



CHAPTER 3

Age-Based Studies on Coral Reef Fishes

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I. Introduction

There exists a vast literature on the age and growth of fishes (Hilborne and Walters, 1992; Secor *et al.*, 1995a). Much of this reflects a century of research on the major stocks of exploited fishes, primarily those of temperate water, open-ocean, and deep-water habitats. In contrast, there is relatively little age-based demographic information available on coral reef fishes. There are a number of reasons for advocating a more comprehensive understanding of the age-based demography of coral reef fishes. The primary reason relates to the increasing exploitation of reef fish stocks by both artisanal and commercial fisheries, some of the latter (e.g., the live fish trade) being internationally based (Jennings and Polunin, 1996; Birkeland, 1997a; Lee and Sadovy, 1998). Demographic information will provide a better basis for reef fish conservation and management.

Assembling age-based data for coral reef fishes will be a complex task. Most species have wide distributions spanning significant geographic gradients (Myers, 1999). Within localized areas a species will occur in a variety of habitats. As poikilotherms, fish are sensitive to prevailing environmental conditions (Atkinson, 1994). Growth and life history patterns of reef fishes can be expected to vary, at geographic, latitudinal, and habitat scales. An emerging picture of the demography of reef fishes suggests three things. Many taxa will be relatively long-lived (Munro and Polunin, 1997), with life-spans exceeding 15 years; they will have highly distinctive patterns of growth and age-based demographic

features will show a strong phylogenetic structure (Hart and Russ, 1996; Newman *et al.*, 1996; Choat and Axe, 1996; Choat *et al.*, 1996). Most importantly, it is becoming evident that size and age in many taxa of reef fishes may be decoupled (Hart and Russ, 1996; Newman *et al.*, 1996, 2000b). Although reef fishes occur in a wide range of sizes, large size may not correlate with longevity. In addition, many species of coral reef fishes may have complex sexual ontogenies, which can in turn influence size and sex-specific growth patterns (Sadovy and Shapiro, 1987; Choat *et al.*, 1996).

The arguments for developing an age-based demography of coral reef fishes are compelling. Estimates of age-specific variation in growth, reproductive, and mortality rates are the foundation of population biology (Cole, 1954; Stearns, 1992). Knowledge of age structure and mean and maximum life-spans is an important element of fisheries science (Beverton and Holt, 1957; Beverton, 1992; Roff, 1984). Warner and Chesson (1985) suggest that under conditions of fluctuating recruitment rates extended life-spans may be expected. If populations of reef fishes do display extended life-spans, with individuals accumulating in older age classes, then these will be especially vulnerable to exploitation (Musick, 1999a). In deep-sea fishes otolith increments have revealed a picture of long life, slow growth, and populations dominated by older individuals (Smith *et al.*, 1995; Stewart *et al.*, 1995; McFarlane and Beamish, 1995). Similar conditions may well occur in many coral reef fish taxa.

As an introduction to the major sections of this chapter we identify three issues that are important for a better understanding of age-based dynamics for coral reef fishes: (1) the methods used in age-based approaches, (2) tropical/temperate comparisons of fish faunas and the distinctive features of coral reef fishes, and (3) the issue of phylogenetic influences on patterns

of growth and longevity among the perciform lineages of coral reefs.

A. Development of Age-Based Approaches

Estimation of fish age is best achieved through analysis of incremental structures that occur in otoliths. The most useful information is provided by counts of annuli obtained from sections of sagittal otoliths. The choice of sagittal otoliths follows from the demonstration that they continue to accrete calcareous material in a linear fashion throughout the life of the fish, regardless of the pattern of somatic growth (Secor *et al.*, 1995a). This also provides a means of obtaining estimates of age from otolith weight data (Worthington *et al.*, 1995). The patterns of spatial variation in fish growth indicate, however, that it will be necessary to calibrate the relationship between age and otolith weight for each sampling locality.

Other structures such as scales, fin spines, and vertebral centra may also record annual increments, but there are drawbacks to their use for tropical fishes, especially if species are long-lived. The most conveniently sampled structures are scales. However, there may be difficulties in detecting annuli near the margins of scales in long-lived species (Secor *et al.*, 1995a). Some species shed scales easily and hence possess numerous replacement scales that do not record the entire growth history, and many taxa such as acanthurids do not possess scales suitable for reading. Analysis of otolith structure, composition, and weights remains the most effective method for aging of fishes. For long-lived species the most unbiased results are obtained from sectioned rather than whole otoliths (Secor *et al.*, 1995a).

Despite the capacity of otoliths to provide a basis for age estimation, there have been relatively few attempts to use this approach for coral reef fishes. This reflects in part the initially discouraging results of otolith examination in tropical fishes (Munro, 1983). Moreover, many biologists based in the tropics have not had access to appropriate laboratory facilities. Length-based analyses of growth (Pauly, 1998) and reproduction (Sadovy, 1996) have been important in developing a demographic data base for reef fishes. However, if the relationship between size and age is decoupled then length-based analyses may be misleading, especially for long-lived species (Hilborne and Walters, 1992).

Daily otolith increments have proved useful for the analysis of growth patterns in larval juvenile and short-lived fishes (Chambers and Miller, 1995). However,

there may be difficulties associated with the reading of daily rings in fishes living longer than 10 years. For these, annual increments are more appropriate. Fowler (1995) examined sagittal otoliths in 28 species of coral reef fishes and detected interpretable structures suggesting annual increments in 25 of these. Fowler also reviewed information on the validation of annual increments in coral reef fishes. Of 35 instances in which validation has been attempted, only twice was validation not achieved because no periodicity in increment structure was detected. In four examples validation was recorded as "preliminary" only.

Since Fowler's review a number of additional validations of annuli have been achieved for coral reef fishes (Hart and Russ, 1996; Newman *et al.*, 1996; Choat and Axe, 1996; Choat *et al.*, 1996; Manickchand-Heileman and Phillip, 2000; Cappo *et al.*, 2000; Hernamen *et al.*, 2000; Pilling *et al.*, 2000). The most comprehensive studies have been on the family Lutjanidae, for which validation was achieved for 11 coral reef species (Cappo *et al.*, 2000; Newman *et al.*, 2000a,b). Combined with previous estimates of age and growth in reef-associated lutjanid fishes (Loubens, 1980; Manooch, 1987) and work on East Pacific species (Rocha-Olivares, 1998), these studies provide an informative picture of one group of coral reef fishes. Lifespans in excess of 30 years were recorded in a number of species.

The most cost-effective approaches to validation of increments as annual check marks are through chemical markers (Hart and Russ, 1996; Newman *et al.*, 1996; Choat and Axe, 1996; Choat *et al.*, 1996; Cappo *et al.*, 2000; Hernamen *et al.*, 2000) or marginal increment analysis (Manickchand-Heileman and Phillip, 2000; Pilling *et al.*, 2000). There are three types of difficulties in using these approaches for coral reef fishes. First, although examples of sagittal otoliths with clearly defined annuli can be obtained from coral reef fish sampled at low latitudes, the consistency with which rings are displayed may be poor relative to fish from temperate waters (Fowler, 1995). Second, many coral reef fish species are globally abundant but are rare on a local scale (Munday and Jones, 1998). This limits the opportunity for tagging and retrieving chemically marked fishes for validation studies. Third, much coral reef research is still expeditionary in nature. Year-round access is often difficult, a fact that limits the opportunity for marginal increment analysis as a validation tool. However, the last of these difficulties is rapidly vanishing as tropical fisheries authorities realize the value of such information.

A number of additional validation options are available for coral reef fishes. Major environmental

signals at known dates, such as those generated by El Niño events, may modify growth schedules of fishes and be incorporated into otolith structures (Meekan *et al.*, 1999). Age determinations based on elemental or isotopic concentrations in otoliths provide a technically demanding but potentially valuable approach to the issue of validating the temporal basis of otolith increments (Campana, 1999). Annual periodicity in Sr:Ca ratios derived from the analysis of sagittal otoliths has been reported for one coral reef species (Sadovy and Severin, 1992). Variation in oxygen isotope cycles reflecting annual patterns of temperature provides a potential avenue for validation (Campana, 1999). However, their utility for fishes that occur in environments with limited annual temperature ranges has yet to be tested. Chemical techniques require sophisticated laboratory facilities. For many tropical countries marginal increment analysis may be the most cost-effective means of age validation.

The chemical dating of otoliths based on the decay of radioisotopes provides an accurate method for determining age in fishes, especially longer lived species (Campana, 1999). To date, the main focus for such age determinations has been on long-lived temperate water and deep-water fishes. Work on temperate sciaenid fishes (Pereira *et al.*, 1995; Jones and Wells, 1998) based on radiometric validations has provided estimates of life-spans in the order of 60–110 years. Kalish (1993) suggested the analysis of radiocarbon derived from nuclear testing and incorporated into the otolith matrix as an objective and accurate age validation procedure. The study of Kalish *et al.* (1996) is particularly significant in that it provided age estimations of *Thunnus maccoyi* in excess of 30 years, 50% longer than estimations that had been incorporated into management models for this species. However, age groups of fishes most sensitive to nuclear bomb radiocarbon are those born between 1958 and 1965 (Campana, 1999). Even long-lived fishes are now starting to pass beyond this window of opportunity.

Future validation of age estimates in coral reef fishes must also investigate the use of stable isotopes and radioisotopes, ideally based on international collaboration with respect to analytical facilities. Despite the complexity of these techniques and their interpretation (Campana, 1999), they hold the greatest promise of precision and objectivity of age determinations, especially when used in association with more traditional approaches. Problems associated with viewing of increment structures in individual fishes from low latitudes may be resolved by using validation techniques based on a combination of chemical markers and otolith growth models (Cappo *et al.*, 2000).

B. Tropical–Temperate Comparisons

The majority of our information on fish growth patterns and age-based population dynamics comes from the study of the great temperate water fish stocks, including clupeoids, gadids, and pleuronectids (Beverton and Holt, 1957). There is now a comprehensive information base on these groups, a reflection of their prior abundance and economic importance, but relatively little information on shallow-water perciform fishes (Beverton, 1992; He, 2001). Are studies of temperate groups an appropriate foundation for the development of an age-based approach to the demography of coral reef fishes dominated by perciformes?

Coral reef fishes and their habitats display highly distinctive characteristics that differ substantially from temperate groups listed above. A number of reef fish taxa, including acanthurids and lutjanids, display distinctive age-specific growth patterns (Newman *et al.*, 1996; Choat and Axe, 1996). Young fish grow rapidly until they reach maturity then abruptly reduce somatic growth. This results in a highly characteristic “square” growth curve with numerous age classes accumulating in a few size classes. In contrast, tropical serranid fishes of the genus *Plectropomus* show relatively short life-spans and growth curves more consistent with those displayed by clupeoid, gadid, and pleuronectid fishes (Beverton, 1992). Both types of growth curves are illustrated in Fig. 1. The “square” growth curves are characteristic of a number of coral reef fishes, including lutjanids and acanthurids, and may generate age-specific properties very different from those seen in the more characteristic growth curves of temperate species.

The physical structure and hydrodynamic environment of coral reefs are more complex (Boehlert, 1996) than are those of higher latitudes. Fisheries biologists in temperate waters can access a substantial body of information on the gyres and current systems that influence movement patterns and larval transport of fishes (Sinclair, 1988). Fisheries research in higher latitudes has built on networks of fisheries laboratories and workers with collaborative research agendas. The establishment of age-based approaches has been one of these. The result has been a common approach to methodologies and an integrated perspective on fish population dynamics. For example, knowledge of the hydrodynamic environment of the coastal seas and of the seasonal patterns of spawning in temperate species has played an important part in the recognition of fish stocks and their distinctive demographic characteristics (Beverton and Holt, 1957; Harden-Jones, 1968; Cushing, 1976; Isles and Sinclair, 1982).

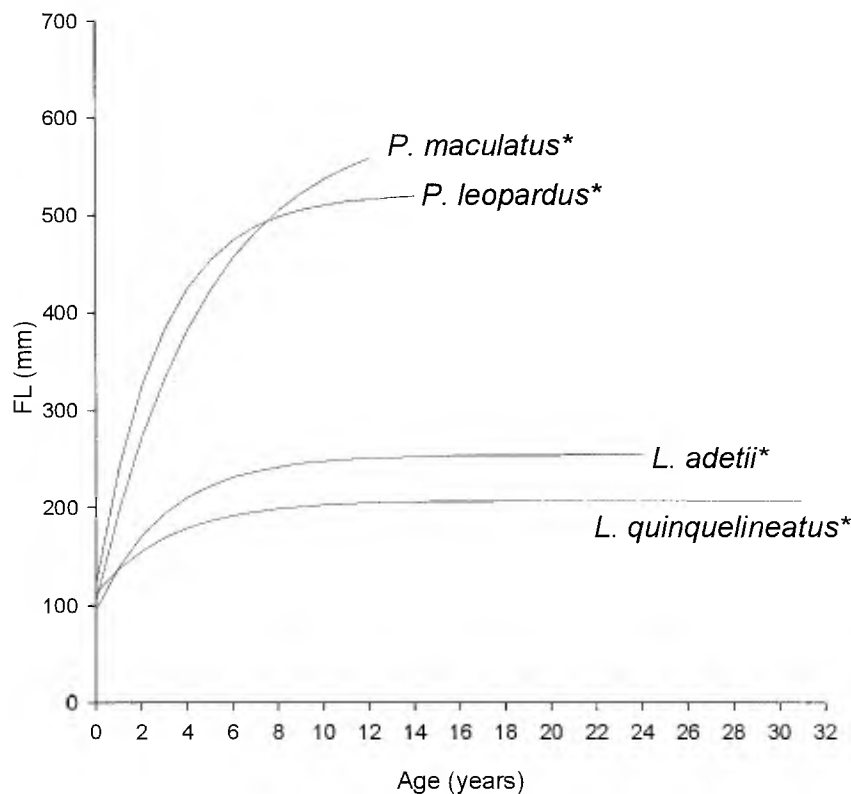


FIGURE 1 von Bertalanffy growth curves fitted to size-at-age data for two species of *Plectropomus* and two species of *Lutjanus* to show contrasting growth and longevity patterns. *Plectropomus* data from Ferreira and Russ (1992, 1994); *Lutjanus* data from Newman *et al.* (1996). *, Age increments validated.

In contrast, fisheries for coral reef species are often localized, artisanal, and targeted to multispecies assemblages (Dalzell and Adams, 1997; Jennings and Lock, 1996). This reflects the widely distributed, circumtropical nature of coral reefs and their accessibility through a variety of fishing methods. There have been limited opportunities for the development of common methodologies, or to focus research on a few representative taxa. The complexity of the hydrodynamic environments of coral reefs has made analysis of dispersal patterns difficult (Leis, 1991a; Boehlert, 1996), although work by Jones *et al.* (1999) has revealed a surprising degree of recruitment back to natal reefs. Studies of genetic structuring (Planes, 1993; Shulman and Bermingham, 1995) are providing a perspective on levels of gene flow and connectivity in reef fish populations. However, there is still little information on the spatial variation in demographic structure of reef fish populations or on the degree of concordance between demographic and genetic characteristics.

In the absence of a comprehensive understanding of age-based dynamics the use of length-based approaches has provided a substantial data base and the opportunity to compare the life histories of temperate and tropical fishes (Pauly, 1998). Such a comparison was

provided by Pauly (1994), who argued that tropical fishes have smaller asymptotic sizes, shorter life-spans, higher fecundities, and higher natural mortalities.

The argument that tropical fishes possess smaller mean sizes, shorter life-spans, and higher mortality rates compared to their temperate counterparts has considerable significance for coral reef fisheries. However, it is unclear that the exploited fishes of coral reefs have a smaller average asymptotic (maximum) size compared to their temperate water counterparts. Coral reefs harbor numerous taxa of small fishes, especially in the speciose families Gobiidae, Blennidae, Apogonidae, and Pomacentridae. In these families the maximum size rarely exceeds 100 mm standard length (SL). However, in a number of abundant but heavily exploited taxa (Acanthuridae, Haemulidae, Labridae, Lethrinidae, Lutjanidae, Scaridae, and Serranidae) the mean length for species is close to or greater than 300 mm SL. Moreover, the maximum size achieved by species ranges from 100 to 1000 mm SL in many families (Munday and Jones, 1998; Randall *et al.*, 1990; Böhlke and Chaplin, 1993). Although tropical fish faunas harbor many small species, the distinctive feature is the range of sizes achieved within a taxon, rather than the mean size.

Second, is there a consistent relationship between longevity and size? In a preliminary analysis of 38 taxa, Thresher (1991) identified a positive relationship between maximum size and maximum age. However, additional aging has revealed long life-spans in small species (Newman *et al.*, 1996; Choat and Axe, 1996). A phylogenetic component in the distribution of life-spans would introduce additional variability into size/longevity relationships. For example, small species of lutjanids may have slower growth rates and longer lives compared to large serranids of the genus *Plectropomus* (Ferreira and Russ, 1992, 1994; Newman *et al.*, 1996).

Finally, are tropical reef fishes more fecund than their temperate equivalents? Comparisons between tropical and temperate species are difficult to obtain. Intuitively it seems that tropical fishes should produce more eggs per year compared to temperate fishes, because the latter may be constrained to seasonal breeding episodes. For example, Davis and West (1993) suggest a monthly frequency of up to 22 spawning episodes for a tropical lutjanid. Robertson *et al.* (1999) monitored population spawning behavior of *Thalassoma bifasciatum* and found that an average of 75% of mature females spawn on a given day but that the clutch size among such females averaged only approximately one-third of the size-specific maximum.

What is clear is that tropical fishes display a wide range of spawning periodicities (Robertson, 1991a; Sadovy, 1996; Robertson and Kaufman, 1998) and that it will be difficult to make general comparisons with temperate species. Two useful comparative measures can be identified: (1) annual fecundity as a percentage of body weight—this may be much higher in species that spawn frequently throughout the year compared to those that spawn less frequently, because clutch weight does not exceed 35% of total weight, even among species that spawn only once per year (Burt *et al.*, 1988; Robertson, 1990); and (2) lifetime fecundity (Sadovy, 1996; Jones and Wells, 1998). However, there are few estimates of this for any tropical fishes and particularly for the larger species. Warner and colleagues have provided robust estimates of lifetime fecundities for *Thalassoma bifasciatum* (Warner, 1984a). Doherty (1983b) has also estimated lifetime fecundity for a pomacentrid and Kuwamura *et al.* (1996) for gobies. There are few estimates available for the larger species of coral reef fishes. Reproductive patterns in coral reef fishes are complex, with protogyny the dominant mode in many abundant species. With the exception of *Thalassoma bifasciatum* the age distribution of reproductive effort in protogynous species is not well understood in any tropical fish.

C. Comparison of Age and Growth Patterns among Lineages

Tropical reef fish faunas include several distinctive evolutionary lineages (Tyler *et al.*, 1989; Helfman *et al.*, 1997) with different morphologies and reproductive modes. The majority of species within this group are perciformes with dispersive larvae (Sale, 1991a). Beyond this it is not possible to generalize life history characteristics across lineages and the great diversity precludes detailed demographic analysis by taxon. However, estimates of longevity among the different lineages can provide a basis for identifying different life histories in reef species and their capacity to respond to exploitation.

To illustrate the diversity of life histories in reef fishes we will compare data on size and age among two ecologically similar but phylogenetically distinct lineages of reef fishes. The lineages chosen, surgeonfishes (Acanthuridae) and parrot fishes (Scaridae), are speciose groups of percomorph fishes, representatives of the suborders Acanthuroidei and Labroidei, respectively. The Acanthuridae are a monophyletic and highly distinctive lineage within the acanthuroid fishes (Tyler *et al.*, 1989; Winterbottom and McLennan, 1993; Tang *et al.*, 1999). The scarid and labrid fishes in association with the odacids display a number of structural characteristics of the pharyngeal apparatus that support the argument of the existence of a single major lineage of labroid fishes (Kaufman and Liem, 1982). However, evidence for monophyly, especially molecular information, remains a key issue in the analysis of labroid phylogeny (Johnson, 1993). Species in both lineages share a number of similar ecological features (Choat, 1991). The size ranges and numbers of species in each family are almost identical (Munday and Jones, 1998), although the Acanthuridae have a greater mean size. Both are circumtropical in distribution with paleontological evidence of occurrence in tropical reef environments from the Eocene (Acanthuridae) and the Miocene (Scaridae) (Bellwood, 1994, 1996a,b). Although all scarids are basically benthic-feeding-grazers, acanthurids show greater ecological diversity. A number of species, especially in the genera *Naso* and *Acanthurus*, are midwater plankton feeders as opposed to grazers of shallow reef substrata (Jones, 1968).

Each lineage has a distinctive set of morphological and structural characteristics. Scarid fishes exhibit typical labroid features of a fusiform body with a total length to greatest body depth ratio of ~2.2 and a substantial skeletal investment in a pharyngeal apparatus with a grinding mode of action. Acanthurid fishes are laterally compressed, with a total length to

greatest body depth ratio of ~ 2.9 , have a muscular gizzard rather than a grinding pharyngeal apparatus, and have a highly distinctive set of single knives or multiple fixed blades on the tail base. Further details of the structural characteristics and evolutionary relationships within each group may be found in a variety of publications (Bellwood, 1994; Winterbottom and McLennan, 1993). Despite differences in structural and morphological features the most abundant taxa in each lineage display similar feeding patterns (Clements and Choat, 1995; Choat and Clements, 1998).

Collectively these two taxa represent a substantial proportion of reef fish biomass, with individual taxa, especially those in the genera *Scarus*, *Acanthurus*, and *Ctenochaetus*, being the most abundant fishes in the size range of 200–400 mm SL. Both groups are of major ecological importance in reef dynamics, with grazing activities implicated in removal of algal biomass and bioerosion (Bellwood, 1995a; Bruggemann *et al.*, 1994b; Steneck, 1988). The pattern of ecological similarities and structural and reproductive contrasts makes these abundant reef fishes good candidates for a comparative investigation of life history and demographic features. The key variables are size distributions, growth rates, patterns of growth, age structures, and maximum life-span in populations of representatives of each taxon.

We also refer to published data available for other groups of reef fishes, especially lutjanids and serranids (Manooch, 1987; Fowler, 1995; Sadovy *et al.*, 1992), a reflection of their traditional importance in reef fisheries. However, the expanding scale of reef fishing (Dalzell and Adams, 1997; Jennings and Lock, 1996) has resulted in an increased pressure on other groups of large reef fishes for which we have relatively little demographic information. Those abundant fishes, usually identified as coral reef herbivores, now bear the brunt of increasing fishing on many reef systems.

In summary, age-based approaches will provide a sound foundation for the analysis of reef fish population dynamics. However, the resultant picture is likely to be highly complex. This reflects both the nature of the reef environment and the diverse perciform assemblages that inhabit coral reefs and sustain multispecies fisheries. Attempts to compare tropical and temperate fish faunas will be confounded by this complexity, due to decoupling of age and size and the diverse reproductive behaviors and ontogenies of reef fishes. Phylogenetic factors are likely to contribute strongly to the diversity of life histories and reproductive modes seen in reef fishes.

II. Hypotheses for Testing and Refinement

Our intention for the remainder of this chapter is to present the issues as hypotheses for further testing and refinement. The most desirable outcome would be more attempts to estimate ages and the validation of age-based life history features in coral reef fish. Our approach is guided by three observations: (1) there are relatively few examples of size-at-age data for coral reef fishes, although the published information suggests a variety of growth patterns and maximum life-spans. (Manooch, 1987); (2) lineages of reef fishes differ considerably with respect to mean life-span and reproductive mode (Munday and Jones, 1998); and (3) many coral reef fishes are protogynous, with populations composed of large males and smaller females, which intuitively one would expect to be older and younger, respectively (Helfman *et al.*, 1997). However, for most protogynous species we lack information on age-specific growth rates, age structures, and life-spans that would allow a test of this expectation.

Further discussion will follow the sequence of the five questions listed below, using acanthurids and scarids as examples.

- What is the distribution of life-spans in the chosen groups and are they consistent or do they vary among regions?
- Is there a predictable relationship between body size and maximum age and is any such relationship consistent among taxa?
- Are there taxon-specific patterns in growth curves generated by size at age data among the different groups?
- Are maximum age estimates and growth parameters consistent over geographic and environmental gradients in the same taxa?
- In protogynous species are size and age distributions concordant?

A. What Is the Distribution of Life-Spans among Acanthurids and Scarids: Are They Consistent or Do They Vary among Regions?

To investigate this question we have compared species of acanthurids and scarids sampled from the western Pacific and the tropical Atlantic regions. Four questions are posed. (1) Are there taxon-specific

differences in longevity among these groups? (2) Are taxon-specific differences consistent between regions? (3) Are there overall differences in longevity among regions? (4) Are these differences reflected in otolith dimensions in each taxon and region?

In order to compare life-spans we used an estimate of maximum age based on the mean of the upper 25% of the annuli counts for each species. Given the relatively small sample sizes for some species this provided a more robust and conservative estimate than an estimate of T_{\max} based on the oldest individual in the sample (Beverton, 1992). To examine the relationship between otolith dimensions and age we used the ratio of the distance from the otolith core to the edge of the proximal margin of the sagittal section (height) to the greatest distance across the dorsal to ventral surfaces of the section (width). The orientation is shown in Fig. 2. The ratio of height to width was used because substantial differences in sagittae size and morphology existed between the two taxa. We made two assumptions about otolith growth. First, sectioned sagittal otoliths will show an increase in thickness (defined as height in Fig. 2) throughout the life of the fish as increments are added through time. Second, the rate of thickening will decrease as distance between increments is reduced in older fishes. The material for the analysis was collected from coral and rocky reefs in the West Pacific Great Barrier Reef (GBR) and the western and central regions of the tropical Atlantic. The taxa sampled are representative of the abundant species at each locality (Meekan and Choat, 1997).

A plot of relative otolith dimensions vs. age revealed a clear structure in the data set (Fig. 2A). The relative height of sagittal otoliths increases in a predictable manner with increasing age even among distinct taxa. The ratio of otolith sectional height to width increased as a power of the mean maximum age, showing that the rate of accretion of otolith width declines as a function of maximum life-span. The specific points from this data set were as follows:

1. Acanthurids had consistently greater maximum ages compared to scarids both in the tropical Atlantic and the West Pacific. With the exception of *Bolbometopon muricatum* (the largest scarid), scarids had maximum ages of <20 years, with most being considerably less than that. Most acanthurids are long-lived and a number of species exceed 30 years.

2. Scarids of the genus *Sparisoma* (tropical Atlantic) had low maximum ages relative to members of the genus *Scarus* from the West Pacific. This could represent both locality and phylogenetic sources of variation.

3. Acanthurids in the West Pacific achieve greater maximum ages than do tropical Atlantic species. Atlantic acanthurids are relatively short-lived, especially those from the Caribbean proper.

4. There are differences in the pattern of otolith growth relative to age in tropical Atlantic vs. West Pacific fishes (Fig. 2A). The relationships are adequately represented by power curves. The patterns were driven by species of the genus *Acanthurus* (Fig. 2B). Atlantic species have relatively thicker otoliths compared to their West Pacific counterparts.

The maximum ages recorded for acanthurids approach those seen in other shallow-water long-lived fishes such as sciaenids (Jones and Wells, 1998), although they are less than those of deep-sea fishes. Atlantic and West Pacific members of the same taxa appear to have shorter life-spans and different otolith growth allometries. A more direct interregional comparison of life-spans and otolith dimensions for scarids must await increased sampling of Atlantic species of the genus *Scarus*.

B. Is There a Predictable Relationship between Body Size and Maximum Age?

Is size a useful proxy for age? The estimates of maximum age provide an opportunity to examine the relationship between size and age in each group (Fig. 3). Estimates of T_{\max} (Beverton, 1992) and the von Bertalanffy parameters for the acanthurid and scarid populations used in Fig. 3 are shown in Table 1. For scarids there is a predictable pattern, with 64% of the variance in maximum age explained by increase in size. Increased sampling will likely tighten this relationship. For example, more comprehensive collections of *Scarus rubroviolaceus* from the Seychelles indicated maximum ages of 18–20 years for fish 400 mm SL. (E. Grandcourt, personal communication). This would make this species consistent with other large scarids (*Chlorurus microrhinos*, *Cetoscarus bicolor*) in terms of size/age relationships. We would also expect the *B. muricatum* age estimates to shift to the right because the preliminary collections did not sample the largest individuals that occur on the Great Barrier Reef. However, it should be pointed out that some smaller species, most notably *Scarus frenatus*, are older than “expected” for their maximum size.

In contrast, no relationship between age and size is discernible among the species of acanthurids. Very small species such as *Zebrasoma scopas* and *Acanthurus nigricans* displayed greater ages than did the

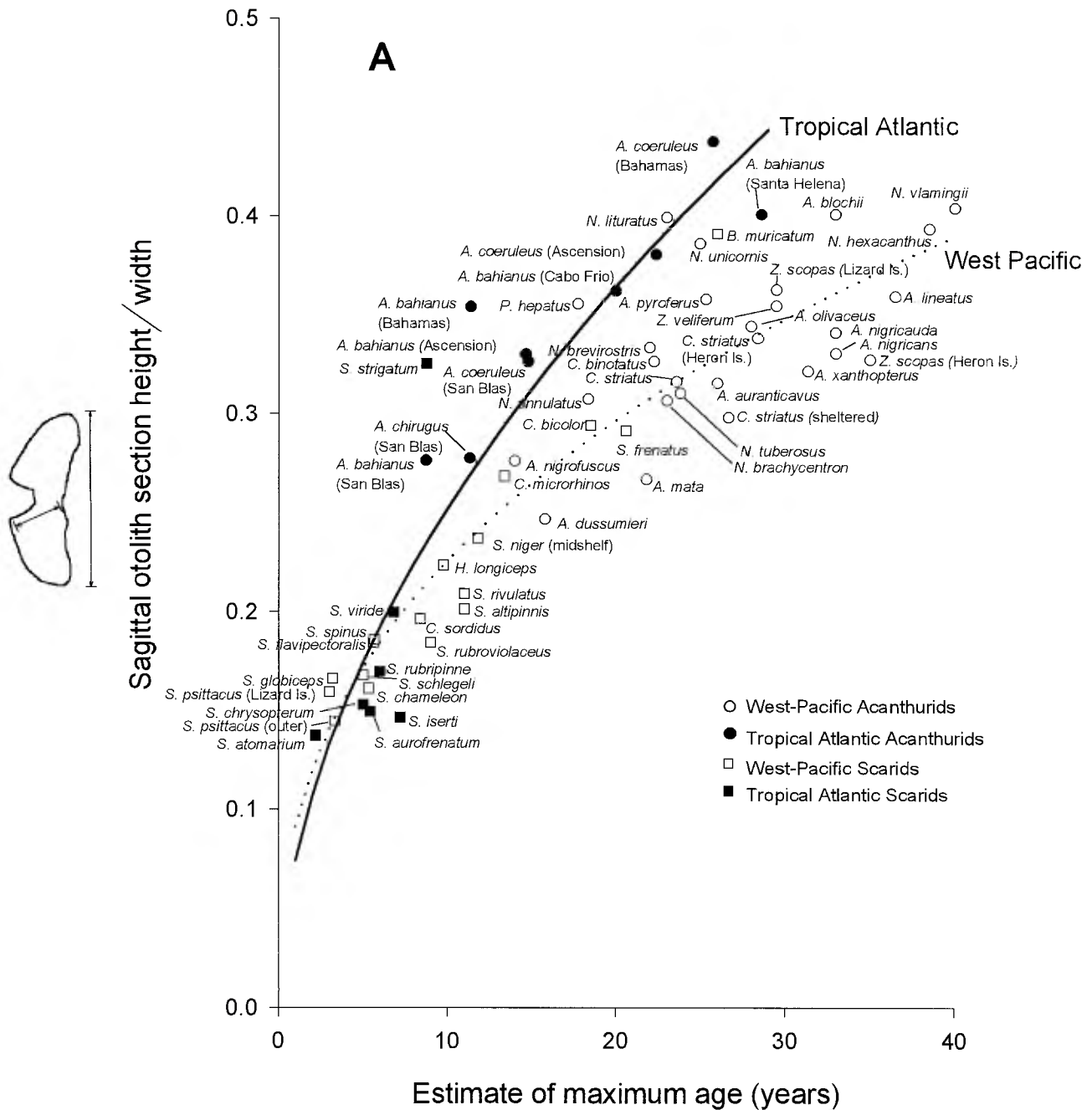


FIGURE 2 (A) The relationship between estimated maximum age and the ratio of sectioned otolith height to width in 50 taxa of acanthurid and scarid fishes sampled from the West Pacific and tropical Atlantic. Maximum age is estimated as the mean of the upper 25% of the sampled age distribution for each taxon. West Pacific: $y = 0.0911x^{0.394}$, $r^2 = 0.791$. Tropical Atlantic: $y = 0.0743x^{0.531}$, $r^2 = 0.774$. (B) The relationship between estimated maximum age and the ratio of sectioned otolith height to width in species of the genus *Acanthurus* from the tropical Atlantic and the West Pacific. For Atlantic and Caribbean data five populations of *Acanthurus bahianus* and three populations of *Acanthurus coeruleus* were included. West Pacific *Acanthurus*: $y = 0.0879x^{0.397}$, $r^2 = 0.551$. Tropical Atlantic *Acanthurus*: $y = 0.0128x^{0.353}$, $r^2 = 0.541$.

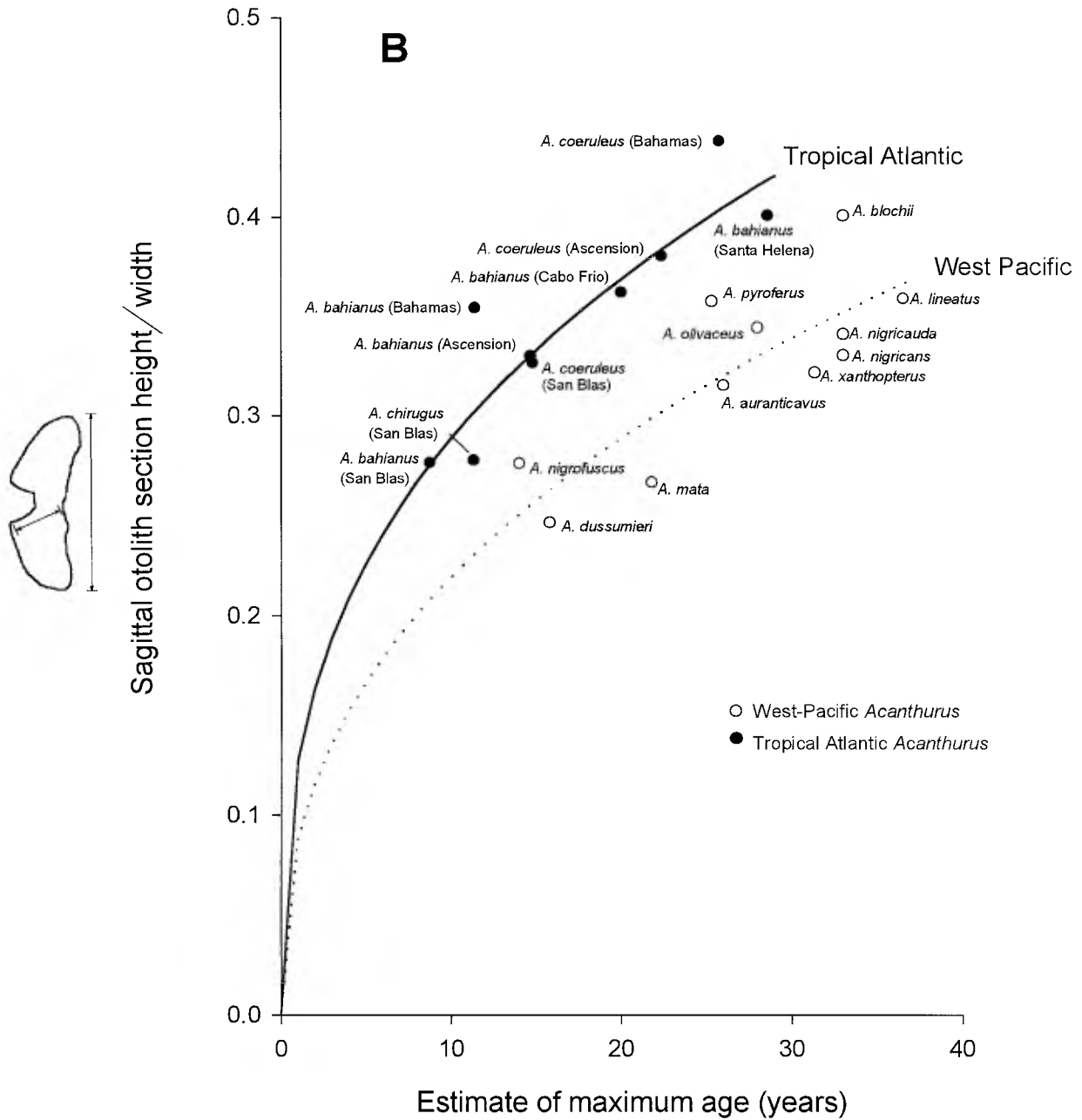


FIGURE 2 (continued)

majority of members of the genus *Naso*, a genus that includes the largest acanthurids. Nor is there any consistent pattern evident within any of the five genera. The largest members of the genus *Acanthurus* sampled in this series, *A. xanthopterus*, *A. mata*, and *A. dussumieri*, were shorter-lived than several of the smaller species, *A. nigricauda*, *A. lineatus*, and *A. nigricans*. A similar lack of patterns occurred in the other speciose

genus *Naso*. In the Acanthuridae size and age are effectively decoupled.

C. Are There Taxon-Specific Patterns in Growth Curves?

We examined patterns of somatic growth using size-at-age data for a selection of species. This

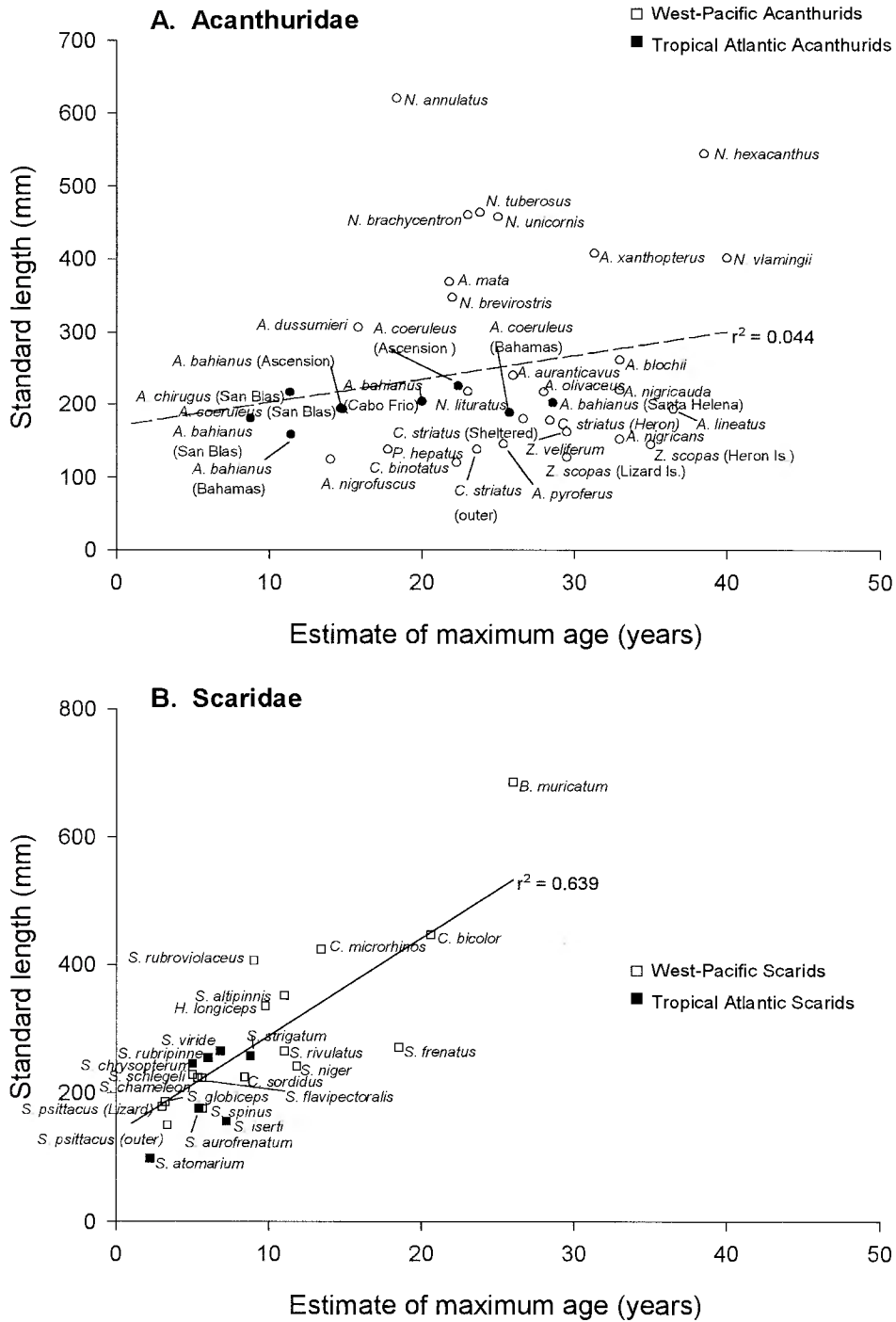


FIGURE 3 The relationship between maximum length and maximum age in 50 taxa of acanthurid and scarid fishes. Lines are least-squares regressions. (A) West Pacific and tropical Atlantic Acanthuridae. (B) West Pacific and tropical Atlantic Scaridae.

TABLE 1 von Bertalanffy Parameters and Estimates of T_{\max} for Acanthurid and Scarid Populations used in Fig. 3

Family/species	Parameter/estimate			Family/species	Parameter/estimate		
	K	L_{∞}	T_{\max}		K	L_{∞}	T_{\max}
Acanthuridae				Acanthuridae (cont.)			
<i>Acanthurus auranticavus</i>	0.676	235	30	<i>Naso unicornis</i>	0.489	386	30
<i>Acanthurus bahianus</i> (St. Helena Is.)	1.241	189	31	<i>Naso vlamingii</i>	0.264	379	45
<i>Acanthurus bahianus</i> (Ascension Is.)	1.061	176	19	<i>Zebrasoma scopas</i>	0.425	133	33
<i>Acanthurus bahianus</i> (Cabo Frio)	1.201	183	22	<i>Zebrasoma veliferum</i>	0.282	208	27
<i>Acanthurus bahianus</i> (San Blas)	1.584	148	10	Scaridae			
<i>Acanthurus bahianus</i> (Lee Stocking Is.)	0.985	156	13	<i>Bolbometopon muricatum</i>	0.136	694	33
<i>Acanthurus blochii</i>	0.250	276	35	<i>Cetoscarus bicolor</i>	0.255	421	21
<i>Acanthurus chirugus</i> (San Blas)	0.705	200	13	<i>Chlorurus microrhinos</i>	0.301	430	15
<i>Acanthurus coeruleus</i> (Ascension Is.)	0.403	193	37	<i>Chlorurus sordidus</i> (Heron Is.)	0.493	229	8
<i>Acanthurus coeruleus</i> (San Blas)	0.477	183	16	<i>Chlorurus sordidus</i> (midshelf)	1.083	193	9
<i>Acanthurus coeruleus</i> (Lee Stocking Is.)	0.817	174	27	<i>Chlorurus sordidus</i> (outer)	1.215	158	8
<i>Acanthurus dussumieri</i>	0.296	308	28	<i>Hipposcarus longiceps</i>	0.278	350	12
<i>Acanthurus lineatus</i>	0.462	183	42	<i>Scarus altipinnis</i>	0.253	377	13
<i>Acanthurus mata</i>	0.219	383	23	<i>Scarus chameleon</i>	0.716	231	6
<i>Acanthurus nigricans</i>	0.280	143	34	<i>Scarus frenatus</i> (midshelf)	0.844	232	19
<i>Acanthurus nigrofuscus</i>	0.783	120	16	<i>Scarus frenatus</i> (outer)	1.251	195	7
<i>Acanthurus olivaceus</i>	1.066	210	33	<i>Scarus iserti</i> (San Blas)	1.235	117	8
<i>Acanthurus pyroferus</i>	0.422	143	28	<i>Scarus niger</i> (midshelf)	0.736	238	16
<i>Acanthurus xanthopterus</i>	0.287	426	34	<i>Scarus niger</i> (outer)	0.989	176	23
<i>Ctenochaetus striatus</i> (exposed)	0.974	154	32	<i>Scarus psittacus</i> (midshelf)	1.190	172	5
<i>Ctenochaetus striatus</i> (sheltered)	0.803	175	36	<i>Scarus psittacus</i> (outer)	1.505	175	4
<i>Ctenochaetus striatus</i> (Kimbe Bay)	0.802	105	28	<i>Scarus rivulatus</i> (midshelf)	0.220	309	8
<i>Naso annulatus</i>	0.213	626	23	<i>Scarus schlegeli</i>	0.403	239	8
<i>Naso brachycentron</i>	0.429	434	31	<i>Sparisoma atomarium</i> (San Blas)	1.828	101	3
<i>Naso brevirostris</i>	0.402	304	25	<i>Sparisoma aurofrenatum</i> (San Blas)	0.669	178	7
<i>Naso hexacanthus</i>	0.221	527	44	<i>Sparisoma chrysopterum</i> (San Blas)	0.627	258	5
<i>Naso lituratus</i>	0.755	211	39	<i>Sparisoma rubripinne</i> (San Blas)	0.811	238	7
<i>Naso tuberosus</i>	0.428	459	25	<i>Sparisoma strigatum</i> (St. Helena Is.)	0.993	252	10
				<i>Sparisoma viride</i> (Lee Stocking Is.)	0.458	357	9
				<i>Sparisoma viride</i> (San Blas)	0.559	280	7

selection was made to facilitate comparison within and between each taxonomic group and between fishes from different biogeographic regions. Figure 3 shows that the relationship between maximum size and maximum age differed between the two groups. Were there also differences in patterns of somatic growth in acanthurids and scarids? The analyses are based on estimates of the von Bertalanffy growth function with parameters L_t (length at time t), L_{∞} (mean asymptotic length), K (the growth coefficient that defines the growth rate to L_{∞}), and t_0 (the hypothetical age at which a fish would have length 0). To facilitate comparisons between the groups the intercepts of the growth curves generated by the model were constrained to approximate sizes for recruitment from the pelagic to benthic populations in each taxon (Leis and Rennis, 1983). These were 25 mm SL for West Pacific acanthurids,

27 mm for Atlantic acanthurids (Robertson, 1991b), and 10 mm SL for scarids from both regions.

Information from other groups of reef fishes [for example, the snapper genus *Lutjanus* (Newman *et al.*, 1996) and the serranid genus *Plectropomus* (Ferreira and Russ, 1992, 1994)] shows that species in different genera have different growth patterns and life-spans. In the former there is rapid initial growth to an asymptotic size that remains constant over the reproductive life of the fish, with 60–80% of linear growth being accomplished within the first 15% of the life-span. The species illustrated in Fig. 1 are small but long-lived. This effectively decouples size and age. In contrast, although the species of *Plectropomus* achieve substantially greater sizes compared to the lutjanids, they are relatively short-lived, with somatic growth occurring over a greater part of the size range, resulting in a

discernible relationship between age and size. Although one obvious interpretation of these differences is that shorter life-spans of *Plectropomus* reflect the effects of fishing for these sought-after species, this is not the case (Ferreira and Russ, 1995).

Size-at-age data for 15 species of scarid and 17 species of acanthurid were fitted to the von Bertalanffy growth function (Figs. 4 and 5; Table 2). The growth curves confirmed the relative distribution of ages seen in Fig. 1, with the mean maximum age of acanthurids being 29 years and that of scarids 12 years. For both groups the Atlantic and Caribbean taxa had lower maximum ages than did equivalent-sized West Pacific species. However, the von Bertalanffy parameters K and L_{∞} for both groups had similar mean values, although K for scarids was higher than it was for acanthurids (0.733 vs. 0.566). Mean L_{∞} values were 288 mm for scarids and 295 for acanthurids. The two groups generated different growth curves.

The genera *Acanthurus*, *Ctenochaetus*, and *Zebra-soma* showed rapid initial growth, achieving a consistent L_{∞} value and resulting in the characteristic square growth curve similar to that seen in small lutjanids (Newman *et al.*, 1996). This was most obvious in small species of the genus *Acanthurus*, such as *A. olivaceus* and *A. lineatus*. Atlantic acanthurids displayed the same type of square growth curves seen in West Pacific congeners despite having life-spans only half that of equivalent West Pacific species. These small acanthurids generated high K values. Members of the genus *Naso* were long-lived. Most displayed flat growth curves although *N. annulatus* and *N. tuberosus* were exceptions. Despite greater sizes of the *Naso* species the distribution of life-spans was similar to that seen in *Acanthurus*, *Ctenochaetus*, and *Zebra-soma*. For scarids the growth curves for the selected species also reflected the distribution of life-spans shown in Fig. 1. For the West Pacific species the relationship between size and age can be clearly seen in the distribution of life-spans from the smallest (*Scarus psittacus*) to the largest (*Bolbometopon muricatum*) species. The greatest age recorded was 33 years for *B. muricatum*, although this will be a conservative estimate, because the samples did not include the largest individuals observed. The Caribbean species again showed shorter life-spans compared to the West Pacific species. When examined on the same temporal scale as the West Pacific species the Caribbean scarids of the genus *Sparisoma* show very short life-spans characterized by continuous and rapid somatic growth.

The von Bertalanffy parameters K and L_{∞} can be plotted to provide summaries of growth performance in a variety of taxa. Pauly (1998) has presented such a summary based on 4826 sets of parameter estimates

of the von Bertalanffy growth function. The negative relationship generated by plotting K on L_{∞} identifies the "growth space" used by fishes. We have provided a similar plot for the 47 species sampled (Fig. 6). This generated the familiar negative relationship, confirming the conclusions of Pauly (1994, 1998) that fishes either tend to remain small and have high K values or become large and have low K values (Fig. 6A).

The value K represents only one aspect of the fish growth regime, that rate at which L_{∞} is approached. Other growth-related features that may be important to management are not reflected in such plots. For example, despite major differences in longevity between acanthurids and scarids these taxa were not obviously partitioned in Fig. 6. Thus although the parameters K and L_{∞} allow comparison of growth patterns they do not capture the important life history features that arise from differences in life-span. Couplets of species closely associated in Fig. 6 as a result of their similar K and L_{∞} values have life-spans varying by a factor of 2–4, e.g., *Chlorurus microrhinos* ($K = 0.307$, $L_{\infty} = 428$, $T_{\max} = 15$) vs. *Acanthurus xanthopterus* ($K = 0.298$, $L_{\infty} = 425$, $T_{\max} = 33$); *Chlorurus sordidus* ($K = 1.117$, $L_{\infty} = 193$, $T_{\max} = 9$) vs. *Acanthurus olivaceus* ($K = 1.144$, $L_{\infty} = 209$, $T_{\max} = 33$); and *Hipposcarus longiceps* ($K = 0.282$, $L_{\infty} = 350$, $T_{\max} = 12$) vs. *Naso vlamingii* ($K = 0.282$, $L_{\infty} = 376$, $T_{\max} = 45$).

If K is plotted on T_{\max} (Fig. 6B) a negative trend is present but with greater scatter than the relationship between K and L_{∞} . Moreover, the taxa predictably segregate in terms of T_{\max} . This can be seen in estimates of size at sexual maturity as a proportion of L_{∞} , and age at sexual maturity as a proportion of T_{\max} (Table 3). Four groups of fish are considered: West Pacific species of *Acanthurus* and *Naso* and West Pacific scarids of the genera *Chlorurus* and *Scarus* (Table 3). For *Acanthurus* and *Naso*, respectively, sexual maturity is achieved at 6 and 15% of T_{\max} . For the scarids the estimate is 19%. For the acanthurids 86 and 85% of size at L_{∞} is achieved by sexual maturity. For scarids the estimate is 68%. The value 6% of T_{\max} for *Acanthurus* is lower than the value for *Chlorurus* and *Scarus* by a factor of three and is indicative of a life history pattern with an extended reproductive span.

D. Within a Taxon, Are Maximum Age Estimates and Growth Parameters Consistent over Geographic and Environmental Gradients?

Most species of reef fishes occur in a number of distinctive habitats within a reef and also have broad

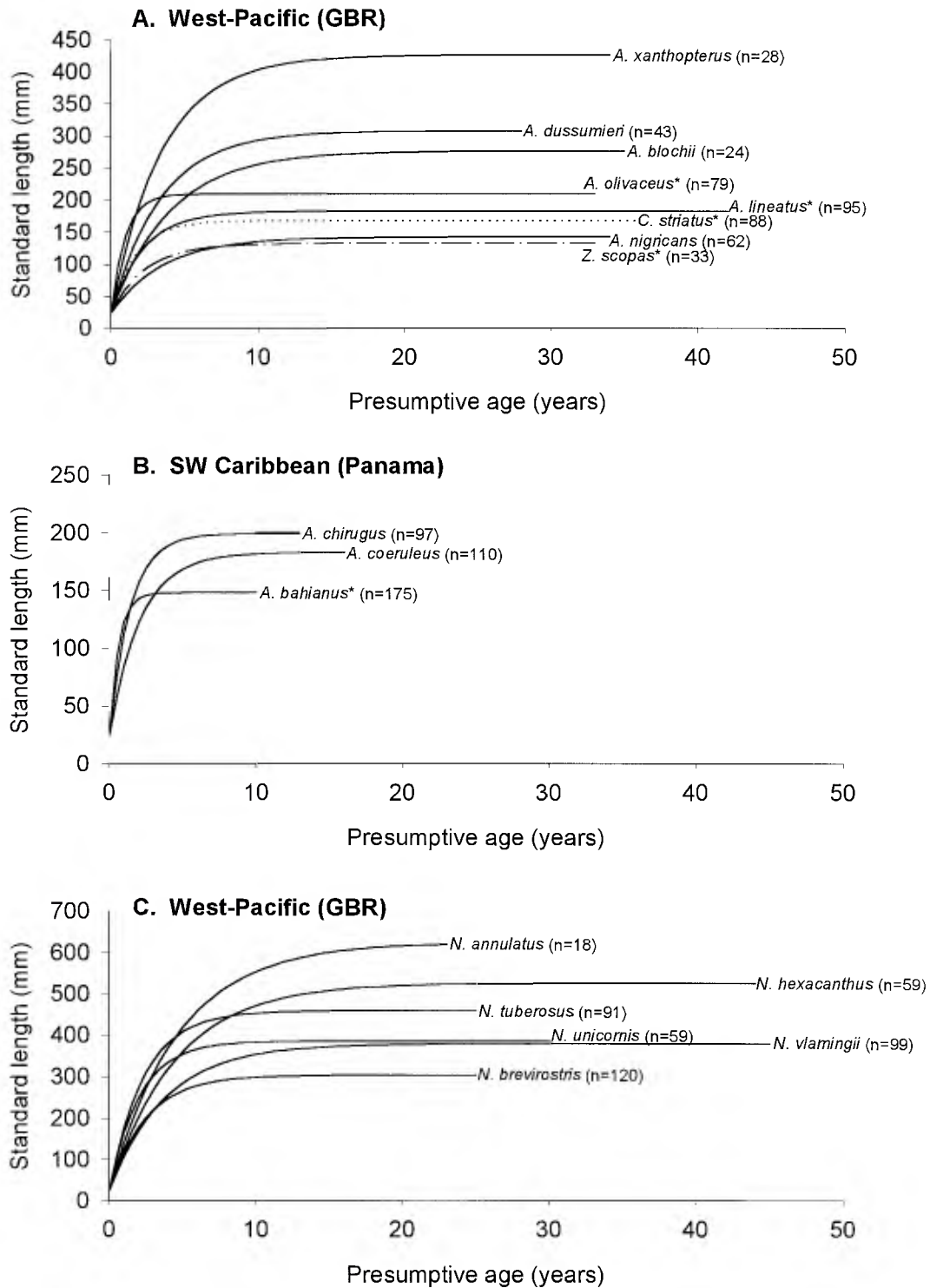


FIGURE 4 von Bertalanffy growth curves fitted to size-at-age data for 17 acanthurid taxa (von Bertalanffy parameters in Table 1; size-at-age data available from J. H. Choat). (A) West Pacific (northern GBR) taxa of *Acanthurus*, *Zebrasoma*, and *Ctenochaetus*. (B) Caribbean taxa of *Acanthurus* from the San Blas sampling locality. (C) West Pacific (northern GBR) taxa of *Naso*.

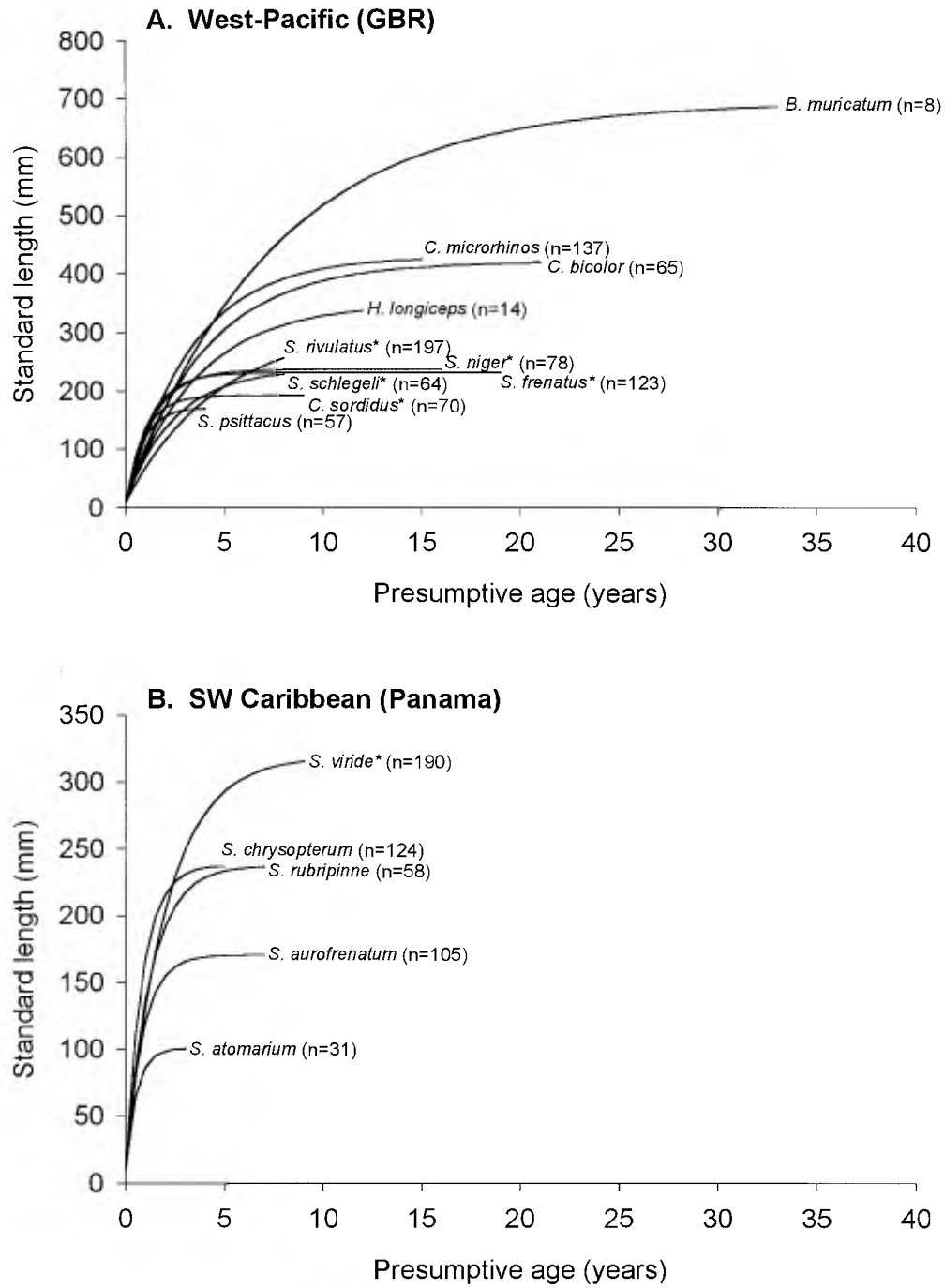


FIGURE 5 von Bertalanffy growth curves fitted to size-at-age data for 15 scarid taxa (von Bertalanffy parameters in Table 1; size-at-age data available from J. H. Choat). (A) West Pacific (northern GBR) taxa of *Bolbometopon*, *Chlorurus*, *Hipposcarus*, and *Scarus*. (B) Caribbean taxa of *Sparisoma* from the San Blas sampling locality.

TABLE 2 von Bertalanffy Parameters: Sample Size and Size Range for Acanthurids (Fig. 4) and Scarids (Fig. 5)

Family/species	Parameter/estimate				Size range
	L_{∞}	K	t_0	n	
Acanthuridae					
<i>Acanthurus bahianus</i>	148.32	1.584	-0.12	175	31-198
<i>Acanthurus blochii</i>	276.07	0.250	-0.38	24	129-328
<i>Acanthurus chirugus</i>	199.61	0.705	-0.19	97	55-230
<i>Acanthurus coeruleus</i>	183.48	0.477	-0.31	110	30-206
<i>Acanthurus dussumieri</i>	307.67	0.296	-0.29	43	140-334
<i>Acanthurus lineatus</i>	182.74	0.462	-0.32	95	92-206
<i>Acanthurus nigricans</i>	142.86	0.280	-0.69	62	84-160
<i>Acanthurus olivaceus</i>	209.74	1.066	-0.12	79	95-248
<i>Acanthurus xanthopterus</i>	426.25	0.287	-0.21	28	111-473
<i>Ctenochaetus striatus</i>	168.00	0.591	-0.27	88	103-197
<i>Naso annulatus</i>	625.76	0.213	-0.19	18	179-630
<i>Naso brevirostris</i>	303.75	0.402	-0.21	120	86-364
<i>Naso hexacanthus</i>	527.18	0.221	-0.22	59	148-577
<i>Naso tuberosus</i>	459.39	0.428	-0.13	91	144-517
<i>Naso unicornis</i>	385.77	0.489	-0.14	59	176-494
<i>Naso vlamingii</i>	379.10	0.264	-0.26	99	136-459
<i>Zebrasoma scopas</i>	132.82	0.425	-0.49	33	76-157
Scaridae					
<i>Bolbometopon muricatum</i>	693.81	0.136	-0.11	8	231-710
<i>Cetoscarus bicolor</i>	420.56	0.255	-0.09	65	155-461
<i>Chlorurus microrhinos</i>	429.89	0.301	-0.08	137	105-499
<i>Chlorurus sordidus</i>	192.95	1.083	-0.05	70	98-245
<i>Hipposcarus longiceps</i>	350.07	0.278	-0.10	14	191-374
<i>Scarus frenatus</i>	232.36	0.844	-0.05	123	109-295
<i>Scarus niger</i>	238.01	0.736	-0.06	78	121-278
<i>Scarus psitticus</i>	172.10	1.190	-0.05	57	104-215
<i>Scarus rivulatus</i>	308.50	0.220	-0.15	197	88-290
<i>Scarus schlegeli</i>	238.81	0.403	-0.11	64	89-249
<i>Sparisoma atomarium</i>	101.08	1.828	-0.06	31	50-101
<i>Sparisoma aurofrenatum</i>	170.89	1.163	-0.05	105	91-234
<i>Sparisoma chrysopteron</i>	237.97	1.176	-0.04	124	74-278
<i>Sparisoma rubripinne</i>	237.57	0.811	-0.05	58	112-272
<i>Sparisoma viride</i>	318.96	0.498	-0.06	190	32-379

geographical distributions. Plasticity in growth and reproductive parameters in poikilotherms in response to environmental variation is well known (Atkinson, 1994). The issues of geographic variation and plasticity in growth and life history parameters are critical to our understanding of reef fish population dynamics. The capacity to age fishes over major parts of their geographic range provides a means of assessing systematic trends in life history parameters in response to both latitudinal and local gradients in environmental conditions. This approach requires estimation of ages of fishes by examining annuli in sectioned otoliths in fishes collected adjacent to the equator. Such sampling is still in its infancy, although sectioned otoliths from the

Seychelles, 4° south latitude, show consistent and regular increment structures (E. Grandcourt, personal communication). The examples presented here are taken from size-at-age data collected from two species of widely distributed acanthurid, *Acanthurus bahianus* in the West and central Atlantic and *Ctenochaetus striatus* from southern and central western Pacific reefs (Fig. 7).

The two sampling gradients had the following features. For *A. bahianus* the gradient in the tropical Atlantic extended from Cabo Frio (southwestern Atlantic) to the Bahamas (northwestern Atlantic), covering in absolute terms 16° of latitude and 6° Celsius range in mean annual temperature. For *C. striatus*,

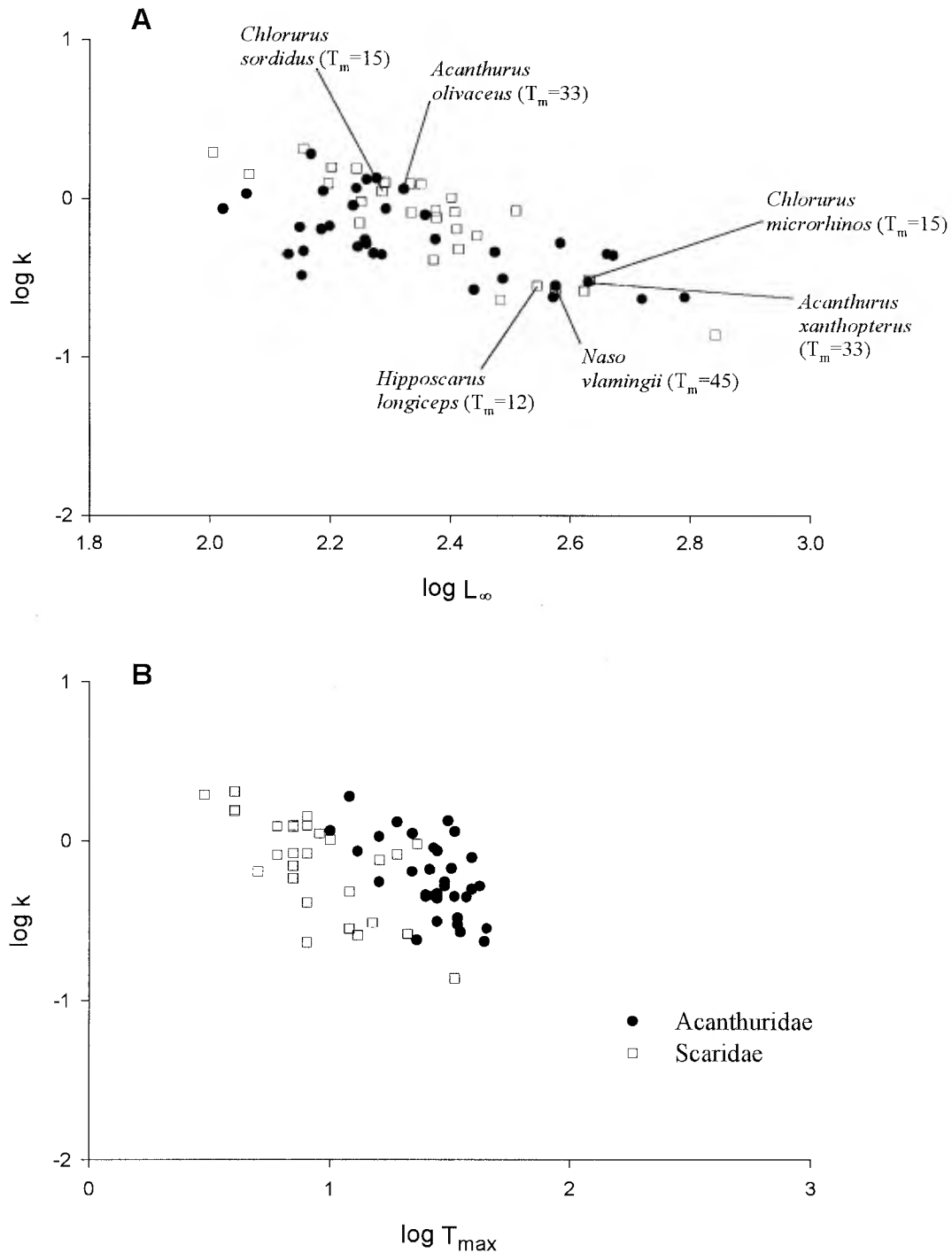


FIGURE 6 (A) Relationship between K and L_{∞} for 34 acanthurid populations (25 taxa) and 28 samples of scarid populations (22 taxa). The three couples of species show pairs of acanthurids and scarids with similar combinations of K and L_{∞} values but with distinctive T_{max} values (see text). (B) Relationship between K and T_{max} for the same data set.

TABLE 3 Estimates of K and Values for L_{∞} , T_{\max} , T_m (Age at Maturity), and L_m (Size at Maturity) for Six Species of Acanthurid and Six Species of Scarid

Family/species	Parameter/estimate						
	L_{∞}	K	T_{\max}	T_m	L_m	A^a	B^b
Acanthuridae							
<i>Acanthurus olivaceus</i>	210	1.066	33	2	180	86%	6%
<i>Acanthurus lineatus</i>	183	0.462	42	3	160	87%	7%
<i>Ctenochaetus striatus</i>	168	0.591	36	2	135	80%	6%
<i>Naso brevirostris</i>	304	0.402	25	4	250	82%	16%
<i>Naso hexacanthus</i>	527	0.221	44	7	450	85%	16%
<i>Naso tuberosus</i>	459	0.428	25	4	350	76%	16%
Scaridae							
<i>Chlorurus microrhinos</i>	430	0.301	15	4	300	70%	27%
<i>Cetoscarus bicolor</i>	421	0.255	21	5	300	71%	24%
<i>Chlorurus sordidus</i>	193	1.083	9	1.5	100	52%	17%
<i>Scarus frenatus</i>	232	0.844	19	2	180	78%	11%
<i>Scarus niger</i>	238	0.736	16	2	175	74%	13%
<i>Scarus psittacus</i>	172	1.190	4	1	110	64%	25%

^a $A = \%L_{\infty}$, the proportion of L_{∞} achieved at sexual maturity.

^b $B = \%T_{\max}$, the proportion of T_{\max} achieved at sexual maturity.

the gradient in the southern and central Indo-Pacific extended from Heron Island (southern GBR) to Kimbe Bay (New Britain), covering 18° of latitude and 4° mean annual temperature. Acanthurids were sampled in as close as possible to similar habitats at the following localities. For *A. bahianus* the localities were St. Helena and Ascension Island (south central Atlantic), Cabo Frio (southern Brazil), San Blas Point (southwestern Caribbean), and Lee Stocking Island (Bahamas, northwestern Atlantic). Over this range *A. bahianus* occurs on both rocky and coral reefs. For *C. striatus* the localities were Heron Island (southern Great Barrier Reef), Lizard Island (northern Great Barrier Reef), and Kimbe Bay (New Britain). For the West Pacific, gradient samples at different sites in the vicinity of Lizard Island are included (Choat and Axe, 1996). Size-at-age data from sagittal otoliths were used to construct growth curves and to estimate K , L_{∞} , and T_{\max} from samples from each locality. At Heron Island insufficient specimens were obtained to construct a growth curve, although samples at the upper end of the size range were available to provide an estimate of T_{\max} .

Plotting estimates of T_{\max} against latitude revealed a positive relationship between maximum age estimates and latitude for the West Pacific but not for the Atlantic locations. In the South Atlantic, latitude and temperature are not closely coupled due to the influences of cold oceanic currents (Santa Helena) and upwelling (Cabo

Frio). A plot of T_{\max} on mean annual sea temperature revealed a negative relationship between age and temperature in both the West Pacific and the Atlantic localities. Sampling at Lizard Island localities incorporating a range of habitat types confirmed the presence of localized variation in life history features.

The size-at-age data from each locality were fitted to the von Bertalanffy equation to display comparative growth patterns. The West Pacific material (*C. striatus*) showed a reduction in asymptotic size and shorter life-spans at Kimbe Bay site (5° south latitude) (Fig. 8A). The samples from Kimbe Bay showed an L_{∞} 41% lower compared to the sheltered reef samples from Lizard Island. A clearer case for latitudinal variation in growth and life history parameters is seen in the analysis for *A. bahianus* (Fig. 8B). The characteristic square growth curve occurred at each locality, but the maximum sizes and ages achieved varied systematically with location. The L_{∞} for the San Blas samples was 20% smaller than that for the St. Helena samples. The 95% ellipsoidal confidence regions around the von Bertalanffy parameters were used to compare the growth functions among populations (Kimura, 1980) (Fig. 8C). Statistically significant variation among locations occurred in the life history parameters. The tropical Atlantic populations of Santa Helena, Cabo Frio, and Ascension showed significantly higher L_{∞} compared to the Caribbean populations from Bahamas and San Blas.

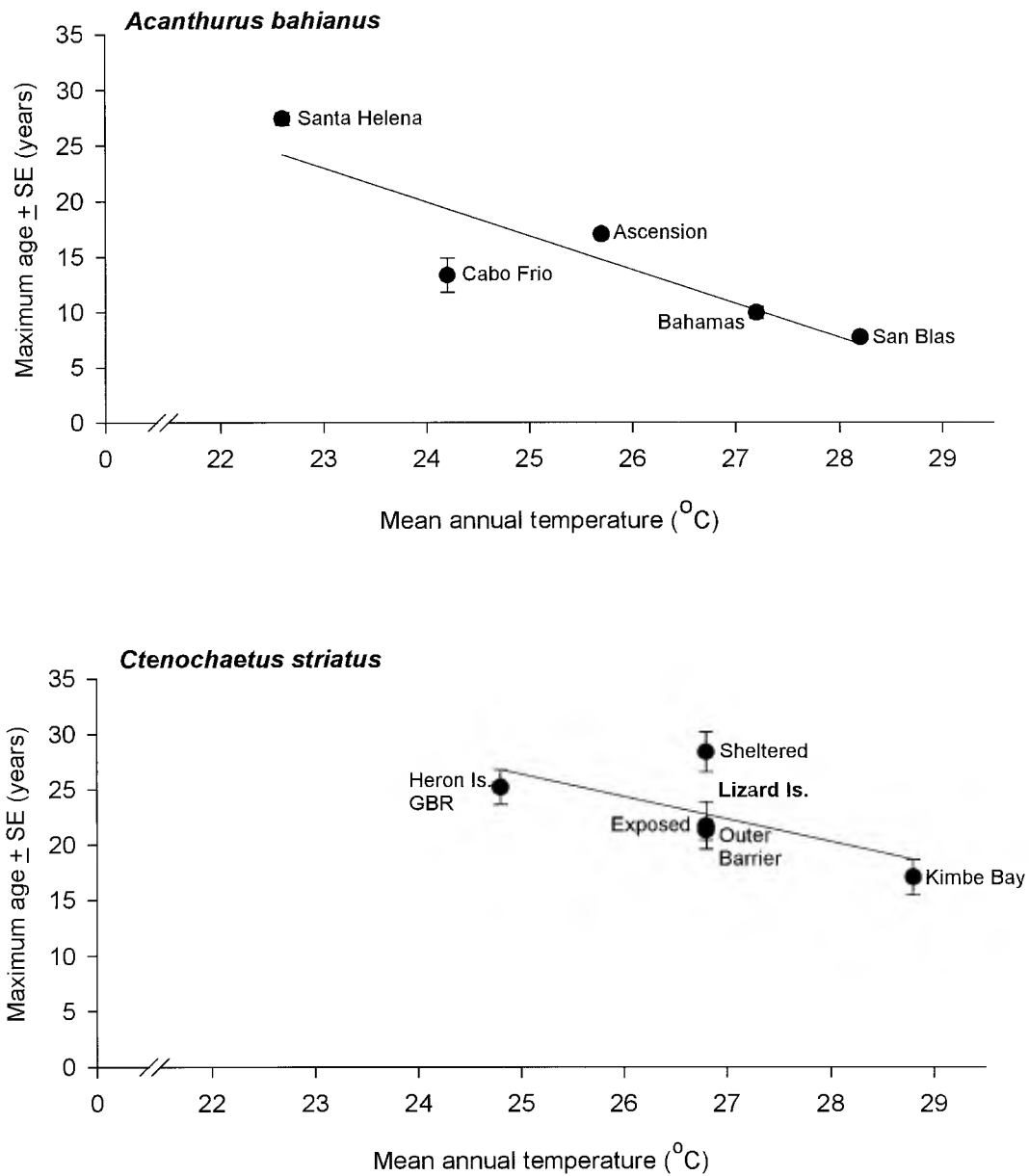


FIGURE 7 Relationship between estimates of maximum age and average annual sea surface temperature for populations of *Acanthurus bahianus* sampled at five geographic localities from the tropical Atlantic and Caribbean and five populations of *Ctenochaetus striatus* samples from three localities on the Great Barrier Reef and New Britain. The Lizard Island locality was subsampled by habitat. Temperature data from IGOSS (1998) and D’Croz and Robertson (1997). Localities are at the following latitudes: for the Indo-Pacific—Heron Island, 24°S; Lizard Island, 14°S; Kimbe Bay, 5°S; for the tropical Atlantic and Caribbean—Santa Helena, 16°S; Ascension, 8°S; Cabo Frio, 23°S; San Blas, 9°N, Bahamas, 24°N.

Each species maintained similar patterns of variation in longevity and growth over a wide range of environmental conditions but showed systematic changes in K , L_{∞} , and T_{\max} correlated with variation in temperature. This included a threefold increase in T_{\max} in *A. bahianus* from the San Blas Archipelago to St. Helena.

E. In Protogynous Species Are Size and Age Distributions Concordant?

A large number of coral reef fishes are protogynous hermaphrodites (Sadovy, 1996). Labroid fishes are the most abundant protogynous hermaphrodites on

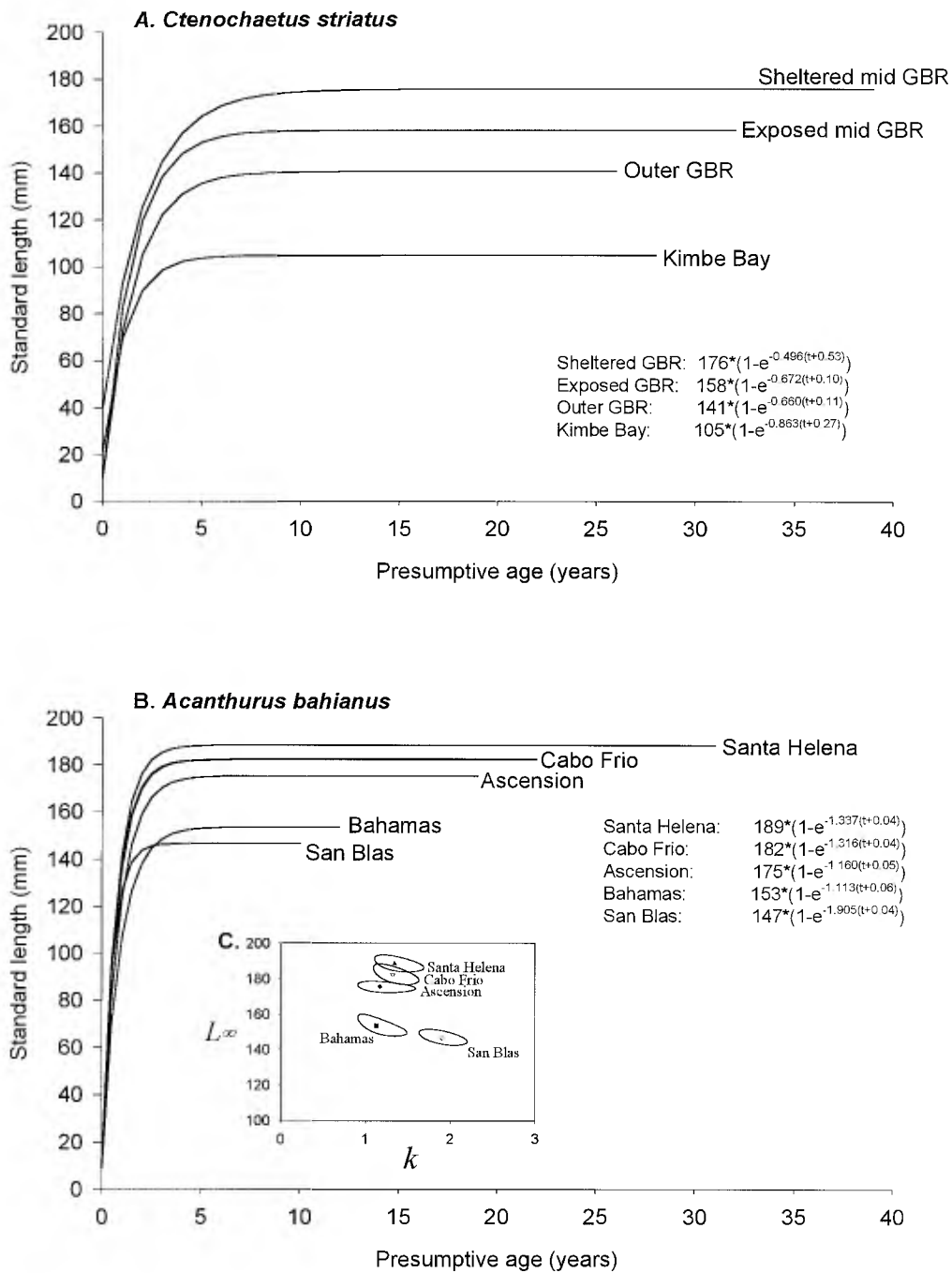


FIGURE 8 von Bertalanffy growth curves fitted to size-at-age data for four populations of *Ctenochaetus striatus* and five populations of *Acanthurus bahianus* (size-at-age data available from J. H. Choat). (A) *Ctenochaetus striatus* growth curves and von Bertalanffy equations for four populations. (B) *Acanthurus bahianus* growth curves and von Bertalanffy equations for five populations. (C) Comparison of five von Bertalanffy growth curves for populations of *Acanthurus bahianus* showing cross-sections of 95% confidence regions around least-squares estimates of K and L_{∞} following Kimura (1980).

coral reefs, with scarids being the numerically dominant taxon of larger protogynous fishes. Scarids well illustrate the need for age-based approaches to the analysis of protogynous life history patterns. Sexually dichromatic scarids present a picture of large terminal males and smaller initial-phase females. Intuitively one would expect that the population should also be partitioned by age. Large terminal males represent the oldest members of the population, whereas females are smaller and younger and are recruited into the terminal male population by sex reversal, following the loss (removal or departure) of large terminal males. Females are young, abundant, and have a capacity to replenish the large-male population by sex reversal. Representative size frequency distributions of three species of scarids illustrate these points (Fig. 9). However, when size/age relations are considered a more complicated picture emerges. Size-at-age plots for protogynous species such as these are often messy, with a considerable range of sizes in different age groups. Partitioning plots by sex reduces the variation, especially in intermediate age groups (Choat *et al.*, 1996). At a given size, secondary (sex-changed) males are larger than females. However, small mature females may represent some of the oldest members of the population. Comparison of age and size distributions (Fig. 9) for the three scarids illustrates these points. In the case of *Scarus frenatus* and *C. microrhinos* age plots revealed a number of females that are as old as, but substantially smaller than, the largest terminal-phase males.

In summary, a review of growth parameters and age structures in two ecologically similar groups of reef fishes confirms that analysis of the population dynamics of reef fishes is likely to be complex. There will be marked variation in the patterns of growth, in the relationships between size and age, and in the distribution of maximum ages among different lineages. Protogynous patterns of sexual development and sex-specific differences in growth rate will be a further complicating factor.

Reliable estimates of maximum age and of age structure are of critical importance in evaluating the population dynamics of reef fishes and their capacity to respond to altered recruitment and mortality rates.

III. Discussion

Age-based studies of tropical reef fishes have been relatively slow moving. In some instances good descriptions of age-specific demography have been obtained from the otoliths of fishes from low-latitude reef environments (Sadovy *et al.*, 1992). However, for many

others, including species under increasing fishing pressure, we lack such information. This is partly due to the perception that otoliths of fishes from low-latitude reef systems do not show consistent formation of annual rings. Detection and analysis of periodic rings in otoliths sampled from fishes in low-latitude coral reef systems is a challenge. It is our experience that consistent patterns can be demonstrated, although it is necessary to examine large numbers of otoliths to achieve this. There are relatively few instances in which the first otolith examined reveals incremental structures of the clarity seen in temperate reef fishes.

In size-at-age plots presented here we have used the term "presumptive age." In many taxa the annual periodicity of check marks has not been validated. For most reef species validation has been achieved through chemical marking of calcareous structures or marginal increment analysis. However, validation that satisfies protocols of independent methodologies and application over the full range of the age distribution are difficult to achieve in coral reef fishes due to their diversity, relative rareness of individual species, and, in many instances, extended life-spans.

Much of the debate concerning age estimation in fishes has been focused appropriately on the accuracy and precision by which otolith increments are recognized, validated, and counted. This can be problematical in species with numerous increments crowded near the margins of otolith sections. Moreover, the processes controlling increment formation in tropical fishes are poorly understood (Fowler, 1995). Understanding the interplay between physiological and environmental factors in the formation of internal otolith structures will facilitate a more accurate approach to the analysis of age-based dynamics. The fact that some temperate species form clearly defined increments in their sagittae that are not referable to an annual schedule of deposition (Morales-Nin *et al.*, 1998) confirms the need for validations. However, an emerging consensus of age determination studies is that consistent increments observed in sectioned sagittal otoliths in both tropical and temperate species may be reliably interpreted as having an annual periodicity. There may be exceptions to this interpretation. For example, Milton *et al.* (1995) suggested that rings observed in the otoliths of lutjanids may not be formed annually (but see Cappo *et al.*, 2000). Despite such issues it is important to provide age estimations as hypotheses for further testing and to help prioritize future work.

The potential problems faced in coral reef fisheries are similar to those encountered in fisheries for deep-water species. The inability of management procedures to prevent the serious overexploitation of deep-water

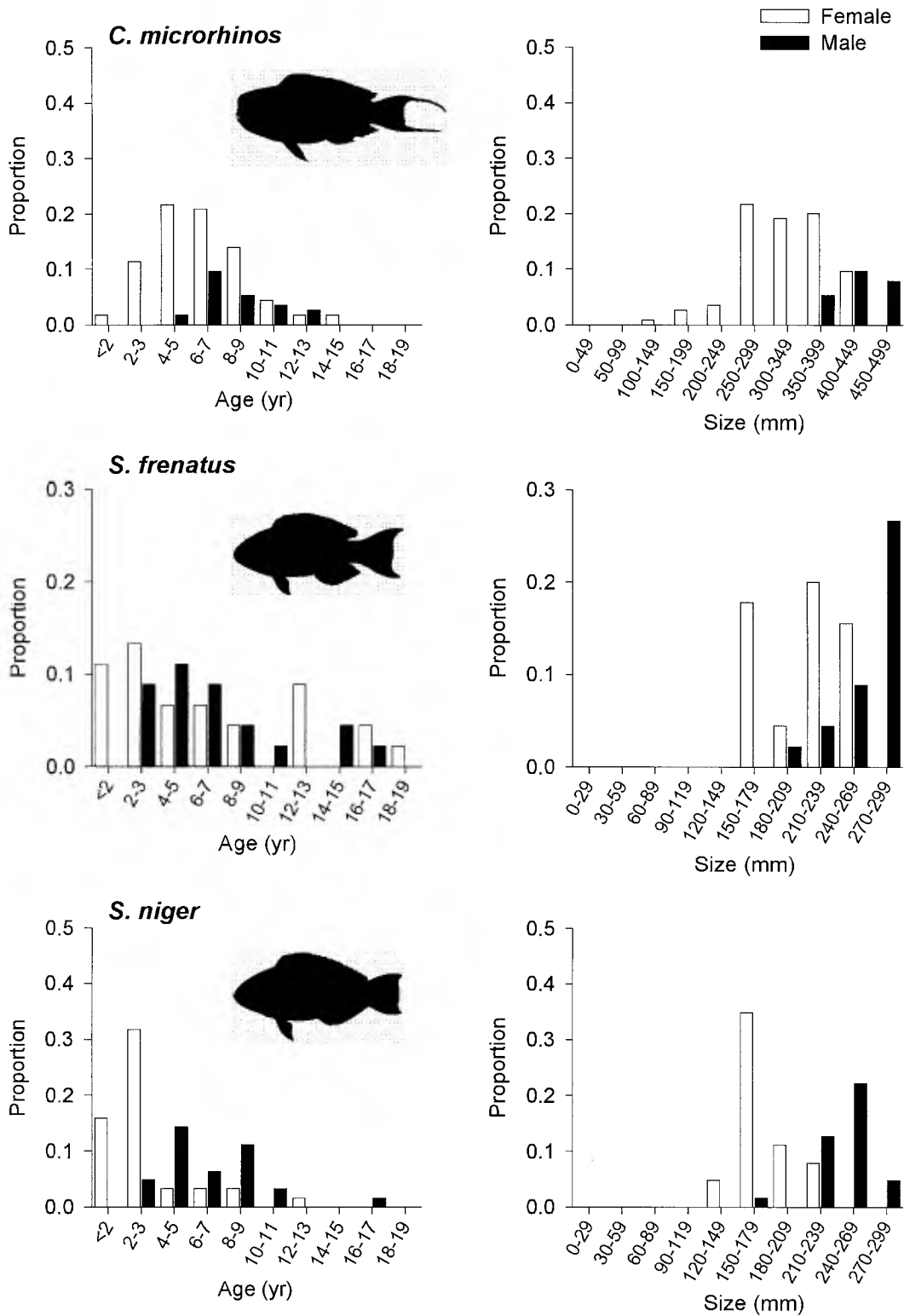


FIGURE 9 Age and size distributions by sex for three species of protogynous scarids: *Chlorurus microrhinos*, *Scarus frenatus*, and *Scarus niger* sampled from the West Pacific (GBR).

fishes, especially the orange roughy *Hoplostethus atlanticus* (Tracey and Horn, 1999), can be traced in part to the lack of appreciation that the fishery was targeting long-lived and slow-growing fishes. The basic issue for fisheries and life history studies is not one of determining whether the particular otolith section reveals either 6 or 10 presumed annual check marks, but whether the fish lives 10 years or 40 years. Underestimation of ages may lead to unrealistically high estimates of growth and natural mortality rates, an issue that has been especially problematical in, but not confined to, deep-water fishes.

There is increasing recognition of the need to conserve reef fish stocks and to gather the information necessary to identify levels of vulnerability based on life history features. Roberts and Hawkins (1999) identified extended life-spans, slow growth rates, and low natural mortality rates as characteristics that will render marine species vulnerable to extinction through human activities, including overexploitation. Roberts (1997a) also identified the difficulties facing managers of multispecies fisheries targeting taxa with a range of life history features. An additional dimension to this problem is seen in the taxa used by Roberts (1997a) to identify contrasting life history tactics. Acanthurids were provided as examples of r selected species and serranids were provided as examples of K selected species, i.e., rapidly growing, short-lived vs. slow-growing, longer lived, respectively. A number of workers (see Musick, 1999a, for a summary) have pointed out that r selected species may have higher maximum sustainable yields compared to K selected species. Our data indicate that, in contrast to the previous conclusions, in many reef environments acanthurids rather than serranids may have life history features more characteristic of a K selection regime. The estimates of growth rates and longevity from size-at-age data that provide the core of this chapter are an attempt to provide a more inclusive framework for the analysis of reef fish population phenomena. They are designed as hypotheses to be challenged or confirmed by additional studies on the age-structure of tropical fishes and as alternatives to length-based approaches. Given the variation in relationships between size and age discussed here, the most appropriate outcome would be an increased emphasis on age estimations and the validation of presumed annual check marks in the otoliths of coral reef fishes.

A recurring theme in studies of coral reef fishes concerns the extent to which we may generalize about ecological and life history attributes. The analysis of life-spans in acanthurid and scarid fishes shows that ecologically similar species can differ substantially in demographic characteristics. The literature suggests that this type of partitioning among different lineages

of reef fishes is common. For example, some pomacentrids with a total length of 60 mm may have maximum ages of approximately 16–18 years (Fowler and Doherty, 1992; Doherty and Fowler, 1994a), similar to ages achieved by the serranids *Plectropomus maculatus* and *Plectropomus leopardus* for fork lengths of 680 and 500 mm, respectively (Ferreira and Russ, 1992, 1994), and *Epinephelus guttatus* for a 458-mm fork length (Sadovy *et al.*, 1992). Very large serranids such as *Epinephelus itajara* (2065-mm fork length) may be only 33 years old (Bullock *et al.*, 1992), equivalent to many acanthurids that are 160–210 mm in fork length, or a tenth of the length and a thousandth of the serranid weight. Age estimates for lutjanids demonstrate that relatively small species may be substantially longer lived compared to large serranids (Newman *et al.*, 1996). Such decoupling of size and age and differences in vital rates between and within lineages of reef fishes mean that it will be difficult to generalize about responses to environmental change or human impacts without a considerable data base on life history characteristics.

The growth patterns generated by the size-at-age data revealed different patterns of growth among our two chosen taxa. Acanthurids displayed square growth curves, partitioned into a short ascending arm where rapid growth to achieve asymptotic size and sexual maturity occurs followed by an extended life-span where reproductive output occurs with minimal somatic growth. Similar patterns have been recorded for small species of lutjanids (Newman *et al.*, 1996). These growth patterns show certain similarities to temperate sciaenids (Jones and Wells, 1998) and deep-water oreosomatids (Stewart *et al.*, 1995) and hoplostethids (Smith *et al.*, 1995), in which growth to the start of the horizontal arm of the growth curve occurs in approximately the first 18–25% of the life-span. The scarids generate more familiar growth curves in which size increases gradually throughout life, although there are exceptions (Choat *et al.*, 1996). The growth patterns observed in large scarids such as *C. microrhinos* are similar to those of a number of serranids (Ferreira and Russ, 1994; Sadovy *et al.*, 1992) and gadid, clupeoid, and pleuronectiform fishes (Beverton, 1992).

Analytical treatments of fish growth and life history features (Beverton, 1992; Pauly, 1998) rely heavily on the von Bertalanffy parameters, K and L_{∞} . Making useful comparisons based only on these parameters is difficult. First, fishes with very different life history features may have similar values of K and L_{∞} (Fig. 6). These parameters do not capture differences in longevity that can generate different life history features, notably the reproductive lifetime. Second, von Bertalanffy growth curves are frequently fitted to

truncated size-at-age data that do not adequately span the age range. A number of studies have recognized the consequences of exclusion of particular age classes from estimates of growth parameters and the difficulties this causes for the comparison of growth among species or populations (Mulligan and Leaman, 1992). The estimated values of K and t_0 are sensitive to the age composition of the sample, with exclusion of the younger age classes in particular resulting in the underestimation of K (Ferreira and Russ, 1994). This effect will be particularly problematical in species with square growth curves (Craig, 1999). Some standardization of the structure of data sets used to estimate K and L_∞ is required. In comparisons within a taxon we constrained the growth curve to the estimated size at settlement.

Sensitivity of K to the age composition of the sample causes a number of difficulties in the estimation of growth parameters for coral reef fish populations. First, coral reef fishes are subject to a wide range of fisheries practices and the age of "recruitment" to a fishery may vary accordingly. Very small individuals are selectively targeted in some species, e.g., newly settled siganids (Bryan and Madraisau, 1977). Second, there is relatively little information on age and size at reproductive maturity, and third, there is evidence of very different patterns of growth among species with similar size ranges. Comparisons of K for different regional populations will be confounded if there is no control for the effects of variation in the distribution of ages used in different samples.

Beverton (1992) has provided a number of analytical protocols for comparing life history parameters in fishes, including the concept of the growth-maturity-longevity (GML) plot. This captures important features of life-span and reproductive output in different groups of fishes. Plotting of the dimensionless ratios K/T_{\max} and L_m/L_∞ , where L_m is the length at which 50% of a year-class reach maturity, provides a demonstration of the distinctive differences between the demographic patterns of long-lived cold-water fishes of the genus *Sebastes* (average $T_{\max} = 54$) when compared to the shorter lived Gadiformes (average $T_{\max} = 14$) and Pleuronectiformes (average $T_{\max} = 23$). Such an approach may be informative for reef fishes, provided estimates of K are standardized and more extensive data sets for T_{\max} are available.

Growth parameters and life-spans within a species vary over environmental gradients, although the pattern of growth is preserved. For the acanthurids examined both size and longevity varied substantially over the average annual temperature gradients examined. There are likely to be a number of explanations for these patterns. For example, habitats in lower latitudes

will support a greater diversity and density of fishes (Meekan and Choat, 1997). This in turn may result in decreased asymptotic size through competitively driven reductions in growth rate or increased mortality due to predation. Decreasing temperature may reduce growth rate (Pauly, 1998), which in turn seems to be associated with increased life-spans. A more potent source of variation in life history features may relate to latitudinal variation in reproductive output. Robertson (1991a) examined the relationship between seasonal cycles and reproductive outputs and concluded that relatively benign tropical conditions would permit year-round spawning. Greater amplitude of seasonal cycling would have the capacity to reduce spawning duration and reproductive outputs. Reduced outputs and more variable recruitment expected in tropical species near the latitudinal limits of their range may select for extended life-spans.

A potential source of confounding in the comparisons of longevity is the unmeasured effect of fishing mortality. Fish populations at localities within the Caribbean with intense artisanal fisheries are more likely to be impacted by fishing compared to populations in the peripheral or isolated localities. It could be argued that the short life-spans of fishes from the San Blas Archipelago and Lee Stocking Island might reflect fishing pressure. However, although the San Blas Kuna peoples do harvest the marine resources of the sampled reefs, small herbivorous reef fishes such as *Acanthurus bahianus* are not a targeted catch and the method (traps) most likely to yield such species is not widely used (D. R. Robertson, personal observation). At Lee Stocking Island there is no intensive trap fishery (J. H. Choat and D. R. Robertson, personal observations) for small reef species as occurs in Jamaica and St. Thomas. This issue should be resolved by comparing T_{\max} and age structure in conspecific populations from fished and unfished sites with similar environmental profiles, preferably at the same location.

An alternative explanation to variation in fishing pressure is a trade-off between life-span and reproduction. Individuals at the periphery of their species range may reproduce and recruit less frequently and maintain longer lived populations compared to those at the center of the range. The differences between West Pacific and Caribbean acanthurids and scarids in terms of maximum age achieved are striking. However, we acknowledge that these comparisons may need reinterpretation once the largest Caribbean scarids, *Scarus gaucamia*, *S. coelestinus*, and *S. coeruleus*, are included. Moreover, a more expanded data base is required to ensure that the comparisons between Indo-Pacific and Caribbean scarids are not confounded by phylogenetic factors. It

is also important that studies comparing growth rates, life-spans, and recruitment rates (as a proxy for reproductive outputs) be carried out under conditions that control for fishing mortality and locality effects in each ocean system. Marine reserves offer the best opportunity for such tests that could be accomplished without significant damage to populations of abundant species in either the short or the long term.

The analysis of growth and age structure in protogynous species provides further evidence of distinctive growth patterns in different groups of reef fishes. For scarids there is strong evidence of sex-specific growth differentials resulting in males being larger than females at a given size (van Rooij *et al.*, 1995; Choat *et al.*, 1996). One result is the presence of large, young males in the population. Another is that some females may live as long as males. Sex-specific growth patterns in protogynous species have been attributed to a growth spurt in males at the time of or following sexual transition (Charnov, 1982). Evidence from scarids supports this interpretation (Choat *et al.*, 1996). Some serranid fishes—for example, *Epinephelus guttatus* (Sadovy *et al.*, 1992)—do not, however, show evidence of either long-lived females relative to males or evidence of sex-specific growth patterns. Not only will protogynous species and gonochoristic species require different approaches to harvesting (Sadovy, 1996), but also different lineages of protogynous fishes may have distinct demographics that also require different approaches to management.

Growth spurts in secondary male fishes are arguably associated with the change in energy investment from eggs to sperm. The characteristically small testes of large, fast-growing secondary male scarids suggest a trade-off between somatic and reproductive growth. Francis and Barlow (1993) provide an alternative interpretation for differential growth rates in males and females. Faster male growth rates in Midas cichlids were shown experimentally to be a result of growth trajectories established early in life by a combination of developmental conditions and social interactions. For protogynous species, faster growing members of the population may differentiate as secondary males. Hence faster growth rates may be a predisposing condition for sex reversal, rather than a consequence. Analysis of growth histories of individual fishes through back-calculation of otolith increments would help establish the pattern of growth in secondary males and resolve the issue of resultant growth spurts vs. preestablished growth trajectories. Comparison between protogynous serranid and labroid fishes with a focus on growth chronologies and sex-specific growth patterns would be particularly useful.

Regardless of the detail in interpreting demographic events in protogynous fishes it is clear that age-estimation studies are critical for determining the most appropriate management options. As Sadovy (1996) has indicated, mechanisms governing sex change in reef fishes are sensitive to a number of factors—physiological, behavioral and ecological. Estimates of fecundity for different size and age classes of the female population are critical for both management and life history studies. Estimations of fecundity are complicated by wide variation in mating systems, spawning behaviors, and population and individual spawning periodicities in reef fishes (Robertson, 1991a; Robertson *et al.*, 1999).

Throughout this chapter we have discussed growth phenomena in some species in which validation of annual growth increments has not been achieved. To reiterate, we are in full agreement with the importance of validation, but argue that given the diversity of reef fishes and the manifest and rapidly accelerating influence of fishing pressure, a preliminary analysis of growth patterns is important in determining future research priorities. The possibility that many reef species may be long-lived and display growth patterns that do not sit comfortably with traditional analytical protocols must be noted. The degree of plasticity in growth parameters and vital statistics within species that have wide distributions is also a key issue. Additional studies and validations are required to confirm or challenge the patterns we have described. Increased continuity of access to coral reefs will enhance the prospects for marginal increment analysis. In many situations and especially in equatorial areas validations based on chemical marking of sagittae should be expanded to incorporate otolith growth models (Cappo *et al.*, 2000) and the possibilities of radiochemical dating of otoliths further investigated.

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