not be used as an objective criterion for age estimation. These methodologies, together with length-frequency analysis, were also employed to assess the

age composition and growth of a recently discovered population in Lakes Crescent and Sorell in Tasmania, based on a sample of 333 specimens.

Length-at-age data for 181 populations of carp from different geographical areas were collected from several literature sources and analysed for patterns in growth. Whenever feasible a VBGF was fitted to each data set for computation of growth parameters, otherwise a linear model was used. No pattern in growth based on climate type (Köppen system), latitude and latitudinal zone was recognised. Although based on somewhat simplistic assumptions (no consistent account could be made for other abiotic and biotic factors affecting growth in fish) this study would indicate that, despite local differences in growth among populations, carp would achieve an optimal size regardless of climatic conditions, and a mechanism of countergradient variation also could be involved.

The age, growth and cohort composition of a sample of 539 larvae and juveniles collected in 1994–95 in the lower Murray were investigated. Age determination was based on microincrement analysis of otoliths (lapilli), and validation achieved by a combination of methods, including tetracycline-marking, back-calculation of hatching dates and length-frequency analysis. Cohort composition and intracohort variability in growth of larvae were also studied based on length-frequency distributions and developmental step analysis. Observations on the diet of larvae and early juveniles were also made, with special reference to the time of transition from planktivorous to omnivorous benthic feeding.

The technical literature on carp is enormous: a critical review of previous studies has focussed on several ecological aspects, including (1) impact assessment and options for control, (2) age and growth, and (3) early life history, with special emphasis for the onset of the juvenile period.

Clearly, research is needed to better understand the success of carp as an invasive species in Australia, and to develop ways to limit its detrimental effects. This thesis is the outcome of work designed to contribute such basic information.

DECLARATION

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis, when deposited in the University Library, being available for loan and photocopying.

Signed: **Date:** 11/6/97

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Blichi, my wire-haired fox terrier, has patiently shared with me long days at home and cheered me up during the last three years of my stay in Australia. To him I dedicate my thesis.

1.

INTRODUCTION

> The common carp, my father once wrote, "is a superanimal that, like man, can dominate its habitat". A botanist turned fisheries biologist, my father also recognized the carp as a weed, one of the many hardy immigrants that thrive in habitats disturbed by human activities. His respect for this fish came from years of trying to control carp populations in order to increase the numbers of game fish and waterfowl in Minnesota lakes. His classification of many Minnesota lakes as "carp lakes" reflects the difficulty of this task.
>
> P. B. Moyle (1984)

1.1 Carp and its advent to Australia

The carp (*Cyprinus carpio* L.) is a member of the Cyprinidae, one of the largest families of freshwater fishes (Howes 1991). It is one of the most widely-distributed fish in the world, occurring in diverse environments in all but polar climates, including even brackish water (e.g. Barraclough and Robinson 1971; Geddes 1979) and is present in all continents except Antarctica (e.g. Panek 1987). Balon (1969, 1974, 1995a,b) recognised three groups of wild forms, namely (1) a western dispersant, the European wild carp of the Piedmont Zone of the Danube, (2) an eastern dispersant, the east Asian wild carp from Siberia, and (3) the wild carp from western central Asia, the original area of postglacial dispersal. Pale-ogeographical, historical and linguistic evidence indicate a Caspian origin (Berg 1964) and Roman domestication (Balon 1969, 1974; but see Hoffmann 1995), contrary to earlier, still-circulating beliefs in the Chinese or Vietnamese descent (Balon 1995a,b; cf. Kålås and Johansen 1995; Pierce 1996). Based on the number of gill rakers (Mišík 1958) and other meristic characters (Berg 1964), two poorly-defined subspecies are distinguished: the European common carp (*C. c. carpio*), derived from the western dispersant, and the Asian common carp (*C. c. haematopterus*), from the eastern dispersant. However, the overlap in meristic characters and the possible European origin of *C. c. haematopterus* suggest that the apparent differences among 'subspecies' and domesticated varieties are likely to be related to the presence of altricial and precocial forms (Balon 1995b).

Owing to its ubiquity and importance in aquaculture, descriptions of the basic biology of carp are readily found in monographs and aquacultural manuals (for example, Bănărescu 1964; Berg 1964; Alikhuni 1966; Sarig 1966; Scott and Crossman 1973; Steffens 1980; Merrick and Schmida 1984). Various facets of carp biology, including reviews, are considered in the following chapters, with emphasis on age, growth and early life history, with a discussion also on reproductive ecology and feeding behaviour.

Shearer and Mulley (1978) recounted the story of 'great tragedy and frustration' (Wharton 1971) surrounding the introduction of carp into Australia. Two non-invasive strains ('Prospect' and 'Yanco') were first introduced into Prospect Reservoir (Sydney) and the Murrumbidgee Irrigation Area (Griffith), possibly as early as the 1850s. A third strain ('Boolarra'[1]), originally imported in 1960 from Germany by a Victorian farmer, invaded adjacent areas of the Gippsland region and defied repeated attempts of eradication. In 1964 carp were reported in Lake Hawthorn near Mildura, from where they later escaped into the rivers of the Murray-Darling Basin (MDB). In 1969 the first carp were caught near Renmark in South Australia, and by 1971 a population had become established in Lake Alexandrina near the river mouth (Hall 1981). Carp are present in relatively large numbers in the Paroo River catchment (Gehrke *et al.* 1995), in the northwestern MDB, and now occur in all Australian states, including the island state of Tasmania (Chapter 5).

Clearly, carp in Australian waters are descendants of domesticated strains of various origins that have reverted to a feral state. Shearer and Mulley (1978; cf. Section 1.3) postulated that the closely-related 'Prospect' and 'Boolarra' carp were derived from domesticated European forms, while 'Yanco' carp originated from domesticated Asian stock (see also Section 8.3). Escapees of ornamental varieties (*nishikigoi* or *koi*; cf. Balon 1995a,b) have recently been reported in New South Wales (Harris 1995), indicating that new introductions are still occurring. All these forms are morphologically distinguishable from the wild carp of Eurasia, which has a distinctive notch on the dorsum of the head

[1] Although both 'Boolarra' and 'Boolara' spellings are in the literature, 'Boolarra' is the name of the locality in Gippsland where this strain of carp was first imported by a local farmer. An advertisement from *The Weekly Times* (July 27, 1960), announcing the availability of "a plentiful food supply of fat fish", reads "Boolarra fish farms" and "Boolarra Victoria" (Wharton 1971).

(Balon 1995a,b). Finally, based on scale pattern domesticated carp can be divided into four basic forms, *viz.* scaled, line, mirror and leather (or naked) (Brylińska 1986, in Balon 1995b).

1.2 Known and unknown impacts: data-gathering or contemplation?

Chiare, fresche e dolci acque...
(Crystal-clear, fresh and sweet waters...)
Francesco Petrarca (1304–1374)

'Accidental' releases of fish into rivers and lakes have often met with disastrous effects throughout the world (Courtenay and Stauffer 1984). The deleterious effects of carp in particular were categorised by Costa-Pierce *et al.* (1993) as (1) competition for space and food, (2) habitat alteration, and (3) increased susceptibility of native species to degraded conditions. High densities of carp are often reported in the literature (e.g. Cahn 1929; Cahoon 1953; Rose and Moen 1953; Fletcher *et al.* 1985) and are directly or indirectly linked to the decline of native fish populations. In Australia the distinctive bottom-feeding behaviour of carp (Sibbing *et al.* 1986; Sibbing 1988) has been held responsible for increased turbidity, destruction of aquatic plants, liberation of nutrients from the sediment (promoting eutrophication and algal blooms: Gehrke and Harris 1994; Meredith 1996) and undermining of stream banks and irrigation channels (Harris 1995). Circumstantial evidence indicates that carp may also have contributed to the destruction of snail habitats in the lower River Murray (Sheldon and Walker 1993).

Flow regulation in the MDB has changed the balance of processes involved in the maintenance of the channel and floodplain environments, creating conditions inimical to many native species and favourable to the establishment and spread of exotic fish like carp (e.g. Walker 1986; Walker and Thoms 1993)[2]. Native fish like golden perch (*Macquaria ambigua*), Murray cod (*Maccullochella peeli*) and silver perch (*Bidyanus bidyanus*) are all

[2] Interestingly river regulation in the Danube, amongst other factors, has been responsible for the replacement of carp, a typical wetland spawner, with the smallest sturgeon (*Acipenser ruthenus*), a river channel spawner and formely a rare species in the area (Balon 1995a).

dependent on floods for their spawning migrations and to provide feeding grounds for the young (Cadwallader 1986).

Field observations, circumstantial and other evidence for the detrimental effects of carp on wetlands in North America and elsewhere (e.g. Cahn 1929; Anderson 1950; Cahoon 1953; Taylor *et al.* 1984, and references therein) have encouraged many experimental studies to evaluate the effects of carp on turbidity, nutrient release, macrobenthic and planktonic community structure, interaction with native fish and destruction of aquatic vegetation (e.g. Black 1946; Threinen and Helm 1954; Tryon 1954; Hruška 1961; Olaniyan 1961; Hillbricht-Ilkowska 1964; King and Hunt 1967; Prejs 1973; Zawisza and Ciepielewski 1973; Lamarra 1975; Crivelli 1983; Swar and Gurung 1988; Meijer *et al.* 1990; Qin and Threlkeld 1990; Richardson *et al.* 1990; Riera *et al.* 1991; Wilcox and Hornbach 1991; Breukelaar *et al.* 1994; Cline *et al.* 1994; Tátrai *et al.* 1994; Sidorkewicj *et al.* 1996).

In Australia, Malcolm (1971) investigated the effect of carp on turbidity and aquatic vegetation by aquarium experiments and observations in farm dams. Increases in turbidity and a reduction of plant cover were recorded, but no interaction with other fish species was detected. Fletcher *et al.* (1985) found no association between carp density and turbidity, but cited a critical biomass of 450 kg/ha above which plant damage was possible. Based on these preliminary results, Roberts *et al.* (1995) conducted a replicated experiment in ponds, showing that carp had significant effects on water quality, habitat structure and pond physical characteristics. Robertson *et al.* (1995) provided corroborative data for carp in billabongs.

In a review of North American studies, Taylor *et al.* (1984) emphasised the difficulty of research to quantitatively assess and demonstrate the impact of carp. Specifically, in evaluating the role of carp on vegetation removal they stated that "the multiplicity of effects possible—given the complex manner in which carp interact with virtually every physical and biological component of an ecosystem—has made it difficult to pinpoint simple cause-effect relationships" (p. 336). In regard to effects on water quality they contended that "causality is difficult to verify in natural settings; therefore, proposed cause-effect relations between carp-induced turbidities and such occurrences as displacements of native species, disruption or cessation of reproductive activities, deterioration of spawning

areas, and damage to shallow-water communities [...] must be viewed as conjectural *until more rigorous documentation is obtained*" (p. 338, italics mine).

A major criticism of most studies on carp impact is the lack of rigorous experimental design (Roberts 1997). Although robust techniques for assessment of environmental disturbance in the 'real, but variable, world' have been developed (Underwood 1991, 1992, 1993a,b, 1994, 1996), and sometimes used successfully (Chapman *et al.* 1995), it is questionable whether their use is feasible in studies at a river or basin level (cf. Blanch *et al.* 1996). On the other hand, results from pond or small-scale experiments have limited validity in extrapolations.

In view of the increasing public awareness of the disturbance caused by carp in Australian rivers, the research community is faced with the need for quantitative data. Yet in science "results can be equivocal, several interpretations of data are possible, and conclusions may be incomplete or vague" (Balon and Bruton 1986, p. 227), a point often overlooked by managers and decision-makers. Figures like a critical carp biomass of 450 kg/ha may well give someone, *ceteris paribus*, a 'false sense of security' and provide a starting point for further experimental work, but they do little to advance our understanding or predictive capability. Morison and Hume (1990), commenting on Taylor *et al.*'s (1984) contentions, observed that "such a history raises the question of whether a definitive study could ever be done, and if it was, whether it would lead to better management of carp populations in any case" (p. 111). More recently, Harris (1995, p. 25) stated that "the debate about carp has shifted from 'is there a problem' to 'how can the problem be solved'".

In view of the high densities reached by carp in some Australian inland waters (perhaps up to one individual per square metre: Roberts 1997), it is arguable whether more resources should be allocated to projects designed to determine whether there is an impact. If a cost-effective and heuristic approach for predicting and assessing ecological impacts is necessary, then flexible, empirical methods such as the niche-overlap model of Coates and Ulaiwi (1995) might be adopted *in lieu* of 'comprehensive' data-gathering programs or 'more rigorous' experimental studies. Balon (1989, p. 9), warning against the "severe limitations of any empirical experience" and expressing "skepticism over arrogant opinions based on 'data' alone—invariably of a limited sample size", provocatively asked: "When

shall we be able to read: we are at the moment deeply engaged in contemplating the theoretical implications of our observations?".

1.3 Previous biological studies of carp in Australia

Little is known of the most basic elements of the biology of carp in Australia. Jones (1974) investigated the age and growth of a population in the River Murray in South Australia, based on the interpretation of scales. Although a conventional date of annulus formation was tentatively set to 1 October, it was argued that protracted spawning, favoured by warm water temperatures year-round, would invalidate the use of conventional age estimates, traditionally based on the assumption that fish are born around the same nominal birth-date. As a result, a method was proposed whereby individual fish were assigned to different groups depending on their estimated period of spawning. Other calcified structures were also examined, and evidence was given for the potential value of opercular bones, whereas fin rays and otoliths failed to provide satisfactory results. Formal validation of age assessments (*sensu* Beamish and McFarlane 1983) was not attempted.

The distribution and genetic composition of carp in Australia were described by Shearer and Mulley (1978). Three distinct strains ('Prospect', 'Yanco' and 'Boolarra'; cf. Section 1.1) were distinguished from historical data, morphological characters and allozyme electrophoresis. Hybridisation between 'Yanco' carp and goldfish (*Carassius auratus*) was also reported, and other hybrids between 'Yanco' and 'Boolarra' carp were later identified in the Murrumbidgee Irrigation Area (Mulley and Shearer 1980). Keck (1981) and Hume *et al.* (1983b) developed methods for the identification of carp x goldfish hybrids based on morphological and electrophoretic techniques. Hybrids did not show a morphological intermediacy as expected, but tended to resemble carp. Only in their cranial osteology were intermediate characters observed.

Hall (1981) studied the diet and feeding behaviour of carp in Lake Alexandrina and in the River Murray in South Australia. Filamentous algae, detritus and microcrustaceans were the major food components, and differences in the diet of fish from different size-classes were related to changes in gill raker width. A marked seasonal variation in diet composition was ascribed to fluctuations in the relative abundance of benthic and

planktonic organisms. No reference, however, was made to the diet of 0+ individuals, the smallest fish examined being about 150 mm (total length).

A tagging study designed to determine the movements of carp in backwaters of the lower Murray was undertaken by Reynolds (1983) at Gurra Lakes (near Berri). No spawning migrations were observed, although there was circumstantial evidence for homing behaviour. An important observation was that 0+ fish tend to abandon their nursery grounds and move to other areas, allowing colonisation of new habitats.

The 15-year old 'Carp Program' of the Victorian government (Hume *et al.* 1983a) still represents the primary source of data. In 1979 the government funded a three-year research program to determine the distribution, abundance and life history patterns of carp in Victorian waters, and to document the effects on freshwater habitats (Pribble 1979). A list of references on major biological studies on carp was compiled (Hume *et al.* 1979), and brief reviews produced of the effects of carp on fish, invertebrates, aquatic vegetation and waterfowl (Fletcher and Pribble 1979; Smith and Pribble 1979), and of its biology and behaviour (Hume and Pribble 1980). Another review evaluated the role of genetics in the management of wild populations (Brown 1980). Results of the investigation were presented as annual reports (Pribble 1980; Hume *et al.* 1981, 1982) and all were reviewed in a final report (Hume *et al.* 1983a). Several aspects of carp ecology were investigated, including diet, reproduction, age and growth. Plankton and bottom fauna were the major food items in carp of all sizes, plant matter being of secondary importance. Owing to its omnivorous feeding habit, interactions with native fish due to diet overlap were also predicted. An increase in the gonadosomatic index between summer and winter was reported, and protracted spawning, involving deposition of several batches of ripe eggs, was recorded during spring and early summer. Despite attempts to determine the age profiles of wild populations, logistic problems and limitations of the available techniques failed to provide a reliable method. Otoliths, fin rays and opercular bones were examined, but eventually discarded due to difficulties in preparation and interpretation. Only scales were retained for age estimates, although a lack of annulus deposition in most individuals resulting from prolonged periods of no growth invalidated their use. The age composition of the populations examined was therefore estimated by length-frequency distributions,

useful only for the first few age classes. The same methodology was also employed to describe the growth of 0+ carp.

1.4 Objectives and organisation

Clearly, the ability to age carp is essential for any study of population dynamics, for evaluation of life history patterns and work on environmental impact. Accordingly, the objectives of this study were:

1. **To determine a reliable method of age determination:** age assessments based on annulus counts from a suite of calcified structures (scales, opercular bones and otoliths) are validated (Chapter 2), and the bias and reproducibility of age interpretations evaluated (Chapter 3).

2. **To evaluate models of growth in wild populations:** somatic and otolith growth models are assessed for a population of carp in the lower River Murray (Chapter 4), and these methods implemented to describe the age and growth of a recently discovered population in Tasmania (Chapter 5).

3. **To assess and speculate on growth patterns:** based on literature data, a brief history of studies on carp ageing, followed by an evaluation of the structures employed, is provided (Chapter 6), and growth patterns on a global geographical scale evaluated for the presence of latitudinal clines and the possible role of latitudinal compensation in growth as a life history trait (Chapter 7).

4. **To describe the onset of the juvenile period:** published data on the relative growth of body parts and organs, functional morphology, social interactions, differential growth of individuals and microhabitat use are collated and assessed to determine the time of the onset of the juvenile period (Chapter 8).

5. **To monitor the early life history of a wild population:** age assessments based on otolith microincrement counts in larvae and juveniles are validated and employed, in conjunction with developmental step analysis, to study the growth and cohort composition of a wild population (Chapter 9) and the diet of larvae and early juveniles (Chapter 10).

6. **To review the literature on carp ecology:** previous studies on the environmental impact (Section 1.2), age and growth (Chapters 4, 6 and 7), and early life history (Chapters 8–10) of carp are reviewed and discussed.

The thesis is in two parts: the first (Chapters 2–7) deals with the age and growth of carp 1+ and older, and the second (Chapters 8–10) considers the ecology of the young-of-the-year (0+). Finally, suggestions for further studies are offered in Chapter 11.

2.

AGE AND GROWTH:

VALIDATION OF AGE ASSESSMENT

> The major obstacle to ageing carp encountered [...] was the highly variable growth rates in different habitats with the possibility that growth may cease for extended periods in an irregular fashion. The ability of fish to move between rivers and floodplain billabongs during floods meant that the growth history of a particular fish could not necessarily be associated with the habitat in which it was caught. Checks observed in their scales may have corresponded to an annulus or to an extended period without growth. These problems would not be overcome by the use of opercular bones or any other structure.
>
> D. J. Hume *et al.* (1983a)

2.1 Introduction

Techniques to determine the age of individual carp are a prerequisite for studies of population dynamics (e.g. Beamish and McFarlane 1987), but there are virtually no supporting data for carp in Australia. As discussed in Section 1.3, Jones (1974) and Hume *et al.* (1983a) attempted to develop methods for ageing carp in the Murray-Darling Basin (MDB), but encountered problems related to variable annual growth rates between individuals and protracted spawning periods. Population age data are essential to assess the suitability of control methods like water-level manipulations, intensive fishing, habitat restoration, viral agents, immunocontraception and gene manipulation (Roberts 1997), and to allow determination of recruitment and year class strength (cf. Mann 1991).

This study was designed to evaluate and validate the accuracy of age assessments from a suite of calcified structures (scales, opercular bones and otoliths) in carp from the lower River Murray in South Australia. The bias and reproducibility of age interpretations are discussed in Chapter 3, and an evaluation of growth models is provided in Chapter 4.

2.2 Materials and methods

2.2.1 Terminology

In the following the terms *opercular bone* and *operculum*, and *calcified structure* or, more simply, *structure* are used interchangeably, and the generic term 'otolith' refers to the asteriscus (lagenar otolith; see below). Also, in this and the following three chapters (3–5) the term 'annulus group' (fish with the same number of annuli on an otolith) applies to the validation study. The term 'age group(s)' is reserved for annulus group(s) where formal validation is deemed to have been achieved.

2.2.2 Sampling and preparation

A total 603 carp were collected by gill-netting in backwaters of the River Murray in South Australia, using monofilament nets of 20, 50, 75, 100 and 150 mm stretched mesh. Most fish ($n = 515$) were obtained from monthly samples at Gurra Lakes, near Berri, between July 1994 and July 1995. Small samples were collected from Sunnyside (near Murray Bridge; $n = 35$) and Swan Reach ($n = 49$) between October 1993 and March 1994, and four specimens from Lake Merreti (Chowilla floodplain) were obtained from a local fisherman in July 1994.

From 6–10 scales were removed from the antero-medial region of the body immediately above the lateral line, where normal scales usually are found in carp (Bagenal and Tesch 1978). The scales were cleaned of mucus and stored in paper envelopes. From 4–8 un-regenerated scales per fish were mounted between glass slides after soaking briefly in 20% sodium hypochlorite and rinsing in distilled water.

Opercular bones were excised following McConnell (1952) and stored in water for a few weeks. This provided near-complete maceration of the attached tissue so that later 5–10 min immersion in undiluted sodium hypochlorite and rinsing in water was sufficient preparation for analysis (cf. English 1952a; Rehder 1959).

The lagenar otoliths (*asterisci*) were recovered by the 'open-the-hatch' method (Secor, Dean and Laban 1991). After removal of the brain the otic cleft, containing the elongate

saccular otoliths (*sagittae*) and the 'sagitta-like' asterisci, becomes visible, allowing extraction with fine tweezers[1]. Following removal the asterisci were cleaned by soaking for a few minutes in 5% sodium hypochlorite, then rinsed in distilled water and 90% ethanol, following Secor, Dean and Laban (1991).

2.2.3 Annulus identification

There are differences in the criteria for identification and counting of annuli on the various calcified structures. Techniques for carp scales and opercular bones are well-known, but there is little information for otoliths; these are emphasised below.

2.2.3.1 Scales

The criteria of Chugunova (1963) and Talaat and Oláh (1986a) were followed for scales. These were inspected with a dissecting microscope (10–20X) under transmitted light. An annulus is taken as a transition between two uninterrupted zones of closely-spaced and widely-spaced circuli, with anastomosis as an essential criterion for identification. The scale radius and distance of each annulus from the focus (EPUs) were measured along the antero-ventral axis using an ocular micrometer (15X). The circuli between the last-formed annulus and the anterior margin were also counted. Scales from mirror carp (1·2% of the entire sample) could not be read, contrary to Das and Fotedar (1965) (cf. Section 6.2.1).

2.2.3.2 Opercular bones

The methods of McConnell (1952) and English (1952a) were adopted for reading and interpretation of opercular bones. In this case an annulus is taken as a sharp transition between a translucent and an opaque zone, normally a continuous narrow ridge on the proximal (concave) surface of the opercular bone. Annuli were counted by eye under transmitted light; their visibility usually improved after wetting with water. For older fish, observation of the distal surface under transmitted light sometimes was useful in determining the position of the first and occasionally the second annulus, normally

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[1] In carp, as in all otophysan fish (ostariophysi *sensu* Fink and Fink 1981), the *pars inferior* of the inner ear is distinguished by the presence of the Weberian Apparatus, a series of ossicles connecting the swim bladder to the inner ear (e.g. Fay and Popper 1980). These are responsible for the peculiar morphology of the sagittae and asterisci, a point often overlooked and responsible for some terminological confusion (e.g. Fagade 1980; Landau *et al.* 1988; Mina 1989; see also Vilizzi and Walker 1995 and Section 6.2.6).

obliterated by ossification around the fulcrum. The opercular radius and the distance of each annulus from the fulcrum were measured with dial callipers (± 0·05 mm), following Hostetter and Munroe (1993).

2.2.3.3 Otoliths

Wichers (1976) and Hume *et al.* (1983a) reported failed attempts to read otoliths, but did not indicate which pair was used. In apparently the only two studies where carp otoliths have been used successfully (Raina 1987; Pinilla *et al.* 1992), neither the otoliths or the criteria were specified.

The morphology of carp asterisci invalidates the use of standard terminology (e.g. Jensen 1965; Pannella 1980), and Berinkey's (1956) scheme is used here. Whole otoliths are best viewed immersed in water, with the distal side facing the observer and the ventral margin up, using a dissecting microscope (20–40X) and a dark background (reflected oblique light). Under these conditions an annulus is seen as a transition between a translucent (dark) and an opaque (light) zone. Annuli were counted on the distal side of the otolith, along the antero-dorsal region, at the level of the spike, a projection analogous to the antirostrum of the non-otophysan teleost sagitta (e.g. Pannella 1980). When fewer than 5–6 annuli were present they generally could be followed through to the posterior and ventral side, an important feature that distinguishes true from false annuli, which appeared as discontinuous transitions. When more annuli were present this criterion could not be applied because of crowding of the annuli towards the ventral region. Annual increments (paired alternate opaque and translucent zones taken to represent one year of growth) often were composed of an irregular number of pseudoannuli. These are conspicuous in the otoliths of some marine fish (e.g. Griffiths and Hecht 1986; Withell and Wankowski 1988, 1989). In carp, pseudoannuli are formed during the second and occasionally the third and fourth years of growth. Three categories (classes) can be defined to aid interpretation of changes in zone patterns (the same features, with minor variations, apply to opercular bones):

- Class A: all annual increments include an opaque and a translucent zone, without pseudoannuli (Fig. 2.1a);

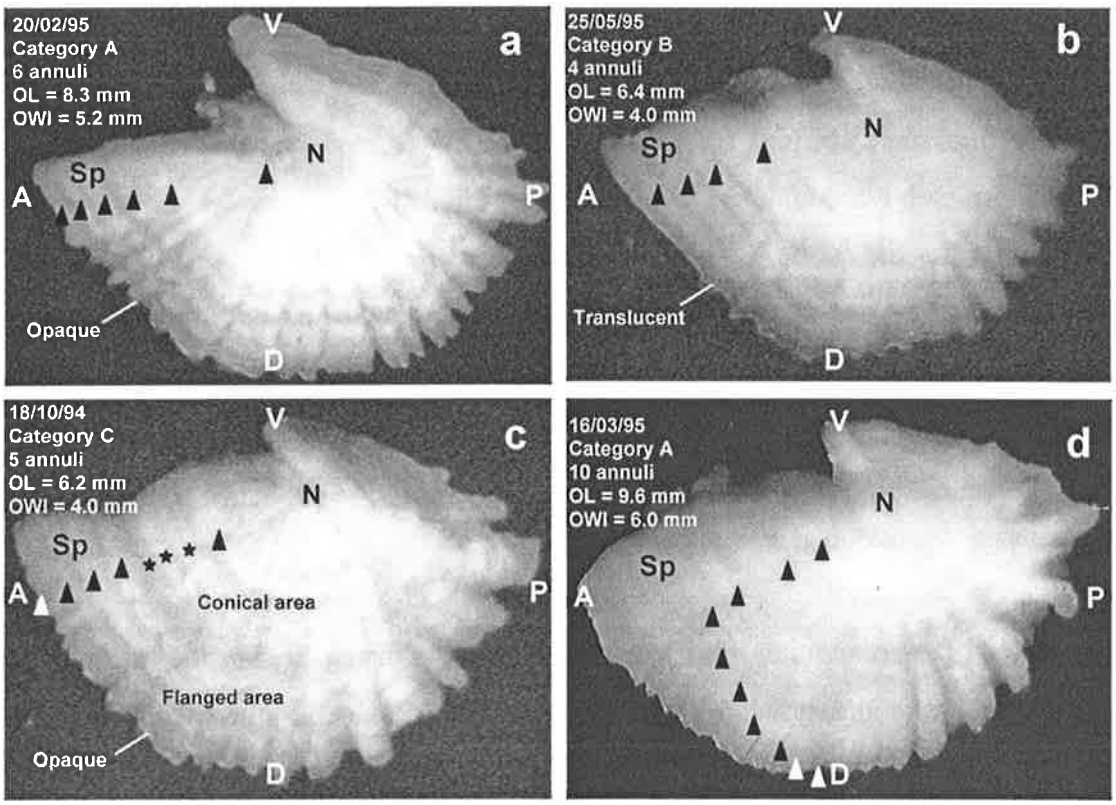

Figure 2.1 Morphological categories of carp otoliths (asterisci) defined to aid interpretation of changes in zone patterns. Under reflected oblique light on a dark background an annulus is a transition between a translucent (dark) and an opaque (light) zone, here indicated by a triangle. Pseudoannuli are marked with an asterisk. The edge type (i.e. opaque or translucent), the date of capture of the fish and the number of annuli are also reported. Sp: spike; A: anterior edge; P: posterior edge; D: dorsal edge; V: ventral edge; N: nucleus; OL: otolith length; OWI: otolith width. (a) Class A (6 annuli), opaque edge, summer; (b) class B (4 annuli), translucent edge, late autumn; (c) class C (5 annuli), newly-formed opaque zone, spring; (d) class A (10 annuli).

- Class B: annual increments as above but lacking a sharp transition between translucent and opaque zones, although annuli are recognisable (Fig. 2.1b);

- Class C: pseudoannuli present in the second annual increment. The region between the nucleus and the second annulus is often conical or at least protruding, and further annuli, when present, are located in a flanged area (Fig. 2.1c).

In fish with more than 6–7 annuli further deposition of calcium carbonate on the dorsal side of the otolith causes increased curvature. Under these conditions the translucent and opaque zones are closely spaced and alternate regularly, assuming a tiered arrangement (Fig. 2.1d).

When possible the left otolith of each pair was sectioned using a low-speed lapidary saw, following standard techniques (Bedford 1983; Augustine and Kenchington 1987). Three successive transverse sections (0·4–0·5 mm) were cut through the nucleus and polished with 1200 grit carborundum paper to enhance the visibility of the zones. The sections were examined under the same lighting conditions used for analysis of whole otoliths (transmitted light proved unsatisfactory), and the morphological categories described above were applied. A measure of otolith thickness could not be obtained from the sections, as calcium carbonate deposition in older fish was almost exclusively limited to the dorsal side of the otolith and did not cause a corresponding increase in overall depth. Attempts to find a reliable measure of dorsal curvature were unsuccessful.

The distance of each annulus from the nucleus and the distance from the nucleus to the edge (*radius*) were measured (± 0·005 mm) using a dissecting microscope linked via camera to a desktop computer and Optimas™ image analysis software. In whole otoliths measurements were taken along an imaginary line parallel to the ventral edge of the dorsal spike. In sectioned otoliths the annuli were measured along a line connecting the nucleus to the mid-point of the dorsal margin. When there was consistent curvature on the dorsal side (in otoliths from older fish) measurements were taken along two lines, the break being where the change in curvature occurred.

2.2.4 Data analysis

Marginal Increment Analysis (MIA) was used to validate counts of annuli. This is a two-step procedure consisting of Marginal Increment Ratio Analysis (MIRA) and Edge Type Analysis (ETA) (Haas and Recksiek 1995). The 'edge interpretation problem' (R. I. C. C. Francis *et al.* 1992) was also addressed.

2.2.4.1 MIRA

Calculation of the Marginal Increment Ratio (MIR) in all calcified structures was based on the formula:

$$MIR = [(CE - CLA) / (CLA - CSA)] \times 100$$

where:

CE = distance from centre of origin (C: focus in scales, fulcrum in opercular bones, nucleus in otoliths) to the outer edge (E) (thus, CE is equivalent to the radius);

CLA = distance from centre of origin to the last-formed annulus (LA);

CSA = distance from centre of origin to the second last-formed annulus (SA).

When only one annulus is present the denominator in the formula is the distance of the annulus from the centre of origin (CLA).

2.2.4.2 Edge interpretation and ETA

To identify more precisely the edge in the calcified structures, a modification of a technique proposed by Anderson *et al.* (1992a,b) was used: from the MIR value the last-formed annulus was judged as 'C' (close), 'N' (now due) or 'Z' (other). For scales and opercular bones the edge was scored C if MIR ≤ 25%, Z if 25% < MIR < 75%, and N if MIR ≥ 75%. In whole and sectioned otoliths it was not possible to detect a newly-formed opaque zone when its width was less than 10–40% of the previous increment, and the edge was scored C if MIR ≤ 50%, Z if 50% < MIR < 75%, and N if MIR ≥ 75%. The margins of whole and sectioned otoliths and opercular bones were recorded as opaque or translucent. Attempts to define the edges of scales from the spacing of circuli (i.e. widely- or closely-spaced) were not successful.

2.3 Results

2.3.1 Marginal increment ratio analysis

If a new annulus is formed once a year and MIR values for fish caught at regular (e.g. monthly) intervals are plotted against time, a dip (minimal MIR values) should be evident during the period of annulus formation (spring/summer). Conversely, peak MIR values should be apparent during the period of little or no growth (autumn/winter).

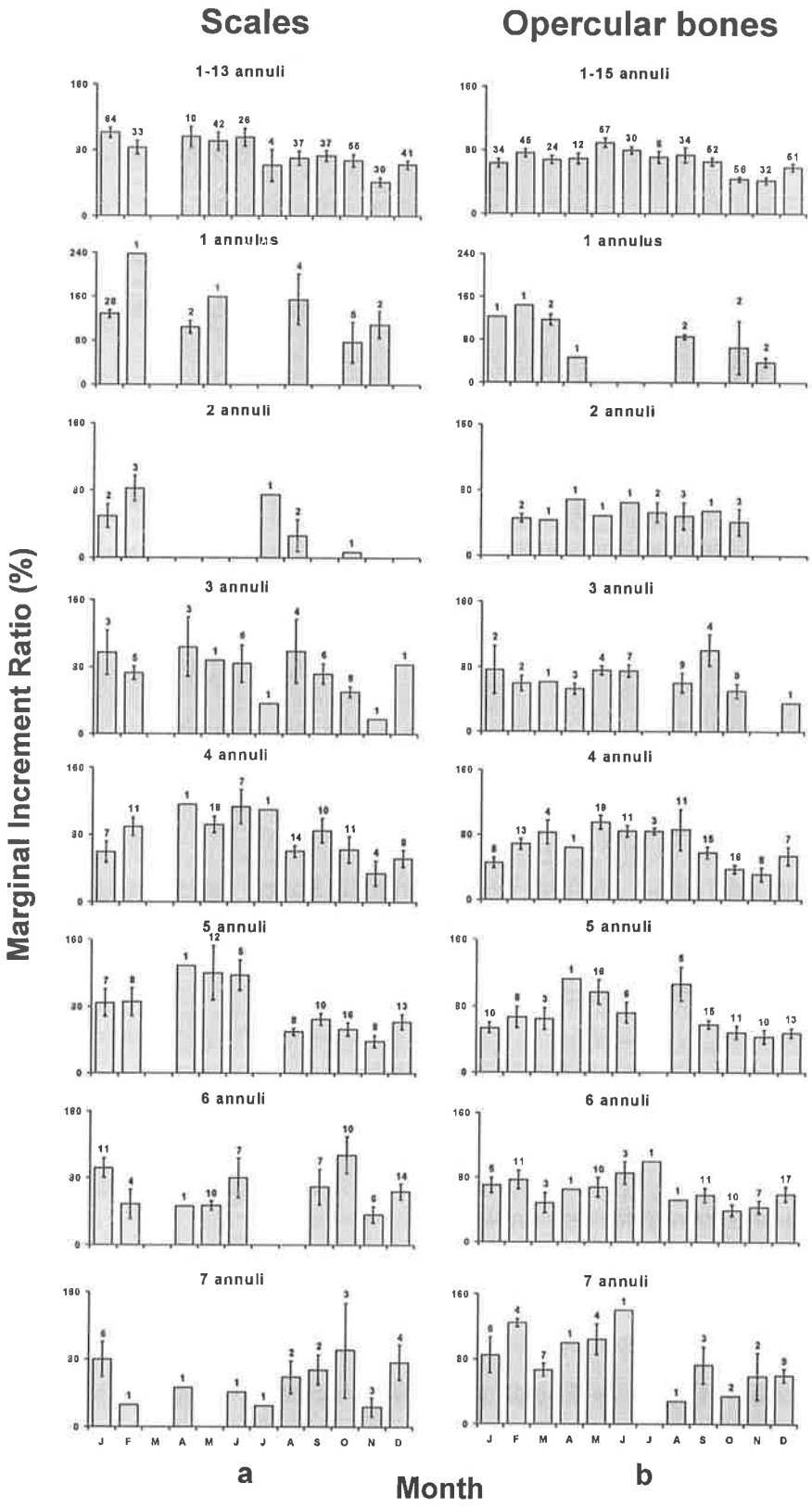

Figure 2.2 Mean monthly values (± SE) of the marginal increment ratio (MIR), expressed as a percentage of the previous increment. Data for pooled annulus groups and for 1–7 annuli are shown. (a) Annulus counts based on scales; (b) annulus counts based on opercular bones.

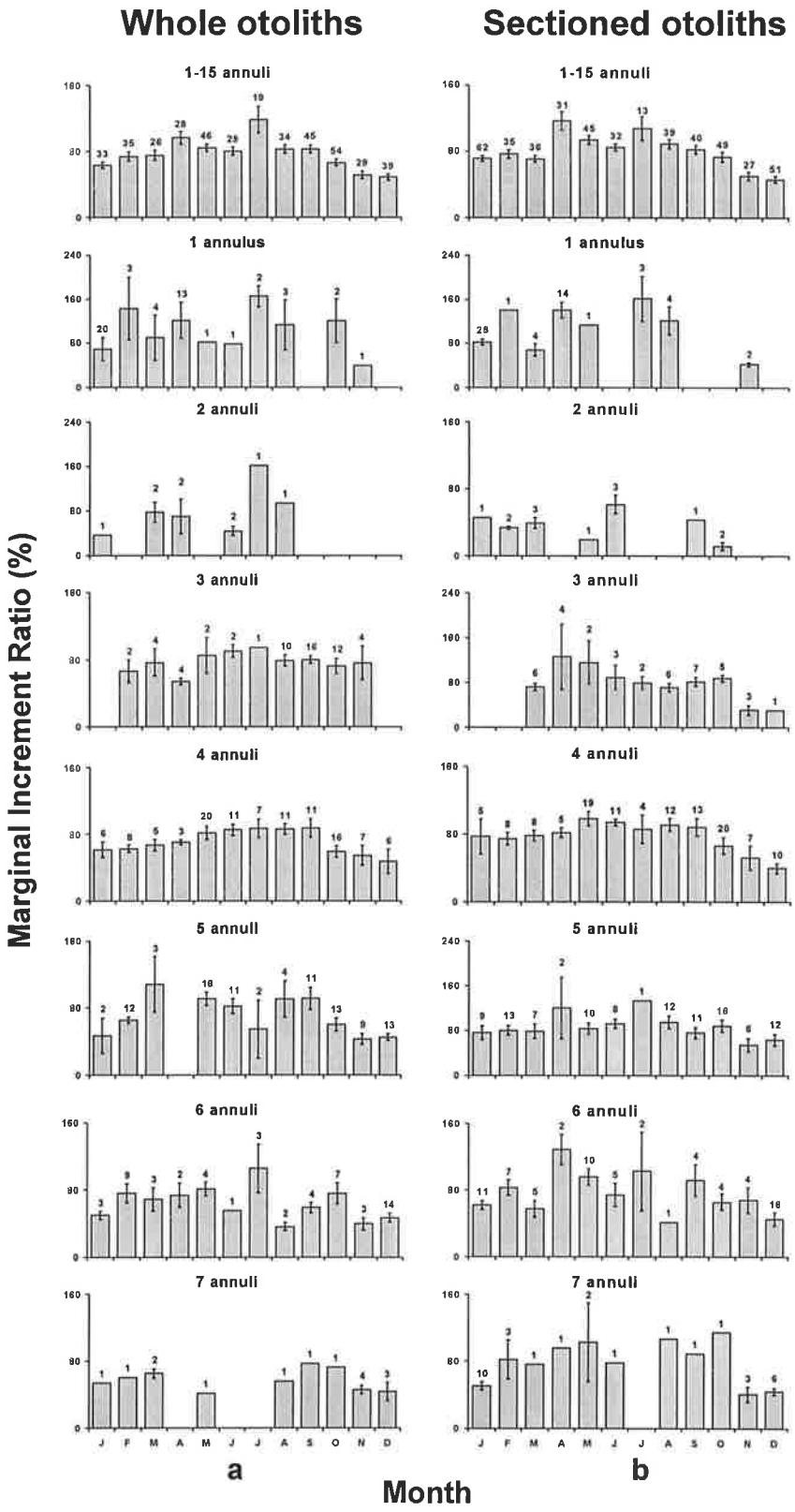

Figure 2.3 Mean monthly values (± SE) of the marginal increment ratio (MIR), expressed as a percentage of the previous increment. Data for pooled annulus groups and for 1–7 annuli are shown. (a) Annulus counts based on whole otoliths; (b) annulus counts based on sectioned otoliths.

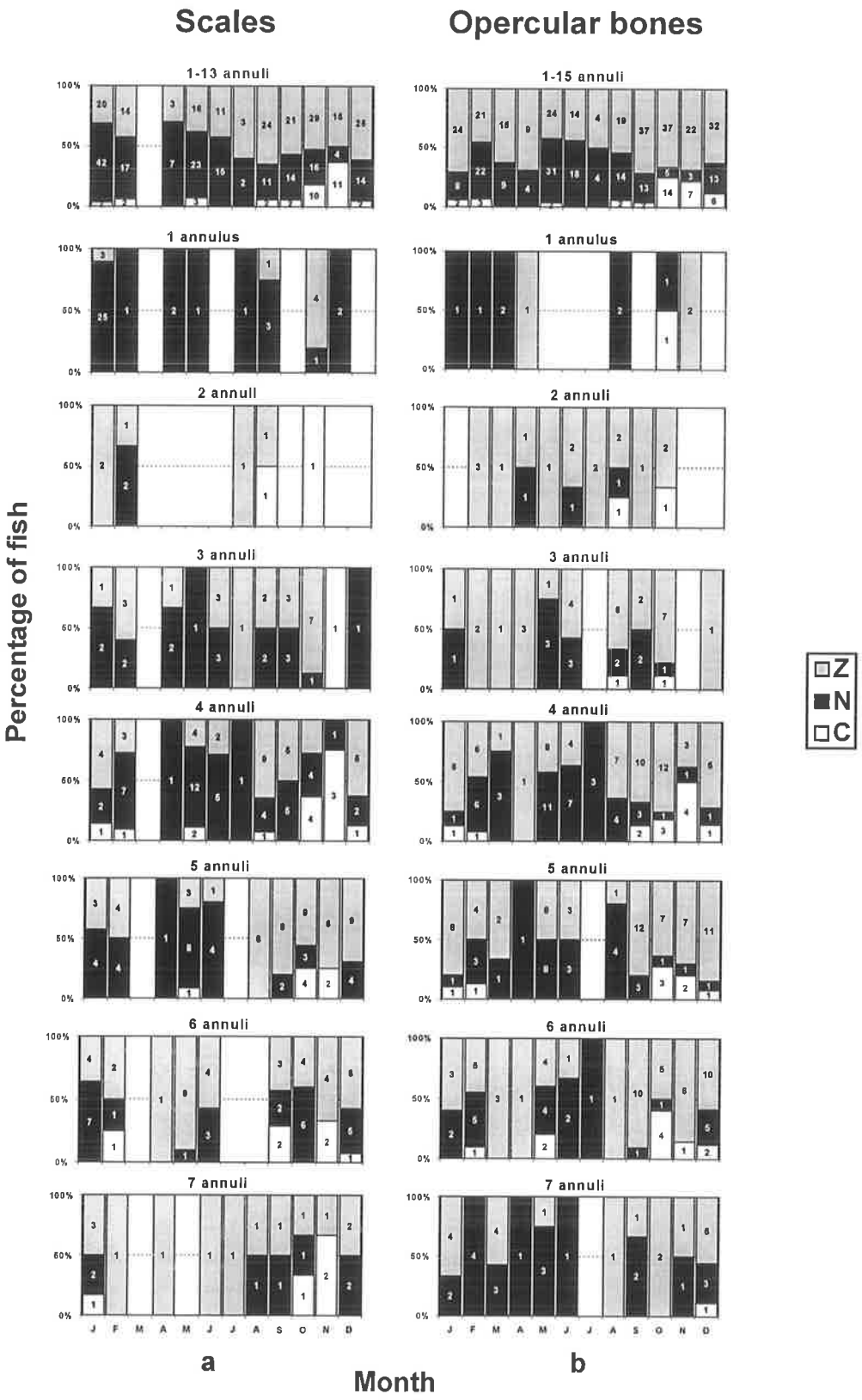

Figure 2.4 Percentage of scales and opercular bones scored as C (MIR ≤ 25%), Z (25% < MIR < 75%) or N (MIR ≥ 75%). Data for pooled annulus groups and for 1–7 annuli are shown. (a) Annulus counts based on scales; (b) annulus counts based on opercular bones.

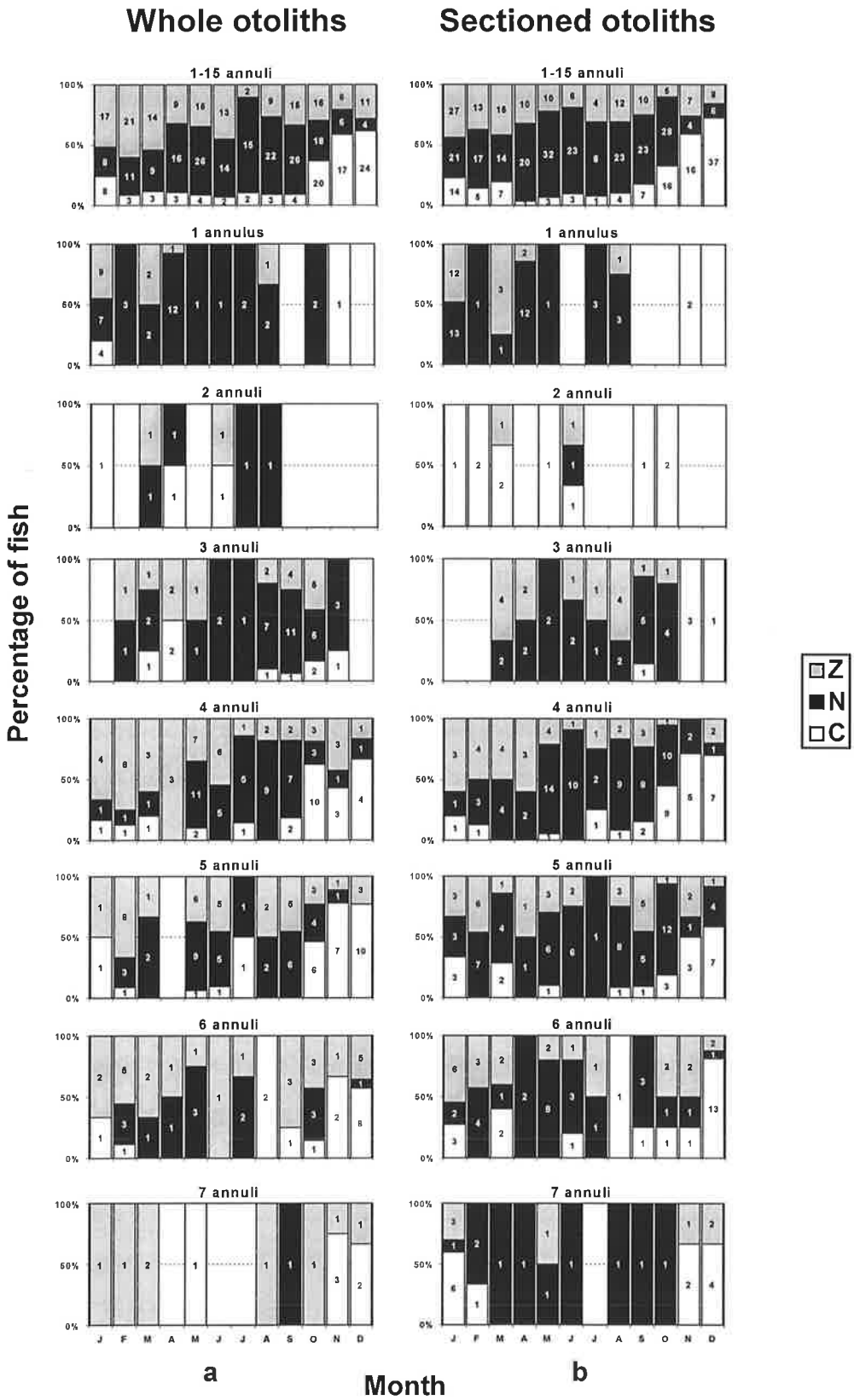

Figure 2.5 Percentage of whole and sectioned otoliths scored as C (MIR ≤ 50%), Z (50% < MIR < 75%) or N (MIR ≥ 75%). Data for pooled annulus groups and for 1–7 annuli are shown. (a) Annulus counts based on whole otoliths; (b) annulus counts based on sectioned otoliths.

After pooling annulus groups, a dip was evident in October–December. This is visible for opercular bones and scales (Fig. 2.2a,b top), but is more pronounced for whole and sectioned otoliths (Fig. 2.3a,b top). The time of annulus formation appeared to be November/December for otoliths, compared to October/November for scales and opercular bones. The difference could have arisen from the difficulty to detect a newly-forming annulus in some otoliths until the corresponding opaque zone was well-developed (this required an adjustment in the criteria for the definition of edge-type categories as described above).

A major drawback with pooling annulus groups is that variations in timing of annulus deposition among age groups may obscure the seasonal pattern of annual increment development (Williams and Bedford 1974). Thus, a separate analysis for each annulus group is mandatory if the range of validated ages is to be determined. When MIR values for all calcified structures were plotted against time for annulus groups 1–7 (beyond this point MIRA becomes trivial because annual increments become negligible), a consistent seasonal pattern was seen for annulus groups 1, 4, 5, 6 and, to a lesser extent, 3 and 7. Given the limited sample size, firm conclusions could not be drawn for any calcified structure when only two annuli were present (Figs 2.2 and 2.3).

2.3.2 Edge interpretation

In pooled annulus groups small marginal increments, corresponding to type C edges, predominated in October/November for scales and opercular bones, and in October–January for whole and sectioned otoliths (Figs 2.4a,b and 2.5a,b top). Edge type C otoliths were also found, but in very low proportions, throughout autumn and winter. This 'noise' probably stemmed from the criterion adopted for determination of edge type categories. Preliminary trials based on the criteria for scales and opercular bones were inconclusive for otoliths, and the correction applied here is preferable even if there are some mismatches. Well-developed annual increments (type N) became progressively more common from January to July for scales, February to August for opercular bones, and February to September for otoliths (whole and sectioned). A consistent pattern suggesting new annulus formation at the beginning of the growing season was identified in annulus groups 3, 4, 5 and 6 for all structures. In annulus group 1, the rapid development of the second-year increment, compounded with the relative thinness of the associated opaque zone (in

opercular bones and otoliths) and of the zone of closely-spaced circuli (in scales), probably was the reason for the low numbers of edge type C structures recorded between October and December. Again, no definite conclusions could be drawn for annulus group 2, given the small sample size.

2.3.3 Edge type analysis

Although a higher percentage of opercular bones with an opaque margin was recorded for annulus groups 3–6 during spring and summer, opaque edges were still common in July/August (Fig. 2.6). In annulus groups 1–2 all opercular bones were scored as translucent, probably reflecting the overall thinness of the bone when less than three annuli were present (Fig. 2.7a). For the pooled annulus groups the percentage of whole otoliths with an opaque edge consistently increased from October to December and decreased from January to March. When annulus groups 1–7 were examined separately the percentage of whole otoliths with an opaque edge was still higher in late spring/early summer in annulus groups 3–6. In annulus group 1 translucent edges occurred almost year-round, again because of the rapid development and relatively small width of the first opaque zone. Curiously, no consistent pattern was identified in sectioned otoliths: opaque zones in the proximity of the margin (type C) were present in most annulus groups throughout the year (Fig. 2.7b).

2.3.4 Scale outer circuli counts

In pooled annulus groups the number of circuli beyond the last-formed annulus was minimal in November. This pattern was still recognised when annulus groups were plotted separately, with the possible exceptions of groups 2 and 7, owing to small sample sizes (Fig. 2.8).

2.3.5 Annulus distance

The mean distance from the nucleus increased up to annuli 12 and 13 in whole and sectioned otoliths respectively, and that of the fulcrum increased up to annulus 11 in opercular bones, with standard deviations reasonably constant across annulus groups. Conversely, in scales the mean annulus distance from the focus increased only up to annulus 7 and the corresponding standard deviations usually were consistently higher than those recorded for the other structures (Fig. 2.9a–d).

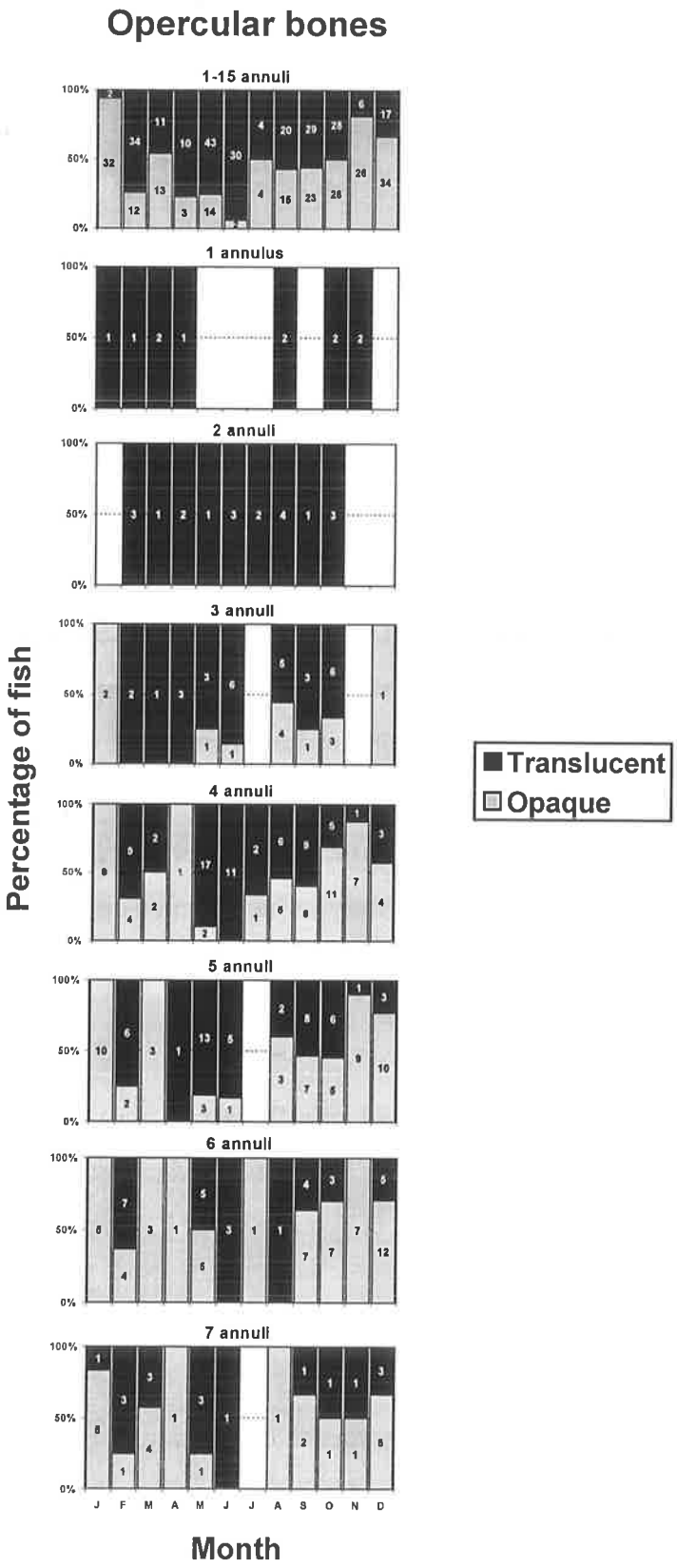

Figure 2.6 Percentage of opercular bones with an opaque or translucent margin under transmitted light. Data for pooled annulus groups and for 1–7 annuli are shown.

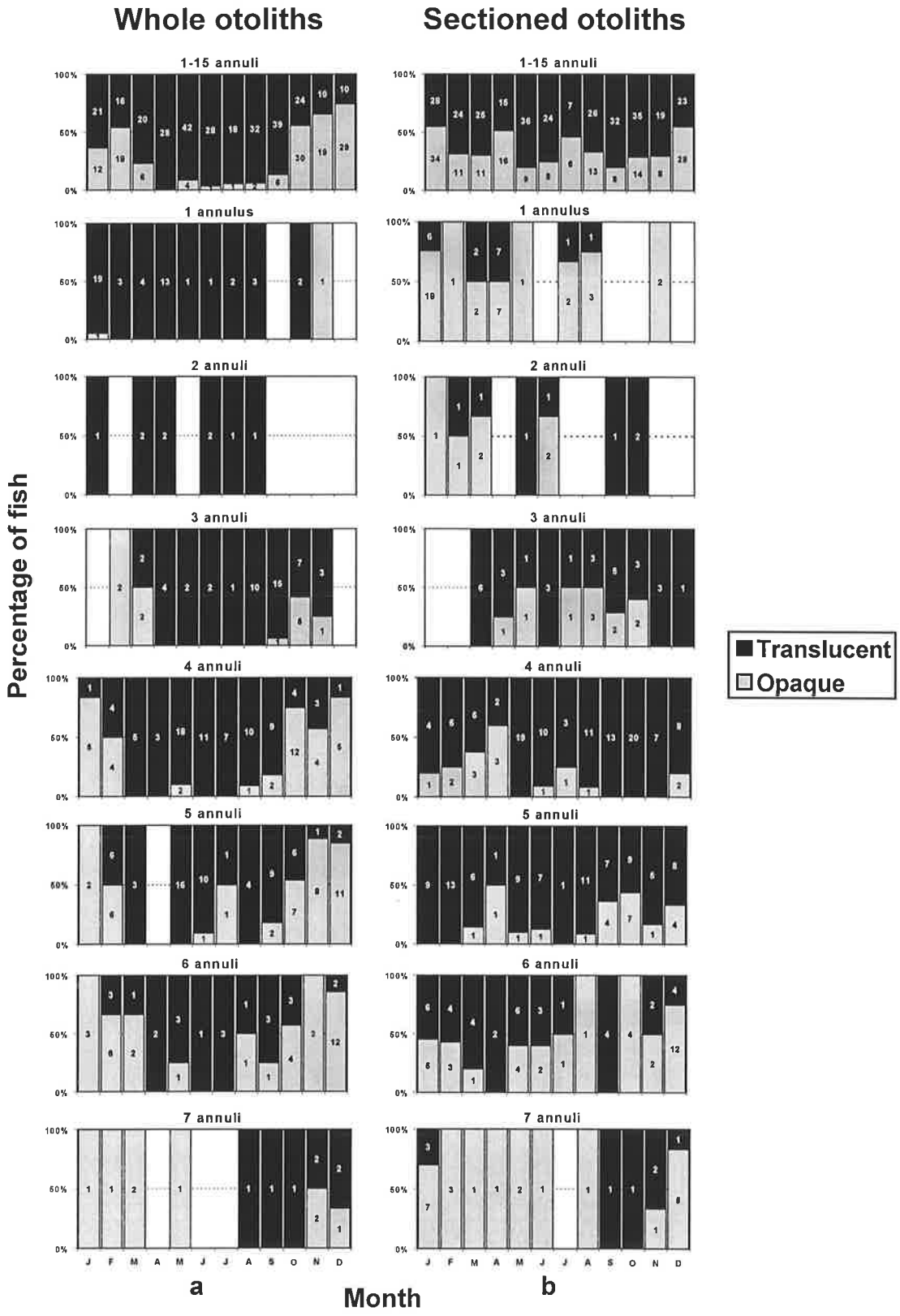

Figure 2.7 Percentage of whole and sectioned otoliths with an opaque or translucent margin under reflected light. Data for pooled annulus groups and for 1–7 annuli are shown. (a) Annulus counts based on whole otoliths; (b) annulus counts based on sectioned otoliths.

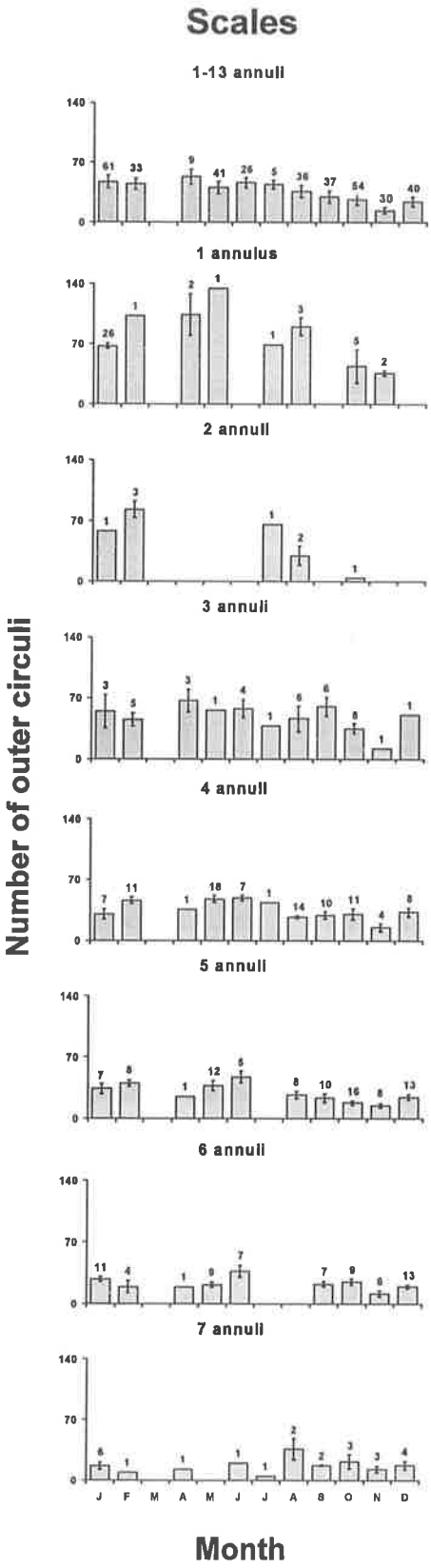

Figure 2.8 Number (± SE) of circuli beyond the last-formed annulus in scales. Data for pooled annulus groups and for 1–7 annuli are shown.

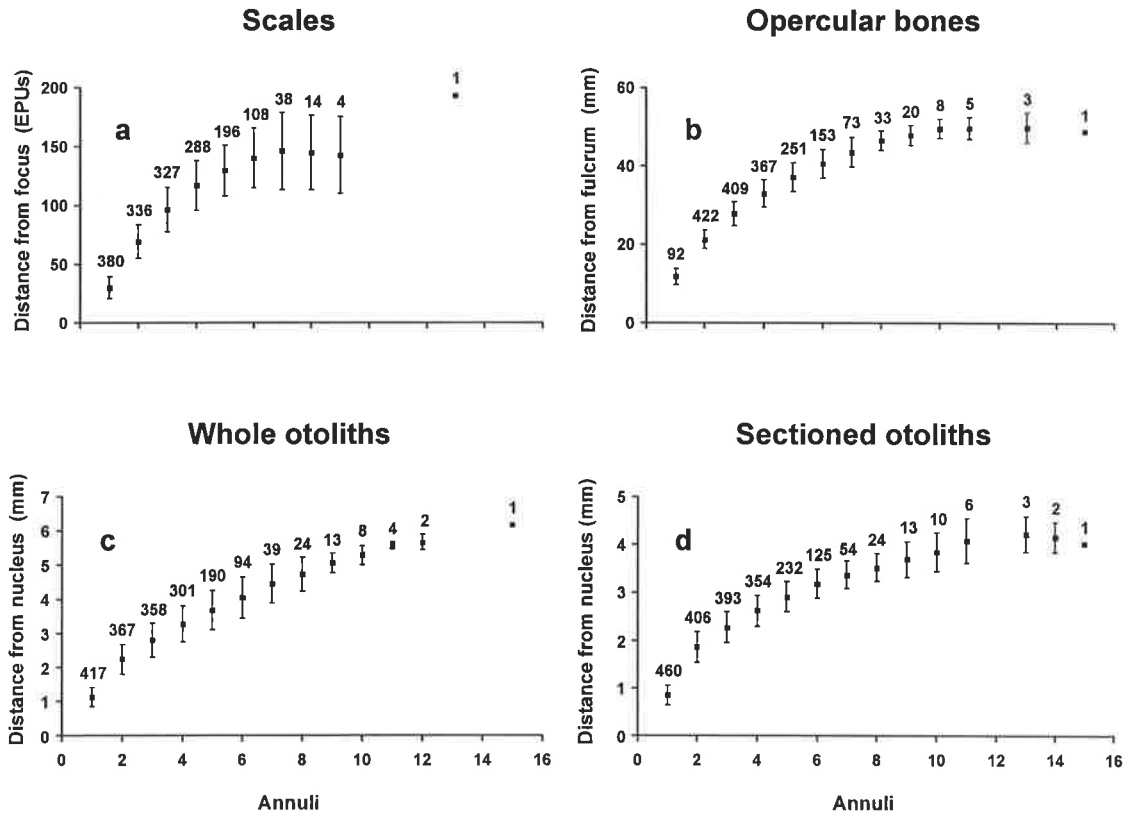

Figure 2.9 Mean annulus distance (± SD) from the centre of origin (focus in scales, fulcrum in opercular bones, nucleus in otoliths). Annulus counts are based on the corresponding structure. (a) Scales; (b) opercular bones; (c) whole otoliths; (d) sectioned otoliths.

2.4 Discussion

Age determination in fish always is prone to some subjectivity (Boehlert 1985), so that routine validation of age assessments obliges the user to indicate accuracy (R. I. C. C. Francis *et al.* 1992). MIA is used widely in fish and fisheries biology *in lieu* of direct validation procedures like mark-and-recapture and capture of fish of known age. These are the most reliable and effective techniques, but beyond the scope of most studies. In this context the type of validation achieved here cannot be regarded as wholly 'successful' in the sense of Beamish and McFarlane (1983), as it is applicable only to the first seven age groups of the sampled population. Another limitation of MIA is that reliance on spatial patterns on calcified structures (corresponding to regularly alternating zones of different optical properties, usually reflecting temporal (i.e. seasonal) changes in physiological activity: Simkiss 1974) makes the method susceptible to spatial and temporal fluctuations in environmental conditions like water temperature and food availability.

Finally, species-specific variability in the morphology of calcified structures may restrict the applicability of conventional MIA techniques used in studies of other fish, prompting for alternative approaches tailored to the species under investigation. It is only in this context that evaluation of a validation technique is possible and this, as already noted, is a convergence of several interrelated factors.

Although decreases in MIR in October–December were apparent up to age group 7 for all structures, the values were never less than 20–30% of the previous incremental zone, and were independent of the estimated ages of the fish and the structure considered. Variations in time of annulus deposition among fish of a different age class are to be expected as a result of differences in relative growth and ontogenetic intervals (i.e. the juvenile, adult and senescence periods *sensu* Balon 1971, 1975b). However, the variability remaining when age groups were examined separately appears to be related to intrinsic and extrinsic factors linked to both the limitations of the ageing technique and to ecophysiological variation among individual fish of any one age class. Carp may spawn through most of the year in the lower River Murray (Jones 1974; see also Chapter 11), possibly even at water temperatures below 18 °C, which is commonly regarded as a lower limit (Sarig 1966). Jones reported that Young-Of-the-Year (YOY) carp were found "in shallow swampy areas of the river throughout the year" (p. 73), probably as a result of protracted flooding in 1974 that may have increased the availability of spawning sites for adult carp and food for larvae and juveniles. Jones' contention was supported by scale morphology (the number and spacing of circuli around the focus) indicating five cohorts of YOY carp (cf. Section 1.3). Although in the lower Murray spawning conditions for carp may occur occasionally in winter, several confounding factors may prejudice the reliability of interpretations of scale morphology. Mann and Steinmetz (1985) showed that the relative widths of the first year of growth in scales of rudd (*Scardinius erythrophthalmus*) varied as a result of differences in individual growth rates within the same age class, the first annulus being further from the focus in fast-growing than in slow-growing individuals. They attributed these variations to differences in microhabitat characteristics and growth rates between years, although genetic variation (cf. carp: Wohlfarth 1977) may also play a role. Another limitation to MIA became evident in this study when reading otoliths with a newly-forming annulus along the edge, usually seen (under reflected light) as a narrow opaque zone within a translucent matrix, making the margin itself appear translucent. The new opaque zone

usually is recognisable only when it attains 20–40% of the previous annual increment, so that an otolith with an incipient zone would be scored as having a translucent edge. This has been recorded for the otoliths of other cyprinids (Mina 1989), and clearly would affect determinations even after grinding or sectioning. Indeed, in this study otolith sections provided no real advantage over whole otoliths in terms of the visibility of newly-formed opaque zones.

The absence of strong periodicity in annulus formation was confirmed by the ETA results, although the morphology of the calcified structures again seems to have had a confounding influence. In opercular bones, and especially in whole otoliths, the numbers of structures with an opaque edge, as expected, were greater in the growing season than in winter, and sectioning obscured these patterns. Although it has been argued that sectioned otoliths, generally considered superior to whole otoliths (e.g. Beamish 1979a,b), should enhance the visibility and resolution of zonation, especially in older individuals and perhaps those resuming their seasonal growth, this did not appear to be so for carp. A detailed analysis of the value and reliability of scales, opercular bones, and whole and sectioned otoliths for age determinations in carp is given in Chapter 3. Here, it may be noted that sectioning does obscure alternating translucent and opaque zones, especially near the edge, preventing identification of transitions in the same growth zones as the ones normally visible in whole otoliths.

A goal of the validation component of this study was to identify a semi-objective criterion to assist in interpretation of the edges of calcified structures. The method of Anderson *et al.* (1992a,b) was modified to accommodate variation in the relative width and appearance of annual increments, especially the opaque zones in otoliths. This method was superior to ETA in resolving difficulties encountered in the interpretation of zonation patterns. The increased resolution is most evident because the presence of 'aberrant' opaque edges in fish sampled in late autumn and winter is suppressed by giving more emphasis to the relative width of the last annual increment than to its appearance. Another advantage of this method is that it allows a margin of precision for the designated common birth-date, given that this may vary over the range of the species (cf. Chapter 4). As an alternative, qualitative approach to describing seasonal trends in scale morphology, the numbers of outer circuli provided a reasonably satisfactory indication of the annual

formation of new annuli, although pronounced irregularities narrowed the range of age classes to which this method could be applied, especially in fish with more than 4–5 annuli.

By comparing MIRA, ETA and a modified method as means for resolution of the edge interpretation problem, this study demonstrates that for the calcified structures examined the formation of annuli occurred annually in carp up to seven years old. Although extrapolations should be made cautiously before confirmation by other methods, particularly tagging programs, the regular alternation of opaque and translucent zones observed in the opercular bones and whole otoliths of older carp is also strongly suggestive of annual periodicity. Previously reported difficulties in determining the age profiles of wild carp populations in Australia, due to protracted spawning conditions and a lack of a pronounced seasonality (Jones 1974; Hume *et al.* 1983a), therefore can be overcome by methods designed to minimise the confounding effects of these factors on the formation of periodic patterns in scales, opercular bones and otoliths.

2.5 Conclusion

By validating age estimates for the first seven years of age in carp from the lower Murray, with a qualification for age class 2 where the sample size was small, problems in age determinations for this species in Australia can be circumvented by the adoption of *ad hoc* ageing techniques based on regular patterns in scales, opercular bones and otoliths. More research is needed to extend the range of validated ages to the entire life span, possibly using mark-and-recapture studies and/or by radiometric analysis of otoliths (e.g. Fenton and Short 1992).

3.

AGE AND GROWTH:

CONSISTENCY OF AGE INTERPRETATIONS

> Initially opercular bones, otoliths, and fin spines, were also taken from some fish to determine the best structure for ageing carp. Otoliths were found to be too small and difficult to extract, bones were bulky to store, required cleaning and drying after collection and were often opaque and difficult to read.
>
> D. J. Hume *et al.* (1983a)

3.1 Introduction

Several methods for assessing the reliability of fish age interpretations from calcified structures have been developed in the last 20 years (Campana *et al.* 1995), and indications of the consistency of estimates now are mandatory in age and growth studies. Percent agreement, a simple measure of precision, has been superseded by indices like the Average Percent Error (APE: Beamish and Fournier 1981), the Coefficient of Variation (V or CV: Chang 1982) and the index of precision (D: Chang 1982), all independent of the ages of the fish. There are also graphical methods (e.g. the age bias plot of Campana *et al.* 1995) to indicate linear and non-linear age estimation bias, another key to consistent interpretations.

Calcified structures like scales, otoliths, flat bones, vertebrae and fin rays often have been used separately to interpret the age of fish, and other studies have compared suites of structures to corroborate age interpretations or resolve problems with identification of structure-dependent periodic patterns (e.g. Maraldo and MacCrimmon 1979; Erickson 1983; Sharp and Bernard 1988). In cyprinids, scales and to a lesser extent opercular bones are widely used (Mann 1991), and otoliths (especially lapilli) also have been employed successfully (e.g. Backe-Hansen 1982; Mills 1988; Mina 1989; O'Maoileidigh and Bracken 1989).

In carp, *Cyprinus carpio* L., there are several potential structures (cf. Vilizzi and Walker 1995), and comparative studies are relatively well-documented. For example, English (1952a) and Rehder (1959) found scales and opercular bones to be good indicators of age and growth, and Wichers (1976) and Bishai and Labib (1978) judged fin rays and vertebrae respectively to be most convenient and reliable (cf. Chapter 6).

In south-eastern Australia, concern over the spread of carp and their impact on rivers and wetlands has encouraged researchers to seek methods for control (Brumley 1991; Harris 1995; cf. Section 1.2). A fundamental step is to develop methods to determine the ages of carp, and hence the age profiles of populations. This chapter presents an evaluation of a suite of calcified structures (scales, opercular bones, whole and sectioned otoliths (asterisci)) from carp in the River Murray, South Australia. The aim was to determine which structure(s) could be reliably used in routine assessments of the age profiles of wild populations. The criteria for evaluation were (1) the overall readability of a structure, (2) the extent of the between-structure, within-interpreter and between-interpreter bias and precision of annulus counts, and (3) differences in the estimates of growth parameters from annulus counts for different structures.

Methods for the collection and preparation of samples are described in Chapter 2, where validation of the age assessments is provided. An evaluation of growth models is given in Chapter 4.

3.2 Methods

3.2.1 Terminology

In this chapter the term *interpreter* is used as synonymous with *ager* or *reader*, and *interpretable* and *uninterpretable* with *readable* and *unreadable*, respectively. Also, *annulus count(s)* (or simply *count(s)*) will be equivalent to *annulus reading(s)* (or simply *reading(s)*), and *interpreting the age* of a fish will be preferred to *ageing* a fish.

3.2.2 Experimental layout

The study was in three stages involving five interpreters (A–E) with varying degrees of experience in fish age interpretation techniques.

3.2.2.1 Stage 1. Comparison of structures and consistency by Interpreter A

Preliminary annulus counts were made by Interpreter A (the author) on 471 scales, 468 opercular bones, 563 whole otoliths and 546 sectioned otoliths. Three replicate counts were needed for the whole otoliths before satisfactory confidence in their interpretation was achieved, but one count was enough for scales and opercular bones. This disparity reflects the lack of established criteria for the interpretation of carp otoliths, despite an extensive literature on methods for analysis of structures like scales and opercular bones (cf. Sections 6.2.1 and 6.2.2). Satisfactory interpretation of annulus counts on sectioned otoliths also was achieved after one series of counts, as the appearance of zones was comparable to that in the unsectioned otoliths. The overall interpretability of each structure was evaluated in the first count. Whenever a pattern (alternating opaque and translucent zones in opercular bones and otoliths, or closely- and widely-spaced circuli in scales; cf. Chapter 2) could not be consistently identified the preparation was scored *uninterpretable*. These were discarded in the second count, with small numbers of opercular bones and whole otoliths (n = 5), lacking annuli, from 0+ fish. All *interpretable* structures, except sectioned otoliths, were then examined a second time by Interpreter A. This was two months after the first count, and involved 380 scales, 440 opercular bones and 417 whole otoliths. The interpreter had no indication of the date of capture, length or weight of the fish.

3.2.2.2 Stage 2. Consistency by Interpreters A and E

The second stage involved Interpreter E, who had no prior experience with fish age interpretation techniques. Counts by Interpreter E were evaluated in a preliminary training session lasting about three days, after which she examined the sample of interpretable scales, opercular bones and whole otoliths examined by Interpreter A. Again, Interpreter E had no knowledge of the body morphometrics and date of capture of the fish.

3.2.2.3 Stage 3. Precision by Interpreters B, C and D

The third stage was a two-part experiment involving three researchers with diverse experience in fish age interpretation methodologies. Interpreters B and D both had some prior experience, and Interpreter C was an expert in terms of both experience and number of calcified structures examined. All were given a one-day familiarisation course, to ensure a consistent approach.

In the first part of the Stage 3 experiment the interpreters were required to count annuli on 90 preparations consisting of 30 scales, 30 opercular bones and 30 whole otoliths. They were given the same 90 preparations, chosen randomly from triplets from 362 fish, including all possible combinations of interpretable and uninterpretable structures determined by Interpreter A. They were aware of the possible presence of uninterpretable preparations. Each structure was randomly assigned a number from 1–30 so that there was no numerical correspondence between structures of the same triplet; indeed, the interpreters did not know that there were triplets from the same fish. They were asked to complete their counts in one day, independently of one another. They had no information about the date of capture, length or weight of the fish.

The second part of the Stage 3 experiment was identical except that the three interpreters (B, C, D) performed their analyses at different times from one another (1–2 months after the first count), and Interpreters B and D relied on image analysis to enumerate annuli on whole otoliths. All structures scored as uninterpretable by Interpreters B, C and D on the first occasion were discarded for the second count.

3.2.3 Data analysis

Stage 1 comparisons were to determine the interpretability of the structures, the visibility of the first and second annulus and the bias and precision of annulus counts. As sectioned otoliths provided annulus counts comparable to those from whole otoliths throughout the range of annuli enumerated, they were eventually discarded. Subsequent counts were on scales, opercular bones and whole otoliths (i.e. second count by Interpreter A; all counts by Interpreters B, C, D and E).

The within-Interpreter A bias and precision of counts on scales, opercular bones and whole otoliths were analysed by statistical and graphical methods. For each pair of replicate counts on each structure this included (1) an age frequency table, (2) an age bias plot, and measures of (3) APE and V for pooled annulus counts, (4) APE, the percent agreement (PAG) and an index of percent bias (Kimura and Lyons 1991), with corresponding plots for mean annulus counts at each annulus group, and (5) parameter estimates for the Von Bertalanffy Growth Function (VBGF). Following Kimura and Lyons (1991), the nominal age (= number of annuli) used to compare replicate annulus counts by Interpreter A on the

same structure at each annulus group was the rounded mean. Further, in comparing annulus counts between structures, and between counts by Interpreters A and E on scales, opercular bones and whole otoliths, the coefficient of variation, an age bias plot and an age frequency table were used. VBGF parameter estimates also were fitted to length-at-annulus data from the annulus counts by Interpreters A and E on the three structures.

The results from Stage 3 were analysed only for precision, as the small sample sizes prevented evaluations of bias. Precision was measured by APE and V, and statistical tests were performed to compare the reproducibility of counts within and between interpreters.

The reproducibility of replicate counts for the two structures found to provide the most reliable and consistent interpretations (i.e. opercular bones and whole otoliths) was tested for each structure by two-way nonparametric ANOVA (Zar 1984). The factors in these analyses were the type of annulus pattern on the structure (classes A–C, as defined in Section 2.2.3.3) and the annulus group (arbitrarily: I = 1–3 annuli, II = 4–7 annuli, III ≥ 8 annuli). The response variable was the coefficient of variation, based on three replicate counts (two counts from Interpreter A and one from Interpreter E).

VBGFs were fitted by nonlinear procedures to age estimates from different structures and interpreters, followed by *post hoc* statistical comparisons between and among models. The methods are described in Section 4.2.4. Following Chang (1982) the coefficient of variation is preferred to measure precision, given its statistical rigour and flexibility, but the average percent error or corresponding index (IAPE) are provided for comparison with other data. The rules for recognition of annuli are followed, and the term *annulus* is used instead of age (estimated or validated).

3.3 Results

3.3.1 Stage 1. Comparison of structures: bias and reproducibility

The numbers and corresponding percentages of interpretable and uninterpretable scales, opercular bones, whole and sectioned otoliths are shown in Table 3.1. Interpretability was not independent of the type of structure: scales and opercular bones respectively provided the lowest and highest number of interpretable preparations. Whole and sectioned otoliths

had similar interpretability, suggesting that no real improvement was achieved by sectioning. In most scales recorded as uninterpretable, most annuli could not be recognised because of partial or complete resorption. In other cases no clear pattern of alternating zones of widely- and closely-spaced circuli could be seen, often because there were strong irregularities in the arrangement of the circuli. Although opercular bones showed the highest interpretability, these results could be misleading because the position of the first and sometimes the second annulus could not be determined consistently. In opercular bones with less than three annuli the thinness of the bone usually inhibited the interpretation of pseudoannuli often present during the first two years of growth. When 3–6 annuli were present the first annulus, when visible, appeared at the transition between a translucent zone at the level of the fulcrum and a more opaque zone marking the inception of the second year of growth. In opercular bones with more than six annuli ossification at the level of the fulcrum completely obscured the first and, occasionally, the second annulus. As noted, whole and sectioned otoliths had a similar interpretability, mid-way between that of scales and opercular bones. Faded, narrow, discontinuous and randomly intersecting opaque zones in a translucent matrix were typical of uninterpretable whole otoliths, and sectioning did not improve their visibility. In all interpretable whole and sectioned otoliths the first annulus was always identifiable, unlike that in scales and opercular bones.

Table 3.1 **Numbers and corresponding percentages (in parentheses) of interpretable and uninterpretable calcified structures.** All values for scales, opercular bones and whole otoliths are based on the first count by Interpreter A. Only one count was done on sectioned otoliths. The chi-square probability value is indicated.

Calcified structure	Interpretable	Uninterpretable
Scale	380 (80·7)	91 (19·3)
Opercular bone	444 (94·9)	24 (5·1)
Whole otolith	492 (87·4)	71 (12·6)
Sectioned otolith	465 (85·2)	81 (14·8)
$\chi^2 = 50{\cdot}28$ ($P = 7{\cdot}0E{-}11 < 0{\cdot}001$)		

3.3.2 Stage 1. Comparison of structures: bias

In comparing the four structures for bias and reproducibility all possible pairwise combinations were examined, and the corresponding values for IAPE and V are shown in Table 3.2. As expected, counts from whole and sectioned otoliths were more precise than those from other combinations. The least reproducibility was seen in comparison between opercular bones and sectioned otoliths. Bias was also studied by means of a frequency table and an age bias plot for each of the six possible combinations, shown below. In all these comparisons, the wider deviations from equivalence at higher annulus counts may be simply an artefact of small sample sizes.

Table 3.2 **Reproducibility of annulus counts based on all pairwise comparisons of four calcified structures.** IAPE: index of average percent error; V: coefficient of variation; Sc: scale; Op: opercular bone; WOt: whole otolith; SOt: sectioned otolith; A1: first count by Interpreter A; A2: second count by Interpreter A.

Calcified structure	*n*	IAPE (%)	V (%)
OpA1 / ScA1	323	8·38	11·85
WOtA2 / ScA1	297	8·94	12·65
SOt / ScA1	324	8·45	11·95
WOtA2 / OpA1	337	9·30	13·15
SOt / OpA1	362	10·57	14·94
SOt / WOtA2	357	7·01	9·92

3.3.2.1 Opercular bones and scales

There was good agreement up to eight annuli. Opercular bones under-estimated scale annulus counts when the scales had more than eight annuli. One scale with six annuli accompanied an operculum with 15 annuli (Table 3.3, Fig. 3.1a).

3.3.2.2 Whole otoliths and scales

Little bias was detected between whole otoliths and scales up to six annuli, but scale annulus counts thereafter increased disproportionately (Table 3.4, Fig. 3.1b).

3.3.2.3 Sectioned otoliths and scales

The pattern was similar to that for scales and whole otoliths. There was a tendency for counts to be inflated at three scale annuli and under-estimated at 7–8 scale annuli. Four sectioned otoliths with more than 10 annuli corresponded to scales with 6–7 annuli (Table 3.5, Fig. 3.1c).

3.3.2.4 Whole otoliths and opercular bones

Interpretations were broadly similar, but with some striking deviations. Opercular bones under-estimated otolith annulus counts of 2–3 annuli, and slightly over-estimated them at seven and nine annuli. Two whole otoliths with 12 and 15 annuli corresponded to opercular bones with 6 and 7 annuli, respectively (Table 3.6, Fig. 3.1d).

3.3.2.5 Sectioned otoliths and opercular bones

Annulus counts from opercular bones were under-estimated when 2–4 sectioned otolith annuli occurred, and over-estimated beyond seven annuli. No bias was apparent when only five annuli were present. One sectioned otolith with 14 annuli corresponded to an opercular bone with only seven annuli (Table 3.7, Fig. 3.1e).

3.3.2.6 Sectioned otoliths and whole otoliths

Sectioned otoliths over-estimated whole otolith counts at 2–4 annuli, and there were wide deviations over seven annuli. The caveat regarding small sample sizes should not be forgotten (Table 3.8, Fig. 3.1f).

Table 3.3 **Age frequency table comparing annulus counts by Interpreter A based on scales and opercular bones.** Data are numbers of calcified structures and counts in agreement are shown in bold type. ScA1: first count of scales; OpA1: first count of opercular bones. See also Fig. 3.1a.

ScA1/ OpA1	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Total
1	**7**	5																12
2	2	**2**	1	1														6
3		8	**18**	7	5													38
4		2	10	**45**	25	1	2		1									86
5				24	**32**	22	2	1										81
6			1	9	16	**29**	6		1		1				1			64
7			1	1	1	4	**7**	5	2	1			1					23
8			1		1	1	1		3	1	1							9
9				1		1			**1**									3
10																		0
11																		0
12																		0
13													**1**					1
14																		0
15																		0
16																		0
17																		0
Total	9	17	32	88	80	58	18	6	8	2	2	0	2	0	1	0	0	323

Table 3.4 **Age frequency table comparing annulus counts by Interpreter A based on scales and whole otoliths.** Data are numbers of calcified structures and counts in agreement are shown in bold type. ScA1: first count of scales; WOtA2: second count of whole otoliths. See also Fig. 3.1b.

ScA1/ WotA2	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Total
1	**27**																	27
2	4	**1**				1												6
3	2	4	**14**	12	3	1												36
4			22	**37**	11	5	1	1										77
5			5	29	**24**	10	1											69
6			1	6	25	**15**	3	2			1							53
7			1		4	5	**4**	2	2									18
8			1		2	1	2	**1**		1								8
9				1	1													2
10																		0
11																		0
12																		0
13									1									1
14																		0
15																		0
16																		0
17																		0
Total	33	5	44	85	70	38	11	6	3	1	1	0	0	0	0	0	0	297

Table 3.5 **Age frequency table comparing annulus counts by Interpreter A based on scales and sectioned otoliths.** Data are numbers of calcified structures and counts in agreement are shown in bold type. ScA1: first count of scales; SOtA: single count of sectioned otoliths. See also Fig. 3.1c.

ScA1 / SOtA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Total
1	**32**	1																33
2	3	**4**			1													8
3		2	**10**	13	3													28
4			14	**41**	24	5												84
5		2	1	33	**24**	10	7			1								78
6			2	9	20	**21**	8	1	1		1		1					64
7			1	2	3	7	**4**		1						1			19
8					2	1	2	**1**		2								8
9					1													1
10																		0
11																		0
12																		0
13										1								1
14																		0
15																		0
16																		0
17																		0
Total	35	9	28	98	78	44	21	2	2	4	1	0	1	0	1	0	0	324

Table 3.6 **Age frequency table comparing annulus counts by Interpreter A based on opercular bones and whole otoliths.** Data are numbers of calcified structures and counts in agreement are shown in bold type. OpA1: first count of opercular bones; WOtA2: second count of whole otoliths. See also Fig. 3.1d.

OpA1 / WOtA2	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Total
1	7																	7
2	7	**5**	3	2	1	1												19
3	1	2	**13**	15	3													34
4			20	**47**	17	4	1											89
5			8	21	**36**	8	2											75
6			3	10	25	**21**	2	3		1		1						66
7				2	8	9	**3**	1	1						1			25
8						2	2	**4**		1								9
9						2	2	2										6
10									1	**1**								2
11							1	1										2
12																		0
13									2									2
14																		0
15											1							1
16																		0
17																		0
Total	15	7	47	97	90	47	13	11	4	3	1	1	0	0	1	0	0	337

Table 3.7 **Age frequency table comparing annulus counts by Interpreter A based on opercular bones and sectioned otoliths.** Data are numbers of calcified structures and counts in agreement are shown in bold type. OpA1: first count of opercular bones; SOtA: single count of sectioned otoliths. See also Fig. 3.1e.

OpA1 / SOtA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Total
1	**9**	1																10
2	3	**3**	4	6	1													17
3	1	3	**8**	12	8	1												33
4		2	10	**46**	31	6	3	1										99
5			5	21	**25**	19	6	2		1								79
6		1		17	18	**24**	9	2										71
7				6	7	8	**5**	2	1		1			1				31
8				1	2		3		2									8
9						3	2	1		1	1							8
10										**1**					1			2
11							1				**1**							2
12																		0
13										1								1
14																		0
15													1					1
16																		0
17																		0
Total	13	10	27	109	92	61	29	8	3	4	3	0	1	1	1	0	0	362

Table 3.8 **Age frequency table comparing annulus counts by Interpreter A based on whole and sectioned otoliths.** Data are numbers of calcified structures and counts in agreement are shown in bold type. WOtA2: second count of whole otoliths; SOtA: single count of sectioned otoliths. See also Fig. 3.1f.

WOtA2 / SOtA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Total
1	**44**	2		1														47
2		**3**	2	2														7
3		2	**22**	20	6	1												51
4			7	**56**	26	4	2	1										96
5			2	14	**41**	20	4	2										83
6		1	1	4	12	**20**	4	2	1									45
7				3	1	2	**2**	1	1	1	1							12
8				1		2	3	**1**			1							8
9										1	1				1			3
10						1			1	**1**								3
11													1					1
12																		0
13																		0
14																		0
15														1				1
16																		0
17																		0
Total	44	8	34	101	86	50	15	7	3	3	3	0	1	1	1	0	0	357

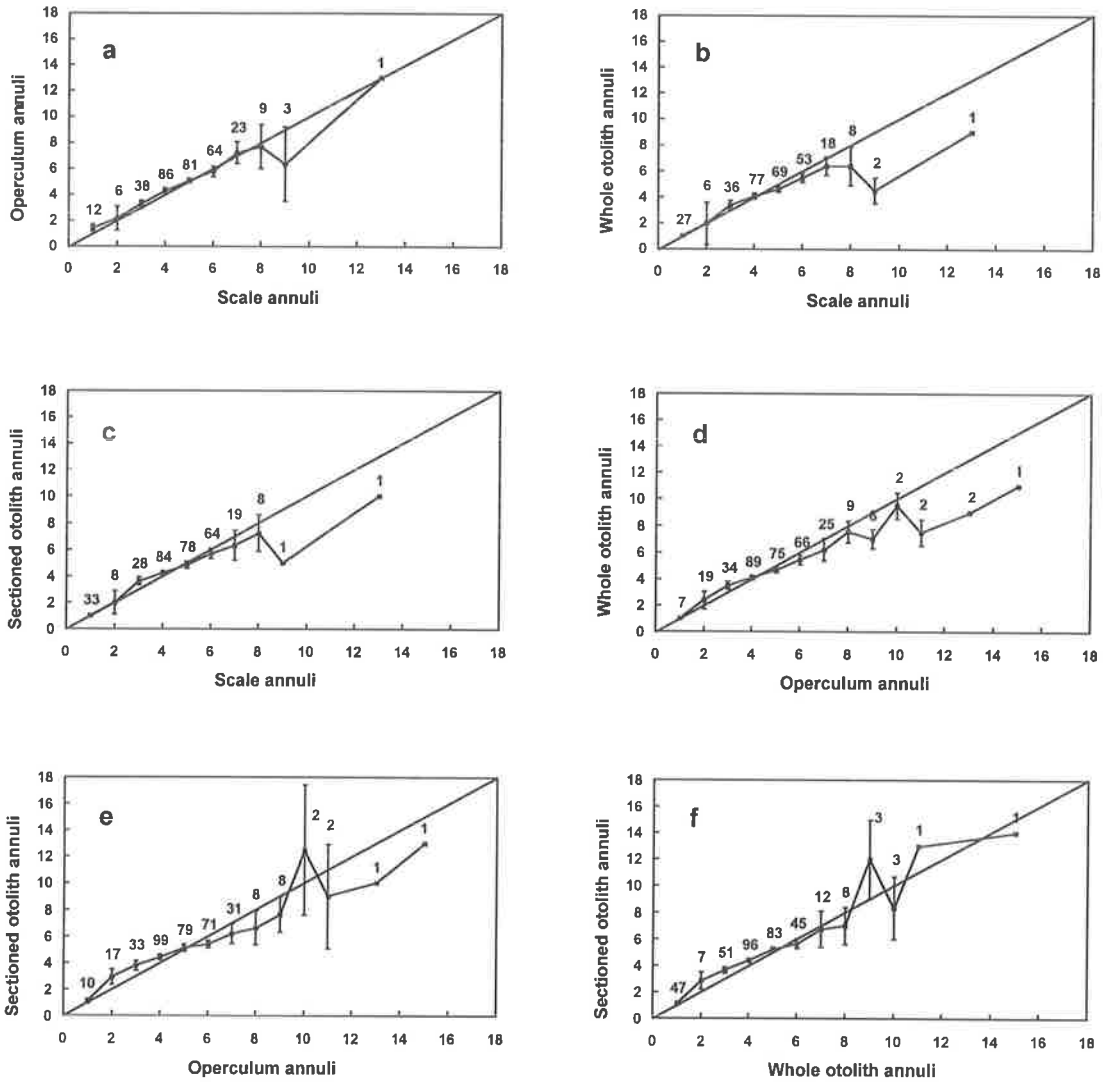

Figure 3.1 Age bias plots for all pairwise comparisons between four calcified structures. The sample size and 95% confidence limits at each annulus group and the 1:1 equivalence line are indicated. Annulus counts from scales and opercular bones are based on the first count by Interpreter A, those from whole otoliths on the second count and those from sectioned otoliths on the single count by the same interpreter. (a) Opercular bones and scales; (b) whole otoliths and scales; (c) sectioned otoliths and scales; (d) whole otoliths and opercular bones; (e) sectioned otoliths and opercular bones; (f) sectioned otoliths and whole otoliths. See also Tables 3.3–8.

3.3.3 Stage 1. Consistency by Interpreter A

To complete these comparisons, a VBGF was fitted to each of the four length-at-annulus data sets for each calcified structure (Table 3.9). An *F*-test showed no significant differences among the curves ($P > 0{\cdot}05$), suggesting that annulus counts from the different structures were equally effective in describing growth.

As no difference in the visibility of annuli was apparent in sectioned otoliths, subsequent discussion of the consistency of age interpretations is based on data from scales, opercular bones and whole otoliths.

Replicated annulus counts by Interpreter A had similar reproducibility, indicated by values of V (Table 3.10). Age bias plots showed that in his second count Interpreter A under-estimated annulus counts (relative to the first count) when more than seven annuli were present in scales and whole otoliths and more than 10 annuli in opercular bones (the counts for opercular bones therefore were consistent for a greater range of annulus counts than for scales and whole otoliths). In whole otoliths the confidence limits were wider over seven annuli than for scales and opercular bones, and there was a tendency toward over-estimation in the second count when two annuli were enumerated in the first count (Tables 3.11–13, Fig. 3.2a–c).

The bias and precision of counts by Interpreter A were assessed for each structure at each annulus count (counts were averaged over the two replicates). Precision was measured as the coefficient of percent agreement and the coefficient of variation, and bias was calculated as the difference between the two replicate counts for each structure, averaged over preparations with the same mean number of annuli (Table 3.14; Fig. 3.3a–c).

In all structures the percent agreement fell below 50% when more than six annuli were present. For scales and opercular bones V was 10–20% at all annulus counts, and in whole otoliths it was over 25% at two annuli and near 25% at eight annuli.

Comparisons of VBGF models fitted to length-at-annulus data showed no significant differences in curves for the first and second counts on scales and opercular bones ($P > 0{\cdot}05$), but significant differences for whole otolith data (Table 3.9).

Table 3.9 **Comparison of length-at-annulus von Bertalanffy growth functions, based on annulus counts from different calcified structures and interpreters.** Values (± asymptotic SE) for the parameters in each model and tests of significance are reported. FL_∞: asymptotic fork length; K: Brody coefficient; t_0: estimated time at which the length of the fish was 0 (Ricker 1975). *F* values are based on an analysis of residual sum of squares (ARSS), following Chen *et al.* 1992 (cf. Chapter 4).

Group	*n*	FL_∞ (mm)	K (yr^{-1})	t_0 (yr)	*F*
All calcified structures					
Scale (Interpreter A, first count)	380	595·6 ± 14·1	0·413 ± 0·040	0·410 ± 0·105	1·736 ns ($P = 0·076$)
Opercular bone (Interpreter A, first count)	440	663·8 ± 18·0	0·276 ± 0·029	− 0·173 ± 0·225	
Whole otolith (Interpreter A, second count)	417	644·1 ± 21·4	0·305 ± 0·034	0·020 ± 0·159	
Sectioned otolith (Interpreter A, single count)	460	629·9 ± 20·1	0·313 ± 0·035	0·065 ± 0·151	
Scale					
Interpreter A (first count)	380	595·6 ± 14·1	0·413 ± 0·040	0·410 ± 0·105	2·239 ns ($P = 0·082$)
Interpreter A (second count)	380	642·9 ± 18·5	0·306 ± 0·029	0·210 ± 0·117	
Opercular bone					
Interpreter A (first count)	440	663·8 ± 18·0	0·276 ± 0·029	− 0·173 ± 0·225	0·393 ns ($P = 0·758$)
Interpreter A (second count)	440	663·1 ± 18·6	0·270 ± 0·029	− 0·186 ± 0·240	
Whole otolith					
Interpreter A (first count)	417	569·2 ± 12·6	0·486 ± 0·056	0·371 ± 0·136	3·795 ($P = 0·010 < 0·05$)
Interpreter A (second count)	417	644·1 ± 21·4	0·305 ± 0·034	0·020 ± 0·159	
Scale					
Interpreter A (first count)	380	595·6 ± 14·1	0·413 ± 0·040	0·410 ± 0·105	9·148 ($P = 6·0E–06 < 0·001$)
Interpreter E (single count)	380	647·2 ± 20·6	0·277 ± 0·027	0·211 ± 0·133	
Opercular bone					
Interpreter A (first count)	440	663·8 ± 18·0	0·276 ± 0·029	− 0·173 ± 0·225	0·148 ns ($P = 0·931$)
Interpreter E (single count)	440	665·5 ± 20·6	0·280 ± 0·032	− 0·043 ± 0·236	
Whole otolith					
Interpreter A (second count)	417	644·1 ± 21·4	0·305 ± 0·034	0·371 ± 0·136	2·636 ns ($P = 0·050$)
Interpreter E (single count)	417	683·0 ± 24·2	0·250 ± 0·026	− 0·049 ± 0·155	

Table 3.10 **Reproducibility of annulus counts within Interpreter A and between Interpreters A and E based on three calcified structures.** IAPE: index of average percent error; V: coefficient of variation.

Calcified structure	Within Interpreter A			Between Interpreters A and E		
	n	IAPE (%)	V (%)	*n*	IAPE (%)	V (%)
Scale	380	5·61	7·94	380	9·15	12·94
Opercular bone	440	5·32	7·52	440	6·99	9·89
Whole otolith	417	5·64	7·97	417	6·23	8·80

Table 3.11 **Age frequency table comparing replicate annulus counts by Interpreter A based on scales.** Data are numbers of scales and counts in agreement are shown in bold type. ScA1: first count; ScA2: second count. See also Fig. 3.2a.

ScA1 / ScA2	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Total
1	**41**	3																44
2		**6**	3															9
3		2	**24**	9	4													39
4		2	4	**55**	21	6	2	1	1									92
5				9	**54**	19	3	3										88
6			1	1	13	**40**	12	2	1									70
7	1		1		2	7	**7**	4	2									24
8			1		2	1		**5**	1									10
9							1	1	**1**									3
10																		0
11																		0
12																		0
13										1								1
14																		0
15																		0
16																		0
17																		0
Total	42	13	34	74	96	73	25	16	6	1	0	0	0	0	0	0	0	380

Table 3.12 **Age frequency table comparing replicate annulus counts by Interpreter A based on opercular bones.** Data are numbers of opercular bones and counts in agreement are shown in bold type. OpA1: first count; OpA2: second count. See also Fig. 3.2b.

OpA1 / OpA2	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Total
1	**9**	1	1															11
2		**12**	8															20
3		2	**27**	11	2													42
4		1	10	**76**	25	3	1											116
5			2	14	**52**	21	6	3										98
6			1	2	12	**49**	15	1										80
7					3	14	**18**	4			1							40
8					1		3	**5**	2		1	1						13
9								5	**4**	1	1	1						12
10							1	1			1							3
11										1	**1**							2
12																		0
13											2							2
14																		0
15										1								1
16																		0
17																		0
Total	9	16	49	103	95	87	44	19	6	3	7	2	0	0	0	0	0	440

Table 3.13 **Age frequency table comparing replicate annulus counts by Interpreter A based on whole otoliths.** Data are numbers of whole otoliths and counts in agreement are shown in bold type. WOtA1: first count; WOtA2: second count. See also Fig. 3.2c.

WOtA1 / WOtA2	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Total
1	**49**	4																53
2	1	**3**	3	1	2													10
3		2	**39**	14	2													57
4			11	**71**	17	1	1											101
5			2	18	**54**	13	1				1							89
6			1	5	13	**31**	6	2	1	1								60
7					4	7	**5**	2										18
8			1		2	2	2	**3**										10
9				1	2			2	**3**	1		1						10
10						1		1		**2**								4
11				1				1	1									3
12																		0
13																		0
14																		0
15																		0
16															1			1
17											1							1
Total	50	9	57	111	98	55	15	11	5	4	2	1	0	0	1	0	0	417

Table 3.14 **Bias and precision of annulus counts by Interpreter A at each annulus group based on three calcified structures.** ScA1: first count of scales; ScA2: second count of scales; OpA1: first count of opercular bones; OpA2: second count of opercular bones; WOtA1: first count of whole otoliths; WOtA2: second count of whole otoliths. Precision is measured as the coefficient of percent agreement (PAG) and the coefficient of variation (V), while bias is calculated as the difference between the two counts on each structure, averaged over preparations with the same mean number of annuli. The nominal age (= annuli) is the rounded mean (cf. Kimura and Lyons 1991).

Annuli	ScA1 / ScA2				OpA1 / OpA2				WOtA1 / WOtA2			
	n	PAG %	V (%)	Bias (%)	*n*	PAG (%)	V (%)	Bias (%)	*n*	PAG (%)	V (%)	Bias (%)
1	41	100·0	0·0	0·0	9	100·0	0·0	0·0	49	100·0	0·0	0·0
2	9	66·7	15·7	−16·7	14	85·7	8·4	−10·7	8	37·5	29·5	−18·8
3	31	77·4	7·6	3·2	38	71·1	8·7	−3·5	45	86·7	4·2	−2·2
4	73	75·3	7·0	−2·4	101	75·2	5·6	−0·2	102	69·6	7·5	−2·2
5	93	58·1	8·3	−3·2	97	53·6	8·3	−2·1	96	56·3	8·0	2·5
6	81	49·4	8·9	−2·7	92	53·3	7·3	−3·3	64	48·4	8·7	2·1
7	35	20·0	13·9	−6·1	52	34·6	9·0	−2·5	27	18·5	14·7	10·6
8	13	38·5	9·2	−8·7	12	41·7	5·5	−1·0	12	25·0	21·3	−2·1
9	3	33·3	5·5	0·0	14	28·6	9·3	3·2	6	50·0	5·4	7·4
10					4	0·0	18·0	−25·0	5	40·0	8·8	8·0
11					4	25·0	8·4	−6·8	1	0·0	20·2	−27·3
12	1	0·0	18·4	25·0	2	0·0	11·8	16·7				
13					1	0·0	28·3	38·5				
14									1	0·0	30·3	42·9
15												
16									1	0·0	4·6	6·3

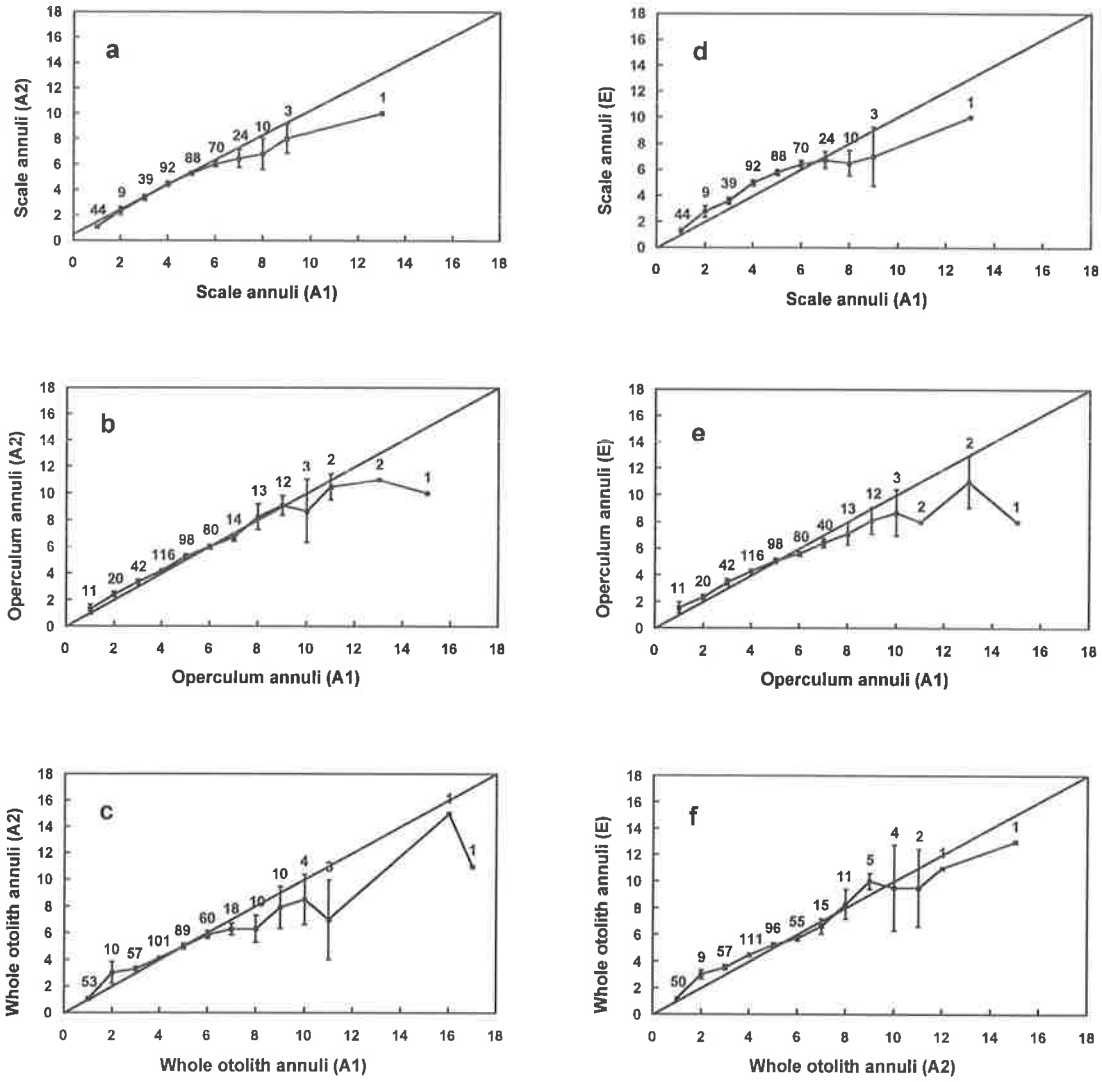

Figure 3.2 Age bias plots for pairwise comparisons between replicate annulus counts from the same and from different interpreters based on three calcified structures. The sample size and 95% confidence limits at each annulus group and the 1:1 equivalence line are indicated. A1: first count by Interpreter A; A2: second count by Interpreter A; E: single count by Interpreter E. (a) Second and first count of scales by Interpreter A; (b) second and first count of opercular bones by Interpreter A; (c) second and first count of whole otoliths by Interpreter A; (d) single count by Interpreter E and first count by Interpreter A of scales; (e) single count by Interpreter E and first count by Interpreter A of opercular bones; (f) single count by Interpreter E and second count by Interpreter A of whole otoliths.

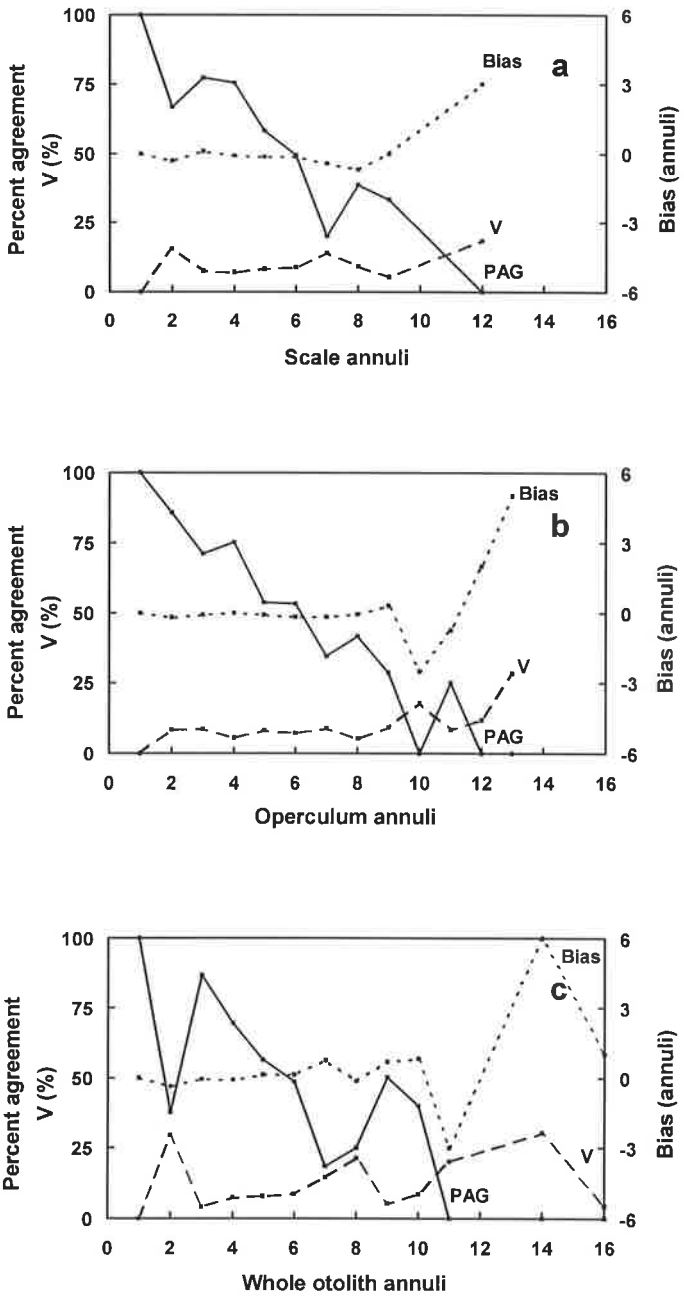

Figure 3.3 Bias and precision of annulus counts based on three calcified structures. PAG: percent agreement; V: coefficient of variation. Bias is calculated as the difference between two replicate counts for each structure, averaged over preparations with the same mean number of annuli. All counts by Interpreter A. (a) Annulus counts from scales; (b) annulus counts from opercular bones; (c) annulus counts from whole otoliths.

3.3.4 Stage 2. Consistency by Interpreters A and E

The reproducibility of counts between Interpreters A and E (Table 3.10) was least for scales, better for opercular bones and best for whole otoliths. The age bias plot for scales showed that Interpreter E over-estimated counts by Interpreter A below six annuli and under-estimated counts above 8 annuli (Table 3.15, Fig. 3.2d). Interpreter E also under-estimated counts for opercular bones when more than six annuli were counted by Interpreter A (Table 3.16, Fig. 3.2e). However, there was close agreement between the two from 1–6 annuli. Counts on whole otoliths agreed up to eight annuli, although Interpreter A over-estimated when 2–3 annuli were present. The overall precision of counts when more than 10 annuli were present was higher in whole otoliths than in scales and opercular bones (Table 3.17, Fig. 3.2f).

VBGFs fitted to age estimates by Interpreter A (first count for scales and opercular bones and second count for whole otoliths) and Interpreter E showed significantly different curves ($P < 0{\cdot}001$) for scales, but no significant differences between the curves for opercular bones and whole otoliths (Table 3.9).

Table 3.15 **Age frequency table comparing annulus counts by Interpreters A and E based on scales.** Data are numbers of scales and counts in agreement are shown in bold type. ScA1: first count by Interpreter A; ScE: single count by Interpreter E. See also Fig. 3.2d.

ScA1 / ScE	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Total
1	**33**	9	2															44
2		**3**	5	1														9
3		1	**21**	11	5	1												39
4			3	**33**	34	9	12	1										92
5			1	8	**24**	36	14	5										88
6				2	13	**20**	25	8	2									70
7			1		2	7	**9**	4				1						24
8			1		1	2	3	**3**										10
9					1		1		**1**									3
10																		0
11																		0
12																		0
13										1								1
14																		0
15																		0
16																		0
17																		0
Total	33	13	34	55	80	75	64	21	3	1	0	1	0	0	0	0	0	380

Table 3.16 **Age frequency table comparing annulus counts by Interpreters A and E based on opercular bones.** Data are numbers of opercular bones and counts in agreement are shown in bold type. OpA1: first count by Interpreter A; OpE: single count by Interpreter E. See also Fig. 3.2e.

OpA1 / OpE	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Total
1	**6**	4	1															11
2		**14**	6															20
3		5	**17**	16	4													42
4		2	9	**71**	27	4	2	1										116
5			3	20	**51**	18	5		1									98
6				3	36	**34**	6		1									80
7					8	15	**12**	4		1								40
8					1	4	5	**1**		2								13
9						1	6	1	**1**	2		1						12
10							1		1	**1**								3
11								2										2
12																		0
13										1		1						2
14																		0
15								1										1
16																		0
17																		0
Total	6	25	36	110	127	76	37	10	4	7	0	2	0	0	0	0	0	440

Table 3.17 **Age frequency table comparing annulus counts by Interpreters A and E based on whole otoliths.** Data are numbers of whole otoliths and counts in agreement are shown in bold type. WOtA1: first count by Interpreter A; WOtE: single count by Interpreter E. See also Fig. 3.2f.

WOtA1 / WOtE	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Total
1	**44**	4	2															50
2		**1**	7	1														9
3		2	**29**	21	4	1												57
4			5	**63**	33	9	1											111
5			2	13	**54**	20	6	1										96
6				3	17	**28**	6	1										55
7					4	1	**7**	3										15
8						2	3	**1**	2	2		1						11
9									**1**	3	1							5
10					1					**2**			1					4
11								1			**1**							2
12											1							1
13																		0
14																		0
15													1					1
16																		0
17																		0
Total	44	7	45	101	112	61	23	7	3	7	3	1	2	0	0	0	0	417

3.3.5 Stage 3. Precision by Interpreters B, C and D

Based on counts by Interpreters A–D the average interpretability of scales was lower than for opercular bones and whole otoliths (Table 3.18). Interpreter D counted annuli on all structures, as did Interpreter C for opercular bones and otoliths. Fewer scales were scored as interpretable by Interpreter A, and the number of interpretable whole otoliths was the same for Interpreters A and B. Only one of the six scales recorded as uninterpretable by Interpreter A was scored as such by Interpreter B, and the only scale considered uninterpretable by Interpreter C was also uninterpretable by Interpreter B but not Interpreter A. Only one of the two whole otoliths uninterpretable for Interpreter A was also uninterpretable for Interpreter B.

Table 3.18 **Percentages and corresponding numbers (in parentheses) of interpretable and uninterpretable calcified structures.** Values for scales and opercular bones are based on the first count by all interpreters, while values for whole otoliths are based on the second count by Interpreter A and the first count by Interpreters B, C and D. Sample sizes in parentheses.

Interpreter	Scale	Opercular bone	Whole otolith
A	80·0 (24)	100·0 (30)	93·3 (28)
B	90·0 (27)	96·7 (29)	93·3 (28)
C	96·7 (29)	100·0 (30)	100·0 (30)
D	100·0 (30)	100·0 (30)	100·0 (30)
Average	91·7	99·2	96·7

The average within-interpreter precision of counts by Interpreters B–D was lowest in otoliths, highest in scales, and intermediate in opercular bones. A similar result was obtained in comparisons between Interpreter A and Interpreters B–D (not shown). The between-interpreter precision (B–D and A) was higher in scales, lowest in whole otoliths, and intermediate in opercular bones. However, Friedman's tests (two-way nonparametric ANOVA) indicated no significant differences among structures either for the within-interpreter or between-interpreter reproducibility of counts ($P > 0{\cdot}05$; Table 3.19).

3.3.6 Comparison of opercular bones and whole otoliths by categories

No significant interaction occurred between morphological category and structure in the reproducibility of interpretations (measured by V) for opercular bones and whole otoliths

($P = 0{\cdot}143$). However, Friedman's tests showed that in opercular bones the reproducibility between annulus groups was significantly different ($P < 0{\cdot}01$), although there were no such differences between morphological categories. *Post hoc* Tukey-type pairwise comparisons indicated no significant differences in the coefficients of variation for annulus groups I and II, and I and III, although groups II and III did have different values. In whole otoliths, reproducibility did not differ between either morphological category or annulus group.

3.4 Discussion

Two notable outcomes are that (1) growth curves based on counts from the four calcified structures (scales, opercular bones, whole and sectioned otoliths) equally described the length-at-annulus relationship, and that (2) no substantial bias in annulus counts was detected in systematic comparisons of the structures to reveal structure-dependent over- or under-estimation of annuli. However, small-scale discrepancies did occur, and these may be the key to understanding the confounding effects that structure-specific factors could have had on interpretability and the bias and reproducibility of interpretations.

Scales, flat bones and otoliths grow at different rates relative to fish length. Casselman (1990) showed that in several fish the otoliths and, to some extent, the cleithra continued to grow allometrically as the fish approached its asymptotic length, but that this was not the case for scales, which often underwent resorption and erosion. Indeed, scale resorption in carp is a major impediment to reliable interpretations of annulus patterns (Carlander 1969), and may be an effect of starvation (Ichikawa 1953 in Simkiss 1974). Several authors (e.g. McConnell 1952; English 1952a; Rehder 1959) have found opercular bones to be better indicators of age and growth. Annulus counts from otoliths also should indicate the age of older fish more accurately than scales. Unfortunately, information on the use of carp otoliths is fragmentary (Vilizzi and Walker 1995; Chapter 6), and only Raina (1987) and Pinilla *et al.* (1992) apparently did not experience difficulties in interpretation of these structures. Finally, sectioned otoliths generally are regarded as superior to whole otoliths, especially in estimating the ages of older fish (Beamish and McFarlane 1987), but this method has not previously been applied to carp.

Table 3.19 **Within-interpreter and between-interpreter reproducibility of annulus counts based on three calcified structures.** Values for the index of average percent error (IAPE), the coefficient of variation (V: in italics) and the number of preparations (in parentheses) are given for each calcified structure. The within-interpreter reproducibility is based on two replicate counts by all interpreters, while the between-interpreter reproducibility is from the first count by all interpreters. Probability values for Friedman's tests are also reported.

	Within interpreters (B–D)			Between interpreters (A and B–D)		
Interpreter	Scale	Opercular bone	Whole otolith	Scale	Opercular bone	Whole otolith
B	10·79; *15·26* (27)	7·56; *10·70* (29)	12·54; *17·73* (28)	9·57; *13·53* (27)	10·52; 14·*87* (29)	13·28; *18·78* (28)
C	9·19; *13·00* (29)	14·09; *19·92* (30)	12·81; *18·11* (30)	10·64; *15·04* (29)	10·99; *15·54* (30)	12·02; *17·00* (30)
D	7·37; *10·43* (30)	12·18; *17·22* (30)	11·63; *16·45* (30)	9·71; *10·41* (30)	10·68; *14·71* (30)	12·82; *18·13* (30)
Average	9·12; *12·90*	11·28; *15·95*	12·33; *17·43*	9·97; *12·99*	10·73; *15·04*	12·71; *17·97*
	$\chi_r^2 = 0{\cdot}333$ ns ($P = 0{\cdot}368$)			$\chi_r^2 = 0{\cdot}667$ ns ($P = 0{\cdot}717$)		

Some of the results from this study may appear to contradict findings reported in the literature. However, the perceived similarity of annulus counts based on whole and sectioned otoliths stems from the peculiar morphology of carp asterisci relative to the sagittae of non-otophysan fish (*sensu* Fink and Fink 1981; Chapter 2), and this was the primary reason for rejection of otolith sections from further analyses. Patterns of calcium carbonate deposition in the otoliths of older fish were responsible for the slight under-estimation of annulus counts seen in comparisons with opercular bones. Later annuli in whole otoliths often were indistinct due to the overall translucency of the margin, and sectioning further disrupted patterns recognisable in the whole otoliths, magnifying the variations in the respective annulus counts. On the other hand, difficulties in discerning the first 1–2 annuli in opercular bones caused these structures to under-estimate annulus counts when compared to whole and sectioned otoliths. This problem did not emerge in interpreting scales, even though the exact position of the first annulus often had to be estimated.

Evaluation of within- and between-interpreter reproducibility showed relatively high values for IAPE (or V), compared to those reported in the literature. Although a standard measure of the reproducibility of interpretations in fish age and growth studies probably cannot be defined, values for IAPE below 10% may be taken as an acceptable level of precision (Powers 1983). In this study IAPE values for carp were 5·3–14·1%, higher than those reported for Murray cod (*Maccullochella peeli*, 3·0–5·4%: Anderson *et al.* 1992a) and golden perch (*Macquaria ambigua*, 3·9–5·6%: Anderson *et al.* 1992b) in the Murray-Darling Basin (MDB). However, the reproducibility of counts here was dependent also on the expertise gained over time by the individual interpreters. Thus, counts by Interpreter E, who spent several weeks on the entire set of interpretable structures, were more precise than those from the three other interpreters, giving IAPE values from 5·3–9·1%. Conversely, IAPE values from Interpreters B–D ranged from 7·4–14·1%, with 13 of 18 values above 10%.

No attempt was made to reconcile different annulus counts from Interpreters A and E (who analysed the whole set of preparations), and growth modelling employed age estimates by Interpreter A (the second count from whole otoliths, the only count from sectioned otoliths

and the first counts from opercular bones and scales, in that order) (cf. Chapter 4). Given the impossibility of knowing the *true* age of the fish, counts by Interpreter A were taken to be the most precise. The choice of otoliths (whole and sectioned) for estimation of growth parameters was dictated primarily by the need to clearly identify the positions of the first and second annuli (this became too subjective in opercular bones and to some extent scales). On the other hand, as most otoliths from older fish could not be reliably aged (at least with the techniques used here) and would therefore be *uninterpretable*, the use of opercular bones would offset the variability in annulus counts seen in the age bias plots for otoliths.

Pseudoannuli (present in all structures during the second year of growth) (cf. Section 2.2.3.3) and variations in annulus patterns with age did not appear to affect the reproducibility of age interpretations. In whole otoliths, however, the presence of pseudoannuli during the first 3–4 years (in class C preparations) probably was responsible for bias at older ages in the replicate counts by Interpreter A. After this experience, the second count of whole otoliths was deemed more reliable than the first. The lack of bias between annulus counts on whole otoliths from Interpreter A (second count) and Interpreter E at all ages suggests that these problems were largely overcome. As a result, the classification of opercular bones and otoliths into arbitrary morphological categories was of real value in identifying patterns likely to confound age interpretations. The same criteria were used in the preliminary training of the interpreters.

Interpretations of annulus patterns in carp scales, opercular bones and otoliths are not easy and instruction and experience are required for precise and unbiassed assessments. We recommend the use of both opercular bones and whole otoliths in routine age interpretations of carp in the MDB. The use of opercular bones to age older fish (10+ years) should help to resolve difficulties in detection of later annuli in otoliths. Whole otoliths are recommended as a means to age carp up to 10 years, and are essential if the locations of the first 2–3 annuli are to be accurately determined. The visibility of otolith annuli is not improved by sectioning. Scales are less easily interpretable, but may be useful in less rigorous assessments of the age profiles of carp populations (they may be the only option in examinations of historical collections). Scale samples do not harm the fish, and could be of value in tagging programs where the fish are injected with markers like

oxytetracycline (McFarlane and Beamish 1987; cf. Section 6.2.1). In monitoring the dynamics of carp populations researchers undertaking routine age assessments could exchange collections of calcified structures (Kimura *et al.* 1979; Boehlert and Yoklavich 1984; Boehlert 1985), ensuring that the bias and precision of counts do not deteriorate over time.

4.

AGE AND GROWTH:

EVALUATION OF MODELS

> Any scholar immersed in the details of an intricate problem will tell you that its richness cannot be abstracted as a dichotomy, a conflict between two opposite interpretations.
>
> S. J. Gould (1987)

4.1 Introduction

Modelling fish growth is an important outcome of studies designed to interpret the age profiles of populations from their calcified structures. Thus, it is often of interest to compare the growth rates of fish stocks from different geographical areas, or of males and females within the same population, or to describe year-to-year variation in growth as a response to changing abiotic and biotic factors (e.g. Weatherley and Gill 1987). However, no general agreement exists among fish biologists as to which mathematical model would best describe the growth of fish (reviews in Ricker 1979; Moreau 1987; see also Section 7.4).

In this chapter estimated ages for carp in the lower River Murray, based on interpretations of a suite of calcified structures (Chapters 2 and 3), are employed in modelling somatic and otolith growth. Whenever feasible, an integrated approach will be adopted whereby combinations of growth functions are evaluated and applied to describe the growth of the population under study.

Methods for collection and preparation of samples are explained in Chapter 2, where techniques for validation of age assessments are discussed. The consistency (i.e. bias and precision) of age interpretations is dealt with in Chapter 3.

4.2 Methods

4.2.1 Terminology

In this chapter the term *estimated age(s)* is employed in referring to growth models; this is determined by the presence of both validated and unvalidated (therefore putative) annulus groups in the data set/model combinations.

4.2.2 Sample measurement

Fish were measured for total Weight (W, ± 1·0 g) and Total Length (TL), Fork Length (FL) and Standard Length (SL), to within 1 mm. The following regressions apply:

$$FL = -12{\cdot}167 + 0{\cdot}929\ TL \qquad (n = 601, r^2 = 0{\cdot}999),$$

$$FL = 8{\cdot}667 + 1{\cdot}097\ SL \qquad (n = 602, r^2 = 0{\cdot}995).$$

A subsample of fish (n = 308) was measured for Body Depth (BD, ± 1·0 mm), taken as the distance between the dorsal and ventral sides of the body (from immediately anterior to the dorsal spine to immediately posterior of the pectoral fin, following Mišík (1958)). An 'Index of Obesity' (IO) was calculated as the ratio of SL and BD, to identify deep-bodied or obese morphs (cf. Balon 1977). The fork length was used in all further analyses as this was the more easily and reliably obtained measurement. Fish with macroscopically differentiated gonads were sexed; others were classified as juveniles.

The length (OL) and width (OWI) of both asterisci (hereafter 'otoliths') were measured with dial callipers (± 0·05 mm) and the weight (OW, ± 0·1 mg) recorded with a digital balance after drying at 50 °C for 24 h (Secor, Dean and Laban 1991).

4.2.3 Designation of a birth-date and ages adjustment

October 1 was taken as the nominal birth-date of each annual cohort of carp in the sampled population. This choice was dictated primarily by the time of formation of new annuli in the calcified structures when values for MIR (all structures) and for the number of outer circuli (scales) approach a minimum (cf. Chapter 2). Further, carp in the lower Murray generally have a major spawning event in October (cf. Chapter 11).

Setting a common date in this way has implications for ages estimated from annulus counts, as an adjustment is required whenever an annulus is formed before or after the designated birth-date. Three factors must be taken into account, namely (1) the number of annuli on each structure (equivalent to the estimated age of the fish), (2) the month of capture, and (3) the MIR value (Table 4.1). If, regardless of the number of annuli, a fish was caught between August and September and a new annulus was already forming (hence MIR ≤ 25% for scales and opercular bones, or MIR ≤ 50% for otoliths), its estimated age was decremented by one year. If, again regardless of the number of annuli, a fish was caught in October (the nominal month of birth) and the corresponding MIR ≥ 75% (i.e. a new annulus was due), its estimated age was incremented by one year. For fish caught between November and February a third factor, namely the number of annuli counted on the corresponding structures, comes into play. Thus, if a fish with more than one annulus was about to form a new annulus in November (i.e. MIR ≥ 75%), its estimated age was incremented by one year. The same adjustment was made for fish with structures having more than 2, 3 and 4 annuli, captured in December, January and February respectively, with MIR ≥ 75%. No adjustment was needed for fish captured between March and July.

Table 4.1 **Computation of the adjustment in annulus counts based on a nominal birth-date of October 1 for each annual cohort.** Annuli: number of annuli counted on a calcified structure; MIR: marginal increment ratio.

Month of capture	Annuli	MIR (%)	Estimated age (yr)
January	≤ 3		Annuli
	≥ 4	≥ 75	Annuli + 1
February	≤ 4		Annuli
	≥ 5	≥ 75	Annuli + 1
March–July			Annuli
August–September		≤ 25[A]	Annuli – 1
		≤ 50[B]	Annuli – 1
October		≥ 75	Annuli + 1
November	1		1
	≥ 2	≥ 75	Annuli + 1
December	≤ 2		Annuli
	≥ 3	≥ 75	Annuli + 1

[A] Scales and opercular bones.

[B] Whole and sectioned otoliths.

4.2.4 Data analysis

For modelling purposes, age was expressed as a decimal according to:

age (as integer) + (days from October 1 to date of capture) / 365

Six growth models, including the Von Bertalanffy Growth Function (VBGF), four quadratic models with combinations of log-transformed and decimal variables and a cubic model were employed to describe growth in length (cf. Chen *et al.* 1992). Growth in weight was modelled using the Beverton and Holt's (1957) adaptation of the VBGF for length. In addition, VBGF and log-log quadratic functions (LLQF) were fitted to body-depth-at-age data (Table 4.2).

Table 4.2 **Mathematical functions evaluated in describing the somatic growth of carp.** t: time expressed as a decimal; FL_t, BD_t, W_t: fork length, body depth and weight, respectively, at time t; FL_∞, BD_∞, W_∞: asymptotic fork length, body depth and weight, respectively; K: Brody coefficient of growth; t_0: theoretical time at which the length of the fish was 0 (Ricker 1975); b: exponent from weight-length relationship. All logarithms to the base 10.

Type	Abbreviation	Mathematical function
Decimal-decimal quadratic	DDQF	$FL_t = a_1 + b_1t + c_1t^2$
Log-decimal quadratic	LDQF	$FL_t = a_1 + b_1Log(t + 1) + c_1Log(t + 1)^2$
Log-log quadratic	LLQF	$Log(FL_t) = a_1 + b_1Log(t + 1) + c_1Log(t + 1)^2$
Decimal-log quadratic	DLQF	$Log(FL_t) = a_1 + b_1t + c_1t^2$
Decimal-decimal cubic	DDCF	$FL_t = a_1 + b_1t + c_1t^2 + d_1t^3$
von Bertalanffy (FL)	VBGF	$FL_t = FL_\infty(1 - exp(-K(t - t_0)))$
von Bertalanffy (BD)	VBGF	$BD_t = BD_\infty(1 - exp(-K(t - t_0)))$
von Bertalanffy (W)	VBGF^b	$W_t = W_\infty(1 - exp(-K(t - t_0)))^b$

The six length-at-age models were fitted to the four data sets from examination of calcified structures. Linear models for males and females were compared for goodness of fit (r^2) by means of a randomised blocks ANOVA, with the growth function as the fixed effect and the structures as blocks (cf. Zar 1984). Bonferroni-corrected pairwise comparisons were then made between the resulting growth models, and VBGFs for each sex were compared by a modified procedure for Analysis of the Residual Sum of Squares (ARSS), following Chen *et al.* (1992).

As age estimates from all four structures were not always available for each fish, due to problems of interpretability or the absence of one or more of the structures, estimated ages

from whole otoliths, sectioned otoliths, opercular bones and scales, in this order, were used in modelling growth. These priorities were determined in a separate evaluation of calcified structures (cf. Chapter 3).

The MGLH module of SYSTAT™ v 5.03 (Wilkinson 1990) was employed for fitting linear models. For all VBGFs, starting values for L_∞, W_∞ and BD_∞ (for body growth), OL_∞ and OWI_∞ (for otolith growth), K and t_0 were obtained by the Ford-Walford method (Ricker 1975; Kimura 1980), and the NONLIN module of SYSTAT™ was used to calculate least squares estimates and asymptotic standard errors for all parameters. In fitting the VBGF to the length-at-age and weight-at-age data for males and females the t_0 value of the VBGF for the combined sexes, including juveniles, was set as a constraint in the model. Weight-length regressions for fish and otoliths were fitted using the NONLIN module of SYSTAT™.

Multiple linear regression models were employed in an attempt to estimate carp age from otolith and body morphometrics. Otolith Weight (OW), Otolith Length (OL), Otolith WIdth (OWI), FL and W, their quadratic and cubic terms, and the interactions OW*OL, OW*OWI, OL*OWI, FL*W were included in the model, with the estimated whole otolith age as the dependent variable. Models were fitted to males and females by stepwise regression, using $\alpha = 0{\cdot}10$ for both entry and exit criteria.

The Anderson-Darling statistic was employed as a test for normality (Snedecor and Cochran 1989) and homoscedasticity was tested by a variance ratio test or Bartlett's test, when applicable (Sokal and Rohlf 1981). When the assumptions of normality and homoscedasticity were not satisfied equivalent non-parametric tests were used. Finally, residuals from all linear and nonlinear regressions were plotted against fitted values of the dependent variable to check that assumptions of independence of errors, zero mean, constant variance and normal distribution were met.

4.3 Results

A total 539 carp were successfully interpreted for age, including 379 specimens from scales, 440 from opercular bones, 417 from whole otoliths and 460 from sectioned otoliths. Summary statistics for length- and weight-at-age of juveniles, males and females are shown in Table 4.3.

Table 4.3 **Summary statistics for fork length (FL) and body weight (W) of juvenile, male and female carp.** The estimated ages of the fish are based on annulus counts from whole otoliths, sectioned otoliths, opercular bones and scales, in this order.

		FL (mm)				W (g)			
Estimated age (yr)	*n*	Mean	± SE	Min	Max	Mean	± SE	Min	Max
Juveniles									
1	63	207·4	6·9	96	341	213·8	21·8	19	817
2	5	292·4	24·2	230	373	474·2	117·3	205	850
Males									
1	2	358·0	13·0	345	371	843·5	95·5	748	939
2	7	368·0	24·4	268	464	1001·1	180·9	409	1730
3	27	436·4	17·4	268	600	1825·5	201·2	341	4222
4	56	448·6	9·9	259	602	1837·7	117·8	312	3791
5	56	500·9	9·5	319	656	2458·0	129·8	541	4956
6	31	516·3	13·7	317	638	2756·6	193·2	690	4620
7	21	566·1	14·2	417	678	3454·9	224·6	1214	5180
8	6	606·3	20·0	520	654	4035·3	399·8	2521	5514
9	2	628·5	10·5	618	639	4287·5	272·5	4015	4560
10	1	643				4483			
11	2	643·0	6·0	637	649	4956·5	343·5	4613	5300
12	1	577				3365			
Females									
2	4	388·5	28·6	308	435	1194·5	230·1	582	1611
3	26	433·3	12·0	336	555	1658·7	135·3	706	3390
4	77	510·5	6·9	356	623	2560·7	96·9	788	4468
5	60	540·3	9·7	352	641	3096·9	146·3	830	5000
6	48	554·2	10·2	383	655	3364·3	171·5	1051	5340
7	20	581·1	17·3	365	681	3941·1	298·0	904	6880
8	12	605·7	18·3	491	685	4023·8	300·6	1918	5320
9	3	656·0	22·6	629	701	5232·0	745·0	4140	6656
10	6	645·8	10·6	604	682	4627·8	203·9	3925	5160
11	2	668·0	20·0	648	688	5329·5	910·5	4419	6240
15	1	686				5540			

4.3.1 Comparison of length-at-age functions

The VBGF and five polynomial functions fitted to each of the four length-at-age data sets (Fig. 4.1a–d) resulted in a total of 24 coefficients of determination (Table 4.4).

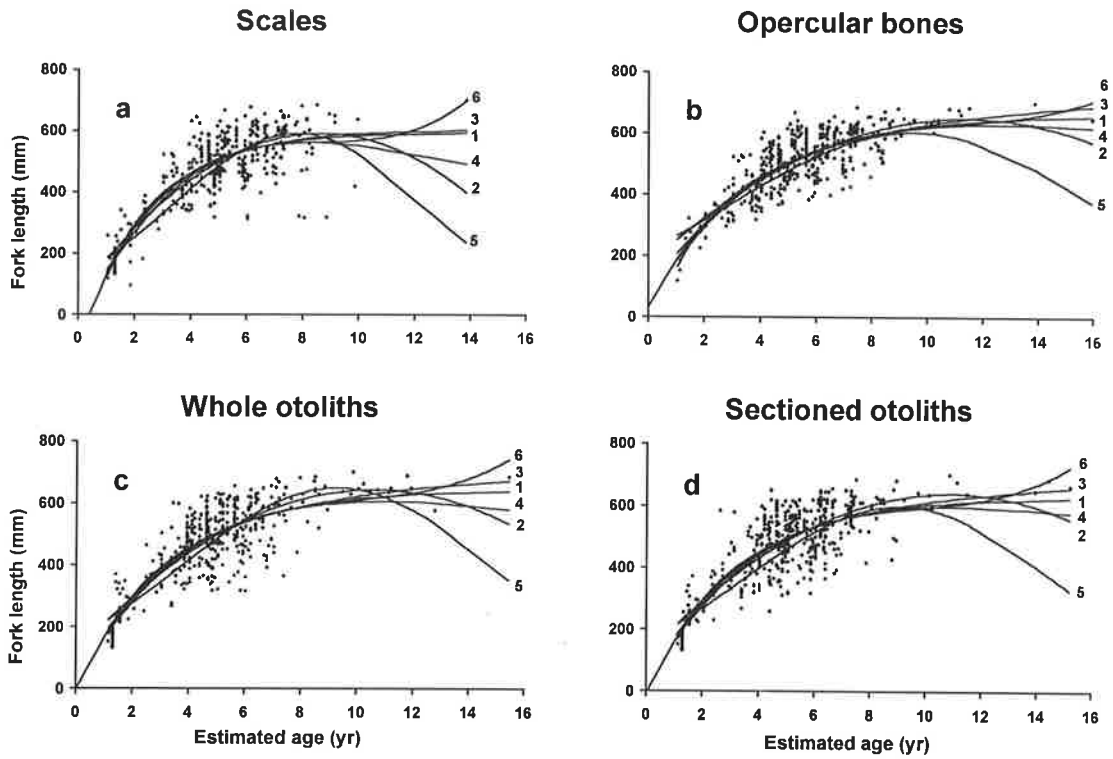

Figure 4.1 Comparison of six length-at-age functions for modelling growth in carp. Estimated ages are based on the corresponding calcified structure. (1) Von Bertalanffy (VBGF), (2) quadratic (DDQF), (3) log-decimal quadratic (LDQF), (4) log-log quadratic (LLQF), (5) decimal-log quadratic (DLQF), and (6) cubic (DDCF) function. Estimated ages from (a) scales, (b) opercular bones, (c) whole otoliths, and (d) sectioned otoliths.

***Table 4.4* Coefficients of determination (r^2) resulting from fitting of six growth curves to four length-at-age data sets.** Annuli counts from scales, opercular bones, whole and sectioned otoliths. Acronyms as in Table 4.2.

Calcified structure	VBGF	DDQF	LDQF	LLQF	DLQF	DDCF
Scale	0·729	0·700	0·727	0·807	0·749	0·730
Opercular bone	0·640	0·622	0·640	0·698	0·631	0·635
Whole otolith	0·685	0·664	0·687	0·757	0·696	0·680
Sectioned otolith	0·687	0·665	0·690	0·769	0·708	0·684

The lowest value was recorded for a DDQF fitted to age estimates based on opercular bones, and the highest value was for a LLQF fitted to scale-based age estimates. A randomised blocks ANOVA indicated significant differences in the mean r^2 values for growth functions (Table 4.5). Bonferroni-adjusted pairwise comparisons between growth functions showed significant differences between the LLQF and other functions, with the first providing best goodness of fit. Conversely, the DDQF resulted in lower r^2 values

compared to other models. No significant differences occurred among r^2 values for the VBGF and the other three functions (DLQF, LDQF, DDCF). The LLQF, by virtue of its precision, and the VBGF, with wider applicability and more biological realism (Moreau 1987), were chosen to model growth in length.

Table 4.5 **Matrix of Bonferroni-adjusted pairwise comparison probabilities.** Six growth functions are examined and the result of a test following a randomised blocks ANOVA to test for differences between coefficients of determination (r^2) as indicators of the goodness of fit of the model is given. Significant differences between growth models at a probability level $\alpha = 0{\cdot}05$ are shown in bold type. Acronyms as in Table 4.2.

Model	VBGF	DDQF	LDQF	LLQF	DLQF	DDCF
VBGF	1·000					
DDQF	**0·006**	1·000				
LDQF	1·000	**0·004**	1·000			
LLQF	**< 0·001**	**< 0·001**	**< 0·001**	1·000		
DLQF	0·705	**< 0·001**	0·936	< 0·001	1·000	
DDCF	1·000	**0·020**	1·000	**< 0·001**	0·215	1·000
$F = 86{\cdot}226$ ($P < 0{\cdot}001$)	DDQF	DDCF	VBGF	DLQF	LDQF	LLQF

4.3.2 Comparison of growth between sexes

Growth in length between males and females, described by the VBGF and LLQF, was significantly different (Table 4.6, Fig. 4.2a,b). Preliminary fits of the VBGF to length-at-age data for males and females resulted in unrealistic estimates for the model parameters, especially L_∞ and t_0, and the t_0 value calculated for the whole sample (males, females, juveniles) was used to estimate the values of L_∞ and K for each sex. Growth rates, indicated by K, were similar between the sexes, but the asymptotic length reached by the females was higher than that for the males.

As no significant differences were apparent in the weight-length relationships for males and females (Table 4.6, Fig. 4.2c), pooling was valid, with the pooled *b* being close to that for allometric growth (Ricker 1975). The *b* values for males and females, calculated from the corresponding weight-length relationships, were used in modelling growth in weight with the modified VBGF (Table 4.6, Fig. 4.2d). In VBGFs fitted to the length-at-age data the t_0 values for males and females were calculated from a model including the pooled

sexes and juveniles. The females showed a faster rate of growth in weight than males, and their asymptotic weight also was relatively high. Again, significant differences were evident in the growth in weight between sexes.

4.3.3 Growth in body depth and index of obesity

There was a high correlation between body depth and fork length:

$$BD = 21{\cdot}685 + 0{\cdot}245FL \quad (r^2 = 0{\cdot}862, n = 301).$$

Two models, a VBGF and a LLQF, were fitted to the body depth-at-age data for males and females (Table 4.6, Fig. 4.2e,f). The growth rate in body depth was faster in females, although they had a lower asymptotic value than males. However, the VBGF parameter estimates reported here are tentative, as no adjustment for t_0 was possible because of a lack of convergence for the estimates when attempting to fit models to males and females constrained for the t_0 value estimated for the combined sexes. Finally, there were significant differences in the growth of body depth for the two sexes, described by the VBGF and LLQF.

Values for the index of obesity (IO) for the whole sample of fish ranged from 2·6–3·8, with a mean of 3·14. The mean IO values for males and females were significantly different ($P < 0{\cdot}05$), although their ranges were comparable.

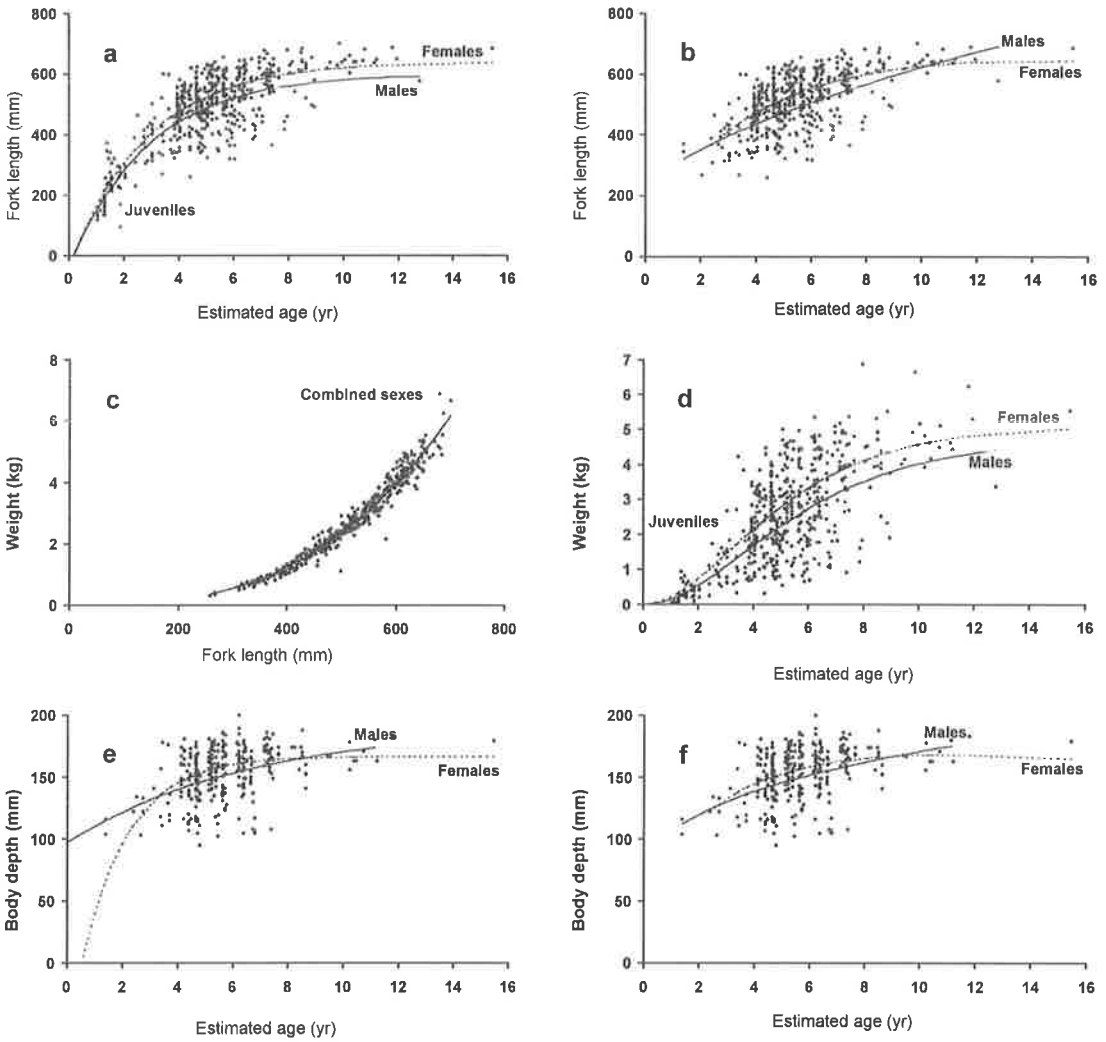

Figure 4.2 Somatic growth of male and female carp. Estimated ages are based on annulus counts from whole otoliths, sectioned otoliths, opercular bones and scales in this order. (a) Growth in length as described by the von Bertalanffy growth function (VBGF): juvenile fish are included as the t_0 values were calculated from a model including the pooled sexes and juveniles; (b) growth in length according to a log-log quadratic function (LLQF); (c) weight-length relationship: only the curve for the combined sexes is shown as there were no significant differences between males and females; (d) growth in weight as described by the Beverton and Holt's (1957) modification of the VBGF: juvenile fish are included as the t_0 values were calculated from a model including the pooled sexes and juveniles; (e) growth in body depth according to the VBGF; (f) growth in body depth as described by the LLQF. Parameters for all models are given in Table 4.6.

Table 4.6 **Models describing the somatic growth of male and female carp.** Values (± (asymptotic) SE) for the parameters in linear and non-linear models and tests of significance between the sexes are reported. The residual sum of squares and the value and corresponding probability for the *F*-ratio test are also indicated for all comparisons of growth curves between sexes. When no significant differences at a probability level $\alpha = 0{\cdot}05$ were detected the model for the combined sexes is given. All logarithms to the base 10. All acronyms and symbols as in Table 4.2.

Statistics	Males + Females	Males	Females
FL VBGF			
n	471	212	259
FL_∞ (mm)^A	625·4 ± 13·6	600·3 ± 21·7	639·2 ± 15·9
K (yr^{-1})^A	0·344 ± 0·021	0·346 ± 0·035	0·353 ± 0·026
t_0 (yr)^{A,B}	0·174 ± 0·116	0·174 ± 0·116	0·174 ± 0·116
r^2	0·336	0·318	0·350
RSS	2519257·149	1193324·483	1180721·550
DF	469	210	257
F	9·522 (*P* = 4·9E–07 < 0·001)		
Model		$FL_t = 600(1–\exp(–0{\cdot}346(t–0{\cdot}174)))$	$FL_t = 639(1–\exp(–0{\cdot}353(t–0{\cdot}174)))$
FL LLQF			
n	471	212	259
a_1	2·196 ± 0·095	2·357 ± 0·125	2·007 ± 0·153
b_1	0·835 ± 0·233	0·371 ± 0·320	1·348 ± 0·365
c_1	– 0·250 ± 0·143	0·046 ± 0·204	– 0·567 ± 0·216
r^2	0·335	0·340	0·339
RSS	2·059	1·033	0·889
DF	468	209	256
F	16·573 (*P* = 1·1E–07 < 0·001)		
Model		$Log(FL_t) = 2{\cdot}357+0{\cdot}371(Log(t+1))+0{\cdot}046(Log(t+1))^2$	$Log(FL_t) = 2{\cdot}007+1{\cdot}348(Log(t+1))–0{\cdot}567(Log(t+1))^2$
LWR			
n	484	217	267
a^A	4·6E–08 ± 9·0E–09	4·8E–08 ± 1·2E–08	4·6E–08 ± 1·3E–08
b^A	2·856 ± 0·030	2·848 ± 0·040	2·857 ± 0·045
r^2	0·963	0·970	0·955
RSS	29·202	9·385	19·803
DF	482	215	265
F	0·108 ns (*P* = 0·897)		
Model	$W = 4{\cdot}6E–08FL^{2{\cdot}856}$	$W = 4{\cdot}8E–08FL^{2{\cdot}848}$	$W = 4{\cdot}6E–08FL^{2{\cdot}857}$

Table 4.6 (continued)

Statistics	Males + Females	Males	Females
W VBGF[b]			
n	471	212	259
W_∞ (kg)[A]	4·994 ± 0·288	4·749 ± 0·447	5·123 ± 0·335
K (yr^{-1})[A]	0·297 ± 0·017	0·279 ± 0·026	0·314 ± 0·022
t_0 (yr)[A,B]	− 0·242 ± 0·370	− 0·242 ± 0·370	− 0·242 ± 0·370
b	2·856 ± 0·030	2·848 ± 0·040	2·857 ± 0·045
r^2	0·336	0·350	0·318
RSS	502·994	195·127	275·018
DF	469	210	257
F	10·703 (P = 7·4E–09 < 0·001)		
Model		$W_t = 4{\cdot}749(1–\exp(–0{\cdot}279(t+0{\cdot}242)))^{2{\cdot}848}$	$W_t = 5{\cdot}123(1–\exp(–0{\cdot}314(t+0{\cdot}242)))^{2{\cdot}857}$
BD VBGF			
n	301	121	180
BD_∞ (mm)[A]	173·0 ± 7·2	191·3 ± 35·9	166·7 ± 4·3
K (yr^{-1})[A]	0·300 ± 0·101	0·151 ± 0·125	0·591 ± 0·209
t_0 (yr)[A]	− 1·920 ± 1·385	− 4·179 ± 3·972	0·544 ± 1·018
r^2	0·164	0·200	0·135
RSS	104916·749	44941·859	56908·090
DF	298	118	177
F	2·961 (P = 0·033 < 0·05)		
Model		$BD_t = 191(1–\exp(–0{\cdot}151(t+4{\cdot}179)))$	$BD_t = 167(1–\exp(–0{\cdot}591(t+0{\cdot}544)))$
BD LLQF			
n	301	121	180
a_1	1·827 ± 0·098	1·938 ± 0·132	1·697 ± 0·189
b_1	0·641 ± 0·238	0·308 ± 0·346	0·977 ± 0·439
c_1	− 0·247 ± 0·146	− 0·024 ± 0·227	− 0·452 ± 0·254
r^2	0·163	0·200	0·124
RSS	0·959	0·432	0·502
DF	298	118	177
F	3·948 (P = 0·020 < 0·05)		
Model		$Log(BD_t) = 1{\cdot}938+0{\cdot}308(Log(t+1))–0{\cdot}024(Log(t+1))^2$	$Log(BD_t) = 1{\cdot}697+0{\cdot}977(Log(t+1))–0{\cdot}452(Log(t+1))^2$

[A] Asymptotic standard errors.

[B] Calculated from a model including the pooled sexes and juveniles.

Table 4.7 **Models describing otolith growth in male and female carp.** Values (± (asymptotic) SE) for the parameters in linear and non-linear models and tests of significance between the sexes are reported. The residual sum of squares and the value and corresponding probability for the *F*-ratio test are also indicated for all comparisons of growth curves between sexes. When no significant differences at a probability level $\alpha = 0{\cdot}05$ were detected the model for the combined sexes is given. OL: otolith length; OWI: otolith width; OW: otolith weight; LDSF: log-decimal simple linear regression function; DDSF: simple linear regression function. All logarithms to the base *e*. Other acronyms and symbols as in Table 4.2.

Statistics	Males + Females	Males	Females
OL VBGF			
n	353	164	189
OL_∞ (mm)[A]	10·109 ± 0·265	9·068 ± 0·308	10·868 ± 0·372
K (yr^{-1})[A]	0·231 ± 0·014	0·281 ± 0·026	0·208 ± 0·015
t_0 (yr)[A,B]	− 1·307 ± 0·225	− 1·307 ± 0·225	− 1·307 ± 0·225
r^2	0·452	0·389	0·525
RSS	229·060	99·280	108·464
DF	351	162	187
F	11·937 (*P* = 1·9E–07 < 0·001)		
Model		$OL_t = 9{\cdot}1(1–\exp(–0{\cdot}281(t+1{\cdot}307)))$	$OL_t = 10{\cdot}9(1–\exp(–0{\cdot}208(t+1{\cdot}307)))$
OL LDSF			
n	353	164	189
a	3·556 ± 0·243	4·132 ± 0·312	3·009 ± 0·347
b	2·508 ± 0·145	2·013 ± 0·189	2·952 ± 0·204
r^2	0·459	0·411	0·527
RSS	225·966	95·736	107·882
DF	351	162	187
F	19·152 (*P* = 1·6E–11 < 0·001)		
Model		$OL_t = 4{\cdot}132+2{\cdot}013\ln(t)$	$OL_t = 3{\cdot}009+2{\cdot}952\ln(t)$
OWI VBGF			
n	353	164	189
OWI_∞ (mm)[A]	6·953 ± 0·215	6·307 ± 0·260	7·422 ± 0·313
K (yr^{-1})[A]	0·187 ± 0·012	0·220 ± 0·021	0·169 ± 0·014
t_0 (yr)[A,B]	− 1·514 ± 0·276	− 1·514 ± 0·276	− 1·514 ± 0·276
r^2	0·483	0·435	0·529
RSS	91·981	40·554	46·850
DF	351	162	187
F	6·092 (*P* = 4·7E–04 < 0·001)		
Model		$OWI_t = 6{\cdot}3(1–\exp(–0{\cdot}220(t+1{\cdot}514)))$	$OWI_t = 7{\cdot}4(1–\exp(–0{\cdot}169(t+1{\cdot}514)))$

Table 4.7 (continued)

Statistics	Males + Females	Males	Females
OWI LDSF			
n	353	164	189
a	2·200 ± 0·155	2·571 ± 0·202	1·814 ± 0·227
b	1·608 ± 0·093	1·390 ± 0·122	1·962 ± 0·134
r^2	0·484	0·443	0·533
RSS	91·895	39·958	46·468
DF	351	162	187
F	11·042 (P = 6·1E–07 < 0·001)		
Model		OL_t = 2·571+1·390ln(t)	OL_t = 1·814+1·962ln(t)
OW DDSF			
n	353	164	189
a	– 3·480 ± 1·995	1·115 ± 2·599	– 6·369 ± 2·837
b	7·895 ± 0·351	6·588 ± 0·468	8·781 ± 0·489
r^2	0·591	0·550	0·633
RSS	44219·751	16153·789	25189·618
DF	351	162	187
F	12·140 (P = 1·4E–07 < 0·001)		
Model		OL_t = 1·115+6·588t	OL_t = – 6·369+8·781t

[A] Asymptotic standard errors.

[B] Calculated from a model including the pooled sexes and juveniles.

4.3.4 Otolith growth

As for somatic growth, the growth of otoliths in length, width and weight was described by both linear and nonlinear models. Although there were no significant differences between the length and width of the right and left otoliths ($Z = 0{\cdot}089$, $P = 0{\cdot}929$; $Z = 0{\cdot}002$, $P = 0{\cdot}999$ for length and width, respectively), their weights were different ($Z = 0{\cdot}730$, $P = 0{\cdot}006 < 0{\cdot}01$). This may have reflected difficulties encountered upon extraction, as the procedure may occasionally damage the otolith at the level of the *fossa acustica* (Berinkey 1956). However, a tentative 'sensitivity analysis', involving fitting of growth models to both right and left otoliths, resulted in no appreciable visual differences. Therefore, in further calculations the length, width and weight of the left otoliths were used and their growth modelled using ages estimated from whole otoliths.

Two curves, namely a VBGF and first-order linear model with log-transformed ages (LDSF), were fitted to the otolith length- and otolith width-at-age data (Fig. 4.3a–d) for both sexes. The t_0 values for the VBGFs for males and females were calculated from VBGFs fitted to the entire sample, including the juveniles. This resulted in more robust estimates for the parameters in the model. Males had lower asymptotic values for otolith length and otolith width than females, although they always showed a higher rate of growth (Table 4.7). In contrast, otolith weight generally increased linearly with age, although only 55% (males) and 63% (females) of the variance was explained by the model (Fig. 4.3e). Finally, ARSS tests always indicated significant differences in otolith growth between males and females.

Table 4.8 **Correlation matrix for otolith morphometrics and age in carp.** Estimated ages (Age) from annulus counts based on whole otoliths. All abbreviations as in Table 4.2.

Males/*Females*	Age	FL	OW	OL	OWI
Age	1·000	*0·582*	*0·796*	*0·707*	*0·729*
FL	**0·541**	1·000	*0·769*	*0·852*	*0·824*
OW	**0·742**	**0·805**	1·000	*0·910*	*0·924*
OL	**0·647**	**0·868**	**0·896**	1·000	*0·934*
OWI	**0·688**	**0·864**	**0·922**	**0·926**	1·000

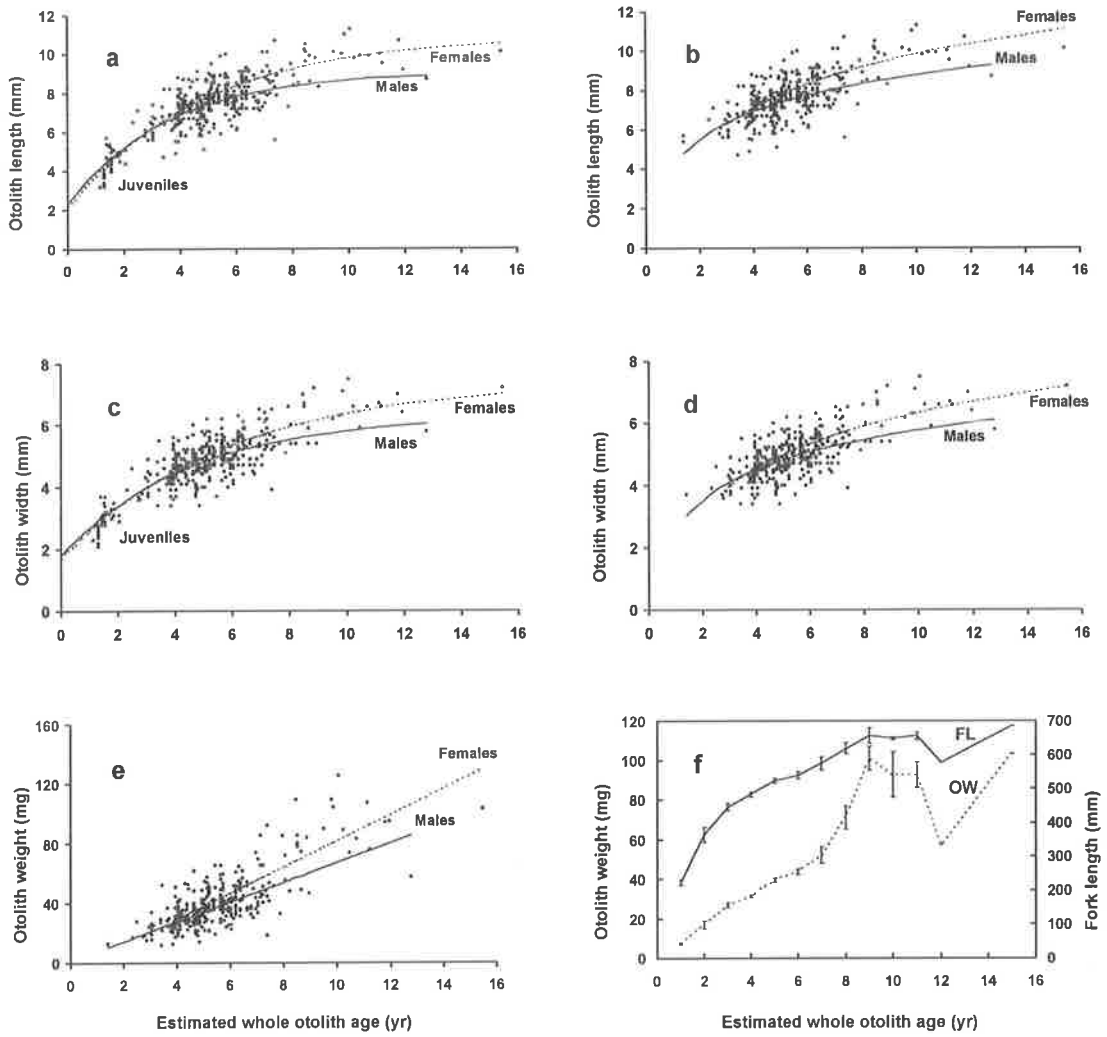

Figure 4.3 Otolith growth in male and female carp. All estimated ages are based on annulus counts from whole otoliths. (a) Growth in otolith length according to the von Bertalanffy growth function (VBGF): juvenile fish are included as the t_0 values were calculated from a model including the pooled sexes and juveniles; (b) growth in otolith length based on a log-decimal simple regression function (LDSF); (c) growth in otolith width according to the VBGF: juvenile fish are included as the t_0 values were calculated from a model including the pooled sexes and juveniles; (d) growth in otolith width based on a log-decimal simple regression function (LDSF); (e) growth in otolith weight as described by a simple linear regression function (DDSF); (f) changes in fork length (FL) and otolith weight (OW) in each estimated age group. Error bars are ± SE. Parameters for all models are given in Table 4.7.

Correlation matrices for otolith morphometrics and age (Table 4.8) showed that in both sexes otolith weight had the strongest linear relationship with age, followed in order by otolith width, otolith length and fork length. Changes in otolith weight within the same estimated age group were also correlated to fluctuations in fork length, especially at older ages (Fig. 4.3f). However, multiple linear regression models to estimate fish age from

body and otolith morphometrics did not yield satisfactory results. For the males, a model including otolith weight and the interaction term FL*W described only 56% of the variation in age, and for females otolith weight alone was retained in the model and accounted for only 63% of the total variance (Table 4.9).

Table 4.9 **Multiple linear regression models for estimation of age from body and otolith morphometrics.**

Variable	Coefficient	± SE	*P*
Males (n = 164)			
Constant	2·085	0·241	< 0·001
OW	0·107	0·011	< 0·001
FL*W	– 0·522E–06	0·207E–06	0·013 ns
Multiple r^2 = 0·562			
Females (n = 189)			
Constant	2·492	0·186	< 0·001
OW	0·072	0·004	< 0·001
Multiple r^2 = 0·633			

4.4 Discussion

Precision, *realism* and *generality* are three key attributes that an ideal model should possess. Ricker (1979) referred to goodness of fit and convenience as the only valid criteria in choosing a growth curve, and cites a number of papers concerning the mathematico-physiological theory of growth regulation. Moreau (1987) also addressed the problem of quality of fit and convenience, and opined that "much ingenuity has been expended in trying to relate growth models to growth processes" (p. 81). Chen *et al.* (1992, p. 1233) reported that "advocates of the PFs [polynomial functions] emphasize their mathematical simplicity rather than their biological usefulness". In fact no model could satisfy all of the above requirements—a precise-realistic-general model inevitably would require trade-offs between each attribute. In this study an integrated approach was adopted.

Several models have been proposed to describe growth in length or weight in fish (reviews in Ricker 1979; Moreau 1987; see also Section 7.4). Chen *et al.* (1992) noted that comparisons among growth functions have seldom been made (but see Beckman *et al.* 1990), especially between the VBGF and polynomial functions, and recommended that "before selecting the growth function for a growth data set, a systematic comparison should be done among growth functions being considered for use" (p. 1234). In keeping with this

recommendation, the analyses here indicate that a parabola with log-transformation of both predictor and response variables (here referred to as LLQF, equivalent to PF3 of Chen *et al.* 1992) provided the best fit, and was chosen by virtue of its precision and ease of computation. However, the VBGF was retained as an alternative model to allow comparisons with published data and provide 'quasi-biological' parameters for describing growth. Chen *et al.* (1992) also suggested use of the VBGF in their study of six species, with the LLQF as an alternative linear function. In contrast, most comparative studies of the VBGF and polynomial models imply a mutually exclusive choice between the two approaches. Roff (1980; see also Knight 1968) proposed 'retirement' of the VBGF, urging fisheries biologists to rely exclusively on polynomial functions, but his call has gone largely unheeded (McDowall 1994). In the present paper we have attempted to avoid the pitfalls of misleading dichotomies (Gould 1987) by adopting an integrated approach. This may be unorthodox, and may even appear tautological, but it does provide two complementary perspectives.

When modelling growth in males and females no appreciable improvement in goodness of fit was gained from the LLQF rather than the VBGF, in contrast to the preliminary comparison of growth models. This is explained by considering that the lower portion of the growth curve, especially the VBGF, will be truncated in the absence of younger fish, resulting in an incomplete data set. No histological examinations of the gonads of immature fish were made, so that their sex remained unknown. Rowling and Reid (1992) circumvented this problem by re-fitting a VBGF to length-at-age data sets for male and female gemfish (*Rexea solandri*) after including data for juvenile fish. In that study growth parameters were compared using likelihood-ratio tests (Kimura 1980), whereas in the present study *F*-tests were used for gross comparisons among growth curves. In modelling growth for each sex taking the t_0 value from a VBGF fitted to pooled length-at-age data for juveniles, males and females provided more realistic parameter estimates. For the LLQF no such refinement was attempted mainly because of difficulties arising in biological interpretation of the parameters. As mentioned, histological confirmation of the sex of juveniles would allow a test of the validity of linear models in tandem with the VBGF.

The maximum estimated ages for males and females in this study were 12 and 15 years, respectively, and the females attained asymptotic lengths and weights greater than the

males. The dearth of information on the age and growth of carp in Australia does not allow comparisons, except that Jones (1974) cited mean total lengths for 1-, 2- and 3-year old carp from the lower River Murray of 440, 630 and 720 mm respectively, consistently higher than those reported here. A review of the voluminous literature on age and growth studies of carp is given in Chapter 6 and 7, but it is of interest here to report von Bertalanffy parameters for some populations in the world to allow comparisons with River Murray carp (Table 4.10).

In a discourse on the origin and domestication of carp Balon (1995a, p. 8) stated that "domesticated pond forms when released or escaped into rivers or lakes always revert into feral states not unlike the original wild form", this being a "powerful, elongated and torpedo-shaped animal" in which "the dorsal contours of its head and body continue in one smooth curve". Further, Balon (1977) earlier reported that deep-bodied or obese morphs, resembling high-backed cultured varieties (Wohlfarth 1984), can develop in wild populations with access to extremely abundant food resources. The mean IO value of 3·9 recorded in this study agreed with that of 3·8 reported by Shearer and Mulley (1978) for the 'Boolarra' strain of carp, which is ubiquitous in the Murray-Darling Basin (the IO values reported here are TL/BD, referred to TL rather than FL, to allow comparison with Shearer and Mulley). Given the ranges reported in Balon (1977), namely 3·5–4·0 in wild carp and 2·2–2·8 in domesticated carp, the Murray population (IO = 3·14, based on FL) appears to be a slightly deep-bodied feral morph. Hall (1981) described the diet of carp in the lower Murray as filamentous algae, macroinvertebrates and detritus, indicating opportunistic feeding behaviour that is typical of the species (cf. Section 1.3). The lower asymptotic value for BD observed for the females was unexpected considering that changes in condition, especially prior to spawning, should affect their body depth. However, Balon (1995a, p. 17) observed that in wild carp maturation of the ovaries causes an increase in body width rather than depth so that the fish maintains a "torpedo-like body at all times, possibly as a prerequisite for overcoming strong currents to reach inundated areas for spawning at high water levels".

Following the seminal study by Boehlert (1985), several researchers have investigated the possibility of using otolith weight as a means to estimate the age profiles of fish populations (e.g. Worthington *et al.* 1995), and analyses of otolith morphometrics have

become routine in age and growth studies of species other than carp (Brothers 1987). In this study the variation in age explained by otolith weight, even after inclusion of additional morphometric variables, was too low to warrant computation of an otolith weight vs age relationship. This was not unexpected, as the peculiar morphology of carp asterisci may have been an additional source of variability, stemming from the uncoupling of otolith and somatic growth rates (Wright *et al.* 1990; but see Secor and Dean 1992). As a result, the otolith growth models reported here are intended only for descriptive purposes. The growth in length and weight of otoliths might be described interchangeably using a VBGF or linear function, as for somatic growth.

Table 4.10 **Von Bertalanffy growth parameters and maximum age for some populations of carp in the world.** L_∞: asymptotic fork length (FL), unless otherwise stated. All symbols as in Table 4.2.

Source	Sex	Length			Weight				Max age (yr)	Area of study
		L_∞ (mm)	K (yr^{-1})	t_0 (yr)	W_∞ (kg)	K (yr^{-1})	t_0 (yr)	b[D]		
Prochelle and Campos (1985)	Combined	527[B]	0·290	0·000					10	River Cayumapu (Chile)
Ramos *et al.* (1985)	Combined	492	0·270	−0·380	1·890	0·270	−0·380	2·911	8	Rio Tejo (Portugal)
Talaat and Oláh (1986b)	Combined	741[B]	0·177	−0·324					9	Körös Reservoir (Hungary)
Sharma (1987)	Combined	1039[B]	0·134	−1·095						Gobindsagar Reservoir (India)
Erdem (1988)	Males	815	0·800	−0·678	5·204	0·105	−0·569	2·306	7	Tödürge Lake (Turkey)
Erdem (1988)	Females	789	0·902	−0·863	7·062	0·114	−0·632	2·306	7	Tödürge Lake (Turkey)
Cengizler and Erdem (1989)	Males	597	0·115	−0·811	3·339	0·114	−0·811	2·695	7	Hafik Lake (Turkey)
Cengizler and Erdem (1989)	Females	503	0·182	−0·665	2·048	0·181	−0·664	2·733	7	Hafik Lake (Turkey)
Harka (1989)	Combined	828[A]	0·162	0·076					8	Kisköre Lake (Hungary)
Çetinkaya (1992a)	Males	640	0·071	−2·710	3·221	0·071	−2·710	2·786	10	Akşehir Lake (Turkey)
Çetinkaya (1992a)	Females	897	0·046	−2·850	9·099	0·046	−2·850	2·821	14	Akşehir Lake (Turkey)
Pinilla *et al.* (1992)	Combined	556[A]	0·403	0·093					4	Laguna de Fuquene (Colombia)
Ritter-Ortiz *et al.* (1992)	Combined	613[C]	0·197	−0·005					10	Atlangatepec Dam (Mexico)
Hoc opus	Males	600	0·346	0·174	4·749	0·134	−0·242	2·848	12	River Murray (Australia)
Hoc opus	Females	639	0·353	0·174	5·123	0·134	−0·242	2·857	15	River Murray (Australia)

[A] Standard length.

[B] Total length.

[C] Measure of length not reported.

[D] Exponent from weight-length relationship.

5.

AGE AND GROWTH:

THE CARP IN LAKE CRESCENT, TASMANIA

> Who hasn't heard some of the following ideas from anglers? "Carp are bad fish; they can't survive even in sewers." "Carp are oily and taste terrible because they eat weeds and junk off the bottom." "Carp are lazy, sloth-like fish; no challenge to sportsmen."
>
> B. Shupp (1987)

5.1 Introduction

Lakes Sorell and Crescent are at 820 m altitude on the eastern edge of Tasmania's Central Plateau: Sorell (catchment 103 km^2) drains into Crescent (57 km^2) via the Interlaken Channel, thence the Clyde River. The two lakes support a commercial fishery for the native short-finned eel (*Anguilla australis*), and there is also a recreational fishery for the exotic brown trout (*Salmo trutta*) and rainbow trout (*Oncorhyncus mykiss*). An endemic galaxiid (*Galaxias auratus*) is also found (A. Sanger, Inland Fisheries Commission, Hobart, pers. comm.).

Another exotic fish, the carp, was reported from the lakes in 1992. This is the first report from Tasmania since a population was found (and later eradicated) near Burnie, NW Tasmania, in the early 1970s (A. M. Olsen, Adelaide, pers. comm.). The options for control and eradication may include poisoning, drawdown and intensive fishing (Roberts 1997), but basic biological data are needed for evaluation. This study determined the age and growth characteristics of the Crescent-Sorell population using techniques developed for carp in the River Murray, South Australia (Chapters 2–4).

5.2 Materials and Methods

5.2.1 Samples and preparation

An aggregate sample of 333 fish was provided by the Inland Fisheries Commission from electrofishing and netting in February–March 1995, September–November 1995 and January–February 1996. All but four specimens came from Lake Crescent (Table 5.1). The fish were sexed, when possible, and measured for Fork Length (FL, ± 1·0 mm) and total Weight (W, ± 1·0 g). Otoliths (asterisci) were recovered from 189 fish, their preparation and examination following the method outlined in Sections 2.2.2 and 2.2.3.3 (Fig. 5.1).

Table 5.1 **Sampling sites and date of collection of carp in Lakes Crescent and Sorell, Tasmania.**

Locality	Date	*n*
Crescent	1.II.1995	10
Crescent	2.II.1995	22
Crescent	7.II.1995	7
Crescent	8.II.1995	1
Crescent	15.II.1995	12
Crescent	22.II.1995	50
Crescent	4.III.1995	26
Sorell	4.III.1995	4
Crescent	14.III.1995	20
Crescent	22.III.1995	56
Crescent	28.III.1995	18
Crescent	29.III.1995	2
Crescent	27.IX.1995	13
Crescent	5.X.1995	8
Crescent	9.XI.1995	2
Crescent	23.XI.1995	20
Crescent	6.I.1996	42
Crescent	14.II.1996	1
Crescent	21.II.1996	19

5.2.2 Validation and ages adjustment

Three replicate otolith counts were made, and data from the last count used for age estimation and growth modelling. Given the relatively small sample size it was not possible to evaluate the bias and precision of the interpretations. Validation of age

interpretations was based on Marginal Increment Analysis (MIA), and followed procedures described in Section 2.2.4.

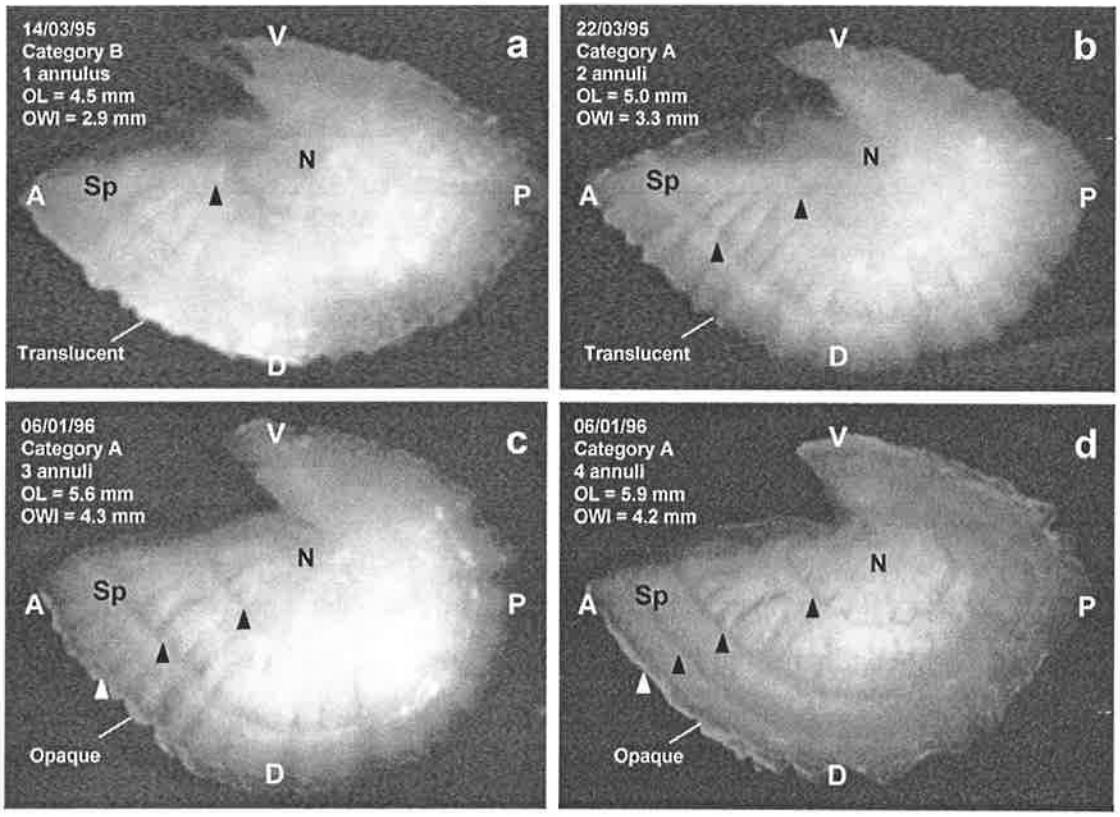

Figure 5.1 Otoliths (asterisci) from carp in Lake Crescent, Tasmania. Viewing conditions and explanation of the symbols as in Fig. 2.1. Morphological categories (classes) as in Section 2.2.3.3. The edge type (opaque or translucent), the date of capture and the number of annuli are indicated. Each annulus is marked with a triangle. (a) Class B (1 annulus); (b) class A (2 annuli); (c) class A (3 annuli); (d) class A (4 annuli).

Ages adjustment allowing for the time of capture and the relative growth of whole and sectioned otoliths was as in Section 4.2.3, with minor modifications. January 1 was taken as the nominal birth-date of each annual cohort. The age of a fish with MIR ≤ 50% (new annulus forming), caught in November–December, was decremented by one year regardless of the number of annuli. Similarly, the apparent age of a fish caught in January with MIR ≥ 75% (new annulus due) was incremented by one year regardless of the number of annuli. In February the age of a fish with more than one annulus, but about to form a new annulus (MIR ≥ 75%), was increased by one year, and in March the same adjustment was applied to fish with more than two annuli and MIR ≥ 75%. Adjustments were not needed for fish caught from April to October (Table 5.2).

Table 5.2 **Computation of the adjustment in annulus counts based on a nominal birth-date of January 1 for each annual cohort of carp in Lakes Crescent and Sorell, Tasmania.** Annuli: number of annuli counted on whole and sectioned otoliths; MIR: marginal increment ratio.

Month of capture	Annuli	MIR (%)	Estimated age (yr)
January		≥ 75	Annuli + 1
February	1		1
	≥ 2	≥ 75	Annuli + 1
March	≤ 2		Annuli
	≥ 3	≥ 75	Annuli + 1
April–October			Annuli
November–December		≤ 50	Annuli – 1

5.2.3 Data analysis

Length-frequency data and MIA were used to estimate the age composition of the population. Fork lengths for the three subsamples were compared by one-way ANOVA, and mean annulus distances from the nucleus in whole otoliths from River Murray and Crescent-Sorell carp were compared by two-way ANOVA (sampling area x number of annuli). Differences between means were located using Tukey's HSD test for unequal samples sizes (Spjotvoll and Stoline 1973). Comparisons of growth in males and females, analyses of residuals and validation of parametric methods followed procedures described in 4.2.4. Statistical analyses employed SYSTAT™ v 5.03 (Wilkinson 1990) and STATISTICA™ v 5.0 (Statsoft Inc. 1995).

5.3 Results

5.3.1 Length-frequency analysis

Length-frequency distributions for each of the three subsamples were approximately unimodal. ANOVA and *post hoc* comparisons indicated no difference in mean FL in 1995 (Fig. 5.2a,b), but the mean FL for the 1996 catch was higher than for either catch in 1995 ($P < 0{\cdot}01$) (Fig. 5.2c).

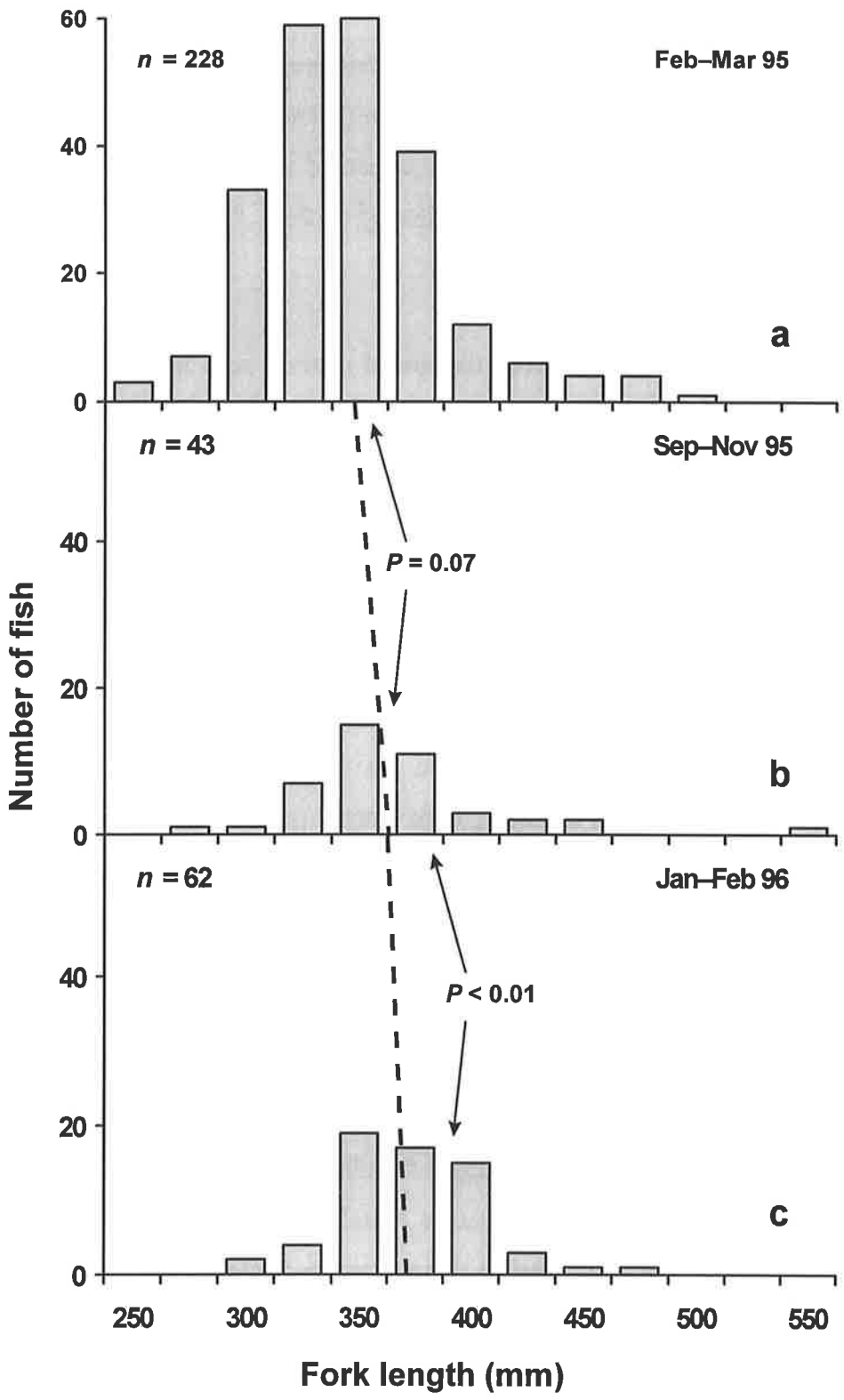

Figure 5.2 Length-frequency distributions of carp from Lakes Crescent and Sorell (Tasmania) during 1995–96. Mean FL values for each subsample are joined by a broken line. Probability values from *post-hoc* comparisons (Spjotvoll/Stoline test) following ANOVA indicate differences between mean FL values. (a) Combined data for February–March 1995; (b) September–November 1995; (c) January–February 1996.

5.3.2 Interpretability of otoliths

Otoliths were recovered from 189 fish: 75 were interpreted for age from whole otoliths, 58 from sectioned otoliths and 56 from both. Three (2·3%) of the 131 whole otoliths and 21 (18·4%) of the 114 sectioned otoliths were discarded as uninterpretable. Interpretability was significantly less for the sectioned otoliths ($\chi^2 = 17{\cdot}95$, $P < 0{\cdot}001$).

5.3.3 Validation of annulus counts

MIA elucidates relationships between the spatial patterns seen in calcified structures and the temporal patterns caused by environmental changes. As comparisons of whole and sectioned otoliths showed no differences in the time of annulus formation and edge characteristics, data for whole otoliths only are considered below. This is appropriate also given the relatively small number of sections.

5.3.3.1 Marginal increment ratio analysis

In pooled annulus groups 1–5 a dip was apparent in January (Fig. 5.3a). MIR increased in February and remained high in November, one month before the nominal birth-date. However, separate analyses of annulus groups 1 and 2 revealed different trends. In otoliths with two annuli MIR remained high throughout the year, peaking in January (Fig. 5.4a). In otoliths with three annuli a dip was visible through January and February. MIR appeared to rise in March and decreased towards the end of the year; however small sample sizes do not allow any definite conclusions (Fig. 5.4b).

5.3.3.2 Edge type analysis

In pooled annulus groups the percentage of otoliths with an opaque edge was high in January and February but markedly lower in March, when most otoliths had a translucent margin. These were observed also in fish caught in September–November (Fig. 5.3b). Otoliths with two annuli had a translucent edge virtually year-round (Fig. 5.4c), while newly-formed opaque edges were especially common in carp with three annuli captured in January (when most specimens were caught) (Fig. 5.4d).

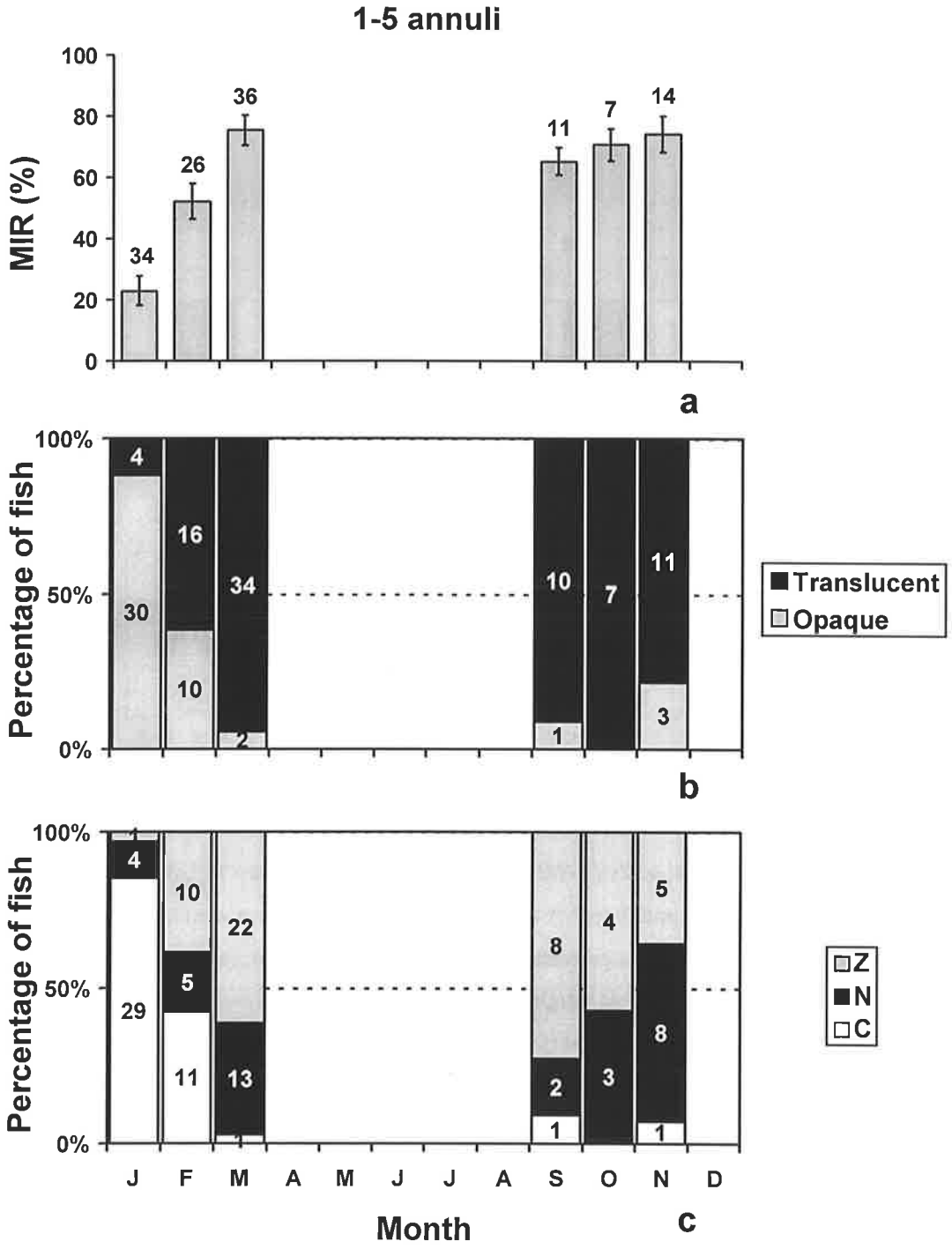

Figure 5.3 Marginal increment analysis (MIA) of whole otoliths from carp in Lakes Crescent and Sorell, Tasmania (pooled annulus groups only). (a) Mean monthly values (± SE) of the marginal increment ratio (MIR), as a percentage of the previous increment; (b) percentage of fish having otoliths with an opaque or a translucent margin (under reflected light), (c) percentage of fish classified as C (MIR ≤ 50%), Z (50% < MIR < 75%), or N (MIR ≥ 75%).

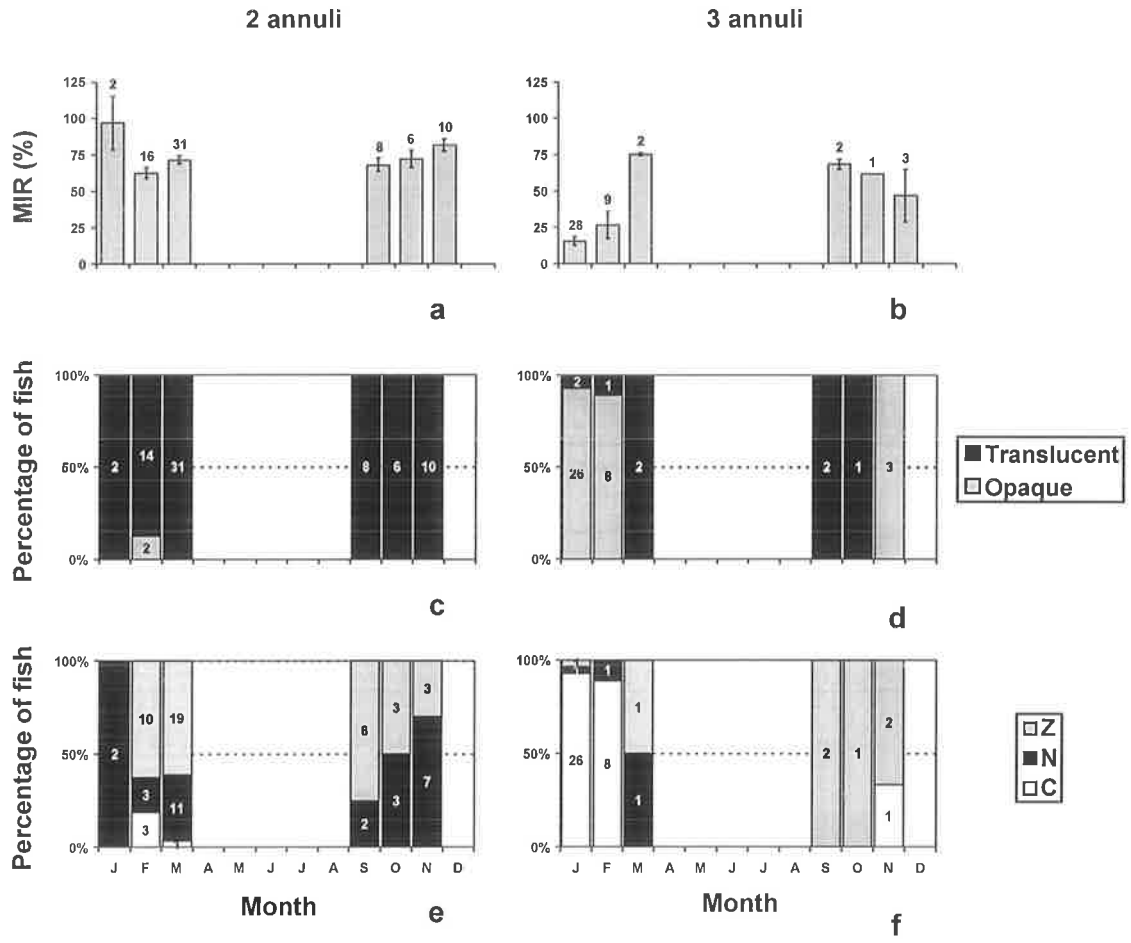

Figure 5.4 Marginal increment analysis (MIA) of whole otoliths from carp in Lakes Crescent and Sorell, Tasmania. Data for 2 (a,c,e) and 3 (b,d,f) annuli are shown. (a,b) Mean monthly values (± SE) of the marginal increment ratio (MIR), as a percentage of the previous increment; (c,d) percentage of fish having otoliths with an opaque or a translucent margin (under reflected light); (e,f) percentage of fish classified as C (MIR ≤ 50%), Z (50% < MIR < 75%), or N (MIR ≥ 75%).

5.3.3.3 Edge interpretation

In pooled annulus groups the distribution of type C, N and Z edges was in keeping with the anticipated formation of a new annulus in January (the nominal month of birth). Indeed, type C otoliths were more abundant in January and February, and the proportions of type N and Z edges increased in November and March–September, respectively (Fig. 5.3c). In annulus group 2 there were few otoliths with type C edges, observed in February and March. This is unexpected, given the distribution of edge types (Fig. 5.4e). A pattern comparable to that noted for MIR and ETA was apparent in annulus group 3, although type Z rather than type N edges appeared to predominate in early spring (Fig. 5.4f).

5.3.3.4 Annulus distance

The mean annulus distance from the nucleus in whole (1–6 annuli) and sectioned otoliths (1–4 annuli) increased progressively, suggesting that ages estimated from annulus counts reflected true ages. The mean distance from the nucleus of the first three annuli in whole otoliths from River Murray carp was significantly less than in Crescent-Sorell ($P < 0{\cdot}001$) (Table 5.3, Fig. 5.5a,b).

Table 5.3 **Summary statistics for the annulus distance from the nucleus in whole otoliths from Crescent-Sorell (Tasmania) and River Murray carp.**

	Annulus distance from nucleus (mm)									
	Lakes Crescent and Sorell					River Murray				
Annulus	*n*	Mean	± SE	Min	Max	*n*	Mean	± SE	Min	Max
1	128	0.947	0.019	0.56	1.83	417	1.145	0.014	0.51	2.26
2	126	1.966	0.022	1.48	2.60	367	2.260	0.023	1.09	3.50
3	53	2.664	0.034	2.01	3.15	358	2.818	0.026	1.42	4.02
4	8	3.078	0.081	2.71	3.38	301	3.284	0.030	1.82	4.47
5	4	3.200	0.112	2.94	3.46	190	3.691	0.042	2.12	4.95

5.3.4 Somatic growth models

The lengths and weights of juveniles, males and females successfully interpreted for age are summarised in Table 5.4. Estimated ages were based on whole or sectioned otoliths and, when both were available for one specimen, the whole otolith was used.

The somatic growth of males and females was modelled using a log-log quadratic function (LLQF: cf. Table 4.2 for terminology). Von Bertalanffy growth functions (VBGFs) could not be fitted owing to lack of convergence in the model parameters, due probably to the limited number of age classes present (only four fish, two males and two females, were older than 4 years). Analysis of Residual Sum of Squares (ARSS) showed that the rate of growth was significantly different between the sexes ($P < 0{\cdot}01$), and separate models were fitted for each (Table 5.5, Figure 5.6a). Pooling was justified as no differences were apparent in the weight-length relationships for each sex ($P > 0{\cdot}05$). The exponent b in the common growth model indicated allometric growth (Table 5.5, Fig. 5.6b).

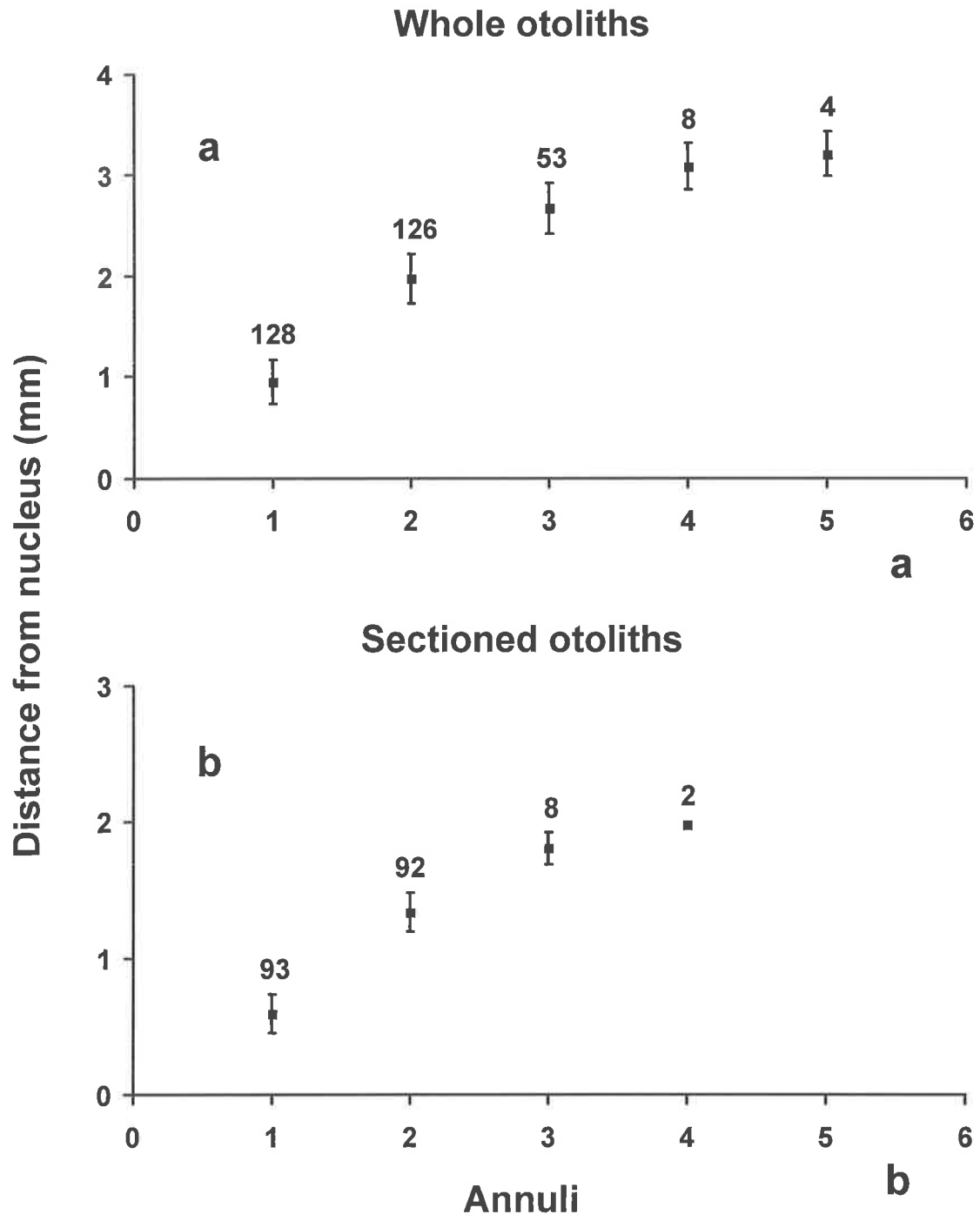

Figure 5.5 Mean annulus distance (± SD) from the nucleus in otoliths of carp from Lakes Crescent and Sorell, Tasmania. Annulus counts based on (a) whole otoliths and (b) sectioned otoliths.

Growth in weight could not be modelled using the Beverton-Holt modification of the VBGF. Again, this was a consequence of small sample size, the limited range of age classes in the population and, to a lesser extent, variability in the body weight in fish at the same age.

***Table 5.4* Summary statistics for fork length (FL) and total weight (W) of juvenile, male and female carp from Lakes Crescent and Sorell, Tasmania.** Estimated ages are based on annulus counts from whole and sectioned otoliths, in this order of priority.

		FL (mm)				W (g)			
Estimated age (yr)	*n*	Mean	± SE	Min	Max	Mean	± SE	Min	Max
Juveniles									
1	2	296·0	26·0	270	322	669·0	111·0	558	780
2	29	317·6	6·2	228	375	823·9	40·8	316	1316
3	3	305·7	22·2	283	350	722·3	159·0	552	1040
Males									
1	1	315				874			
2	39	341·9	4·3	273	400	1036·0	39·4	458	1520
3	41	335·9	4·5	282	420	988·5	40·8	546	1778
4	4	367·0	23·4	302	407	1309·3	265·3	594	1765
5	2	435·5	19·5	416	455	1659·0	345·0	1314	2004
Females									
2	20	341·5	4·7	300	370	1046·0	54·8	600	1485
3	29	362·1	6·8	300	441	1238·9	77·7	681	2200
4	4	395·3	22·6	348	455	1733·5	351·1	1012	2662
5	1	417				1615			
6	1	528				4275			

Length-at-age and weight-length relationships also were modelled for all aged fish (pooled sexes and juveniles). Growth parameters are shown in Table 5.6.

5.4 Discussion

The apparent lack of a new annulus in two-year old fish at the beginning of the growing season (January–February) is perplexing: the mean MIR and the edges of otoliths with two annuli were typical of fish about to form a new annulus, and inconsistent with the low marginal increments and narrow opaque edges expected from annual deposition of zones. This probably is an artefact of the method used, given the presence of a single dominant year-class and the lack of younger age groups. The length-frequency analyses clearly show that a single cohort dominates, consisting of age group II individuals in

Table 5.5 **Models describing the somatic growth of male and female carp in Lakes Crescent and Sorell, Tasmania.** Values (± SE) for the parameters and tests of significance between the sexes are reported. The residual sum of squares (RSS) and the value and corresponding probability for the *F*-ratio test are also indicated for all comparisons of growth curves between sexes. When no significant differences at a probability level $\alpha = 0{\cdot}05$ were detected the model for the combined sexes is given. All logarithms to the base 10. All acronyms and symbols as in Table 4.2.

Statistics	Males + Females	Males	Females
FL LLQF			
n	142	87	55
a_1	2·878 ± 0·119	2·823 ± 0·161	2·797 ± 0·193
b_1	− 1·324 ± 0·390	− 1·085 ± 0·545	− 1·104 ± 0·605
c_1	1·254 ± 0·318	0·986 ± 0·458	1·141 ± 0·470
r^2	0·225	0·078	0·425
RSS	0·217	0·129	0·071
DF	139	84	52
F	5·897 ($P = 3{\cdot}5E{-}03 < 0{\cdot}01$)		
Model		$Log(FL_t) = 2{\cdot}823{-}1{\cdot}085(Log(t+1))+0{\cdot}986(Log(t+1))^2$	$Log(FL_t) = 2{\cdot}797{-}1{\cdot}104(Log(t+1))+1{\cdot}141(Log(t+1))^2$
LWR			
n	255	168	87
a^A	3·9E–08	1·1E–07	2·1E–08
b^A	2·927	2·753	3·028
r^2	0·987	0·989	0·986
RSS	4·694	2·179	2·411
DF	253	166	85
F	2·840 ns ($P = 0{\cdot}060$)		
Model	$W = 3{\cdot}9E{-}08FL^{2{\cdot}927}$	$W = 1{\cdot}1E{-}07FL^{2{\cdot}753}$	$W = 2{\cdot}1E{-}08FL^{3{\cdot}028}$

[A] Asymptotic standard errors not available.

Table 5.6 **Models describing the somatic growth of carp (pooled sexes and juveniles) in Lakes Crescent and Sorell, Tasmania.** Explanation of models as in Table 5.5. All acronyms and symbols as in Table 4.2.

Statistics	All fish
FL LLQF	
n	176
a_1	2·638 ± 0·098
b_1	– 0·609 ± 0·330
c_1	0·273 ± 0·277
r^2	0·215
Model	$Log(FL_t) = 2·638–0·609(Log(t+1))+0·273(Log(t+1))^2$
LWR	
n	332
a^A	3·5E–08
b^A	2·943
r^2	0·900
Model	$W = 3·5E–08FL^{2·943}$

[A] Asymptotic standard errors not available.

1995 and group III individuals in 1996 (notations here follow Jearld 1983). Age group I carp, on the other hand, were always present in very low numbers (two individuals in February, one in March 1995). If an arbitrary 250 mm FL is used to separate I+ from II+ individuals (cf. Fig. 5.2), age group I was inconspicuous in 1995, and probably absent in 1996.

Validation of annulus counts by MIA therefore was based on the dominant 1993 year-class. Two specimens caught in January 1996 accounted for the peak MIR value (Fig. 5.4a) and the presence of 'aberrant' edge types (Fig. 5.4c,e); these probably were 'laggers', yet to form the new annulus laid down by other members of the same annulus group. All carp with two annuli in Fig. 5.4a,c,e (except the two specimens captured in January 1996) were caught in 1995, and specimens with three annuli sampled during January–February 1996 belonged to the same cohort (Fig. 5.4b,d,f). The few III+ specimens caught in September–November 1995 almost certainly were members of a weaker 1992 cohort, represented by only two IV+ individuals in the January 1996 sample. For similar reasons, the low mean MIR for III+ carp in January 1996 is probably atypical, as it relates to the dominant January 1993 cohort and does not include three-year old fish about to form an annulus at the inception of their fourth year (this is the apparently weak January 1992 cohort).

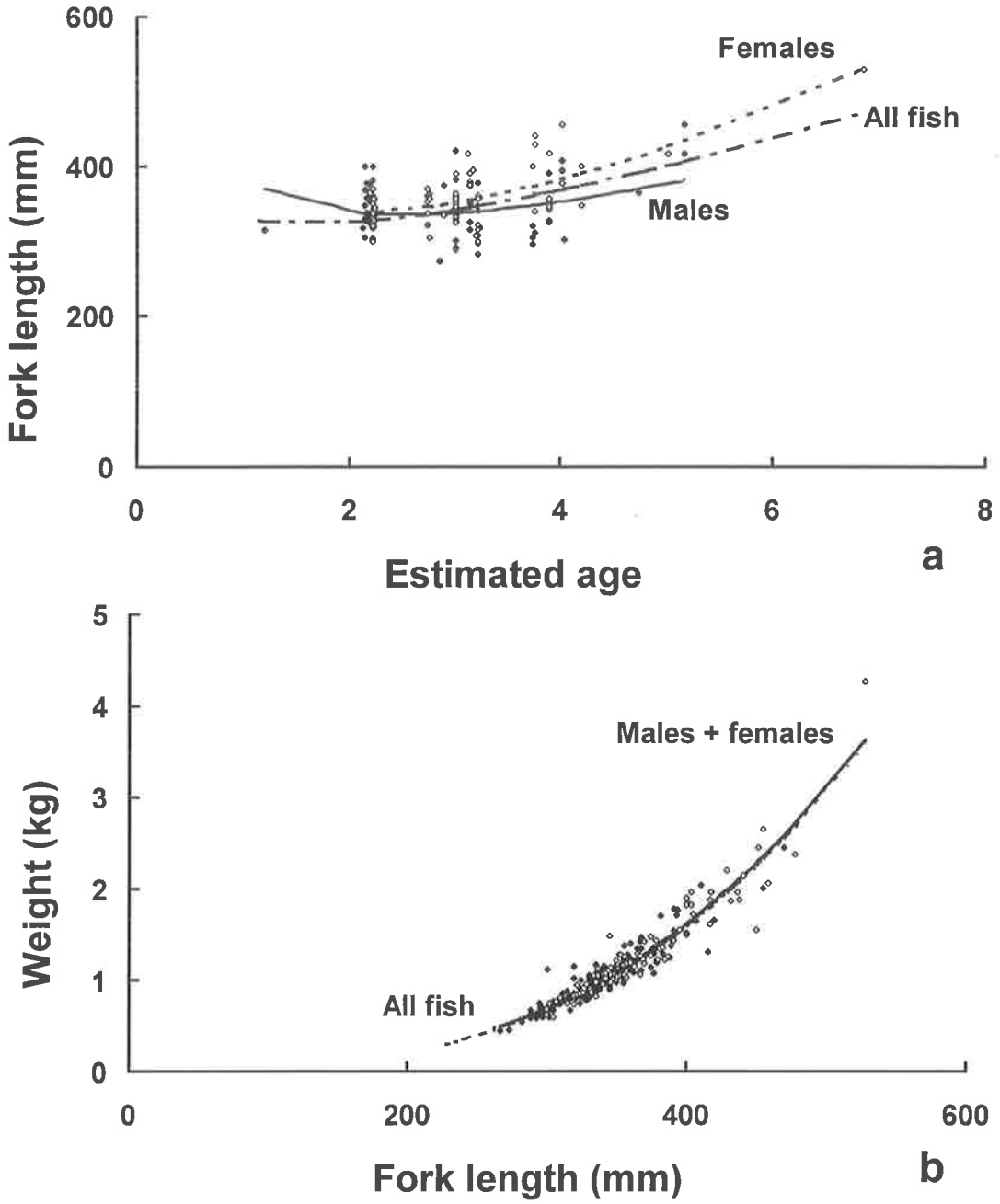

Figure 5.6 Somatic growth of carp in Lakes Crescent and Sorell, Tasmania. Estimated ages are based on annulus counts from whole and sectioned otoliths in this order. Parameters for all curves are given in Tables 5.5 and 5.6. (a) Growth in length described by the log-log quadratic model (LLQF): pooled sexes and juveniles (all fish), males and females; (b) weight-length relationship: pooled sexes and juveniles (all fish), males and females.

Formal validation of these age interpretations was achieved (*sensu* Beamish and McFarlane 1983, 1987) by MIA on otoliths for three-year old fish only. Even so, the patterns of otolith development observed in two-year old individuals (except in the January sample),

and the relative distance of annuli from the nucleus in otoliths from all annulus groups in the population, point to annual deposition of zones over 1–5 years.

These data complement observations on carp in the River Murray (cf. Chapters 2–4). This is illustrated by the tolerance of age estimates to changes in the timing of reproduction. January 1, the nominal birth-date for the Crescent-Sorell population, corresponds roughly to the onset of a protracted period of mean water temperatures exceeding 15 °C, the minimal spawning threshold (Sarig 1966; Guha and Mukherjee 1991). In early 1996 this period included three weeks with temperatures above the indicated threshold (Bullies Marsh, Lake Crescent; Duck Bay, Lake Sorell: Tasmania Inland Fisheries Commission data). However, the 1996 summer was atypical, as a rise in water temperatures above the spawning threshold would have been expected by mid-November. This has important consequences for the estimation of a birth-date. In this study January 1 was chosen based on mean water temperatures and annulus formation in otoliths. However, a more precise estimate would be obtained by future monitoring of year-to-year variation in mean water temperatures in the lakes. Finally, an advantage with this methodology is that difficulties in interpreting results for small sample sizes and/or pronounced annual variation in recruitment are buffered, so that atypical individuals are assigned to the correct annulus group (Anderson *et al.* 1992a,b; R. I. C. C. Francis *et al.* 1992).

The smaller widths of successive annuli in Crescent-Sorell carp may reflect more severe local climatic conditions, compared to those in the Murray, and may explain the lower interpretability of sectioned compared to whole otoliths. In the otoliths of Crescent-Sorell carp, under reflected light, translucent zones appear as dark, thin areas intercalated with wider opaque zones, and the alternations are not clear after sectioning. Winter (slow-growth zones) in otoliths are not necessarily translucent (R. I. C. C. Francis *et al.* 1992), but this appears to be so for carp in Australia (Chapter 2). The narrow zones of Crescent-Sorell carp may reflect a shorter slow-growth period than for carp in the River Murray, where water temperatures exceed the 15 °C threshold for most of the year (Jones 1974).

5.5 Conclusion

The carp population in Lakes Crescent and Sorell should be monitored year-round, with special regard for the timing of reproduction and the annual recruitment of cohorts. Male carp generally mature at ages II–IV and females one year later, at ages III–V (Carlander 1969), and the low number of mature females may partly explain the low recruitment in the lakes in 1994–96. The 1993 year-class is a strong basis for the population to grow.

6.

AGE AND GROWTH:

A CENTURY OF STUDIES ON CARP AGEING

> Van Oosten (1929), in his historical review of the scale method, indicated that, although Hintze demonstrated in 1888 that the age of carp could be determined from examination of scales, Hoffbauer in 1898 usually is recognized as the first to accurately age fish from scales and to validate the results (through the first 3 years), using carp reared in ponds.
>
> K. D. Carlander (1987)

6.1 Overview

Given a century or more of research, and a correspondingly extensive literature on the age and growth of carp (cf. Chapter 7), it is not surprising that many diverse structures and methodologies for age interpretation have been employed. A sample of studies ($n = 68$) (Table 6.1) indicates that scales are by far the most commonly-used calcified structure (82·4%), followed by opercular bones, the dorsal spine and otoliths, the eye lens and vertebrae. This is expected, as scales and opercular bones are routinely employed in age interpretations of many freshwater and marine fish (e.g. Bagenal and Tesch 1978). Otoliths have received less attention, and in the carp literature the type of otoliths examined and the appearance and arrangement of annuli therein are seldom described in detail, if at all (cf. Chapter 2).

The relative values of carp structures are addressed in a subset of the literature ($n = 39$) (Table 6.2). Clearly, no single structure is of general value, although opercular bones generally have been judged superior to scales and, as shown earlier (Chapter 3), are comparable to otoliths, at least in River Murray carp. Casselman (1990) analysed the growth and relative size of scales, cleithra and otoliths, and concluded that calcified structures other than scales continue to grow as the fish does, providing more reliable

estimates of age in older fish. Bones and/or otoliths therefore appear to offer a partial solution to the difficulties related to the morphology and development of scales.

Table 6.1 **Number and percentage of structures used for interpreting the ages of carp based on a representative literature sample of studies.** Percentages do not sum to 100 as more than one structure could have been used in the same study

Structure	*n*	Percentage
Scales	56	82·4
Opercular bones	10	14·7
Spines and fin rays	3	4·4
Vertebrae	1	1·5
Otoliths	3	4·4
Eye lens	2	2·9

Table 6.2 shows the validation procedure (when attempted) and the range of ages validated (*sensu* Beamish and McFarlane 1983, 1987). No validation was attempted in 82% of these studies (Beamish and McFarlane indicated a total of 35%). Although this figure might be deflated by regarding those studies that corroborate age estimates by comparison of annuli in different structures as 'validated *sensu lato*' (e.g. Das and Fotedar 1965; Wichers 1976), it demonstrates that little attention has been paid to validation in carp studies. Many authors appear to have assumed that widely-used methods for age determination, especially the use of scales (e.g. Crivelli 1981), are applicable to all fish. Yet different stocks growing under different environmental conditions, even within a relatively limited geographical range, may show distinct patterns of growth and reproduction that are reflected in the patterns of annuli in their calcified structures (cf. Chapters 2 and 5). Marginal increment analysis (Chapter 2) affords a rough means to analyse these patterns quantitatively and, with techniques like length-frequency analysis (generally applicable to the first few age classes), ought to be routine in studies where more sophisticated methods (e.g. tagging, observations of fish of known age) are precluded.

In light of these considerations, the following sections offer a closer analysis of the various types of structures and methodologies for age interpretation in carp.

6.2 Evaluation of structures

6.2.1 Scales

The ages of cyprinid fish, including carp, traditionally have been determined with scales (Jearld 1983; Mann 1991). Scales were first used by Hoffbauer (1898), whose work paved the way for further developments. Van Oosten (1929) provided further support, and scale interpretation (lepidology) became routine in subsequent work. Johal *et al.* (1984) described the structure of carp scales in detail, highlighting major morphological differences between the Indian and the Czechoslovak common carp (overall shape, number of circuli, production and growth of radii). Talaat and Oláh (1986a,b) evaluated the reliability of scale-based age determinations and growth estimates in a Hungarian population, and suggested criteria for the identification of 'true' and 'false' annuli. The scales of mirror carp (cf. Probst 1949, 1950; Wohlfarth 1984; Brylińska 1986, in Balon 1995b) also have received attention, although there are contrary opinions over their value. Only Das and Fotedar (1965) were able to successfully age mirror carp up to six years old. On the other hand, mirror carp scales proved of no value for a population of known age in a farm pond in Egypt (Bishai and Labib 1978). This is supported by casual observations on mirror carp in the lower Murray (cf. Section 2.2.3.1).

The development, morphology, physiology and genetics of carp scales are well-studied (Kirpichnikov 1937; Golovinskaya 1940; Matsui 1949; Dürr 1957; El-Fiky 1993). The phenomenon of scale absorption in starved fish (Ichikawa 1953, in Simkiss 1974) has obvious implications for age estimation, as the lack of deposition of bony tissue under critical physiological conditions can impair the recognition and interpretation of scale annuli. The literature contains frequent mentions of the limitations of scale-based age determinations, indicating that better understanding of the factors responsible for scale and body growth is necessary for the technique to be implemented successfully (Carlander 1987). Drawbacks with scale-based age determinations include (1) crowding of annuli towards the edge in older fish, (2) supernumerary rings (spawning checks, pseudoannuli), (3) resorption, (4) lack of deposition of the first annulus, and (5) difficulties in locating the first annulus. Advantages are (1) ease of collection and preparation, and (2) the possibility for mark-and-recapture studies (scale removal need not harm the fish).

Table 6.2 **Structures and validation of age estimates based on a representative sample of age and growth studies on carp.** Primary structure(s): main structure(s) employed in interpreting the age of the population under study; Secondary structure(s): alternative structure(s) examined; Attempted structure(s): structure(s) unable to provide reliable age interpretations; Relative value: reliability of structure(s) proposed; Validation: employed methodology for assessing the accuracy of age interpretations (*sensu* Beamish and McFarlane 1983, 1987); Validated ages: range of validated age classes. Sc: scale; Op: opercular bone; Ds: dorsal spine; Ve: vertebrae; El: eye lens; Ot: otolith; Su: subopercular bone; Pa: parietal bone; La: lacrimal bone; Br: branchiostegal bone; Ri: ribs; Pt: pharyngeal teeth.

Author(s)	Primary structure(s)	Secondary structure(s)	Attempted structure(s)	Relative value	Validation	Validated ages
English (1952a)	Sc, Op	Ds	Su	Op > Sc	Not validated	
McConnell (1952)	Op	Sc		Op > Sc	Length-frequency	1–3
Patriarche (1953)	Sc				Strong year class	3–5
Purkett (1957)	Sc				Tagging	Not indicated
Schoffman (1957)	Sc				Not validated	
Sigler (1958)	Op				Not validated	
Rehder (1959)	Sc, Op			Op > Sc	Not validated	
Das and Fotedar (1965)	Sc	Op, Ot, Ve			Not validated	
Carlton and Jackson (1968)	El	Sc, Ds			Not validated	
Astanin and Trofimova (1969)					Known age	1–4
Mauck and Summerfelt (1970)	Sc				Not validated	
Fetodova (1971)	Sc				Not validated	
Stucky and Klaassen (1971)	Sc				Not validated	
Jones (1974)	Sc	Op	Ds, Ot		Not validated	
Živkov (1975)	Sc				Not validated	
Wichers (1976)	Ds	Ve	Sc, Op, Su, Pr, La, Br, Ri, Pt	Op > Ve	Not validated	
Bishai and Labib (1978)	Ve		Op, Ot		Known age	
Kilambi and Robison (1978)	Sc				Not validated	
Tsimenidis (1978)	Op				Not validated	
Tanyolaç (1979)	Sc				Not validated	
Crivelli (1980)	El				Not validated	
Crivelli (1981)	Sc				Not validated	
Hume *et al.* (1983a)	Sc		Op, Ds, Ot		Not validated	

Table 6.2 (continued)

Author(s)	Primary structure(s)	Secondary structure(s)	Attempted structure(s)	Relative value	Validation	Validated ages
Wang Sihua (1983)	Sc				Not validated	
Johal *et al.* (1984)	Sc				Not validated	
Jestin *et al.* (1985)	Ds				Not validated	
Prochelle and Campos (1985)	Sc				Not validated	
Ramos *et al.* (1985)	Sc				MIA	2–5
Talaat and Oláh (1986)	Sc				Not validated	
Mamedov (1987)	Sc				Not validated	
Raina (1987)	Sc, Op, Ot				Not validated	
Sharma (1987)	Sc				Not validated	
Harka (1989)	Sc				Not validated	
Fernández-Delgado (1990)	Sc				Not validated	
Çetinkaya (1992a)	Sc, Op				Not validated	
Demirkalp (1992)	Sc				Not validated	
Pinilla *et al.* (1992)	Ot				Not validated	
Ritter-Ortiz *et al.* (1992)	Sc				Not validated	
Hoc opus	Sc, Op, Ot			Sc < Op = Ot	MIA	1–7

6.2.2 Opercular bones

Opercular bones, originally used for perch, *Perca fluviatilis* (LeCren 1947), have proved to be a valid alternative to scales. They were first employed by McConnell (1952) for a population in northern Utah, where scales had been found unsuitable. English (1952a), Sigler (1958), Rehder (1959), Tsimenidis (1978), Çetinkaya (1992a) and many others have based carp age estimations partly or wholly on opercular bones.

Opercular bones have seldom been used in conjunction with other structures, particularly scales and otoliths, although the use of a suite of structures has long been suggested as a means to circumvent structure-related difficulties in interpretation of annuli patterns (e.g. Beamish and McFarlane 1987). The necessity for reference to complementary structures is evident in the morphological peculiarities of opercular bones. Ridge-like projections radiating from the fulcrum ('buttresses' of McConnell (1952), 'fingers of bone' of English (1952a)) progressively obscure the first 1–3 annuli, so that other structures or age interpretation methodologies (usually length-frequency distributions) are needed (e.g. McConnell 1952).

The relative ease of collection of opercular bones is offset by the time required to prepare them for examination. The conventional methods (boiling for a few minutes to allow skin separation and/or scrubbing with a stiff brush) are all time-consuming, especially when large numbers of fish are to be examined, and are not always successful (cf. Section 2.2.3.2).

6.2.3 Spines and fin rays

The use of fin rays was assessed by Beamish (1981), who emphasised the superiority over scales, especially when scales underestimate the age of older fish. In carp the dorsal spine, a large bone with a strongly-serrated posterior edge (Bănărescu 1964), was first employed for age estimates by Boyko (1940), and the sectioning technique was later refined by English (1952b). Experimental studies using fluorescent markers have been conducted by Meunier and Pascal (1981/1982), who demonstrated the formation of *Lignes d'Arrêt de Croissance* (LAC) in fin rays during winter, providing a physiological basis for their use in age determination. Wichers (1976) and Jestin *et al.* (1985) relied primarily on annuli

counts on the dorsal spine for their age estimates, and English (1952a) and Carlton and Jackson (1968) employed these calcified structures to corroborate interpretations from other structures. In particular, English (1952a) obtained satisfactory results for carp 1–2 years old, overcoming problems with scale and opercular bone interpretations.

As with other structures, fin rays sometimes have yielded contradictory results. Drawbacks often emerge in preparation and sectioning (Jones 1974; Hume *et al.* 1983a). Wichers (1976) noted that consistent deviations in back-calculated growth from dorsal spine annuli were associated with different points along the spine where sections were taken, and this appears to be crucial for validation (Jearld 1983). Nevertheless, as spine collection does not kill the fish this technique may be a valid alternative to the use of scales in mark-and-recapture studies.

6.2.4 Vertebrae and other bones

Vertebrae have been traditionally used mainly in elasmobranchs (Jearld 1983), but also have some application for carp. Bishai and Labib (1978) found that vertebrae, particularly the third vertebra, were the only interpretable structure for a subtropical population of carp. Dark narrow bands were observed from January to March and their formation was correlated with a decrease in water temperature and feeding rate. Wichers (1976) used vertebrae to corroborate age estimates based on fin ray sections, but found them of limited value for older carp because of crowding of annuli along the edge. Wichers also made a systematic study of different bones, including subopercular, parietal, lacrimal and branchiostegal bones as well as ribs and pharyngeal teeth. No satisfactory results were obtained with any of these structures, but this study was a seminal contribution to knowledge of the comparative values of bony structures in carp.

6.2.5 The eye lens

Carlton and Jackson (1968) first proposed the weight of the eye lens as an alternative, semi-objective index of age in carp. Crivelli (1980) re-evaluated the technique on a larger sample, including several age classes indicated by scale counts. In both studies satisfactory results were achieved only for the first age groups, as the eye-lens weights of older fish tend to overlap.

6.2.6 Otoliths

Objective criteria have long been sought to reduce the subjectivity typical of conventional age interpretation techniques. Boehlert (1985) was first to advocate the use of otolith weight, now a routine procedure in most age and growth studies. This did not seem to be of any real advantage for carp, however, as there is typically a low correlation between otolith (asteriscus) weight and age (cf. Section 4.3.4).

In virtually all reports on the use of otoliths in carp, no clear protocols are provided for preparation and examination, and no study specifies unequivocally which of the three pairs of otoliths (lapilli, sagittae, asterisci) were examined. A clear indication of the type of otoliths is essential for cyprinids, where morphological changes of the otic cleft associated with the Weberian apparatus cause major modifications in the shape of the saccular and lagenar otoliths (cf. Chapter 2).

Failed attempts to use otoliths are reported by Jones (1974) and Hume *et al.* (1983a) for carp in Australia (cf. Section 1.3), and by Wichers (1976) and Bishai and Labib (1978) for populations in other regions. The 'small size' of the otoliths is often cited, although it is never clear whether this refers to lapilli, asterisci or sagittae. On the other hand, references to the corroborative value of otoliths include Das and Fotedar (1965), apparently the first to use otoliths in carp, and Raina (1987). Only Pinilla *et al.* (1992) relied exclusively on otoliths for a population of carp in Colombia. These authors detected the formation of opaque zones in winter (December–February) as a response to fluctuations in food availability. This is contrary to present findings for carp asterisci, in which opaque zones are laid at the beginning of the growing season (October in the lower River Murray, December–January in Tasmania), following the development of translucent 'winter' zones (Chapters 2 and 5).

7.

AGE AND GROWTH:

"A MOST SUCCESSFUL COLONIZER"

> Like the early fifteenth century author, who compiled the first known "Treatyse of Fysshynge" in the English language [...]—I am "loth to wryte more than I knowe and have provyyd," so these notes do not pretend to be complete...
>
> S. S. Flower (1935)

7.1 Introduction

References to exceptionally old or large carp are occasionally found in the literature although, as stated by Sarig (1966, p. 3:11), "tales of 100 year old carp are without basic evidence". Hessel (1878, in McCrimmon 1968) claimed an individual of 140+ years, reared in captivity, Flower (1935) cited a mirror carp that lived for 47 y, also in captivity, and Einsele (1956) reported specimens older than 40 y in an Austrian reservoir. With regard to body size, Berg (1964, p. 392) noted that "in June 1886 a carp weighing 32 kg was caught in Lake Garda near Lugano", and gave anecdotal evidence for a 57 kg specimen from the Dnieper delta. Sigler and Miller (1963, in Carlander 1969) indicated a maximum weight of 27 kg for carp in America and 37·4 kg in South Africa (see also Panek 1987). Lengths up to 1 m have been frequently recorded, and still larger individuals are known (Carlander 1969).

References to slow-growing or even dwarfed populations are also found in the literature. Thus, Abdullayev and Khakberdiyev (1972) reported on the ecology of the dwarf carp in the lakes of the Khorezm Province, and highlighted major morphometric differences with respect to normally-growing populations from Lake Ulli-Shor-Kul', while Crivelli (1981) and Fernández-Delgado (1990) pointed to the inhibitory effect of salinity on growth in European populations living in brackish waters.

The above remarks define the extremes of size and age recorded for carp across its distributional range, and indicate the high plasticity for growth manifested by this fish. Balon (1974) reported of pond experiments where artificially dwarfed carp reared under food deprivation could survive for long periods, maintaining their ability to resume growth when returned to an optimal feeding regime. These considerations led Balon (1974, p. 16) to state that " Great viability is a characteristic of wild carp, which tolerate a wide range of environmental factors and are consequently a unique teleost species—a most successful colonizer of the world".

The factors affecting growth in fish have been described by many authors (e.g. Brett 1979; Weatherley and Gill 1987; Wootton 1990), and in cyprinids particularly by Mann (1991). Abiotic factors include temperature, light, salinity, oxygen, pH and water-level fluctuations (Živkov and Petrova 1984), and biotic factors include food quality and availability and population density. The roles of factors vary, of course, at local, regional, continental and global scales.

There is conflicting evidence as to the influence of latitude on size and growth in fish. Thus, Ray (1960) reported that in some Pacific salmons (*Oncorhynchus* spp.) body size tends to increase with latitude, according to Bergmann's Rule, whereas Moyle and Herbold (1987) showed that the opposite was true of western North American cyprinids. Pivnička (1983) attributed growth changes in chub (*Leuciscus cephalus*) and rudd (*Scardinius erythrophthalmus*) to latitude rather than to density, recording a gradual increase in growth from north to south between the 48–58 parallels. No general rule is therefore apparent, suggesting that other regulating factors may mask the effect of latitude (Pivnička 1983; McDowall 1994).

A phenomenon only recently studied in fish is the so-called 'countergradient variation in growth' (Conover 1990). According to this idea the capacity for growth within a species varies inversely with the length of the growing season across a latitudinal gradient. Latitudinal compensation in growth patterns has been documented in marine fish along the eastern North American coast, and laboratory experiments have supported field evidence (Conover and Present 1990; Shultz *et al.* 1996). The adaptive significance of countergradient variation is a reduction in size-selective winter mortality of young-of-the-

year fish by increasing growth and, ultimately, size achieved at the end of the growing season, so that more energy can be stored in the body in the form of easily metabolised lipids (Conover 1992).

Comparisons of growth among populations of carp are common (e.g. Sigler 1958; Živkov 1975; Crivelli 1981; Wang Sihua 1983; Johal *et al.* 1984; Lubinski *et al.* 1986; Mamedov 1987; Harka 1989; Sal'nikov 1989; Fernández-Delgado 1990; Çetinkaya 1992a; Demirkalp 1992), yet very little is known about growth patterns on a global scale. Only Fernández-Delgado (1990), with a sample of 14 studies, identified two groups of fast- and slow-growing populations, observing a significant decrease in growth rate and an increase in age at first maturity with increasing latitude. In that study it was concluded that carp are "capable of a range of phenotypic expressions in response to different environmental situations" (p. 27). However, only the lengths of the first five year classes in each of the analysed populations were considered, and this may have obscured the actual type of growth and maximum size achieved by carp under the latitudinal range considered.

The technical literature on carp is enormous: more than 750 references have been accumulated in the review that underpins the present research program, and the task certainly is incomplete. Following Balon's (1982) advice I have refrained from a 'comprehensive review' of carp age and growth studies, and instead have elected to comment upon a selective, but representative sample. As discussed earlier (Chapter 6), various structures and methodologies have been proposed, contributing to a very large database of growth measurements. In this study length-at-age data are collated and analysed with the aim of revealing patterns in growth as a response to different climatic conditions. However, given the sparse information provided in most references, no attempt has been made to account for the other abiotic and biotic factors contributing to the dynamics of any of the populations. The present study therefore expands on the findings of Fernández-Delgado (1990), and suggests explanations for observed patterns in type and rate of growth as well as optimal size achieved. The possible value of these parameters as a life-history trait is also discussed.

7.2 Materials and Methods

7.2.1 Data collection and criteria for selection

Length-At-Age (LAA) data were gathered from published reports on 181 populations of carp. As it was not always possible to consult the primary source of the information, some LAA values are from secondary sources, essentially internal reports, abstracts and theses or dissertations. Table 7.A (end of chapter) lists all populations examined, alphabetically by the author(s)' name, and also indicates the source of information for secondary references.

As one objective of this survey was to compute population growth parameters (where feasible), datasets including LAA values exclusively for the first few age classes, or for older fish only, were excluded. Further, in the few cases where a single LAA value in a population dataset was not available, this was estimated by linear interpolation from adjacent points. LAA values from direct measurements were preferred to back-calculated ones. Values for males and females were analysed separately.

7.2.2 Data analysis

No general method for measuring fish length has yet been agreed upon in fish and fishery biology (Carlander 1969; but see Ricker 1979). This is especially true for carp, for which measures of standard, fork and total length have been used interchangeably in the literature. It was therefore necessary, for purposes of growth calculation, to choose a length measurement common to all populations examined. Fork Length (FL) was selected, arbitrarily, although observations on carp in the lower Murray (Chapter 4) do support its application in age and growth studies. All Total (TL) and Standard Lengths (SL) were converted to FL according to relationships described in Section 4.2.2. In studies where no indication of the length measurement was given a decision was made according to the following rules:

1. If an indication of the method of measurement *usually* employed by the author(s) in other studies was available then, following Carlander (1969), the same was assumed to have been used in the study considered, and the conversion to FL (if necessary) was made accordingly;

2. If the method was not specified, and could not be guessed at, the reported length was equated with FL.

Two mathematical functions, namely a VBGF and a LLQF (cf. Table 4.2 for nomenclature), were used to describe the growth in length in each carp population. According to Chapter 4, the VBGF was chosen as the primary model whenever it could be fitted to a data set, and the LLQF was preferred in cases where VBGF parameters could not be obtained. This is at variance with the integrative approach previously advocated, where the complementary use of both models was proposed. However, the aim here was to obtain readily-comparable growth parameters, like those provided by von Bertalanffy functions (cf. Moreau 1987). When this could not be achieved, the LLQF was used to describe growth in mathematical terms.

Patterns in growth were explored in terms of geographical distribution based on climate and latitude. To this end the Köppen-Geiger-Pohl classification of climates (Strahler 1992) was adopted as both a descriptive and quantitative scheme, and latitude (either as a continuous or zonal variable) was also used to identify populations. For each population the sampling site was recorded and the corresponding climate type and latitudinal zone identified. When no clear statement of the study area was given (e.g. 'Caspian Sea' or 'Illinois'), a point was selected near the centre of the specified region.

Fitting of growth curves to LAA data followed Section 4.2.4, except that growth models could not be fitted to the original data as only *mean* LAA values were available for each population. Thus, the given values were reduced to a considerably smaller number of observations. As a first step in the curve-fitting procedure, LAA values were plotted to reveal possible indications of an asymptotic trend. The Ford-Walford method (Ricker 1975) was then employed to confirm that VBGF parameter estimates could be obtained. If both conditions were satisfied, a VBGF was fitted by non-linear estimation (Quasi-Newton algorithm) using the Ford-Walford estimates as starting values. In cases where VBGF parameters could not be computed, the LLQF was also fitted by non-linear estimation, for sake of consistency. In the few cases where VBGF parameters were already available from the original study, these were included in the dataset only if FL was used, otherwise the parameters were re-estimated.

Statistical analyses were based on a total of three response and four predictor variables. The dependent variables were (1) asymptotic fork length FL_∞, (2) the Brody coefficient K, and (3) maximum length FL_{max}. The independent variables were (1) latitude, (2) latitudinal zone (0–25, 26–30, 31–35, 36–40, 41–45, 46–50, 51–55, 56–65), (3) Köppen climate type I (A, B, C, D, H), and (4) Köppen climate type II (Af, Aw, BSh, Bsk, BSk, BWh, BWk, Cfa, Cfb, Csa, Csb, Cwa, Dfa, Dfb, Dfc, Dwc: Table 7.1).

Among the dependent variables the VBGF parameters (FL_∞ and K) could be calculated for a total of 106 populations, corresponding to all cases where this model could be fitted successfully, and FL_{max} was available for the whole sample of 181 populations. Two extreme values in the distribution of latitudinal zones (i.e. 0–25, 56–65) covered a wider range because fewer populations have been sampled at those latitudes (cf. Section 7.5).

Table 7.1 **Climate types according to the Köppen-Geiger-Pohl classification system.** Only the climates relevant to this study are indicated.

Climate type	Description
Group A	Tropical
Af	Tropical rainforest
Aw	Tropical rainforest, monsoon type
Group B	Dry
BSh	Steppe, hot
Bsk	Steppe, dry summer, cool
BSk	Steppe, cool
BWh	Desert, hot
BWk	Desert, cool
Group C	Warm temperate (mesothermal)
Cfa	Rainy (humid mesothermal) with hot summer
Cfb	Rainy (humid mesothermal) with warm summer
Csa	Rainy (humid mesothermal) with dry, hot summer
Csb	Rainy (humid mesothermal) with dry, warm summer
Cwa	Rainy (humid mesothermal) with dry winter and hot summer
Group D	Snow (microthermal)
Dfa	Cold, snowy forest (humid microthermal) moist all year with hot summer
Dfb	Cold, snowy forest (humid microthermal) moist all year with warm summer
Dfc	Cold, snowy forest (humid microthermal) moist all year with cool summer
Dwc	Cold, snowy forest (humid microthermal) with dry winter and cool summer
H	Highland

Relationships between latitudinal zone, climate type I and II on one hand and growth model fitted (VBGF or LLQF) on the other were investigated by means of contingency tables. Simple linear regressions were employed in assessing the relationships of FL_∞, K and FL_{max} vs latitude. All statistical analyses were performed with the modules

ANOVA/MANOVA, Nonlinear Regression and Log-Linear Analysis of STATISTICA™ v 5.0 (Statsoft Inc. 1995).

7.3 Results

A graphical representation of the growth in length (FL) for the whole sample of carp populations examined arranged by Köppen climate type is given in Fig. 7.1, and summary statistics for the model variables are shown in Table 7.2.

Contingency analyses indicated no significant relationship between climate groups A–H ($\chi^2 = 4{\cdot}97$, $P = 0{\cdot}29$), climates of type B ($\chi^2 = 4{\cdot}82$, $P = 0{\cdot}31$) and climates of type D ($\chi^2 = 4{\cdot}78$, $P = 0{\cdot}19$) and the fitted growth curve VBGF/LLQF. Only in comparison of C climates with growth models was a significant relationship found ($\chi^2 = 9{\cdot}27$, $P = 0{\cdot}03$*).

The distribution of LAA curves for the carp populations under study, arranged by latitudinal zone, is shown in Fig. 7.2, and descriptive statistics are reported in Table 7.3.

There was no significant relationship between latitudinal zone and fitted growth model ($\chi^2 = 12{\cdot}51$, $P = 0{\cdot}09$), and no trend with latitude for any of the response variables was detected by regression, as the slopes of all regressions lines of FL_∞, K and FL_{max} vs latitude were not significantly different from zero ($r^2 = 0{\cdot}030$, $P = 0{\cdot}08$; $r^2 = 0{\cdot}003$, $P = 0{\cdot}59$; $r^2 = 0{\cdot}008$, $P = 0{\cdot}24$, respectively).

7.4 Discussion

Two results emerge from the present investigation, namely that (1) carp seem to grow either linearly or asymptotically regardless of latitudinal zone or climate type, and (2) no latitudinal cline is apparent in either size achieved (maximum or asymptotic length) or growth rate. This is remarkable given the worldwide distribution of this species.

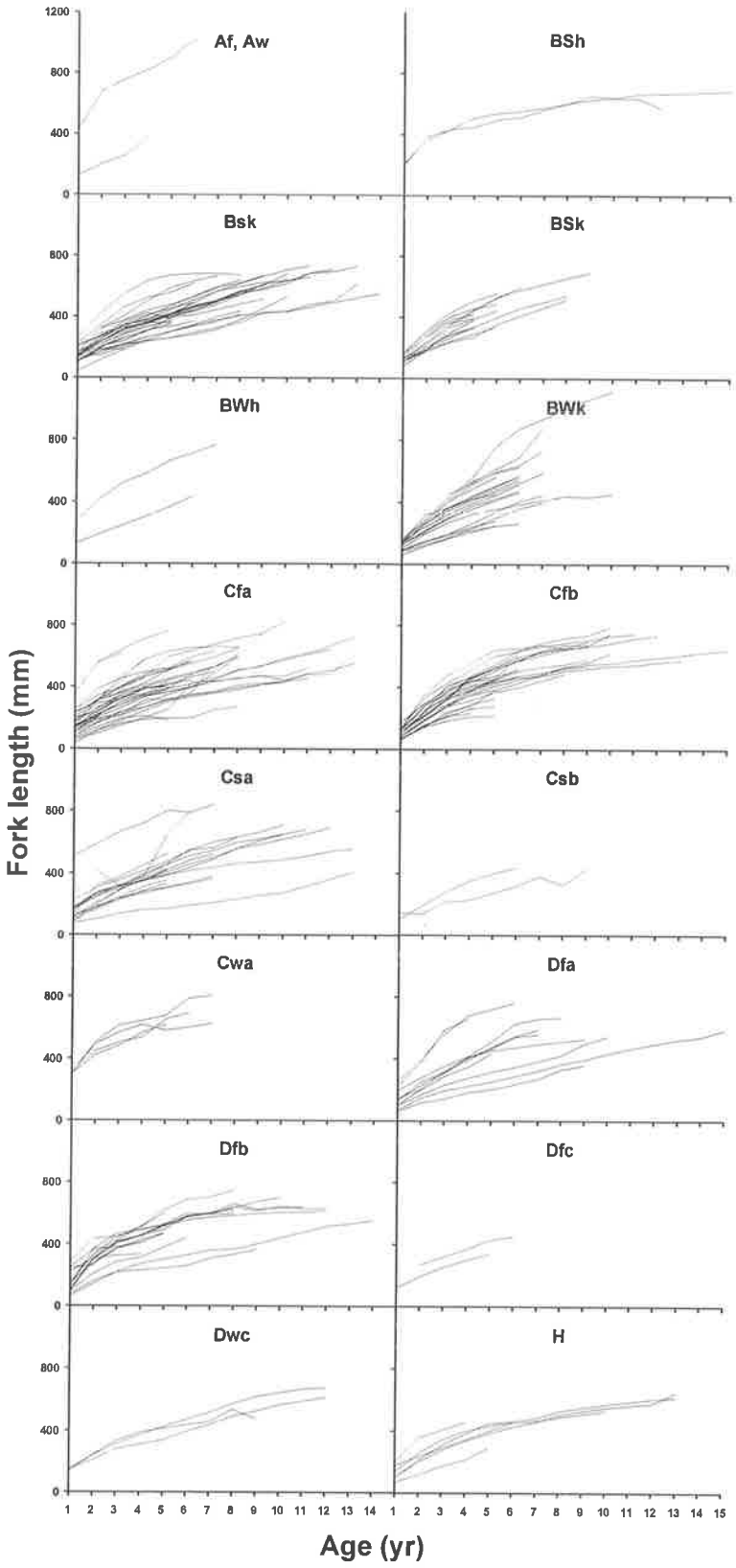

Figure 7.1 Length-at-age curves for populations of carp growing under different climatic conditions based on Köppen climate types (cf. Table 7.1 for an explanation of the symbols).

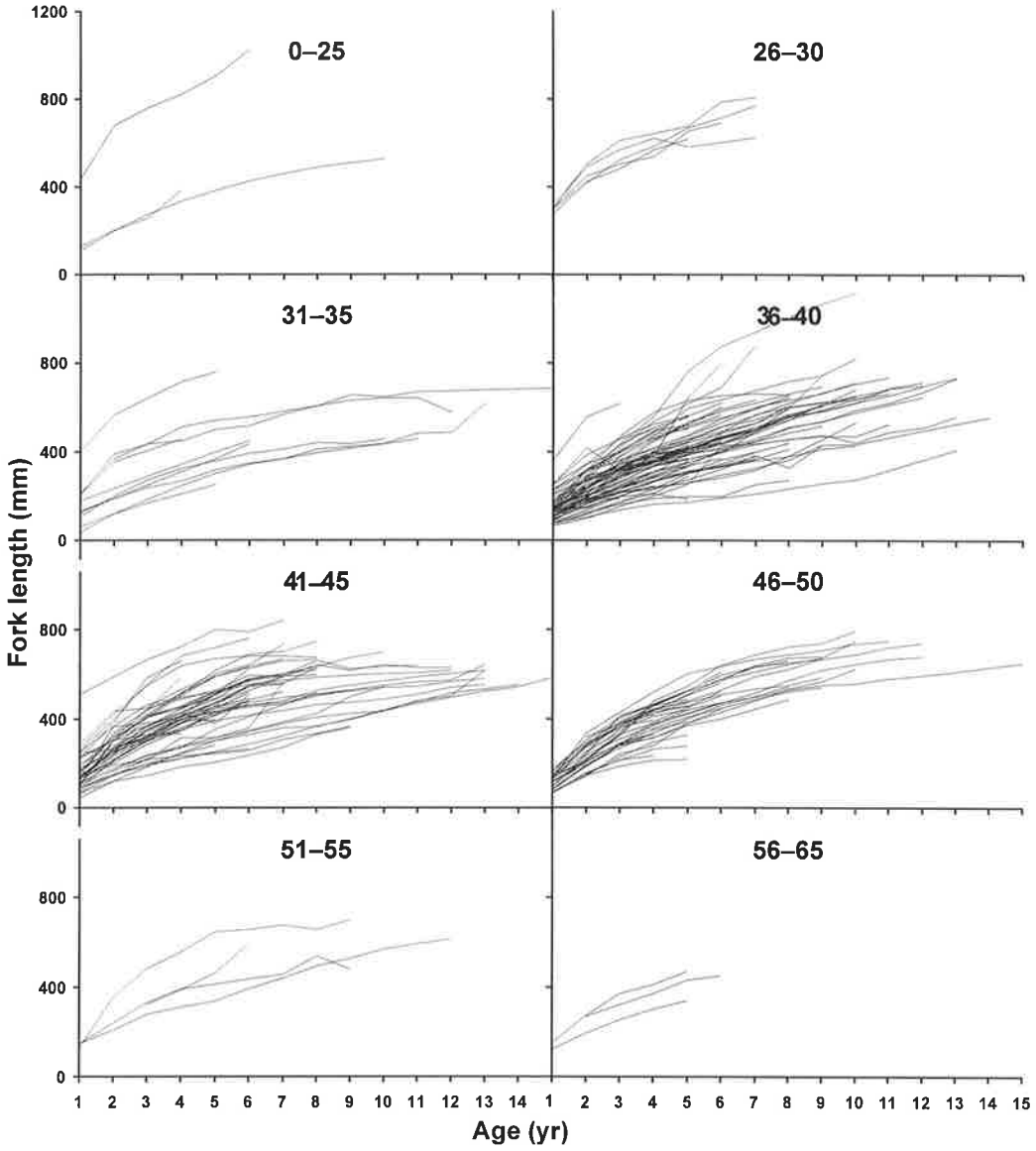

Figure 7.2 Length-at-age curves for populations of carp growing under different latitudinal zones.

The question whether asymptotic growth is real or a mere mathematical artefact has long been debated among fish biologists (e.g. von Bertalanffy 1960; Knight 1968; Ricker 1979; Roff 1980; see also Chapter 4). No consensus exists as to the use of any curve for describing growth. As Ricker (1979, p. 737) put it "none of these curves has been demonstrated to have any physiological basis that might qualify it as *the* growth curve for fishes generally, and frequently two or more of them will describe satisfactorily the same series of observations". McDowall (1994) elaborated on Beverton's (1992) contention that the main difference between fish and other vertebrates is whether the characteristic

Table 7.2 **Summary statistics for VBGF parameters and maximum length in carp populations aranged by Köppen climate groups and types.**

FL_∞: asymptotic fork length; K: Brody coefficient of growth; FL_{max}: maximum fork length. Explanation of the symbols in Table 7.1.

Climate type	*n*	FL_∞ (mm)	± SE	Min	Max	*n*	K (yr^{-1})	± SE	Min	Max	*n*	FL_{max} (mm)	± SE	Min	Max
Af	1	1189					0·263				1	1026			
Aw	1	504					0·372				1	387			
BSh	2	620	19·5	600	639	2	0·350	0·0035	0·346	0·353	2	665	21·5	643	686
Bsk	11	622	48·4	364	897	11	0·351	0·0794	0·046	1·019	28	543	28·3	187	736
BSk	8	579	47·2	458	833	8	0·373	0·0447	0·205	0·558	13	465	31·6	331	695
BWh	1	940				1	0·217				2	601	166·8	434	768
BWk	10	627	48·9	322	799	10	0·265	0·0376	0·123	0·496	19	538	47·8	251	1120
Cfa	21	612	34·6	207	916	21	0·332	0·0559	0·133	1·177	31	541	25·0	210	820
Cfb	18	592	45·1	233	940	18	0·341	0·0326	0·155	0·634	25	543	32·6	218	793
Csa	7	671	65·3	495	958	7	0·168	0·0117	0·135	0·223	17	547	39·8	332	842
Csb	1	623				1	0·210				2	435	3·5	431	438
Cwa	3	761	74·9	613	855	3	0·506	0·2137	0·236	0·928	4	685	43·8	616	806
Dfa	3	740	99·8	561	906	3	0·285	0·0367	0·212	0·322	10	568	36·4	360	761
Dfb	13	610	42·0	336	894	13	0·460	0·1033	0·085	1·300	15	548	32·5	335	749
Dfc											2	395	55·0	340	450
Dwc	2	714	178·5	535	892	2	0·211	0·0920	0·119	0·303	3	609	41·4	535	678
A	2	847	342·5	504	1189	2	0·318	0·0545	0·263	0·372	2	707	319·5	387	1026
B	32	622	26·8	322	940	32	0·325	0·0318	0·046	1·019	64	531	20·6	187	1120
C	50	622	24·2	207	958	50	0·320	0·0300	0·133	1·177	79	548	17·0	210	842
D	18	643	38·4	336	906	18	0·403	0·0777	0·085	1·300	30	551	21·9	335	761
H	4	594	39·5	477	646	4	0·342	0·1374	0·197	0·754	6	496	52·8	289	641

Table 7.3 **Summary statistics for VBGF parameters and maximum length in carp populations arranged by latitudinal zone.** Explanation of the symbols as in Tables 7.1 and 7.2.

Latitudinal zone	*n*	FL_∞ (mm)	± SE	Min	Max	*n*	K (yr^{-1})	± SE	Min	Max	*n*	FL_{max} (mm)	± SE	Min	Max
0–25	3	768	212·6	504	1189	3	0·278	0·0508	0·198	0·372	3	647	193·9	387	1026
26–30	4	806	69·3	613	940	4	0·434	0·1675	0·217	0·928	4	704	48·7	616	806
31–35	7	591	45·7	477	831	7	0·347	0·0804	0·123	0·754	7	529	66·2	251	759
36–40	34	623	25·9	207	916	34	0·295	0·0423	0·046	1·177	34	485	24·2	187	743
41–45	31	652	28·1	322	958	31	0·357	0·0481	0·085	1·300	31	568	23·0	265	842
46–50	24	576	37·0	233	940	24	0·352	0·0286	0·119	0·634	24	494	33·5	218	749
51–55	2	618	83·0	535	701	2	0·397	0·0935	0·303	0·490	2	618	82·5	535	700
56–65	1	562				1	0·358				1	469			

maximum size is reached asymptotically (as in fish) or abruptly (as in birds and mammals), and showed that not only the position of the asymptote can shift considerably within the same species, or that growth can even cease after maturity is reached (as in male western mosquitofish (*Gambusia affinis*)), but also that fish may grow linearly, or close to it, over a considerable portion of their life. It is not surprising, therefore, that populations of carp growing under different conditions can show two types of growth. The question remains whether and how asymptotic or linear growth in carp are related to growing conditions.

As already indicated, there is a considerable amount of unaccounted variation due to factors such as genetic composition, population density, hydrological regime and food availability. Variation in growth capacity is likely to exist among carp stocks resulting from the presence of wild, domesticated and feral forms, with particular domesticated strains being more successful in colonising new habitats than others (e.g. Shearer and Mulley 1978). Growth of carp under artificial conditions (i.e. in ponds, farm dams) can also be markedly different from that in the wild, and may partly explain the absence of an asymptote in some populations (e.g. Bishai and Labib 1978; Khalid 1986). However, linear growth was also typical of many natural and feral, exploited and unexploited populations (e.g. English 1952a; Demirkalp 1992; Ritter-Ortiz *et al.* 1992), suggesting that no pattern exists.

Population density is another important biotic factor. Pivnička (1983) concluded that in roach (*Rutilus rutilus*) and bream (*Abramis brama*) growth was mainly density-dependent, whereas in chub and rudd it was regulated mainly by temperature. Pond experiments have shown that in carp growth under high density may be inhibited by an increase in excretory products (Kawamoto *et al.* 1957) and by the release of a growth-inhibiting hormone (Pfuderer and Francis 1972).

As noted, water-level fluctuations affect the growth of carp, and newly-filled reservoirs provide ideal conditions for fast growth (Živkov and Petrova 1984). In Australia the distribution of size- and possibly year-classes in wild populations is strongly affected by varying hydrological conditions, with entire annual cohorts disappearing (P. C. Gehrke, pers. comm.). These changes in year-class abundance are likely to be caused by fluctuations in food availability (Živkov and Petrova 1984), although water level changes

may also affect reproductive success (e.g. Shields 1957; see also Chapter 11). As a result, variation in population density resulting from differential success in survival and recruitment of 0+ fish would have immediate consequences on annual growth rates (Pivnička 1983).

Given the available data, the absence of a latitudinal or climatic pattern in the type of growth exhibited by carp may be the result of the combined effect of growth-regulatory factors, so that an optimal size, albeit constrained by local conditions, would be achieved following either a linear or asymptotic growth trajectory. The adaptive value of this life-history trait is discussed later, pending an evaluation of the role of latitude and climate on growth parameters.

In carp, countergradient variation may have a role in regulating the growth capacity of populations at different latitudes. The relative length of the growing season varies from 7–9 months at latitudes 24–37 (Welykochatko 1976; Hume *et al.* 1983a; Prochelle and Campos 1985; Fernández-Delgado 1990) to only four months at 50° (Fetodova 1971), and this is paralleled by variation in energy allocation towards reproductive output. Thus, fractional spawning is typical of low-latitude populations (e.g. Welykochatko 1976), whereas a single spawning period (although with intermittent egg release) occurs at higher latitudes (Fetodova 1971).

If countergradient variation influences growth capacity in carp then 'shooting' (or the appearance of fast-growing individuals: Wohlfarth 1977; cf. Chapter 8) in wild populations may also affect the over-winter survival of 0+ fish, as an alternative or complementary means to overcome the constraints of small body size (Miller *et al.* 1988; but see Litvak and Leggett 1992). As a life-history trait, latitudinal growth compensation may allow carp to reach an optimal size so as to maintain an average reproductive output. Mann and Mills (1985) reported that in dace (*Leuciscus leuciscus*) ovarian weight increased with body length, while fecundity reached an asymptote, indicating that larger gonads contained larger eggs. A similar phenomenon has been observed in carp (Zonova 1973), with older (possibly larger) fish producing larger eggs, their relative fecundity progressively decreasing. However, Zonova found no relationship between egg size and survival of carp embryos. This may mean that growth beyond a certain size would not be an advantage for

carp, so that the lack of clines in body size and growth rate observed in the present study may indicate a trade-off between size and reproductive success. The ability of carp to maintain a similar growth potential regardless of climatic and latitudinal changes in environmental conditions may be a key factor for the success of this species in freshwater ecosystems.

7.5 Limitations of the study

In this study an attempt was made to compare growth among climate types and latitudinal zones by ANOVA. However, a power analysis (Zar 1984) revealed that the sample sizes were too small to allow rigorous testing of the hypotheses. In particular, replicate data for 200 and 90 populations would be required, respectively, to have an 80% probability of detecting differences in FL_{∞} and FL_{max} of 50 mm among climate groups B, C and D at a probability level $\alpha = 0{\cdot}05$.

Another limitation of the available database was the uneven spread of populations across the entire geographical range of the species (similar problems were encountered by Kubečka (1994) in a comparison of growth among young-of-the-year fish). The majority of populations in this study came from climate types B and C and latitudinal zones 36–40, 41–45 and 46–50, an effect of the larger number of age and growth studies from Central Europe, Anatolia, Central Asia and North America. This may obviate further global comparisons of growth patterns, especially where the influence of latitude on reproductive strategies and survival of young-of-the-year is to be assessed.

Table 7.A **Age and growth in length for carp in the world.** Author: original study reporting LAA data; Source: reference to the original work cited by the author reporting the LAA data; Site sampling location and country. LR: latitudinal range of the sampling area; CT: climate type according to the Köppen-Geiger-Pohl classification system (Strahler 1992); FL_{max}: maximum mean LA reported; GC: growth curve (linear = LLQF (L) or nonlinear = VBGF (V); see also Table 4.2) fitted to LAA data. Parameters for the LLQF in italics. Other symbols as in Table 4.2.

Author	Source	Site	LR	CT	FL_{max} (mm)	GC	FL_∞(mm) a_l	K (yr^{-1}) b_l	t_0 (yr) c_l
Abdullayev (1969)	Fetodova (1971)	Kuyu-Mazarskoye Reservoir (Uzbekistan)	41–45	BSk	517	L	*1·724*	*1·109*	*– 0·075*
Abdullayev (1969)	Fetodova (1971)	Tudakul' Reservoir (Uzbekistan)	36–40	BSk	338	L	*1·682*	*1·451*	*– 0·470*
Abdullayev and Khakberdiyev (1972)		Lake Ulli-Shor-kul' (Turkmenistan)	41–45	BWk	283	L	*1·482*	*1·730*	*– 0·624*
Akyurt (1987)	Demirkalp (1992)	Almus Baraj Lake (Turkey)	36–40	Bsk	370	L	*1·915*	*0·853*	*– 0·087*
Alpbaz and Hoşsucu (1979)	Demirkalp (1992)	Golmarmara Lake (Turkey)	36–40	Csa	800	L	*2·663*	*– 1·082*	*1·637*
Astanin and Trofimova (1969)		Yegorlyk Reservoir (Russian Federation)	41–45	Dfb	335	V	336	1·300	0·160
Balik and Ustaoglu (1987)	Demirkalp (1992)	Gölcük Lake (Turkey)	36–40	Csa	406	L	*1·752*	*0·431*	*0·246*
Balon (1957)[A]		Lesser Danube above Kolárovo (Slovakia)	46–50	Cfb	648	V	666	0·181	– 0·962
Balon (1957)[B]		Lesser Danube above Kolárovo (Slovakia)	46–50	Cfb	586	V	596	0·335	– 0·008
Barnhart (1955)		Loveland Lake, Colorado (United States)	36–40	Bsk	187	V	634	0·285	0·195
Bauch (1954)	Sarig (1966)	Forte Lake (Hungary)	46–50	Cfb	387	V	478	0·400	– 0·198
Bauch (1954)	Sarig (1966)	Storkow Lake (Germany)	50–55	Cfb	591	L	*2·545*	*– 0·447*	*1·097*
Berg (1964)		Lake Issyk-kul' (Kyrgyzstan)	41–45	BWk	590	V	797	0·183	– 0·072
Berg (1964)		Lake Kamyshlybash (Russian Federation)	56–65	Dfc	340	L	*1·628*	*1·735*	*– 0·741*
Berg (1964)		River Amu-Darya (Turkmenistan)	36–40	BWk	400	L	*1·550*	*1·136*	*0·052*
Berg (1964)		Aral Sea (Kazakhstan)	41–45	BWk	519	L	*1·725*	*1·665*	*– 0·594*
Berg (1964)		Azov Sea (Ukraine)	41–45	Bsk	508	V	512	0·429	0·267
Berg (1964)		Caspian Sea (Russian Federation)	36–40	BWk	564	L	*1·498*	*2·587*	*– 1·255*
Berg (1964)		River Amu-Darya (Turkmenistan)	36–40	BWk	447	L	*1·662*	*1·011*	*0·112*
Berg (1964)		River Kura (Azerbaijan)	36–40	BSk	557	V	689	0·348	0·205
Berg (1964)		Agrakhan Bay (Russian Federation)	46–50	BSk	486	V	541	0·495	0·288
Berg (1964)		Astara (Kazakhstan)	46–50	BWk	458	V	537	0·409	0·204
Berg (1964)[A]		River Kura (Russian Federation)	41–45	BWk	629	V	696	0·496	1·237
Berg (1964)[B]		River Kura (Russian Federation)	41–45	BWk	735	L	*2·289*	*0·570*	*0·069*
Berg (1964)		Ural River (Russian Federation)	56–65	Dfb	469	V	562	0·358	0·126
Berg (1964)		Delta of Volga (Russian Federation)	46–50	BSk	419	V	501	0·492	0·221
Berg (1964)		Delta of Volga (Russian Federation)	46–50	BSk	394	V	458	0·558	0·322
Berg (1964)		Delta of Volga (Russian Federation)	46–50	BSk	331	V	476	0·309	0·105
Berg (1964)		Delta of Volga (Russian Federation)	46–50	BSk	334	V	480	0·311	0·128
Berg (1964)		Volga River (Russian Federation)	46–50	Dfb	469	V	546	0·404	0·195

Table 7.A (continued)

Author	Source	Site	LR	CT	FL_{max}	GC	FL_∞(mm)	K (yr^{-1})	t_0 (yr)
							a_1	b_1	c_1
Bishai and Labib (1978)		Serow Fish Farm (Egypt)	31–35	BWh	434	L	*1·851*	*0·856*	*0·083*
Borzenko (1926)[A]	Carlander (1969)	Caspian Sea (Russian Federation)	36–40	BWk	884	L	*1·693*	*1·856*	*– 0·550*
Borzenko (1926)[B]	Carlander (1969)	Caspian Sea (Russian Federation)	36–40	BWk	1120	L	*1·596*	*2·334*	*– 0·794*
Buck and Cross (1952)	Carlander (1969)	Canton Lake, Oklahoma (United States)	36–40	Cfa	401	V	458	0·438	– 0·068
Cengizler and Erdem (1989)		Hafik (Sivas) Lake (Turkey)	36–40	Csa	365	V	511	0·156	– 0·841
Çetinkaya (1992a)[A]		Akşehir Lake (Turkey)	36–40	Bsk	530	V	640	0·071	– 2·710
Çetinkaya (1992a)[B]		Akşehir Lake (Turkey)	36–40	Bsk	555	V	897	0·046	– 2·850
Christenson (1957)	Carlander (1969)	Mississippi River, Minnesota (United States)	41–45	Dfb	596	L	*1·344*	*2·562*	*– 1·196*
Cook (1955)	Carlander (1969)	Meredith Reservoir, Colorado (United States)	36–40	Bsk	245	L	*2·347*	*– 1·227*	*1·858*
Crivelli (1981)		Ile de Camargue (France)	41–45	Csa	554	V	605	0·157	– 1·358
Das and Fotedar (1965)		Kashmir (India)	31–35	H	447	L	*2·072*	*0·545*	*0·167*
Demirkalp (1992)[A]		Bafra Balik Lakes (Turkey)	41–45	Csa	520	L	*1·915*	*1·172*	*– 0·324*
Demirkalp (1992)[B]		Bafra Balik Lakes (Turkey)	41–45	Csa	630	L	*1·868*	*1·250*	*– 0·290*
Düzgüneş (1985)	Demirkalp (1992)	Mogan Lake (Turkey)	36–40	Bsk	733	L	*2·095*	*0·770*	*– 0·080*
Eddy and Carlander (1939)		Minnesota (United States)	41–45	Dfb	749	V	894	0·234	0·173
Ekmekci (1989)	Demirkalp (1992)	Sariyar Baraj Lake (Turkey)	36–40	Bsk	713	L	*2·169*	*0·453*	*0·146*
English (1952a)[A]		Clear Lake, Iowa (United States)	41–45	Dfa	659	L	*1·762*	*2·251*	*– 1·037*
English (1952a)[B]		Clear Lake, Iowa (United States)	41–45	Dfa	761	V	906	0·322	0·039
Erdem (1980)	Demirkalp (1992)	Akşehir Lake (Turkey)	36–40	Bsk	642	L	1·901	1·158	– 0·216
Erdem (1982)	Demirkalp (1992)	Eber Lake (Turkey)	36–40	Bsk	736	L	1·869	1·245	– 0·295
Erdem (1983a)		Beysehir Lake (Turkey)	36–40	Csa	679	L	1·756	1·493	– 0·472
Erdem (1983a)		Çavusçu Lake (Turkey)	36–40	Bsk	606	L	1·916	1·047	– 0·183
Erdem (1983a)		Egirdir Lake (Turkey)	36–40	Bsk	660	L	1·787	1·367	– 0·385
Erdem (1983b)	Demirkalp (1992)	Çavusçu Lake (Turkey)	36–40	Bsk	681	L	1·817	1·189	– 0·218
Erdem (1984a)	Demirkalp (1992)	Beysehir Lake (Turkey)	36–40	Bsk	647	L	1·850	1·219	– 0·291
Erdem (1984b)	Demirkalp (1992)	Apa Baraj Lake (Turkey)	36–40	Bsk	571	L	1·722	1·619	– 0·575
Erdem (1988)		Tödürge Lake (Turkey)	36–40	Csa	378	V	495	0·188	– 0·391
Fernández-Delgado (1990)		Guadalquivir River (Spain)	36–40	Csb	438	V	623	0·210	0·160
Fetodova (1971)		Bukhtarma Reservoir (Kazakhstan)	46–50	BSk	544	L	1·624	1·616	– 0·470
Fogle (1961)	Carlander (1969)	Oahe Lake, South Dakota (United States)	41–45	Dfb	554	V	766	0·085	– 0·482

Table 7.A (continued)

Author	Source	Site	LR	CT	FL_{max}	GC	FL_∞(mm) a_1	K (yr^{-1}) b_1	t_0 (yr) c_1
Frey (1940)	Carlander (1969)	Kegonsa Lake, Wisconsin (United States)	41–45	Dfb	700	V	736	0·268	0·292
Frey (1940)	Carlander (1969)	Madison Region, Wisconsin (United States)	41–45	Dfb	641	V	654	0·302	−1·038
Frey (1940)	Carlander (1969)	Monona Lake, Wisconsin (United States)	41–45	Dfb	660	V	661	0·366	0·499
Frey (1940)	Carlander (1969)	Waubesa Lake, Wisconsin (United States)	41–45	Dfb	596	V	630	0·406	0·497
Frey (1940)	Carlander (1969)	Wingra Lake, Wisconsin (United States)	41–45	Dfb	617	V	597	0·561	0·510
Geyer and Mann (1939)	Carlander (1969)	Germany	46–50	Cfb	330	V	430	0·352	−0·191
Hancock (1955)	Carlander (1969)	Canton Lake, Oklahoma (United States)	36–40	Cfa	382	V	623	0·168	−0·666
Hargis (1966)	Carlander (1969)	Watts Bar Lake, Tennessee (United States)	31–35	Cfa	455	V	562	0·137	−0·906
Harka (1989)		Kisköre Storage Lake (Hungary)	46–50	Cfb	660	V	940	0·155	−0·001
Houser (1960)	Carlander (1969)	Lawtonka Lake, Oklahoma (United States)	36–40	Cfa	564	V	748	0·210	−0·717
Ikiz (1988)	Demirkalp (1992)	Mamasin Baraj Lake (Turkey)	36–40	Csa	650	V	849	0·139	−0·506
Iowa Conservation Commission (1961)	Carlander (1969)	Missouri River, Iowa (United States)	41–45	Dfa	528	V	561	0·322	0·175
Ivanov (1959)	Fetodova (1971)	Balkhash Lake (Kazakhstan)	41–45	Dfb	366	V	462	0·147	−0·639
Jackson (1954)		Lower Spavinaw Lake, Oklahoma (United States)	36–40	Cfa	743	V	916	0·202	0·339
Jackson (1966)		Spavinaw Lake, Oklahoma (United States)	36–40	Cfa	611	V	632	0·219	−0·908
Jackson (1966)		Lake Eucha, Oklahoma (United States)	36–40	Cfa	634	V	727	0·239	−0·938
Jenkins (1953)	Carlander (1969)	Fort Gibson, Oklahoma (United States)	36–40	Cfa	424	L	*1·495*	*2·006*	*−0·732*
Jenkins (1953)	Mauck and Summerfelt (1970)	Grand Lake, Oklahoma (United States)	36–40	Cfa	653	V	769	0·209	−0·340
Jenkins (1955)	Carlander (1969)	Ardmore Lake, Oklahoma (United States)	31–35	Cfa	759	V	831	0·433	−0·536
Jenkins (1957)		Rod and Gun Lake, Oklahoma (United States)	36–40	Cfa	617	V	644	1·177	0·311
Jester (1974)	Fernández-Delgado (1990)	Elephant Butte Lake, New Mexico (United States)	31–35	BWk	251	V	546	0·123	0·012
Johal *et al.* (1984)		Gagger River, Rajasthan (India)	26–30	BWh	768	V	940	0·217	−0·650
Johal *et al.* (1984)		Gobindsagar River, Himachal Pradesh (India)	26–30	Cwa	691	L	*2·221*	*0·997*	*−0·322*
Johal *et al.* (1984)		Gobindsagar River, Himachal Pradesh (India)	26–30	Cwa	625	V	613	0·928	0·226
Johal *et al.* (1984)		Nangal Lake, Punjab (India)	26–30	Cwa	806	V	855	0·354	−0·286
Johal *et al.* (1984)		Sukhna Lake, Chandigarh (India)	26–30	Cwa	616	V	815	0·236	−0·965
Kanitskiy (1993)		Barguzin River (Russian Federation)	50–55	Dwc	535	V	535	0·303	−0·031
Karabatak (1977)	Demirkalp (1992)	Hirfanli Baraji (Turkey)	36–40	Csa	695	L	*2·068*	*0·692*	*0·002*
Khalid (1986)		Jan Pond (Czech Republic)	46–50	Cfb	475	L	*0·859*	*4·061*	*−2·115*
Khalid (1986)		Lake Dalesice (Czech Republic)	46–50	Cfb	623	L	*1·177*	*2·498*	*−0·915*

Table 7.A (continued)

Author	Source	Site	LR	CT	FL_{max}	GC	FL_∞(mm) a_l	K (yr^{-1}) b_l	t_0 (yr) c_l
Khalid (1986)		Lake Hracholusky (Czech Republic)	46–50	Cfb	749	V	762	0·323	0·374
Khalid (1986)		Lake Klicava (Czech Republic)	46–50	Cfb	749	V	794	0·224	0·419
Khalid (1986)		Lake Orlik (Czech Republic)	46–50	Cfb	679	V	779	0·252	0·469
Khalid (1986)		Levinské Petrovice Pond (Czech Republic)	46–50	Cfb	233	V	271	0·597	0·532
Khalid (1986)		Machovo Jezero Pond (Czech Republic)	46–50	Cfb	738	V	750	0·284	0·537
Khalid (1986)		Pond at Zablati (Czech Republic)	46–50	Cfb	441	L	*1·204*	*2·809*	*– 1·229*
Khalid (1986)		River Berounka (Czech Republic)	46–50	Cfb	486	V	580	0·217	0·242
Khalid (1986)		River Vltava (Czech Republic)	46–50	Cfb	502	L	*1·039*	*3·344*	*– 1·630*
Khalid (1986)		Tobolka Pond (Czech Republic)	46–50	Cfb	793	L	*1·520*	*2·186*	*– 0·815*
Khalid (1986)		Verovice Pond (Czech Republic)	46–50	Cfb	218	V	233	0·634	0·470
Kilambi and Robison (1978)		Beaver Reservoir, Arkansas (United States)	36–40	Cfa	502	V	650	0·257	– 0·892
Kononov *et al.* (1961)	Fetodova (1971)	Dnieper Reservoir (Ukraine)	46–50	Bsk	672	L	*2·243*	*0·509*	*0·074*
Kruglova and Berval'd (1961)	Fetodova (1971)	Veselovka Reservoir (Russian Federation)	56–65	Dfc	450	L	*2·090*	*0·755*	*– 0·096*
Krumholz (1956)	Carlander (1969)	Tennessee (United States)	36–40	Cfa	210	V	207	0·834	0·443
Linton (1961)	Mauck and Summerfelt (1970)	Arkansas River, Oklahoma (United States)	31–35	Cfa	617	L	*0·704*	*3·424*	*– 1·470*
Linton (1961)	Carlander (1969)	Cimarron River, Oklahoma (United States)	36–40	Cfa	273	V	381	0·133	– 0·737
Lopinot (1958)		Illinois (United States)	36–40	Cfa	820	L	*2·221*	*0·071*	*0·541*
Lynch *et al.* (1953)	Carlander (1969)	Two Buttes Reservoir, Colorado (United States)	36–40	Bsk	363	V	364	1·019	0·516
Mamedov (1987)		Nakhicheken Reservoir (Russian Federation)	36–40	BSk	695	V	833	0·205	0·244
Mauck and Summerfelt (1970)		Lake Carl Blackwell, Oklahoma (United States)	36–40	Cfa	524	V	589	0·185	0·178
Mayhew (1957)	Carlander (1969)	Lake McBride, Iowa (United States)	41–45	Cfa	585	L	*1·844*	*1·486*	*– 0·243*
Mayhew (1958)		Lake Keomah, Iowa (United States)	41–45	Cfa	573	L	*2·196*	*0·487*	*0·209*
Mayhew (1964)	Carlander (1969)	Coralville Reservoir, Iowa (United States)	41–45	Dfa	434	L	*1·990*	*0·465*	*0·473*
Mayhew (1965)	Carlander (1969)	Chariton River, Iowa (United States)	41–45	Cfa	394	V	444	0·491	– 0·830
McConnell (1952)		Ogden Bay Bird Refuge, Utah (United States)	41–45	Bsk	682	V	704	0·554	0·198
Minckley (1959)		Big Blue River Basin, Kansas (United States)	36–40	Cfa	556	V	655	0·143	0·690
Mobridge (1965)	Carlander (1969)	Oahe Lake, South Dakota (United States)	41–45	Dfb	622	V	675	0·339	0·491
Nikolsky (1956)	Johal *et al.* (1984)	River Amur (Russian Federation)	46–50	Dwc	678	V	892	0·119	– 0·496
Nikolsky (1961)		Azov Sea (Ukraine)	41–45	Bsk	490	V	569	0·340	0·239
Nikolsky (1961)		Ill River (Kazakhstan)	41–45	BWk	265	V	322	0·282	– 0·174

Table 7.A (continued)

Author	Source	Site	LR	CT	FL_{max}	GC	FL_∞(mm) a_1	K (yr^{-1}) b_1	t_0 (yr) c_1
Nikolsky (1956)	Johal *et al.* (1984)	Aral Sea (Kazakhstan)	41–45	BWk	465	V	736	0·162	−0·153
Nikolsky (1961)		Southern Caspian (Turkmenistan)	46–50	BWk	561	L	*1·722*	*1·506*	*−0·319*
Nikolsky (1961)		Surkhan (Uzbekistan)	36–40	H	289	L	*1·485*	*1·179*	*0·081*
Numann (1958)	Demirkalp (1992)	Akşehir Lake (Turkey)	36–40	Bsk	620	V	727	0·299	−0·213
Numann (1958)	Demirkalp (1992)	Apolyont Lake (Turkey)	36–40	Csa	422	L	*1·453*	*2·194*	*−0·881*
Numann (1958)	Demirkalp (1992)	Beysehir Lake (Turkey)	36–40	Csa	355	V	606	0·180	0·054
Numann (1958)	Demirkalp (1992)	Egirdir Lake (Turkey)	36–40	Bsk	352	V	473	0·273	0·034
Numann (1958)	Demirkalp (1992)	Golmarmara Lake (Turkey)	36–40	Csa	522	L	*1·379*	*3·196*	*−1·928*
Numann (1958)	Demirkalp (1992)	Iznik Lake (Turkey)	36–40	Csa	431	L	*1·571*	*1·894*	*−0·678*
Numann (1958)	Demirkalp (1992)	Mayas Lake (Turkey)	36–40	Csa	332	V	674	0·135	−0·056
Numann (1958)	Demirkalp (1992)	Suleyman Lake (Turkey)	36–40	Bsk	370	V	490	0·300	0·244
Ohio Bureau of Scientific Research (1934)	Carlander (1969)	Ohio (United States)	41–45	Cfa	564	L	*2·115*	*−0·092*	*0·812*
Oliva (1955)		Bohemia (Slovakia)	46–50	Cfb	276	V	321	0·462	0·544
Patriarche (1953)		Lake Wappapello, Missouri (United States)	36–40	Cfa	443	L	*1·843*	*1·053*	*−0·036*
Pinilla *et al.* (1992)		Laguna de Fuquene (Colombia)	0–25	Aw	387	V	504	0·372	0·505
Pivnev (1954)	Fetodova (1971)	Lake Issyk-kul' (Kyrgyzstan)	41–45	BWk	545	V	619	0·328	0·090
Poschalujeva (1929)	Sarig (1966)	Aral Sea (Kazakhstan)	41–45	BWk	480	V	734	0·173	−0·088
Poschalujeva (1929)	Sarig (1966)	River Kura (Azerbaijan)	36–40	BSk	601	L	*1·542*	*2·073*	*−0·717*
Poschalujeva (1929)	Sarig (1966)	Volga River (Russian Federation)	46–50	Dfb	443	L	*1·330*	*2·655*	*−1·333*
Pozalujena (1928)		Aral Sea (Kazakhstan)	41–45	BWk	575	V	799	0·213	0·137
Prochelle and Campos (1985)		River Cayumapu (Chile)	31–35	BWk	456	V	482	0·284	0·118
Purkett (1957)		Salt River, Missouri (United States)	36–40	Cfa	499	V	549	0·333	0·351
Purkett (1957)		Salt River, Missouri (United States)	36–40	Cfa	594	V	696	0·210	−0·063
Purkett (1958)	Carlander (1969)	Missouri (United States)	36–40	Cfa	446	V	553	0·338	0·052
Raina (1987)		Kashmir (India)	31–35	H	455	V	477	0·754	0·261
Ramos *et al.* (1985)		Rio Tejo (Portugal)	36–40	Csb	431	L	*1·522*	*1·591*	*−0·509*
Rehder (1959)		Des Moines River, Iowa (United States)	41–45	Dfa	554	V	752	0·212	0·344
Ritter-Ortiz *et al.* (1992)		Atlangatepec Dam (Mexico)	0–25	H	527	V	612	0·198	−0·001
Sandoz (1961)	Mauck and Summerfelt (1970)	Rock Creek Drainage, Oklahoma (United States)	36–40	Cfa	660	V	699	0·462	0·536
Sandoz (1960)	Carlander (1969)	Rock Creek Drainage, Oklahoma (United States)	36–40	Cfa	426	V	527	0·155	−0·528

Table 7.A (continued)

Author	Source	Site	LR	CT	FL_{max}	GC	FL_∞(mm) a_1	K (yr^{-1}) b_1	t_0 (yr) c_1
Sarig (1966)		Taganrog Reservoir (Azerbaijan)	36–40	BSk	378	L	*1·936*	*0·420*	*0·737*
Schoffman (1942)		Reelfoot Lake, Tennessee (United States)	36–40	Cfa	729	L	*2·132*	*0·518*	*0·091*
Schoffman (1957)		Reelfoot Lake, Tennessee (United States)	36–40	Cfa	646	L	*2·203*	*0·281*	*0·242*
Shaposhnikova (1959)	Astanin and Trofimova (1969)	Tshchikskoye Reservoir (Russian Federation)	41–45	Dfb	408	V	405	1·206	0·197
Shields (1955)	Carlander (1969)	Fort Randall, South Dakota (United States)	41–45	Dfa	590	L	*1·726*	*1·529*	*– 0·404*
Shields (1957)		Gavins Point, South Dakota (United States)	41–45	Dfa	585	L	*1·469*	*1·532*	*– 0·390*
Sigler (1958)		Bear Lake, Utah (United States)	41–45	Bsk	617	L	*0·901*	*2·945*	*– 1·190*
Sigler (1958)		Bear River Refuge, Utah (United States)	41–45	Bsk	667	V	828	0·242	0·072
Starikov (1971)	Kanitskiy (1993)	Posol'skiy floodplain (Russian Federation)	50–55	Dwc	614	L	*1·915*	*0·881*	*– 0·081*
Stucky and Klaassen (1971)		Cedar Bluff Reservoir, Kansas (United States)	36–40	Bsk	438	L	*1·716*	*1·105*	*– 0·146*
Stucky and Klaassen (1971)		Smoky Hill River, Kansas (United States)	36–40	Bsk	411	L	*1·692*	*1·284*	*– 0·345*
Talaat and Oláh (1986b)		Körös Backwater Reservoir (Hungary)	46–50	Cfb	542	V	675	0·175	– 0·239
Tanyolaç (1979)		Lake Eymir (Turkey)	36–40	Bsk	515	L	*1·904*	*0·904*	*– 0·085*
Tanyolaç and Karatabak (1974)	Demirkalp (1992)	Mogan Lake (Turkey)	36–40	Bsk	615	L	*2·359*	*– 0·002*	*0·414*
Thompson (1950)	Carlander (1969)	Grand Lake, Oklahoma (United States)	36–40	Cfa	478	L	*1·880*	*1·002*	*– 0·084*
Tsimenidis (1978)		Vistonis Lake (Greece)	41–45	Csa	842	V	958	0·223	– 2·356
Unterüberbacher (1963)		Neusiedler Lake (Austria)	46–50	Cfb	471	V	539	0·358	0·502
Walburg (1964)	Carlander (1969)	Lewis and Clark Lake, South Dakota (United States)	41–45	Dfa	360	L	*1·494*	*1·206*	*– 0·160*
Wang Sihua (1983)		Hurleg Lake, Qinghai Province (China)	36–40	BSk	446	V	652	0·264	0·532
Welykochatko (1976)		Sao Paulo (Brazil)	0–25	Af	1026	V	1189	0·263	– 0·856
Wichers (1976)		Pathfinder Reservoir, Wyoming (United States)	41–45	H	641	V	639	0·197	– 0·486
Wichers (1976)		Pathfinder Reservoir, Wyoming (United States)	41–45	H	617	V	646	0·220	0·117
Yerli (1988)	Demirkalp (1992)	Koycegiz Lagoon System (Turkey)	36–40	Csa	712	L	*2·133*	*0·743*	*– 0·048*
Youn (1962)	Mauck and Summerfelt (1970)	Spirit Lake, Iowa (United States)	41–45	Dfa	544	L	*1·638*	*1·365*	*– 0·320*
Youn (1962)	Carlander (1969)	Spirit Lake, Iowa (United States)	41–45	Dfa	665	L	*2·005*	*0·962*	*– 0·080*
Živkov (1967)	Johal *et al.* (1984)	Novy Ribnik Fishpond (Slovakia)	50–55	Cfb	700	V	701	0·490	0·591
Živkov (1967)	Johal *et al.* (1984)	River Danube (Slovakia)	46–50	Cfb	524	V	567	0·399	0·353
Živkov (1967)	Johal *et al.* (1984)	Slapy and Orlik Reservoirs (Slovakia)	46–50	Cfb	607	L	*1·245*	*3·359*	*– 1·848*
Živkov (1975)		Batak Dam Lake (Bulgaria)	41–45	Cfb	579	V	573	0·296	0·192
Hoc opus[A]		River Murray, South Australia (Australia)	31–35	BSh	643	V	600	0·346	0·174
Hoc opus[B]		River Murray, South Australia (Australia)	31–35	BSh	686	V	639	0·353	0·174

[A] Males. [B] Females.

8.

EARLY LIFE HISTORY:

THE ONSET OF THE JUVENILE PERIOD

> With metamorphosis it is easy to know where to start, but hard to know where to stop.
>
> G. Wald (1982)

8.1 Introduction

According to Copp and Kováč (1996), the hierarchical life-history model of Balon (1975b, 1990) does not clearly define the larva-juvenile transition in fish with indirect development. They argued that in metamorphic species the process of remodelling, the stabilisation of allometric growth and changes in physiology, behaviour and habitat use are crucial in defining the larva-juvenile transition, and that this transition is inherently unclear because metamorphosis in fish generally is progressive and less dramatic than in, say, metamorphic invertebrates (cf. Flegler-Balon 1989).

The transition from larval to juvenile development has been equated by Balon (1984a) with metamorphosis, a remodelling process involving "extensive changes, from an unfishlike appearance into an adultlike condition", where "temporary organs are replaced by definitive organs" while other characters "persist from the larval period and disappear only later" (Balon 1975b, p. 1664). In fish with direct development (ametamorphic), on the other hand, the embryo develops directly into the definitive phenotype, a juvenile, and as the definitive organs are formed throughout embryogenesis there is no need to remodel larval structures (e.g. Balon 1984a,b, 1985, 1990, 1991; Flegler-Balon 1989). Thus, according to Balon's (1984a) interpretation the larva-juvenile transition in metamorphic fish is indeed well defined, since the process of metamorphosis has been described in many species (e.g. Bertin 1958; Just *et al.* 1981).

The relative duration of metamorphosis varies considerably among fish with indirect development, being a threshold, step or sometimes longer interval (Flegler-Balon 1989). Thus, in the eel (*Anguilla anguilla*) the metamorphosis lasts four months, while in the flounder *Pseudopleuronectes herzensteini* is completed in one week (Balon 1985). Fish with a protracted metamorphic period have been sometimes referred to as 'prejuveniles' in the literature (e.g. Lewis *et al.* 1972; Brothers and McFarland 1981), but more simply called 'metamorphosing larvae' in Balon's life history model (e.g. Balon 1984b, 1985, 1986, 1990). Flegler-Balon (1989, p. 78 and her fig. 4) stated that "metamorphosis starts some time during the larval period" and "its end marks the beginning of the juvenile period", and argued that "what one author considers a larva, is a juvenile in someone else's opinion" (p. 72). This represents a dilemma long recognised by many authors (Flegler-Balon 1989), one that lead Wald (1982) to state that "With metamorphosis it is easy to know where to start, but hard to know where to stop". It is the completion of the process, therefore, rather than metamorphosis itself (equivalent to the larva-juvenile transition) that is ill-defined. However, this probably is a consequence of the different criteria used to determine when metamorphosis in fish (and perhaps other animals) can be regarded as complete. It need not be a flaw in Balon's life history model.

In the following discussion the expression 'onset (or start) of the juvenile period' is preferred to 'larva-juvenile transition'. The latter term is taken as synonymous with metamorphosis.

Copp and Kováč (1996) reconsidered metamorphosis in the roach (*Rutilus rutilus*), and identified an interval at the end of the larval period wherein fish of 15–40 mm Standard Length (SL) (conventionally 'juveniles' or 'small adults') showed protracted allometric growth in several characters (Kováč and Copp 1996), related to larval adaptations for locomotion, visual acuity and microhabitat use. The onset of the juvenile period in this case was equated with the disappearance of larval characters, the appearance of adult structures and the stabilisation of growth ('homeorhetic' growth: Balon 1990). Later work indicates a similar onset in the stone loach (*Barbatula barbatula*), dace (*Leuciscus leuciscus*) and chub (*L. cephalus*) (G.H. Copp, pers. comm.).

Copp and Kováč (1996) suggested that a clear definition of the start of the juvenile period is significant in (1) the use of ontogenetic scales for inter-specific comparisons of morphological development, (2) the study of evolutionary trajectories, (3) the identification of ontogenetic shifts in resource use, and (4) the refinement of fishery recruitment models. In turn, these applications influence the criteria used to define the onset. For example, changes in relative growth and functional morphology are relevant to the first two objectives, whereas shifts in habitat use are relevant to the fourth. The onset thereby is further obscured, as ontogenetic changes in morphology, behaviour and niche breadth may not be synchronous.

A review of literature on the early life history of carp suggests that published data on morphometrics, functional morphology, intra-specific competition and habitat use may shed light on the timing of the onset of the juvenile period in this species. This chapter evaluates these data and suggests directions for research.

8.2 Key studies

8.2.1 Criteria for the 'larva-juvenile transition' in carp

Studies on the early development of fish have viewed ontogeny either as a gradual sequence of 'normal stages', or as a punctuated series of steps and thresholds (hence 'saltatory ontogeny': Balon 1979, 1981b; Crawford and Balon 1994). Work on carp also has followed these models (e.g. Kryzhanovsky 1949; Kryzhanovsky *et al.* 1951, in Balon 1995b; Balon 1958a; Verma 1970, 1971; Hoda and Tsukahara 1971; Peňáz *et al.* 1983; Ahmed *et al.* 1989). Some key studies are cited below.

Smallwood and Smallwood (1931, p. 220) described two larval intervals for carp in North America, namely an inactive period "when the yolk supply is still adequate" and an active period "when important morphological changes take place". With regard to the onset of the juvenile period they wrote (p. 222): "it is difficult to state just when the larval stage ends, but in two weeks the body takes on the characteristic hump just back of the head, the fins have become formed, and the pigmentation begins to have the golden tints that are so

characteristic of the fry stages"[1]. McCrimmon and Swee (1967) observed that scale formation was initiated in fish of 16–18 mm length and complete by 25 mm, and the fins, swimbladder and mouth parts were fully developed in 'young' 21-mm fish. Sarig (1966, p. 3:10) reported that "at the size of 2 cm the fingerlings already resemble adult carp in growth patterns, nutrition, local movements and schooling". Rhouma (1975, p. 108) described the acquisition of juvenile characters thus: "la deuxième semaine la longeur a été de 23 mm, les alevins ont eu la totalité de leurs nageoires et quelques écailles sont apparues à l'implantation de ces nageoires". Balon (1958a) found that in Danubian wild carp the onset of the juvenile period is marked by an almost complete scale cover (see also Balon 1958b), formation of the fin rays and disappearance of the fin fold. In domesticated pond carp, Peňáz *et al.* (1983, p. 19) defined the beginning of the juvenile period (19·1 mm Total Length (TL), age 21 days, at 25 °C) as "the end of metamorphosis, the appearance of scale-cover and the attainment of a body shape similar to that in adulthood". The first juvenile step was marked by the appearance of scale cover (19·1–30·2 mm TL, age 21–29 days), and the second by the presence of complete scale cover and fusion of the nasal septum (30·2 mm TL, age 26 days).

These criteria accord with those for other cyprinids (e.g. Balon 1956). Copp and Kováč (1996) argued, however, that attributes like the onset of scale cover, whilst a key to recognition of juveniles, do not necessarily indicate a threshold in the sense of the saltatory model, because no allowance is made for other potential changes in physiology, behaviour and niche breadth. Some of these changes are examined below.

8.2.2 Relative growth

Hoda and Tsukahara (1971) investigated the relative growth of body parts and organs in carp of 4–300 mm SL. For seven characters (snout length, head length, body depth, caudal peduncle height, length of snout to insertion of dorsal fin, pectoral fin length, pharyngeal arch length), a shift from positive allometry to isometry was apparent at 21·4 mm SL (range 17–24 mm). Allometric growth in eye diameter, mouth gape and opercular opening changed from positive to negative at similar lengths (20, 17, 20 mm SL, respectively).

[1] The notch and hump posterior to the head are peculiar to domesticated carp, even when they have reverted to a feral state (Balon 1974, 1995a,b; see also Section 1.1).

Growth of the intestine was triphasic (negative, positive, positive), with inflection points in the log-log relationship with SL at 9·5 and 22·5 mm. Hoda and Tsukahara (1971, their fig. 13A) also illustrated a 'young' one-month old individual of 25 mm TL. According to Osse (1990, p. 367), "it is quite striking that at a length of some 21 mm, that is at an age of about one month post-hatch (at 23 °C), the generally positive allometry of these dimensions changes into approximately isometric growth".

Oikawa and Itazawa (1985, also 1984a,b) emphasised the relationship between body size and basal metabolic rate. They reported that body height and width increased isometrically at SL > 18 mm, but were positive allometric at smaller lengths. Osse (1990) observed a break at 19 mm SL in the log-log relationship with weight.

8.2.3 Functional morphology

Osse (1990) ventured a functional interpretation of changes in larval and juvenile carp, based primarily on the morphometric data of Hoda and Tsukahara (1971) with reference to locomotion, feeding and respiration. The functional demands of feeding, in particular, warrant attention. Thus, changes in the position of the mouth, from sub-ventral in free embryos (*eleutheroembryos*) to terminal in feeding larvae and downwardly projected in 'juveniles' of 20 mm SL (cf. Hoda and Tsukahara 1971, their fig. 21), mirror the transitions from endogenous to exogenous nutrition and zooplanktivory to benthivory at the beginning of the conventional juvenile period (e.g. Adzhimuradov 1972; Osse 1990). Observations of the diet in the larval and at the beginning of the juvenile period (*sensu* Balon 1958a) support this interpretation (cf. Chapter 10). Further support comes from Hoda and Tsukahara (1971), who recorded an increase in mouth protrusibility at 20–25 mm SL. Osse (1990) also attributed the positive allometric growth of the pectoral fins and mouth gape (to 20 mm and 17 mm SL, respectively), followed by negative allometry, to the functional requirements of feeding. Rapid growth of the pectoral fins and the mouth gape would increase the chance of prey capture by reducing the head yaw caused by angular recoil, and by increasing the radius of the mouth relative to the target (Drost 1987). Finally, a corollary to the pattern of relative growth in body depth and caudal peduncle height observed by Hoda and Tsukahara (1971) is that the body shape (body length/body depth) and peduncle depth factor (peduncle depth/body depth) (*sensu* Webb and Weihs 1986)

attain adult values at SL about 5–6 times the length at hatching (4·49 mm SL: Peňáz *et al.* 1983).

There are clear indications, therefore, of changes in body form and function at 20–25 mm SL, and these appear to be correlated with changes in feeding and locomotion.

8.2.4 Social relations and 'shooting'

Aquarium experiments by Panyushkin (1989) showed that social interactions among carp are apparent even in the first month of life, at 15–30 mm length. Persistent aggregations, however, are identifiable only after the fish attain 35–70 mm length, and are associated mainly with foraging and reactions to external stimuli (e.g. fright responses).

A peculiarity of aquarium and pond carp is the appearance of so-called 'tobi koi' or 'shoot carp' under certain conditions of stocking density and food quality and availability. This phenomenon was studied by Nakamura and Kasahara (1955, 1956, 1957, 1961) and its evolutionary significance and implications for aquaculture and breeding programs are reviewed by Wohlfarth (1977). Shooting is indicated by a strong positive skew in the frequency distribution of length. When food is scarce the fast-growing 'shooters' dominate, slowing or even suppressing the growth of other fish in the population. Shooters do not develop when individual fish are grown in isolation, or when larger fish or fast-growing varieties are added early during growth of the original population, so that its frequency distribution remains symmetrical.

Occasional references to divergent growth patterns appear in other studies. Smallwood and Smallwood (1931, p. 219) observed that "in a month some of the fry were twice the size of the smaller ones". McCrimmon (1968, p. 9) stated that "differences in individual growth, which are influenced by water temperature, stocking density and availability of food, become prominent by the 12th week of life". Ivanova (1978) monitored the growth of 'under-yearlings' fed either natural or supplemented natural diets. 'Quick developers' were not reported under the first feeding regime, although the length distribution of fish reared at a density 1·5 times normal does appear slightly right-skewed (Ivanova 1978, her fig. 2). In the second regime shooters did appear.

The time of appearance of the shooters is significant in the context of the onset of the juvenile period. Belyaev (1976) provided evidence of growth variability in larvae 1–6 days old, but this is unsupported by other work. Nakamura and Kasahara (1955) showed that positively-skewed body-length distributions appeared in a population fed on Cladocera for 20 days, although the distributions of the eggs and younger larvae had been symmetrical. If allowance is made for the eleutheroembryo phase (about 2 days: Peňáz *et al.* 1983; Balon 1995a,b), the age of first appearance of fast-growing individuals, under pond conditions, would correspond to the accepted time for the onset of the juvenile period. This is supported by data for wild larvae 5–21 days post-hatch, and at various developmental steps *sensu* Balon (1958a), showing no indication of fast-growing individuals (cf. Section 9.3.5).

8.2.5 Habitat use

Little is known of the habitat use by larval and juvenile carp, unlike other cyprinids (e.g. Copp 1989, 1992; Copp, Guti, Rovný and Cerný 1994; Garner 1996, 1997a). Casual observations by Beckman and Elrod (1971) for Lake Oahe (North and South Dakota) and Sheaffer and Nickum (1986) for backwaters of the Upper Mississippi River showed that 0+ carp were most abundant in shallow areas associated with flooded vegetation. A more intensive study in Illinois by Richardson (1913) concerned 10–20 mm carp from consecutive spawning seasons in shallow, vegetated waters. Richardson noted that the affinity of 'hatchlings and fingerlings' for these areas made them vulnerable to changes in water level. Sigler (1958, p. 9) considered freshly-flooded, vegetated areas as an ideal habitat where "carp hatch and live from 2 weeks to 2 months", and noted that the young fish tend to abandon their nursery areas after attaining lengths of 75–100 mm (see also Johnson and Dropkin 1994). Circumstantial evidence for this behaviour is provided also by Reynolds (1983) in Australia: from observations in the Murray and Murrumbidgee rivers he speculated that 'smaller fish' (< 200 mm) move out of backwaters to colonise new areas.

8.3 Discussion

Although there is a vast literature on the early ontogeny of carp, the references cited here are sufficient to demonstrate whether the species complies with the model proposed for roach by Copp and Kováč (1996). The foregoing comments indicate significant changes in

carp of 20–25 mm SL (20–30 days post-hatch), corresponding to the accepted onset of the juvenile period in this species. After the onset, the carp resemble adults in morphology, feeding habits, locomotion and perhaps differential growth capacity. Adult modes of life, in regard to habitat use and social behaviour, would be achieved at a greater size and age.

The global genetic heterogeneity of carp stocks (Balon 1995a), including domesticated and feral forms (e.g. Olaniyan 1961; McCrimmon 1968; Toor and Chauan 1975; Welykochatko 1976; Fitzmaurice 1983; Johal *et al.* 1984; Moyle 1984; Prochelle and Campos 1985; Brumley 1991; Costa-Pierce *et al.* 1993; Coates and Ulaiwi 1995; Kålås and Johansen 1995), may obscure the larva-juvenile threshold, notwithstanding variation within local populations (Balon 1985, 1993) that may include altricial and precocial forms (Balon 1995a,b; see also Section 1.1). Balon (1995a, p. 8) postulated differences in the early ontogeny of wild carp from the Danube, Volga and Amur rivers, and ascribed "the enormous variation" in forms to "states of reversal from the domesticated pond form to the feral form". In Australia, Shearer & Mulley (1978) identified three distinct populations ('Boolarra', 'Yanco', 'Prospect'), and suggested that two shared a European ancestry (presumably *C. c. carpio*) and the other was of Asian origin (domesticated *C. c. haematopterus* or, more likely, introgressed European and Asian stocks) (cf. Wohlfarth 1984; Balon 1995a,b; see also Section 1.1).

Adult carp move into shallow, vegetated areas (e.g. Richardson 1913; Sigler 1958; Sarig 1966) after over-wintering (Janković 1971; Johnsen and Hasler 1977; Otis and Weber 1982). Reproductive success and the survival of early life stages are dependent on the availability of flooded nursery areas, and the survival of eggs, larvae and juveniles is threatened by falling water levels (Shields 1957; Swee and McCrimmon 1966). Indeed, water-level manipulations may be a means to control carp in Australia (e.g. Roberts 1997), and the time of transition in habitat use could have considerable relevance for management (cf. Chapter 11).

More attention should be devoted to the implications of shooting for the dynamics of wild carp populations. Wohlfarth (1977) highlighted its potential adaptive value, whereby it would promote reproduction of the faster-growing individuals. Differential growth capacity would allow young 'shooters' to abandon their nursery grounds earlier, increasing

their chances of survival (with consequences for recruitment), and enable populations to disperse and colonise new areas more rapidly. Further, it may play a key role in the over-winter survival of 0+ fish, representing an alternative or complementary means to overcome the constraints imposed by small body size (Miller *et al.* 1988; but see Litvak and Leggett 1992; cf. Section 7.4). Published data and casual observations indicate that shooting is a juvenile phenomenon, but one whose morphological, functional and social advantages remain unclear.

The question posed by Copp and Kováč (1996), whether in fish with indirect development the replacement of larval by adult organs or the stabilisation of allometric growth best defines the onset of the juvenile period, seems not to be relevant in the case of carp. Changes in functional morphology, feeding and possibly differential growth capacity in carp support prior definitions of the onset (Balon 1958a; Peňáz *et al.* 1983), set at 20–25 mm SL, when the definitive phenotype is attained (Flegler-Balon 1989). However, the development of social relations and the shift in habitat use suggest that carp are not 'small adults' in these respects until they attain a greater size and age. These ecological and behavioural changes are not well-understood, but they clearly are significant for recruitment models and control strategies.

9.

EARLY LIFE HISTORY:

AGE, GROWTH AND COHORT ANALYSIS

> The increments first described by Pannella [1971] record both pattern and process [...]. In this they are analogous to the hieroglyphs of ancient Egypt which also show consistent and repeated forms and patterns.
>
> D. H. Secor, J. M. Dean and E. H. Laban (1991)

9.1 Introduction

Very little is known on the early life history of carp in Australia. Only Hume *et al.* (1983a) reported mean lengths for 0+ individuals collected throughout the growing season (September–May) in 1989–91 in the lower Goulburn River (a tributary to the Murray) in Victoria, but no further data on age, growth and cohort composition were provided.

As emphasised by Balon (1990), for understanding life history the patterns and mechanisms of early ontogeny and reproductive styles in fish must be given attention. Thus, a deeper knowledge of the progenetic and early ontogenetic processes in carp in Australia is needed if factors like recruitment and Year-Class-Strength (YCS) are to be understood, and options for population control proposed and evaluated (Roberts 1997).

Otolith microincrements, first discovered by Pannella (1971, 1974), have been extensively studied in fish and fisheries biology (reviews: Campana and Neilson 1985; Jones 1986). They have been identified in both marine and freshwater species, and their daily formation is regarded as general among teleosts (Secor and Dean 1992). An important application of otolith microincrement analysis is the determination of age and early growth of individual 0+ fish, basic for the assessment of size-selective mortality, recruitment and YCS (e.g. Miller *et al.* 1988; Litvak and Leggett 1992; Secor and Dean 1992).

In cyprinids, daily increments in lapilli (the utricular otoliths) have been used to age the fallfish (*Semolitus corporalis*) (Victor and Brothers 1982) and the rose bitterling (*Rhodeus occellatus occellatus*) (Solomon *et al.* 1985). Goldfish (*Carassius auratus*) lapilli also have provided for research on the physiochemical processes regulating calcium carbonate deposition (e.g. Mugiya *et al.* 1981; Mugiya and Odawara 1988; Mugiya and Uchimura 1989; Mugiya 1990). Conversely, the sagittae, routinely employed in most fish, are not useful to age cyprinids (Victor and Brothers 1982; Campana and Neilson 1985). Reference to their use in ageing larval *Mirogrex terraesanctae* (Landau *et al.* 1988) is dubious, as is the illustration given in Muth *et al.* (1988, their fig. 2A). In carp daily increments have not been reported, despite several studies on early growth under natural, domesticated and experimental conditions since Pannella's discoveries (e.g. Ivanova 1978; Dzhafarov 1986; Korwin-Kossakowski 1988; Raat 1989; Johnson and Dropkin 1994).

The objectives of this chapter are (1) to validate the otolith microincrement technique for carp, (2) to describe the growth of field-collected larvae and juveniles and (3) estimate their hatching dates, (4) to study the cohort composition of a wild population, and (5) to evaluate intracohort variability in growth.

9.2 Materials and Methods

9.2.1 Sampling and preparation

In total 539 larvae and juveniles were collected in 1994–95 at Gurra Lakes (near Berri) and Swan Reach. Since variation in body size and type of habitat occupied (Snyder 1983) involved different sampling methodologies, the whole catch hereafter will be divided into four sampling units (groups I–IV) for ease of interpretation. Apart from a collection made in January 1994 at Swan Reach (group I), all 0+ carp caught at Gurra Lakes from April to September 1994 (group II) were a bycatch of samples collected for the age and growth study of older carp (Chapters 2–4). Starting on 21.X.1994 collections occurred weekly until 22.I.1995 (group IIIa,b), except for the second half of December when only one sample was obtained. Two small bycatch collections were also available in February and March 1995 (group IV) (Table 9.1).

Table 9.1 **Material examined for age and growth studies and cohort analysis in 0+ carp.** Sampling group: artificial category defined to assist in interpretation of sampling and preparation procedures; Week: number of weeks after major spawning event set to 14.X.1994 (for sampling groups II and IV only); WLR: weight-length relationship; CA: cohort analysis; GA: growth analysis.

Locality	Collection date	Week	*n*	Sampling group	Analysis	Aged
Swan Reach	25.I.1994		28	I	WLR	
Gurra Lakes	20.IV.1994		5	II	WLR	
Gurra Lakes	12.VII.1994		15	II	WLR	
Gurra Lakes	14.IX.1994		2	II	WLR	
Gurra Lakes	21.X.1994	1	70	IIIa	WLR, CA, GA	54
Gurra Lakes	28.X.1994	2	105	IIIa	WLR, CA, GA	85
Gurra Lakes	4.XI.1994	3	80	IIIa	WLR, CA, GA	58
Gurra Lakes	11.XI.1994	4	37	IIIa	WLR, CA, GA	18
Gurra Lakes	18.XI.1994	5	19	IIIa	WLR, CA, GA	10
Gurra Lakes	25.XI.1994	6	18	IIIa,b	WLR, CA, GA	5
Gurra Lakes	3.XII.1994	7	7	IIIb	WLR, CA, GA	6
Gurra Lakes	11.XII.1994	8	34	IIIb	WLR, CA, GA	17
Gurra Lakes	17.XII.1994	9	42	IIIb	WLR, CA, GA	18
Gurra Lakes	26.XII.1994	10	6	IIIb	WLR, CA, GA	6
Gurra Lakes	7.I.1995	12	20	IIIb	WLR, CA, GA	7
Gurra Lakes	15.I.1995	13	35	IIIb	WLR, CA, GA	18
Gurra Lakes	22.I.1995	14	5	IIIb	WLR, CA, GA	3
Gurra Lakes	20.II.1995	18	3	IV	WLR, CA	
Gurra Lakes	16.III.1995	21	3	IV	WLR, CA, GA	4

Juvenile carp at Swan Reach (group I) were caught with a small seine (10 m x 1 m, 10 mm stretched mesh), while groups II and IV at Gurra Lakes were sampled with monofilament nets (20 and 50 mm stretched mesh). The first six weekly samples from this site (group IIIa) were obtained by sweeping a plankton net (500 μm mesh), fitted with a glass jar at the end, among reed stands and submersed macrophytes, whereas all group IIIb samples were collected with a modified seine (80 m x 2 m, 10 mm stretched mesh) fitted with a collection bag and deployed from a sandy shore of the lake. Carp larvae were distinguished from those of goldfish following Gerlach (1983).

Groups I, III and IV were preserved in 95% ethanol immediately after capture, whereas group II were dissected within 24 h. Group I and II were measured for Standard (SL, mm), Fork (FL, mm) and Total Length (TL, mm) either with dial callipers (± 0·05 mm) or on a measuring board (± 1·0 mm), while in groups III and IV SL and, for juveniles and larvae with developed fins only, FL were measured with dial callipers (± 0·05 mm). The following regressions apply:

$$FL = 0{\cdot}864 + 1{\cdot}108\ SL \qquad (n = 335,\ r^2 = 0{\cdot}997),$$

$$TL = 4{\cdot}887 + 1{\cdot}229\ SL \qquad (n = 50,\ r^2 = 0{\cdot}994).$$

No attempt was made to adjust length measurements for possible shrinkage caused by preservation, although immediate fixation in ethanol has been shown to minimise the effect (Methot and Kramer 1979; Radke 1989; Kingsford and Atkinson 1994).

Total weight (W) was measured to a different level of precision depending on fish size. Thus, carp < 1·0 g (all larvae and a few early juveniles) were weighed to within 0·01 mg on an electronic balance, while heavier specimens were to the nearest 1 g.

All three pairs of otoliths (lapilli, sagittae and asterisci) were excised from a subsample of fish for preliminary evaluation of their comparative age interpretation value (Brothers 1987; David *et al.* 1994). As no microincrements (*sensu* Mugiya *et al.* 1981 and Campana and Neilson 1985) could be identified in either sagittae or asterisci, only the lapilli were used. Otolith extraction in larvae and smaller juveniles (< 80 mm SL) was under a dissecting microscope at low magnification (10–50X). The 'open-the-hatch' method (Secor, Dean and Laban 1991; see also Section 2.2.2) was useful for fish > 40 mm SL, whereas in smaller specimens extraction was possible by placing the fish in a Petri dish and teasing apart the head tissues with dissecting needles. This procedure allows *in situ* identification of the whole set of otoliths, facilitating collection of the lapilli.

9.2.2 Otolith processing and examination

Upon dissection the lapilli (hereafter 'otoliths'), usually one for each fish (right or left), were mounted on microscope slides with thermoplastic cement. No further preparation was required for enumeration of microincrements in smaller otoliths, while grinding was necessary for the larger ones, especially around the perinuclear region where an increase in thickness obscured the innermost increments. Sagittal sections (Pannella 1980) were prepared by manually grinding the embedded otolith from both sides to a thin slice with wet 1200-grade carborundum paper (Hoedt 1992). Although time-consuming and susceptible to failure because of section breakage, this method consistently results in preparations of superior quality for light microscopy (Campana 1984; Campana *et al.* 1987). No further preparation (e.g. polishing) was required.

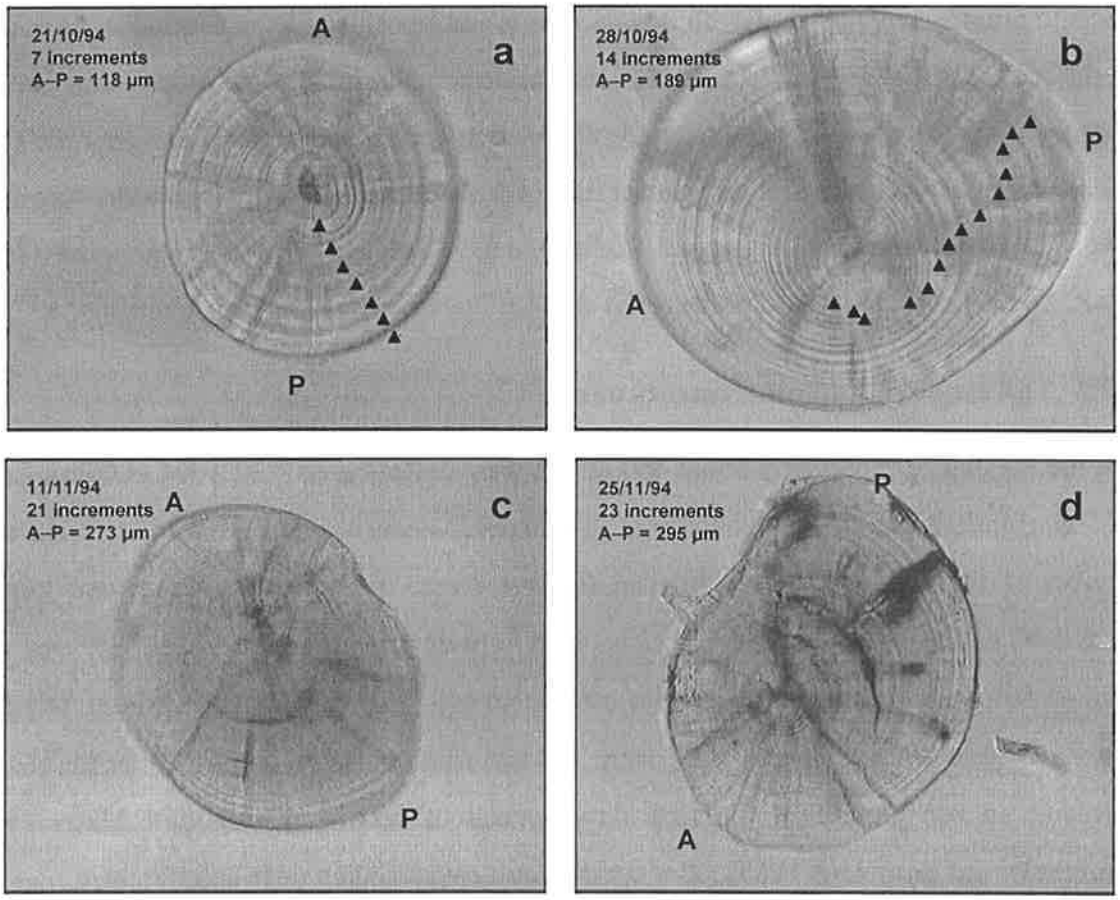

Figure 9.1 Thin-sectioned otoliths (lapilli) of carp. Under transmitted light an incremental zone appears translucent (light) and a discontinuous zone opaque (dark). Microincrements counted in the first two preparations are indicated each by a triangle. A: anterior margin; P: posterior margin; A-P: longest axis of growth. (a) 7 microincrements; (b) 14 microincrements; (c): 21 microincrements; (d) 23 microincrements.

Growth increments were counted under a compound microscope at magnifications of 200–400X, and image analysis software used to assist in pattern recognition. Microincrements were identified as bipartite structures each composed of an incremental and a discontinuous zone (Campana and Neilson 1985), appearing as regularly alternating translucent and opaque zones respectively (under transmitted light). All counts were made ignoring date of capture and size of fish. Increments were counted three times for each otolith, following Lang and Buxton (1993). When two counts were identical or differed by less than three increments, the count from the last of the two counts was accepted. When all counts differed, the middle one was taken unless discrepancies exceeded five increments, in which case the otolith was discarded. When less than 20–30 increments were present these were usually enumerated regardless of the orientation of the otolith, as this was approximately circular in shape (Fig. 9.1a,b). However, with increasing number of increments the otolith

became progressively orbicular, so that an anterior and posterior axes became more evident in the sections (A-P in Fig. 9.1). In this case increments in most otoliths were still counted starting from the nucleus but generally proceeding initially along the posterior axis and subsequently switching to the anterior one where the visibility of patterns improved (Fig. 9.1c,d). Contrary to other studies (e.g. Campana 1984; Volk *et al.* 1994; M. P. Francis *et al.* 1992), no preferential axis for increment counts was identified.

9.2.3 Validation of microincrement counts

For the validation experiment about 800 larvae were collected on 4.XI.1994 at Gurra Lakes and transported live to the laboratory. Three 50 L aquaria were stocked with an even number of fish, which were acclimated for five days. Recirculating water was kept at 22 ± 1 °C and the fish exposed to a 12 h : 12 h light/dark photoperiod. Mortality was very high (> 50%) during the first two days after stocking, and on 9.XI.1994 a total 360 carp were available for marking. Fish were fed *ad libitum* twice daily live brine shrimp (*Artemia salina*) nauplii in the first three weeks of rearing (Bryan and Matty 1980; Vanhaecke and Sorgeloos 1983), after which Tetra-min® flakes were administered.

Otolith marking followed procedures in Muth *et al.* (1988). Two 1 L glass beakers containing a tetracycline hydrochloride (TC) solution of 350 mg/L aerated distilled water (buffered to pH 7·0) were stocked with 120 fish each, incubated for 6 h at 22 °C. During incubation the glass containers were covered with black plastic sheets to minimise possible de-activation of the marker caused by light exposure (Weber and Ridgway 1967). The selected TC concentration has proven a good trade-off between larval survival and mark retention in cyprinids as well as other taxa (Hettler 1984; Tsukamoto 1985; Muth *et al.* 1988). A third 1 L glass beaker containing only distilled water was stocked with the remaining 120 fish, which served as control to determine levels of natural fluorescence (Campana and Neilson 1982). After incubation all fish were returned to the aquaria except for five specimens in each of the three treatments which were immediately sacrificed to evaluate external fluorescence (under a UV lamp), a procedure often employed to determine the success of a marking experiment (Muth *et al.* 1988). Subsequently five fish from each aquarium were sacrificed once a week for the first six weeks and then on day 54, 61, 68 and 91 after treatment. The remaining fish were reared up to day 134 (23.III.1995).

All sacrificed specimens were preserved in 95% ethanol and stored away from light, and their lapilli later prepared and examined by the methods described above, although no grinding was necessary. Otoliths from dead fish were not examined to avoid possible bias due to physiological effects caused by natural mortality (Jearld *et al.* 1993). All micro-increments counts in marked otoliths were made under both normal and ultraviolet light on a fluorescence microscope (200–1000X), without regard for date of sacrifice and fish size.

9.2.4 Identification of developmental steps and cohort analysis

In the laboratory all field-collected fish (aged and unaged) were identified to developmental step following Balon (1958a). The criteria used for the morphological identification of juveniles are explained in Chapter 8, while the steps identified in the larva period are as follows:

Apterolarva (= protopterygiolarva or fin-fold) phase:

Step L'1. The larvae have mixed food, exogenous and endogenous. Remains of the yolk sac are present and minute prey items (particularly Rotatoria) are found in the gut. The larvae swim well but with twitching movements. The posterior chamber of the swim bladder is filled with air and the larvae start breathing through gills. The *vena caudalis profunda* is forming. Some bones begin to ossify.

Step L'2. The larvae feed only exogenously. The ossification process of the lepidotrichia in the caudal fin starts and a first loop appears in the gut. Between 23–26 vertebrae are already ossified.

Step L'3. The larvae are already feeding on large prey. The differentiation of the dorsal and anal fins begins and the hypural bones start to ossify. More than 30 vertebrae are ossified. Mesenchymatic lumps appear in the place of formation of future lepidotrichia of the dorsal and anal fins. The end of the notochord begins to bend upwards.

Pterolarva (= pterygiolarva or fin-formed) phase:

Step L''1. The anterior chamber of the swimbladder is filling with air, while the posterior changes from an elliptical to a pear-shaped form. The ossification process of the spinal chord and the hypuralia ends. In the dorsal and anal fin mesenchymatic lepidotrichia

appear, which later begin to ossify in the dorsal fin. The homocercal tail fin is now forming. Red and orange pigments appear.

Step L''2. The ventral fin begins to form and reaches only up to the first half of the preanal fin and fin-fold. The ribs start to ossify. The anterior chamber of the swimbladder is growing larger than the posterior one. Ossification of the lepidotrichia of the anal fin also begins.

Step L''3. The larvae start to collect food from the bottom. The lepidotrichia are also ossified in the paired fins. The ventral fins overlap half the width of the preanal fin-fold. The anterior part of the swimbladder is three times the size of the posterior one. The embryonic fin-fold appears between the dorsal and caudal as well as between the anal and caudal fin as a narrow strip, or is completely resorbed.

Step L''4. The ventral fin strongly overlaps the edge of the preanal rim, which is quickly resorbed so that at the end of this step there is only a remnant in front of the anus. The scales of the first six rows are forming.

Analysis of length-frequency distributions assisted in the recognition of main cohorts of carp, found to correspond to peaks in spawning activity as determined by back-calculation of hatching dates from microincrement counts (Brothers *et al.* 1983), while developmental step analysis provided information of intra-cohort composition.

Larval growth was studied (1) relative to developmental step, regardless of date of capture, and (2) between successive steps within the same putative cohort, hence including the sampling date (weeks 1–7). In the second case the growth rate G of larvae between successive developmental steps was calculated from the slope 'b' of a regression line through the mean SL values of each pair of steps considered, following Copp (1990b).

9.2.5 Data analysis

In modelling somatic growth length- and weight-at-age curves were fitted based on microincrement counts. Age estimates were not corrected, as deposition of the first increment was assumed to start at hatching (see Section 9.4.1). Somatic growth (length

and weight) was modelled either linearly or non-linearly for larvae and juveniles separately and together. Growth in weight (W) was modelled by a logistic curve of the form:

$$W_t = W_\infty/(1+\exp(-g(t-t_0))),$$

where W_t is the weight at time t, W_∞ the asymptotic weight, g the instantaneous growth rate when $t \rightarrow t_0$, and t_0 the time when the absolute rate of increase starts to decrease (Ricker 1979). Growth in length (SL) was described by either a logistic or Gompertz curve, in the form:

$$SL_t = SL_\infty \exp(-\exp(-g(t-t_0))),$$

where SL_t is the standard length at any time t, SL_∞ the asymptotic standard length, g the instantaneous growth rate when $t = t_0$ and t_0 the time at which the absolute rate of growth begins to decrease (Ricker 1979). A simple regression model (DDSF, cf. Table 4.7 for notation) was sufficient to describe the growth in SL of larval carp. Finally, the weight-length relationship was modelled by piecewise regression analysis on the log-transformed variables.

All statistical analyses were done with the modules ANOVA/MANOVA and Nonlinear Estimation of STATISTICA™ v 5.0 (Statsoft Inc. 1995). Tests of normality and homogeneity of variances were as in Section 4.2.4.

9.3 Results

9.3.1 Validation of microincrement counts

Survival was 100% in all TC-marked fish, and an external fluorescence was present on all larvae sacrificed immediately after treatment ($n = 10$). This indicated that the selected TC-dosage and incubation period met both requirements for marking efficacy and low toxicity. Throughout the experiment mortality was very low, with only three fish (two treated and one control) dead in the first week, and three more (again two treated and one control) upon completion of the experiment.

Table 9.2 **Mean increment counts from lapilli of TC-marked larval and juvenile carp.** First five weeks following treatment.

		Increment count				
Date of sacrifice	Days elapsed	*n*	Mean	± SE	Min	Max
9.XI.1994	7	9	6·1	0·2	5	7
16.XI.1994	14	10	12·6	0·4	10	14
23.XI.1994	21	8	18·6	0·3	17	20
30.XI.1994	28	6	26·5	0·3	25	27
7.XII.1994	35	6	33·3	0·8	31	36

A fluorescent band, usually spanning one or two increments in width, was always visible. However, there was a stark variation in appearance between increments deposited before and after laboratory rearing. The former appeared as distinct alternating pairs of translucent incremental and opaque discontinuous zones, while the latter were faded and much less prominent, and could be generally counted only in otoliths from specimens culled during the first five weeks following marking. This probably explained why increments could not be reliably identified and enumerated on 14% of the marked otoliths processed. Increment counts, which were made starting from the proximal side of the fluorescent band to ensure inclusion of the first increment(s) laid after treatment (Campana and Neilson 1982), closely corresponded with the number of days elapsed from marking (Table 9.2), and the slope 'b' of the regression line of microincrement counts vs number of days since treatment was not significantly different from 1 ($P = 0{\cdot}16$) (Fig. 9.2). Finally, natural fluorescence in un-marked otoliths was generally visible along the edges, although this was always less intense compared to that caused by TC bands in treated otoliths.

For all estimates of age used in cohort analysis and evaluation of growth models microincrements were assumed to form daily.

9.3.2 Microincrement analysis of un-marked otoliths

Up to 86 microincrements were counted in the sample of un-marked otoliths, counts in larger otoliths becoming increasingly difficult, as a result of the increasing curvature of the sagittal plane in the anterior and posterior margins, and/or failure of sectioning through the nuclear region. Subdaily increments were occasionally present, appearing as discontinuous opaque bands intercalated between daily increments. Their incidence, however, was

generally low and limited to the area around the nucleus. In all cases they did not affect interpretation of daily increment patterns for age estimations.

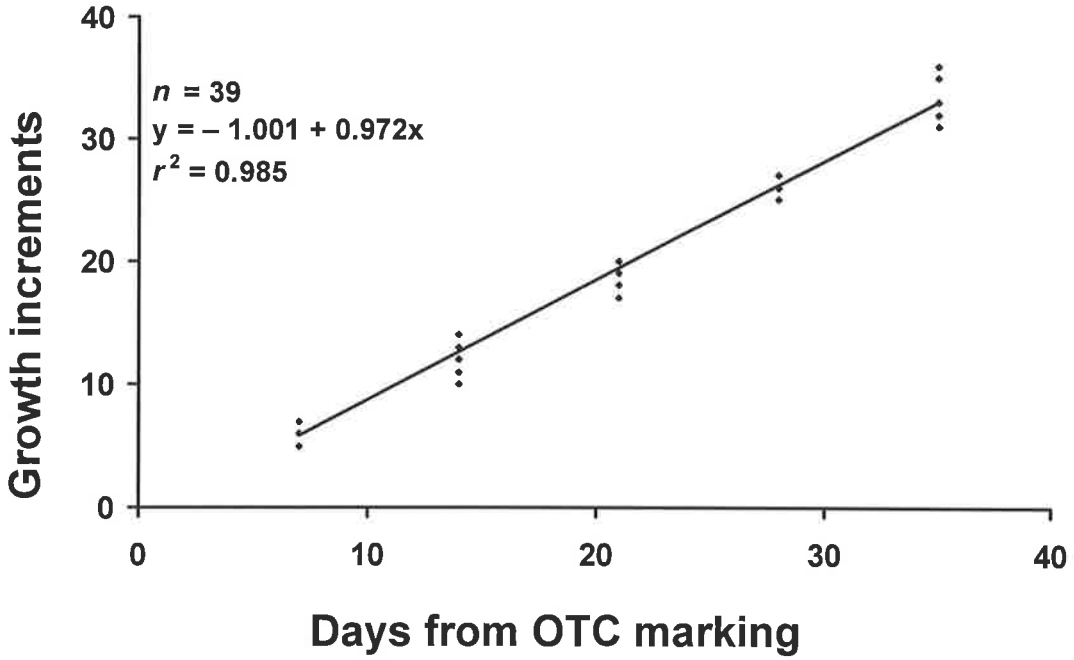

Figure 9.2 Regression of growth increment counts against number of days from OTC marking in otoliths (lapilli) of larval and juvenile carp.

9.3.3 Cohort analysis and estimation of hatching dates

Length-frequency distributions of fish from Gurra Lakes revealed two main cohorts, here indicated as A and B (Table 9.3, Fig. 9.3). Main cohort A, first sampled on 21.X.1994, consisted initially of L'1 and L'2, then L'3–L''1 (week 2), L''1–L''4 (week 3), and L''2–L''4 (week 4) larvae. The first juveniles began to appear on week 4, and by 18.XI.1994 (week 5) no more larvae were sampled. Standard lengths were significantly different among the four sampling dates ($H = 236{\cdot}01$, $P < 0{\cdot}001$). Main cohort B first appeared in samples collected on week 4, when it consisted of L'3 and L''1 larvae. As for main cohort A, juveniles appeared after approximately four weeks (week 8), following a progressive succession of larval steps in weeks 5–7 (L'2–L''3 on week 5, L'3–L''4 on week 6, L''3 and L''4 on week 7). Mean standard lengths for larvae and juveniles in both main cohorts at each sampling date are given in Table 9.3.

Table 9.3 **Sampling dates and length (SL) of two main cohorts (A and B) of larval and juvenile carp.** See also Fig. 9.3.

Sampling date	Main cohort	*n*	SL (mm) Mean	± SE	Min	Max
21.X.1994	A	70	7·47	0·07	5·5	8·7
28.X.1994	A	105	10·18	0·07	6·8	12·3
4.XI.1994	A	80	11·85	0·12	9·0	14·7
11.XI.1994	B	6	9·45	0·28	8·4	10·4
11.XI.1994	A	31	14·58	0·22	12·2	16·9
18.XI.1994	B	14	9·47	0·43	6·4	13·1
18.XI.1994	A	5	19·58	0·61	17·7	20·9
25.XI.1994	B	17	9·58	0·48	7·4	14·4
25.XI.1994	A	1	25·2			
3.XII.1994	B	2	11·25	0·85	10·4	12·1
3.XII.1994	A	5	42·00	1·12	37·8	44·4
11.XII.1994	B	13	26·22	1·51	16·6	35·4
11.XII.1994	A	21	44·62	1·17	35·6	55·0
17.XII.1994	B	10	29·62	2·21	19·6	43·4
17.XII.1994	A	32	56·86	0·51	51·2	64·3
26.XII.1994	B	1	35·8			
26.XII.1994	A	5	70·36	2·69	63·2	77·4
7.I.1995	B	10	41·31	2·47	31·5	57·4
7.I.1995	A	10	74·71	3·36	61·5	89·2
15.I.1995	B	29	42·97	1·24	30·6	60·4
15.I.1995	A	6	91·00	4·56	79·2	106·9
22.I.1995	B	5	37·84	1·47	34·5	43·2
20.II.1995	B	3	48·83	7·82	33·2	57·1
16.III.1995	B	6	46·85	3·63	34·0	57·8
16.III.1995	A	2	96·70	1·80	94·9	98·5

A total of eight putative larval cohorts (*a–h*) were distinguished in samples from the first 7 weeks (Fig. 9.4). The growth rate G between developmental steps was highly variable among cohorts, ranging from 0·029 to 0·729 mm/d (Table 9.4). Even though a negative value (G = – 0·038 mm/d) was recorded in cohort *f* between steps L''2 and L''3, this was probably an artefact of small sample size. Mean G values between successive developmental steps showed no consistent pattern, except for a sudden rise between L''3 and L''4 due to an unexpectedly high value recorded in cohort *a* (Table 9.5).

Back-calculation of hatching dates from microincrement counts revealed two peaks in spawning activity (Fig. 9.5). The first and most pronounced occurred in mid-October and lasted about 10 d, and was followed by a secondary, less intense event in early November lasting about 20 d. Finally, a few more individuals were estimated to have hatched between late November and early December, and as late as early February 1995.

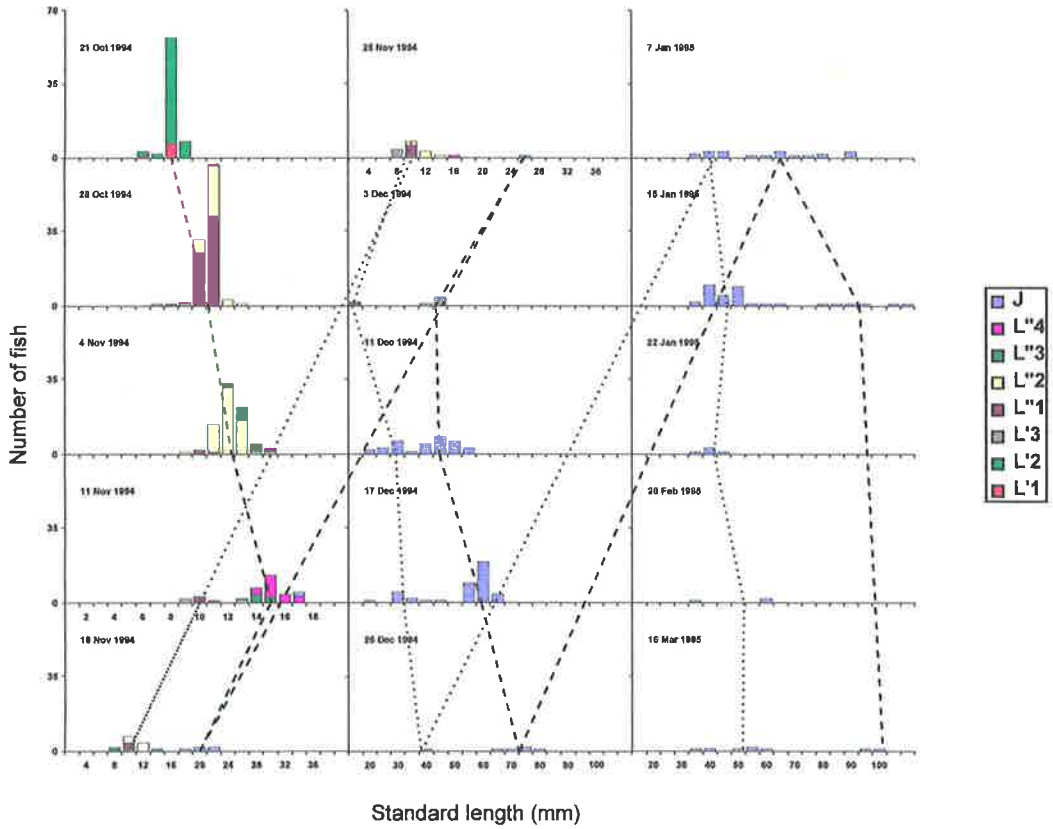

Figure 9.3 Progression of cohorts of larval and juvenile carp. Length-frequency distributions are given for each sampling date (from top left to bottom right). Two main cohorts were recognised during the sampling period, and their growth in standard length is here indicated by a broken (first main cohort (A), sampled starting from 21.X.1994) and a dotted line (second main cohort (B), sampled starting from 18.XI.1994). Larval developmental steps are also indicated (terminology follows Balon (1958a)).

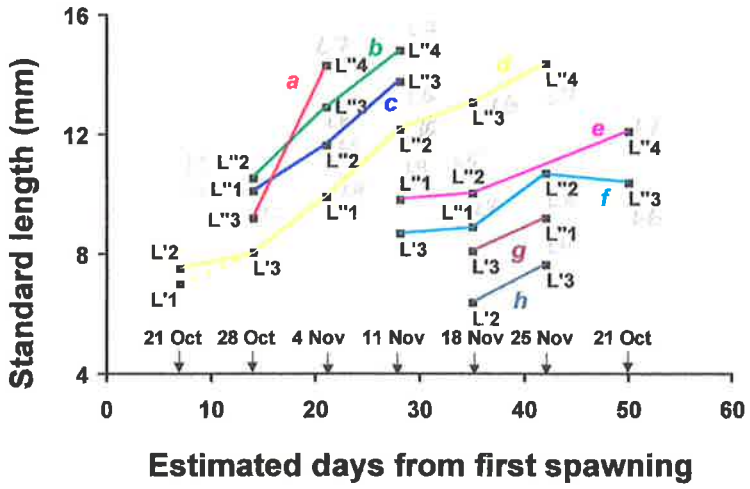

Figure 9.4 Tentative representation of cohort progression in larval carp. Standard length is plotted against number of days from first spawning estimated from increment counts of lapilli. A total of eight cohorts of fish were identified (*a–h*) and the corresponding steps of development (terminology after Balon (1958a)) are indicated.

Table 9.4 **Growth rates between developmental steps of eight different cohorts (*a–h*) of larval carp (October–December 1994).** L_i: initial larval step; L_f: final larval step; Code: initial and final sampling week (1: 21.X.1994; 2: 28.X.1994; 3: 4.XI.1994; 4: 11.XI.1994; 5: 18.XI.1994; 6: 25.XI.1994; 7: 3.XII.1994); D: number of days lapsed from successive sample collections; C: larval cohort; G: growth rate, equivalent to the slope of a regression line fitted to the mean lengths of each pair of developmental steps (cf. Copp 1990b); SL_i: standard length of initial larval step; SL_f: standard length of final larval step. Terminology after Balon (1958a).

					n		Mean		± SE	
$L_i - L_f$	Code	D	C	G (mm/d)	SL_i	SL_f	SL_i (mm)	SL_f (mm)	SL_i (mm)	SL_f (mm)
L'2 – L'3	1–2	7	*d*	0·078	62	3	7·53	8·08	0·53	1·14
L'2 – L'3	2–3	7	*h*	0·180	1	5	6·4	7·66		0·27
L'3 – L"1	2–3	7	*d*	0·265	3	3	8·08	9·93	1·14	0·40
L'3 – L"1	4–5	7	*f*	0·029	2	3	8·70	8·90	0·42	0·82
L'3 – L"1	5–6	7	*g*	0·157	2	5	8·10	9·20	0·28	0·63
L"1 – L"2	2–3	7	*c*	0·220	67	63	10·12	11·66	0·41	0·92
L"1 – L"2	3–4	7	*d*	0·324	3	1	9·93	12·2	0·40	
L"1 – L"2	4–5	7	*e*	0·029	4	7	9·83	10·03	0·43	0·64
L"1 – L"2	5–6	7	*f*	0·257	3	6	8·90	10·70	0·82	1·43
L"2 – L"3	2–3	7	*b*	0·336	33	12	10·55	12·91	0·59	0·75
L"2 – L"3	3–4	7	*c*	0·300	63	8	11·66	13·76	0·92	0·76
L"2 – L"3	4–5	7	*d*	0·129	1	1	12·2	13·1		
L"2 – L"3	6–7	8	*f*	– 0·038	6	1	10·70	10·4	1·43	
L"3 – L"4	2–3	7	*a*	0·729	2	2	9·20	14·30	2·55	0·42
L"3 – L"4	3–4	7	*b*	0·272	12	20	12·91	14·82	0·75	0·97
L"3 – L"4	5–6	7	*d*	0·186	1	1	13·1	14·4		

Table 9.5 **Summary statistics for the growth rate (G) between larval developmental steps in carp.** Terminology after Balon (1958a).

$L_i - L_f$	*n*	Mean	± SE	Min	Max
L'2 – L'3	2	0·1290	0·0510	0·078	0·180
L'3 – L"1	3	0·1503	0·0682	0·029	0·265
L"1 – L"2	4	0·2075	0·0633	0·029	0·324
L"2 – L"3	4	0·1818	0·0860	– 0·038	0·336
L"3 – L"4	3	0·3957	0·1685	0·186	0·729

9.3.4 Growth models

The mean length, weight and estimated age of field-collected larvae arranged by developmental step are given in Table 9.6. These values compare well with those reported in experimental studies by Balon (1958a,b) and Peňáz *et al.* (1983).

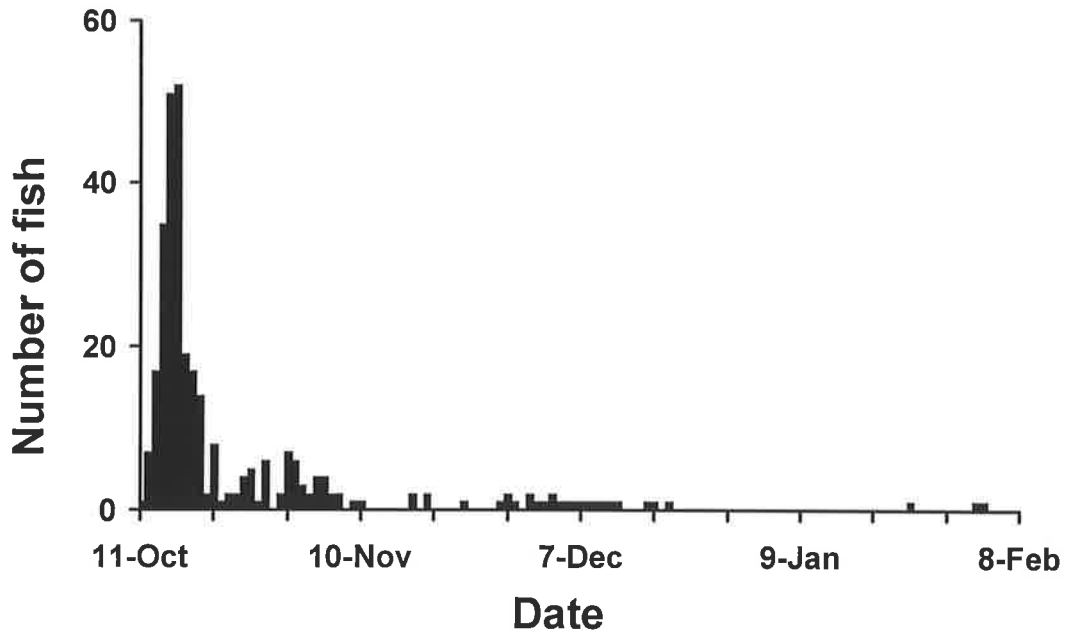

Figure 9.5 Hatching dates for carp in the lower River Murray estimated from back-calculation of microincrement counts in otoliths. Estimated ages are assumed to correspond to the number of days from hatching.

The weight-length relationship indicated a change in slope at 16·8 mm SL, the first juveniles appearing after this transition (Fig. 9.6). Growth in weight for larvae and juveniles (separate and pooled) could only be modelled by a logistic curve, as no satisfactory fit was obtained through a Gompertz equation (Fig. 9.7a–c). Conversely, growth in length (SL) for the pooled data set was described equally well by a Gompertz and a logistic model, providing comparable goodness of fit (r^2 = 0·911 and 0·909, respectively) (Fig. 9.8a). A logistic model was still useful in describing growth in length of juvenile fish, while for larvae this was better fitted by a simple regression line (Fig. 9.8b,c). Parameters for all models and other statistics are given in Table 9.7.

9.3.5 Shooting analysis

Length-frequency distributions were examined separately relative to estimated age (5–6, 12–18 and 21 d) and larval developmental step (L'1–L''4), and the corresponding coefficient of skewness γ_1 calculated in each case. No significant relationship was found by plotting γ_1 values vs either estimated age or larval step (r^2 = 0·16, P = 0·25 and r^2 = 0·21, P = 0·30). Further analyses, including data for juveniles, were not reliable because of small sample sizes.

Table 9.6 **Length, weight and estimated age (from otolith microincrement counts) of larval carp.** Terminology of developmental steps follows Balon (1958a).

	Age (d)					SL (mm)					W (mg)				
Step	*n*	Mean	± SE	Min	Max	*n*	Mean	± SE	Min	Max	*n*	Mean	± SE	Min	Max
L'1	5	5·2	0·5	4	7	8	7·04	2·49	5·8	7·6	8	1·83	1·83	1·2	2·7
L'2	49	5·7	0·1	4	8	63	7·51	0·95	5·5	8·7	63	2·10	2·10	0·6	3·1
L'3	5	14·0	1·4	11	19	12	8·01	2·31	6·8	9·0	12	3·18	3·18	1·8	6·0
L"1	59	14·0	0·3	12	26	82	10·00	1·10	8·2	11·0	82	6·55	6·55	1·9	11·2
L"2	79	16·5	0·3	12	23	110	11·18	1·07	8·9	14·7	110	15·45	15·45	6·1	33·5
L"3	17	19·3	0·8	12	26	24	12·79	2·61	7·4	14·8	24	30·30	30·30	2·5	47·2
L"4	14	23·6	1·0	16	29	24	14·64	2·69	12·1	16·8	24	51·62	51·62	32·6	82·5

Table 9.7 **Models describing the somatic growth of larval and juvenile carp.** Values (± (asymptotic) SE) for the parameters in linear and non-linear models are indicated. W Logistic: logistic function for weight; SL Logistic: logistic function for standard length; SL Gompertz: Gompertz function for standard length; SL DDSF: simple regression model for standard length (see also Table 4.7). In logistic curve, W_∞: asymptotic weight, SL_∞:asymptotic standard length, g: instantaneous rate of growth when $W \rightarrow 0$ or $SL \rightarrow 0$, t_0: time at which absolute rate of increase in weight begins to decrease. In Gompertz growth curve, g: instantaneous growth rate when $t = t_0$ (Ricker 1979).

Statistics	Larvae + Juveniles	Larvae	Juveniles
W Logistic			
n	309	228	81
W_∞ (g/mg)[A]	32·151 ± 3.690[B]	76·333 ± 15.708[C]	36·602 ± 13·780[C]
g (d^{-1})[A]	0·086 ± 0·005	0·215 ± 0·031	0·079 ± 0·014
t_0 (d)[A]	77·482 ± 2·851	23·034 ± 2·107	81·034 ± 9·843
r^2	0·828	0·676	0·759
Model	$W_t = 32·151/(1+\exp(-0·086(t-77·482)))$	$W_t = 76·333/(1+\exp(-0·215(t-23·034)))$	$W_t = 36·601/(1+\exp(-0·079(t-81·034)))$
SL Logistic			
n	309		81
SL_∞ (mm)[A]	99·347 ± 6·922		195·717 ± 124·641
g (d^{-1})[A]	0·061 ± 0·003		0·031 ± 0·009
t_0 (d)[A]	48·686 ± 2·699		83·894 ± 37·628
r^2	0·909		0·696
Model	$SL_t = 99·347/(1+\exp(-0·061(t-48·686)))$		$SL_t = 195·717/(1+\exp(-0·031(t-83·894)))$
SL Gompertz			
n	309		
SL_∞ (mm)[D]	152·195		
g (d^{-1})[D]	0·025		
t_0 (d)[D]	53·711		
r^2	0·911		
Model	$SL_t = 152·2\exp(-\exp(-0·025(t-53·711)))$		

Table 9.7 (continued)

Statistics	Larvae + Juveniles	Larvae	Juveniles
SL DDSF			
n		228	
a		5·651 ± 0·194	
b		0·336 ± 0·013	
r^2		0·749	
Model		$SL_t = 5·651 + 0·336t$	

[A] Asymptotic standard errors.

[B] Weight in mg.

[C] Weight in mg.

[D] Asymptotic standard errors not available.

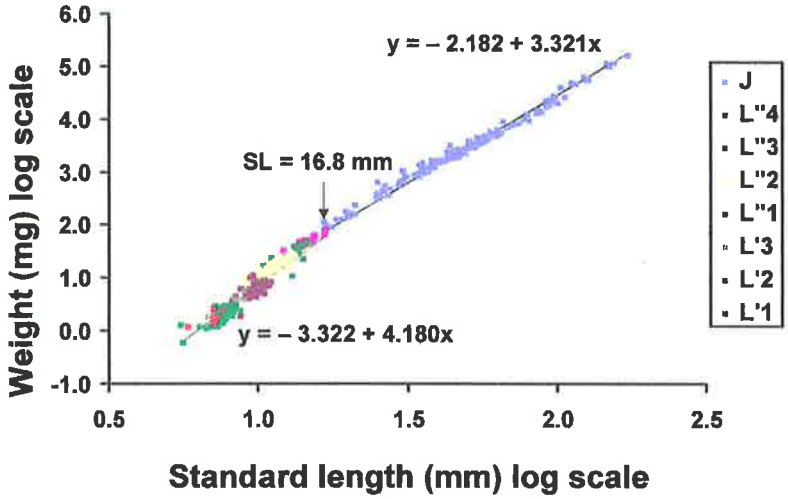

Figure 9.6 Weight-length relationship of carp larvae and juveniles. The arrow indicates the point of break in the regression at the onset of the juvenile period. Terminology after Balon (1958a).

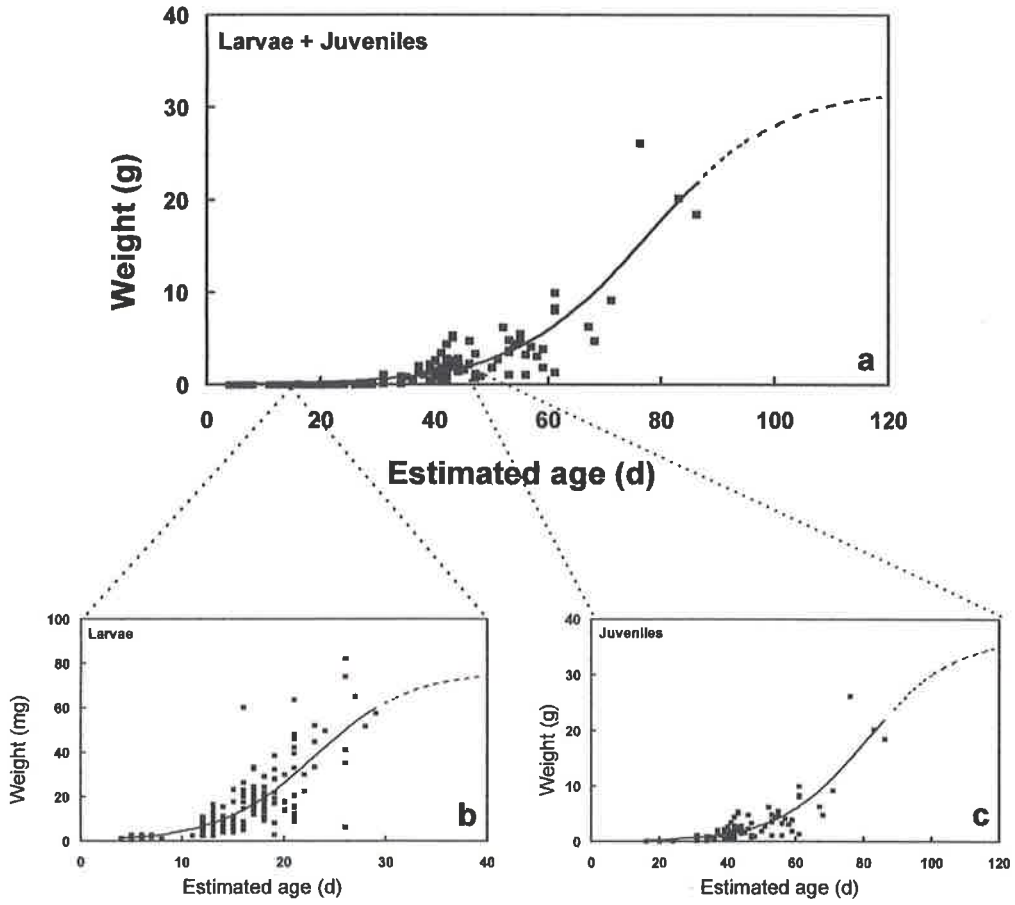

Figure 9.7 Growth in weight of larval and juvenile carp modelled by logistic regressions. Estimated ages are based on otolith microincrement counts. Parameters for all models are given in Table 9.7. (a) Pooled larvae and juveniles; (b) larvae only; (c) juveniles only.

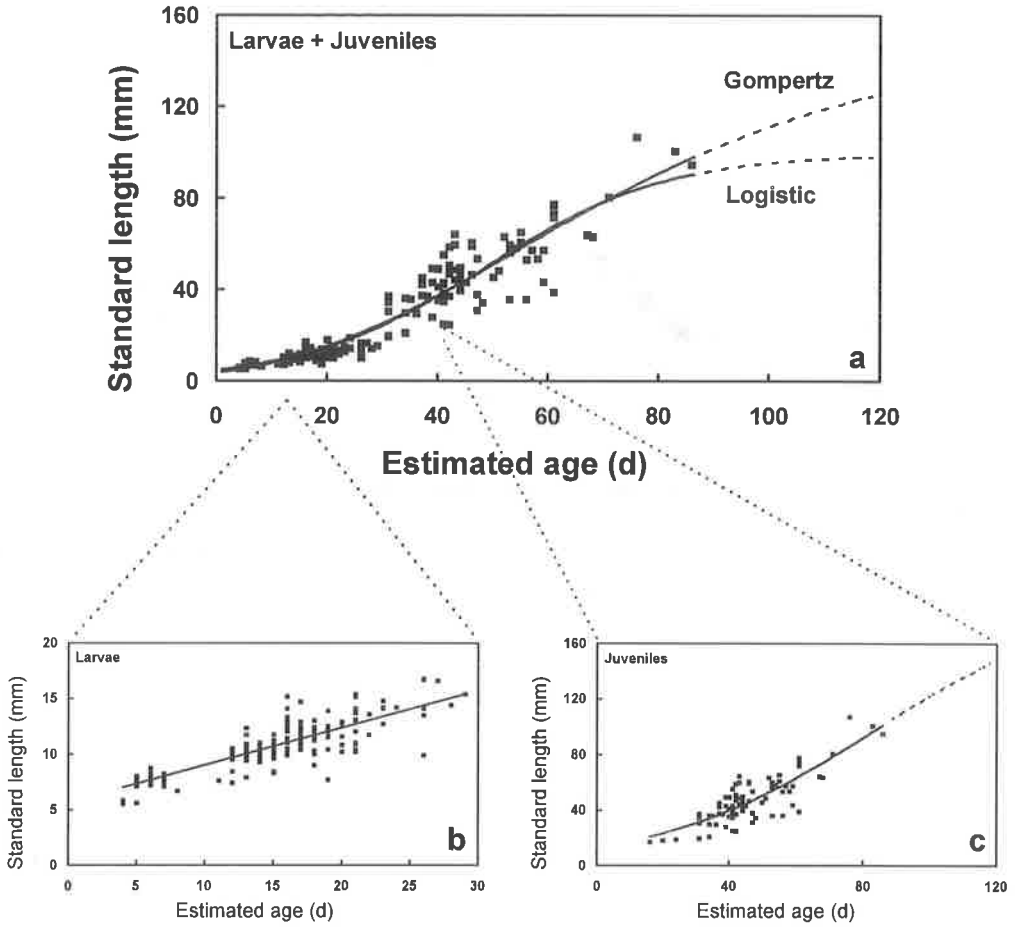

Figure 9.8 Growth in length of larval and juvenile carp in the lower River Murray. Estimated ages are based on otolith microincrement counts. Parameters for all models are given in Table 9.7. (a) Growth of pooled larvae and juveniles fitted by both a logistic and a Gompertz model; (b) growth of larvae only modelled by a simple regression line; (c) growth of juveniles only according to a Gompertz model.

9.4 Discussion

9.4.1 Otolith microincrement analysis

Geffen (1987) summarised the available validation methods for otolith daily increment formation and ranked them by level of reliability. Based on this classification otolith marking and back-calculation of hatching dates, the procedures followed in the present study would be assigned a high and medium-high value, respectively. Also, the high survival of marked fish and clear visibility of fluorescent bands in the corresponding otoliths support previous results (Muth *et al.* 1988) and indicate that the chosen TC dosage and incubation period could be used as a protocol for future laboratory experiments and

mass-marking programs (e.g. Tsukamoto 1985; Lorson and Mudrak 1987; Secor, White and Dean 1991).

No attempt was made in this study to rear and sequentially sacrifice fish from artificially-fertilised eggs, although undoubtedly this is the most desirable validation method (Geffen 1987). This prevented determination of the exact age of first increment formation; instead this was inferred from field observations and literature data. In mid-October 1994 a sudden rise in temperature, accompanied by fine weather and absence of wind, provided ideal spawning conditions for carp at Gurra Lakes. Large numbers of fish congregated in shallow waters and a peak in spawning activity was recorded between 13th–17th of the month (J. Pillar, Loxton, pers. comm.). Based on (a) the mean number of increments (5·2 ± 0·5 SE, Table 9.6) counted in the youngest individuals collected in the first week after spawning (21.X.1994, Table 9.1), and (b) on experimental work reporting formation of otoliths on the second day following activation (approximately one day before hatching) (Peňáz *et al.* 1983), it appears that daily increment formation in carp starts at hatching. It remains to be determined, however, which of the three pairs of otoliths, *viz.* sagittae, lapilli or asterisci, make their first appearance in carp embryos (no indication is given in the literature). Although all otoliths were already visible in the youngest individuals sampled (four increments counted), their formation in teleosts does not appear to be synchronous (e.g. Brothers 1984; Tsukamoto and Kajihara 1987; David *et al.* 1994). It appears that in carp first increment deposition occurs at hatching, although experimental work is needed to confirm or refute this assumption.

A stark variation in increment visibility was noted upon comparison of marked otoliths from laboratory-reared fish with un-marked ones from field-collected larvae and juveniles. This phenomenon, widely reported in the literature (e.g. Warlen 1988; Secor and Dean 1992), has been attributed to a decrease in the magnitude of secondary environmental signals (photoperiod is a primary entrainer) experienced by the fish under laboratory conditions (Campana and Neilson 1985; Jones 1986; Secor and Dean 1992). This may explain why increments in marked otoliths could not be reliably counted after the fifth week following TC-immersion, as their width was probably below the resolution limit of light microscopy (Campana *et al.* 1987). Rearing of larvae and juveniles under experimental conditions more similar to their natural habitat (e.g. in flow-through

enclosures: Øiestad 1981; de Lafontaine and Leggett 1987) may overcome these difficulties.

Although readability was improved in otoliths from field-collected fish, counts could not be reliably made when more than 80–90 increments were present. This was caused by morphological changes in the lapilli reflected by an increased curvature of the sagittal plane (where sections were obtained). M. P. Francis *et al.* (1992) overcame similar problems with ageing young snapper (*Pagrus auratus*) by the combined use of transverse sectioning and SEM examination. However, in that study the sagittae of a non-otophysan fish (*sensu* Fink and Fink 1981; see also Section 2.2.2) were used, so that this methodology may not be applicable to carp lapilli. This contention would be supported by preliminary unsuccessful trials made in the present study involving sectioning through planes other than the sagittal.

9.4.2 Cohort analysis

The application of early developmental steps as an alternative to body size alone has proved effective in studies on the growth and microhabitat use of cyprinids (e.g. Copp and Peňáz 1988; Copp 1990a,b). Cohort analysis, in particular, would benefit from this approach, facilitating spatial and temporal comparisons of inter- an intra-cohort variability in growth.

The two main cohorts (A and B) recognised in this study were separated by a period of about three weeks, and this was supported by back-calculated hatching dates from otolith microincrement counts (Fig. 9.5). Also, further indication of protracted spawning activity in the lakes was given by the presence of fish hatched in late November/early December. Intermittent or batch-wise spawning has often been described in carp (e.g. Ivanov 1971; Janković 1971; Toor and Chauan 1976; Welykochatko 1976), as this species is known for its ability to lay separate batches of eggs in intervals of 1–5 weeks, especially in warmer climates, where the number of successive spawnings can be as high as 5–7 (Welykochatko 1976) (cf. Section 7.4). Also, the number of eggs released in the first batch is higher than in successive depositions (Matsui 1957; Ivanov 1971), and this may explain the lower number of 0+ fish found in main cohort B.

Another reproductive trait typical of carp is the so-called 'repeat spawning within days' (Horvath 1985; Mills 1991), in which portions of a single batch of matured eggs are drawn over several days. It is conceivable that the interaction of this and other factors, including food availability (e.g. Vaas and Vaas-van Oven 1959; Saadi 1965; Matlak and Matlak 1976), temperature oscillations (Konstantinov and Zdanovich 1985) and varying developmental rates (Peňáz *et al.* 1983), will strongly affect intra- and inter-cohort variability in growth. The eight (putative) cohorts (*a–h*) identified here represent therefore only a tentative representation of the actual composition of YOY carp at Gurra Lakes. More intensive sampling programs, preferably daily sampling throughout the spawning period, would provide better resolution and indicate the factors responsible for variation in growth among and within cohorts. For this reason, the larval growth rates given in Tables 9.5 and 9.6, and pictorially represented in Fig. 9.4, should be interpreted with caution.

9.4.3 Growth models

The change in slope in the W-SL relationship calculated at 16·8 mm coincides with the accepted onset of the juvenile period, based on morphological criteria (see Chapter 8). This value appears to be slightly lower compared to the 19 mm reported by Osse (1990) for laboratory-reared fish. Although a shrinkage effect caused by preservation cannot be completely neglected (but see Section 9.2.1), the influence of abiotic and biotic factors experienced by the fish in the natural environment is likely to cause deviations from values recorded under more constant conditions.

Growth in length in pooled larvae and juveniles was equally described by a logistic and a Gompertz curve, which resulted in similar goodness of fit. The value for $SL_\infty = 99$ mm from the logistic model compares relatively well with the mean SL = 111·5 ± 1·3 SE for carp caught in July and September at Gurra Lakes ($n = 17$), whereas the asymptotic value $SL_\infty = 152$ mm from the Gompertz model is in good agreement with the modal lengths around 140 mm reported by Hume *et al.* (1983a). A large variation in the length achieved by carp in the lower Murray before the onset of winter is to be expected as a result of the described spawning habits of this species.

9.4.4 Shooting

The fact that there was no indication of an increase with age or larval developmental step in the several positively-skewed length distributions supports the observations of Nakamura and Kasahara (1955; see also section 8.2.4), namely that faster-growing individuals appear after about 20 d from the start of exogenous feeding (onset of the larva period). Larger samples of juvenile carp would help clarify the role of this phenomenon in wild populations, as it could affect recruitment and ultimately YCS.

10.

EARLY LIFE HISTORY:

OBSERVATIONS ON DIET

> Low amount of yolk is insufficient to build the definitive phenotype and a temporary larva needs to become part of the life history as an external nutrient-acquiring device (highly efficient feeding machine...).
>
> E. K. Balon (1986)

10.1 Introduction

Despite extensive research on the feeding habits and diet composition of 0+ carp in rearing ponds and aquaria (e.g. Alikhuni 1952, 1958; Vaas and Vaas-van Oven 1959; Saadi 1965; Bishai *et al.* 1972; Filatov 1972; Matlak and Matlak 1976; Spataru *et al.* 1980), comparatively little is known about the food of larvae and early juveniles under natural conditions, the majority of studies having concentrated on older individuals, in Australia (Cadwallader 1979; Hall 1981; Hume *et al.* 1983a) and elsewhere (e.g. Moen 1953; Sigler 1958; Bishai *et al.* 1973; Tugarina and Yel'tsova 1974; Stein *et al.* 1975; Toor and Brar 1975; Guziur 1976; Eder and Carlson 1977; Sunder *et al.* 1984; Prochelle and Campos 1985; Ramos *et al.* 1985; Martyniak 1990; Çetinkaya 1992b).

Observations on the food of juveniles in their natural habitat were made by Richardson (1913) and Tugarina and Yel'tsova (1974), while Moen (1953) and Johnson and Dropkin (1994) provided more detailed analyses. However, in none of these studies were ontogenetic changes in diet described. This is of importance if shifts in microhabitat use and resource exploitation, reflecting ontogenetic changes in relative growth and functional morphology, are to be evaluated (see Chapter 8). In the original formulation of the intervals of development in fish Vasnetsov (cf. Balon 1971, 1975b) related the feeding of carp and other species to early life history changes in morphology and physiology. This approach, which allows easier comparisons between populations from different areas than

methods based on body size only, has since been adopted by a number of authors (e.g. Adzhimuradov 1972, and references therein), and will also be followed in this chapter.

The main objective of this investigation was to better define the time of transition from benthivory to planktivory in 0+ carp from the River Murray, and relate it to ecomorphological changes in its life history. This will complement literature data on the functional morphology of larval and juvenile carp indicating that the transition to bottom feeding coincides with the accepted onset of the juvenile period for this species (cf. Section 8.2.3). Finally, another objective of the present observations was to complement casual observations by Hume *et al.* (1983a) in the Murray-Darling Basin.

10.2 Methods

Larval and juvenile carp were collected weekly from Gurra Lakes in October 1994 to January 1995 and processed following methods described in Section 9.2.1 for sampling group III (see also Table 9.1). To minimise possible effects due to daily variation in feeding activity (e.g. Johnson and Dropkin 1994) all collections were made between 10:00–12:00 h. Upon dissection the gut contents of 170 individuals were identified to family or order level under a dissecting microscope at low to medium magnification using keys in Williams (1980), and the number of food items was divided by the Standard Length (SL) of the fish to eliminate size-related differences in stomach capacity (Copp, Warrington and de Bruine 1994). The percentage composition and the number of empty guts were also recorded. Identification of larval developmental steps was as described in Chapter 9. To facilitate comparisons with other studies in which Vasnetsov's notation was used (e.g. Adzhimuradov 1972) the indications given in Balon (1958a) were followed. Thus, in the apterolarva phase the second developmental step (L'2) corresponds to Vasnetsov's step C, and L'3 to D_1. In the pterolarva phase steps L''1, L''2, L''3 and L''4 are instead similar to D_2, E, F and G, respectively. Estimated ages from otolith microincrement counts were as described in Chapter 9.

Table 10.1 **Diet composition of larval and juvenile carp.** The standard length (SL), estimated age (from otolith microincrement counts), percentage of occurrence and number of prey items per SL are reported.

	Developmental interval					
	L'2	L''1	L''2	L''3	L''4	J
SL (mm)						
n	14	17	41	10	12	23
mean	7·64	10·18	11·48	13·35	14·71	36·43
± SE	0·09	0·10	0·15	0·30	0·36	2·51
min	7·1	9·6	9·0	11·7	12·1	16·6
max	8·3	11·0	13·0	14·8	16·7	57·3
Estimated age (d)						
n	11	12	31	5	4	10
mean	9·4	14·8	17·4	20·6	25·8	42·0
± SE	1·3	0·7	0·4	0·9	1·7	2·6
min	5	13	13	18	21	31
max	16	21	22	23	29	61
% composition						
Cladocera	100·0	98·9	98·9	100·0	99·2	83·1
Copepoda		1·1	0·8		0·3	
Decapoda						0·2
Ostracoda						3·5
Corixidae			0·2			0·2
Chironomidae					0·3	0·2
Coleoptera						< 0·1
Hyriidae						< 0·1
Phragmites sp. seeds						12·7
Other seeds			0·2		0·3	0·1
Items per SL						
Cladocera	0·231	0·505	1·088	1·770	1·976	4·939
Copepoda		0·103	0·089		0·068	
Decapoda						0·047
Ostracoda						0·595
Corixidae			0·111			0·057
Chironomidae					0·065	0·046
Coleoptera						0·059
Hyriidae						0·019
Phragmites sp. seeds						1·366
Other seeds			0·088		0·068	0·068

10.3 Results

Empty intestines were found in 53 individuals (30·4% of the sample). These were all larvae in steps L'2 and L''1–L''4. Cladocerans (*Daphnia* sp.) were by far the main food constituent in both percentage composition and number of items per SL (Table 10.1) in larvae and, to a lesser extent, juveniles. Copepods appeared in step L''1, corixids

(*Micronecta* sp.) and seeds in step L''2, chironomids in step L''4. In early juveniles cladocerans were still the most common item consumed, although *Phragmites* seeds were particularly abundant (12·7% of the total composition). Ostracods, corixids, chironomids, decapods (Atyidae and Palaemonidae) and other seeds were also present in smaller quantity. Unlike larvae, the intestines of most juveniles often contained considerable amounts of sand, filling up to one third of the digestive cavity.

10.4 Discussion

Planktivory was the feeding mode of carp throughout the larval period, in accord with Hume *et al.* (1983a), who found microcrustaceans to be the only food group eaten by individuals 15–25 mm SL. This is also supported by literature data, indicating Copepoda and Cladocera as the staple food of carp larvae. Although in small numbers the appearance of corixids in step L''2 (9·0–13·0 mm SL, age 13–22 d) was an indication that larvae progressively acquired the ability to capture more mobile prey. This is supported by Balon's (1958a) observations, showing that larvae 10–11 d post-hatch start feeding on Cladocera.

Adzhimuradov (1972) stated that in step E (≅ L''2) carp become capable of probing the bottom, and reported of studies where benthivory was observed as early as 4–5 d post-hatch, while Balon (1958a) found benthic components in the diet of L''3 larvae. In the present investigation benthic organisms were first recognised after the onset of the juvenile period (cf. Chapter 8), even though microcrustaceans still remained the major food component. Only the presence of large quantities of sand in the digestive tract of juveniles was a clear indication that a bottom-feeding behaviour had been acquired. The low number of benthic organisms accompanied by large amounts of seeds could indicate that juvenile carp were utilising alternative sources of food and continued feeding from the water column possibly as a result of a depauperate benthic fauna. However according to Sibbing (1988) zooplankton is still an important dietary component for 0+ fish in summer, when population densities of chironomids and tubificids decrease.

The objective of this study was to give a summary description of the diet composition of carp during the early life history stages, with special reference to the time of transition to

bottom feeding, and no attempt was made to provide a more detailed analysis for determining the dietary importance of different food categories (e.g. Hyslop 1980), likely to contribute in varying extent to the feeding requirements of 0+ carp. Further research in this direction would help elucidate mechanisms of food selection and qualitative and quantitative changes in diet relative to shifts in microhabitat use.

11.

CONCLUSION AND PROSPECTUS

> One of the most conspicuous fish in commercial catches during my early work on the Slovak part of the Danube (1953 to 1967) was the wild common carp. [...] As a consequence I designed and started a research program on many aspects of the biology of these wild common carp which had been ignored earlier. [...] Subsequently, time has shown that this was the last opportunity for such studies, for towards the end of my 14 years of work on the Danube, these fish became rare and are now listed as endangered.
>
> E. K. Balon (1995b)

Clearly, research is needed to better understand the success of carp as an invasive species in Australia, and to develop ways to limit its detrimental effects. Yet whilst it may be true that "to fully understand the impact of [...] carp, it is necessary to look beyond the immediate aspects of diet, growth and population dynamics and instead focus on ecosystem processes such as nutrient cycling or energy flow" (Roberts *et al.* 1995, p. 1171), it is equally true that knowledge of life history and population dynamics is a prerequisite for both an holistic appreciation of the effects of carp and for prospective methods of control. This thesis is the outcome of work designed to contribute such basic information. It is primarily concerned with methods for determining the ages of individual carp, but contains incidental data on other, related facets of population ecology.

What vulnerable stages are there in the life cycle of carp, specifically ones that might be exploited as a means for population control?

Bruton (1989) observed that non-guarding, altricial fishes like carp typically are successful invaders of abiotically harsh environments, this being especially true of domesticated carp "more able to cope with unpredictable environmental perturbations than their wild ancestor, a highly specialized, precocial form which depends on predictable floods" (Balon 1995b, p. 32). Thus, the absence of predators and the high reproductive potential of carp, among other factors, have significantly contributed to their establishment and spread in

Australia during the last 30 years. On the other hand, the reliance of carp on shallow vegetated areas for spawning, make them vulnerable to hydrological changes. In Balon's (1975a, 1981a, 1990) system of reproductive guilds, the carp is classified as a nonguarding, open substratum egg scattering, obligatory plant spawner (*phytophil*) "adapted to spawn only on freshly flooded plants" so that "if flooded vegetation is not available, spawning cannot take place" (Balon 1975a, p. 834). This applies best to natural populations; there is evidence that domesticated carp may spawn in unvegetated ponds (Toor and Chauan 1976; see also Balon 1995a,b).

Shields (1957) evaluated the effect of water-level fluctuations on carp recruitment in a reservoir in South Dakota, and concluded that timed drawdowns during the spawning season severely limited reproduction. Panek (1987) also pointed to water-level regulation as a control method. In the lower River Murray regulation has transformed the river in a series of weir-pool impoundments (e.g. Walker and Thoms 1993) that potentially would allow easy manipulation of water levels in river-channel and wetland habitats. Indeed, this warrants investigation in other areas of the Murray-Darling Basin (MDB) where timed drawdowns are feasible. It represents an exciting, and so far largely untested, option for management, although it should properly be seen as one of a suite of complementary methods.

In this context, supporting research should focus on (1) reproductive ecology, (2) early ontogeny, and (3) determination of age profiles and Year-Class-Strength (YCS).

It would be vital to know (and be able to predict) the timing of spawning in potential target areas. The problem is unlikely to be simple because, as shown in Section 7.4, the reproductive period and spawning characteristics in carp may vary widely with climatic conditions. In the lower Goulburn River, Hume *et al.* (1983a) reported protracted spawning from October to mid-December, although these always occurred in bursts of 7–15 day intervals of decreasing intensity. In the present study, larval cohort analysis (Chapter 9) has revealed two main cohorts separated by about 4 weeks, including a major spawning event in mid-October and a weaker event in November. The gonadosomatic index for the lower Murray population shows a major peak in October and a secondary one in May, suggesting that carp in this region is a true multiple spawner (cf. Mills 1991),

whereas only one peak occurred in the Goulburn River (Hume *et al.* 1983a). Further studies therefore might assess variation in the reproductive cycle of carp across the MDB and clarify its relation with environmental factors like temperature and hydrological regime. This will be also fundamental for the evaluation of virtually all control methods, including immunocontraception (cf. Roberts 1997).

There are few studies of egg and larval survival in the literature (e.g. Zuromska 1967a,b; Mills 1981). Field and laboratory experiments would indicate the regulating factors, ideally with emphasis on substrate characteristics and exposure to air. Field censuses of the number and density of eggs in the spawning grounds would clarify the relation between egg survival and recruitment. Techniques like Point Abundance Sampling by Electrofishing (PASE) (e.g. Copp and Garner 1996; Garner 1997b) should be evaluated in Australian environments, and perhaps employed to determine the microhabitat use of larvae and 0+ juveniles and the development of habitat suitability indices (Garner 1995). Further, the significance of differential growth among 0+ carp (cf. Chapter 8) for recruitment should be assessed by field observations and laboratory experiments.

Finally, YCS, a variable phenomenon in cyprinid fishes (Mann 1991), should be evaluated in populations from several areas in the MDB and correlated with environmental parameters, including water levels, discharge, rainfall and temperature, so that a model for carp recruitment could be attempted and its applicability tested by future water-level manipulation trials at selected areas in the MDB.

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PAPERS IN SUPPORT

- **Vilizzi, L., and Walker, K. F.** (1995). Otoliths as potential indicators of age in common carp, *Cyprinus carpio* L. (Cyprinidae: Teleostei). *Transactions of the Royal Society of South Australia* **119**, 97–8.

- **Vilizzi, L., and Walker, K. F.** (1997). Age and growth of carp, *Cyprinus carpio* L. (Cyprinidae), in the River Murray, Australia. Validation, consistency of age interpretation and growth models. *Marine and Freshwater Research* (In press.) (This represents the contents of Chapters 2, 3 and 4.)

Addendum

Chapter 2

- Page 13, line 12: EPUs = Eye Piece Units.
- In Figs 2.2–9 the sample sizes are indicated.

Chapter 4

- Page 62, Table 4.2, caption: a_1, b_1, c_1, d_1 are parameters in the model.

Chapter 5

- In Figs 5.3–5 the sample sizes are indicated.

Chapter 6

- Page 103, line 9–11: This assumption may not be true. Recent observations on other cyprinids in the Danube River indicate that only the base of the spine gives accurate readings, thus requiring the death of the fish (Gordon H. Copp, University of Hertfordshire, Hatfield, UK, and Jaroslav Cerny, Slovak Academy of Sciences, Bratislava, Slovakia, pers. comm.).

Chapter 9

- Page 156, lines 13–14: the study by Copp & Penáz (1988) does not per se deal with cohort analysis, but mainly distribution with a bit of general growth information.

References

- The correct citation for Roberts (1997), in press at time of compilation of the thesis, is:
  - **Roberts, J., and Tilzey, R.** (eds) (1997). Controlling carp: exploring the options for Australia. – CSIRO Land and Water, Canberra, 132 pp.
- The following references are missing:
  - **Balon, E. K.** (1993). Dynamics of biodiversity and mechanisms of change: a plea for balanced attention to form creation and extinction. *Biological Conservation* **66**, 5–16.
  - **Swee, U. B., and McCrimmon. H. R.** (1966). Reproductive biology of the carp, *Cyprinus carpio* L., in Lake St. Lawrence, Ontario. *Transactions of the American Fisheries Society* **95**, 372–80.

Erratum

Acknowledgments

- Page xiv, line 15: **Leanne** is **Lianne**

Chapter 2

- Page 12, lines 23–24: **Secor, Dean and Laban 1991** is **Secor *et al.* 1991a**
- Page 13, lines 4: **Secor, Dean and Laban (1991)** is **Secor *et al.* (1991a)**
- Page 14, line 17: **false annuli** is **false annuli (*pseudoannuli*)**
- Page 28, line 20: **Jones'** is **Jones' (1974)**

Chapter 4

- Page 60, line 17: **Secor, Dean and Laban 1991** is **Secor *et al.* 1991a**
- Page 64, Table 4.3, heading: draw two separate lines below FL (mm) and below W (g) to link more clearly the above headings to the statistics below (Mean, ±SE, Min, Max)
- Page 77, line 15: **in this study** is **in the present study**
- Page 78, lines 1–2: **in this study** is **in the present study**

Chapter 5

- Page 91, Table 5.4, heading: draw two separate lines below FL (mm) and below W (g) to link more clearly the above headings to the statistics below

Chapter 6

- Page 102, line 8: **annuli** is **annulus**

Chapter 7

- Page 106, line 3: **pond** is **aquarium**
- Page 114, Table 7.2, caption line 1: **aranged** is **arranged**
- Page 114, Table 7.2, rows 1 and 2, column 7 (*n*),: add number **1** in each of the two cells
- Pages 120–124, Table 7A continued, heading 6 (FL_{max}) add **(mm)** underneath (cf. heading on page 119, first part of table)

Chapter 8

- Page 131, line 12: **Copp, Guti, Rovný and Cerný 1994** is **Copp et al. 1994b**

Chapter 9

- Quotation, line 4: **D. H. Secor, J. M. Dean and E. H. Laban (1991)** is **D. H. Secor et al. (1991a)**
- Page 138, line 13: **Secor, Dean and Laban 1991** is **Secor et al. 1991a**
- Page 147, Figure 9.4, above *x*-axis: the final sampling date **21 Oct** is **3 Dec**
- Page 151, Table 9.7, row 3, column 4: superscript **C** is superscript **B** (i.e., $\mathbf{36{\cdot}602 \pm 13{\cdot}780^{C}}$ is $\mathbf{36{\cdot}602 \pm 13{\cdot}780^{B}}$)
- Page 152, Table 9.7 (continued), footnote B: **Weight in mg** is **Weight in g**
- Page 155, lines 1–2: **Secor, White and Dean 1991** is **Secor *et al.* 1991b**

Chapter 10

- Page 160, lines 17–18, **(Copp, Warrington and de Bruine 1994)** is **(Copp *et al.* 1994a)**

References

- Page 180, line 16: **(1994)** is **(1994a)**
- Page 180, line 19: **(1994)** is **(1994b)**
- Page 182, line 11: **Ekmerçi** is **Ekmekçi**
- Page 183, line 25–26: *Hydrobiologia*, **206** 19–28 is *Hydrobiologia* **206**, 19–28
- Page 191, Line 6: **34–36** is **34–6**
- Page 191, line 16: **16** 19–28 is **16**, 19–28
- Page 191, line 19: *Journal of Ichthyology*, **33**, 148–53 is *Journal of Ichthyology* **33**, 148–53
- Page 191, line 20: **(1977)*** is **(1977)*** (i.e., asterisk is not superscript)
- Page 194, line 22: **(1953)** is **(1953)***
- Page 196, line 17: **Reserach** is **Research**
- Page 199, line 24, volume number 21 is 27 (i.e., *Bulletin of the Japanese Society of Scientific Fisheries* **27**, 73–76)
- Page 205, line 20: **50–56** is **50–6**
- Page 206, line 10: **(1991)** is **(1991a)**
- Page 206, line 13: **(1991)** is **(1991b)**
- Page 215, line 12: **Czeck** is **Czech**