Marine Biology (2006) 148: 1113–1122
DOI 10.1007/s00227-005-0146-7

RESEARCH ARTICLE

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Growth of *Chaetodon larvatus* (Chaetodontidae: Pisces) in the southern Red Sea

Received: 22 March 2004 / Accepted: 15 August 2005 / Published online: 15 November 2005

Abstract Growth and age of *Chaetodon larvatus* were studied using growth bands in otoliths and length-frequency analyses. Otoliths of 180 *C. larvatus* were extracted and measured. Polished sections of sagittae revealed alternating opaque and translucent bands corresponding with a seasonal growth pattern. Both mass and size of the otoliths continue to grow steadily throughout life. Length-at-age data revealed very fast growth during the first year. Growth proceeded at a decreasing rate during the second and the third year; fishes older than 3 years did not grow noticeably. No difference in growth patterns between males and females could be detected. The growth parameters obtained for the whole population are: the asymptotic length (L_∞) = 10.64 cm, growth constant (K) = 1.14 year^{-1} and the theoretical age at length zero (t_0) = −0.30 year. The maximum age recorded was 14 years. Length frequency data collected at a recruitment site confirmed the fast growth of juveniles.

Introduction

Growth studies and age determination are essential for the understanding of the life history of fish species. The two most frequently used methods are interpretation of periodic deposition of calcified tissues and length frequency analyses (Weatherley and Gill 1987). The first method uses growth bands in the scales, otoliths or vertebrae to estimate age while the second is based on the length distribution of fish in a cohort and monitors changes in the distribution with time. Both methods have been widely employed for growth and ageing studies of temperate fishes and yielded good results. Until recently, the methods were not used for tropical fish growth studies for two reasons. First, tropical fish were assumed to lack seasonal growth patterns. This was thought to result in poorly developed growth marks in the hard parts (Brothers 1980). Second, tropical fishes were believed to lack seasonality in recruitment. Protracted recruitment would result in skewed and bimodal length distributions of cohorts. In the absence of a distinct recruitment season, it is difficult to employ the length frequency method for growth studies. However, Longhurst and Pauly (1987) pointed out that in most tropical fishes growth follows predictable seasonal patterns, which can be detected using length frequent data, or by the analysis of seasonal bands in the otoliths.

Many models employing length frequency data to assess growth patterns of fishes from lower latitudes have been developed (Pauly 1987). At the same time developments in the methodology of otolith analysis made wide use of otoliths for ageing of tropical fishes possible (Stevenson and Campana 1992). As a result, growth patterns of a number of tropical fish species have been reported during the last two decades (Buesa 1987; Ntiba and Jaccarani 1988; Morales-Nin and Ralston 1990; Acosta and Appeldoorn 1992; Al-Ghais 1993; Choat and Axe 1996; Choat et al. 1996; Wilson and McCormick 1999; Harris and Collins 2000; Lobropoulou and Papaconstantinou 2000; Newman et al. 2000).

To date, growth studies of coral reef fishes were restricted to a few families including lutjanids, haemulids, sparids and serranids (Choat and Axe 1996). These represent a limited selection of the taxa that make up reef fish assemblages. Information on growth rate and life span is scarce for other families of coral reef fishes. For example, we are aware of only a couple of studies on the growth of butterflyfishes (Ralston 1976; Fowler 1989).

Communicated by O. Kinne, Oldendorf/Luhe

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Butterflyfishes (Chaetodontidae) are prominent members of most tropical reef fish communities. Fifteen species have been recorded from the Red Sea of which seven are endemic to the region (Zekeria et al. 2005). The brown face butterflyfish *Chaetodon larvatus* is endemic to the Red Sea and is the most abundant chaetodontid in the Eritrean coastal waters. Studies of the feeding habits and social behaviour of *C. larvatus* show that adults are obligate corallivores, which live in heterosexual pairs and defend feeding territories (Zekeria et al. 2002; Zekeria and Videler 2002).

In this paper, we investigate the patterns of growth in *C. larvatus*. Otolith analysis and length frequency methods are used independently and results of the two methods are compared.

Materials and methods

Study site

The study was conducted in the southern Red Sea near Massawa, Eritrea (Fig. 1). Fish samples for otolith extraction and length and mass measurements were collected from the reef east of Sheik Said Island while length-frequency data of *C. larvatus* in the field were obtained from Resimedri reef. This reef, which reaches a maximum depth of 10 m, is about 2 km long and forms a narrow fringe along the coast where diverse corals are patchily distributed. Dominant coral genera include *Porites, Echinopora, Montipora* and *Stylophora*. Monotypic coral carpets of branching *Montipora* cover some pockets on the reef. Preliminary surveys showed that these pockets are used as recruitment and nursery grounds by juvenile *C. larvatus*.

Collection and dissection of fish

During the course of this and previous studies in the area data on length, body mass and sex of 612 specimens of *C. larvatus* could be collected.

For the otolith extraction and size measurements in this study, adult *C. larvatus* were sampled at monthly intervals from July 1998 to July 2000 using a barrier net. Juvenile specimens were collected in June and July 1999 using the anaesthetic quinaldine. The fishes were preserved on ice and transported to the laboratory where their total length (mm), standard length (mm), and body mass (g) were measured. The fishes were then dissected and the sex of adult fish was determined by macroscopic examination of the gonads.

Extraction and polishing of otoliths

The largest otoliths, the sagittae, were extracted by dissecting the head of the fish dorsally from the tip of the snout to the anterior end of the dorsal fin base. The otoliths were cleaned with bleach and rinsed in distilled water. The mass of 38 sagittae was measured to the nearest 0.01 g and length measurements were taken along three orthogonal axes to the nearest 0.01 mm. The sagittae were embedded in epon and abraded and polished using carbon paper, alumina slurry, polishing cloth and lapping films sequentially. The otoliths were abraded parallel to both broadest sides until a thin transverse section through the core remained. These sections were examined with transmitted light using a light microscope at 400 times magnification. For each otolith, two independent counts of bands were conducted. The periodicity of annuli formation was inferred from marginal increment analysis.

Visual census of juveniles and adults

Preliminary surveys showed that the distribution of juvenile *C. larvatus* was restricted to areas covered by branching corals whereas adult fish were widely distributed over the whole reef. Due to the spatial variations in distribution between young and adult fish, different methods were employed to estimate the densities and sizes of the two age groups in the field.

Changes in density and length of juvenile fishes were monitored by surveying a fixed site covered by dense branching *Montipora*. Five 50 m^2 quadrats were selected and permanently marked using nylon rope and nails. Each quadrat was subdivided using ropes into 10 m^2 stripes to assist in the counting process and to avoid double counts. The surveys were carried out by diving on the reef between May 1998 and July 1999 at 7–14 days intervals. During each survey, the number of fish within the quadrats was counted and their size estimated to the nearest cm. A cm-scale glued to a PVC slate facilitated length estimation. Moreover, samples of young fish were occasionally collected from nearby sites using the anaesthetic quinaldine to validate the size estimates. Comparisons between estimated and actual length showed that the former is one third higher than actual lengths. Thus, length estimates were corrected accordingly.

Visual census of adult *C. larvatus* was conducted at monthly intervals from May 1998 to July 1999 at each of five 50 m line transects. Data were collected by slowly snorkelling along the permanently fixed line transects and counting the number of *C. larvatus* observed within 2.5 m on either side of the lines. Total length of the fishes was estimated to the nearest 2 cm. All counts were made between 8:00 and 13:00 h and the data were recorded on a PVC slate. Accuracy of estimation of the size of adult fishes was tested by comparing the estimated underwater size of the fish with the actual size of the fish measured after collection. The comparison showed that estimated sizes are one third larger than actual sizes. Thus, the underwater magnification effect was corrected by reducing the estimated sizes by one third.

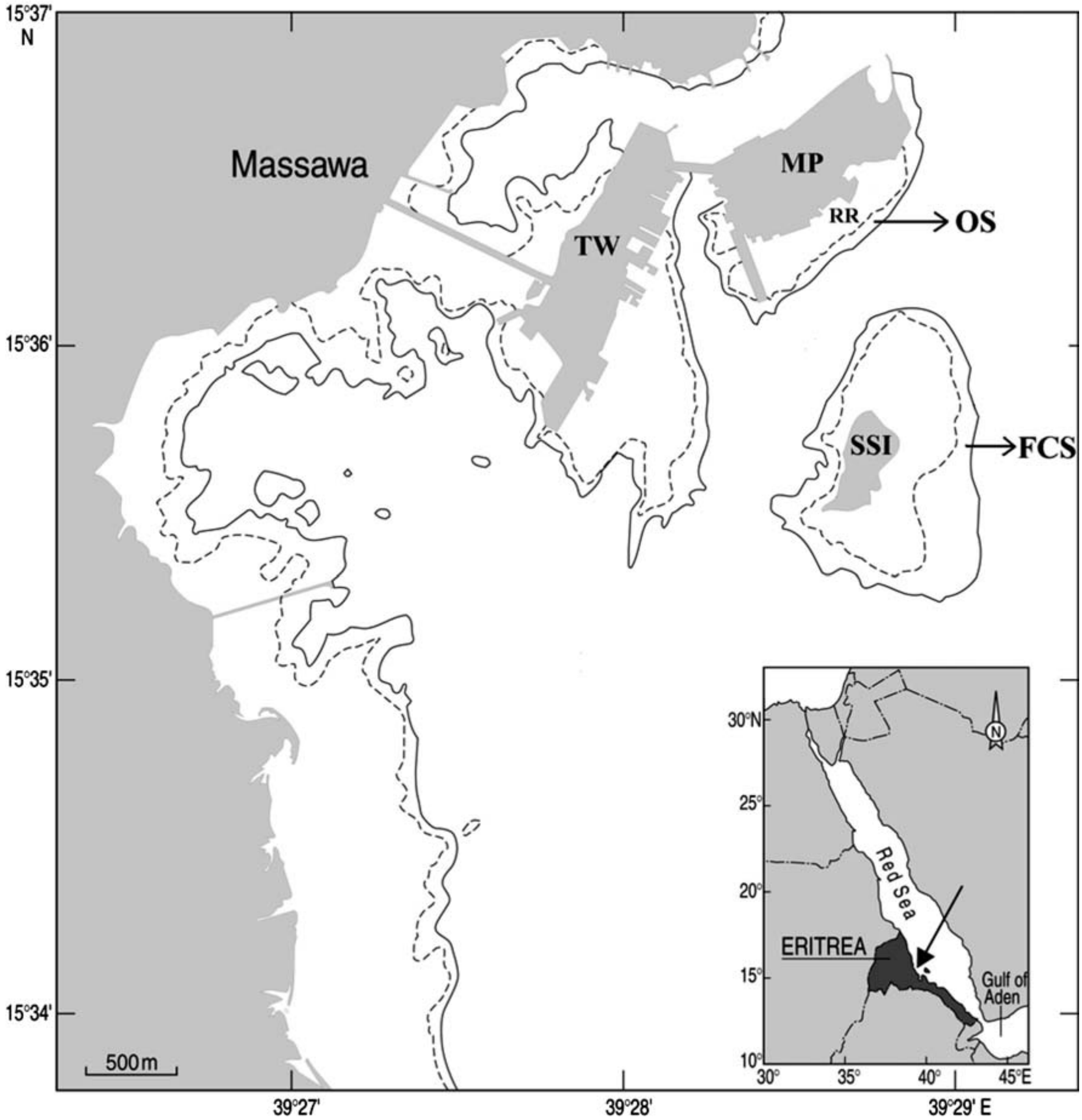


Fig. 1 Study site. *FCS* fish collection site, *MP* Massawa proper, *OS* observation site, *RR* Resimedri reef, *SSI* Sheik Said (Green) Island, *TW* Twalot

Data analysis

The von Bertalanffy growth curve ($L_t = L_\infty(1 - e^{-K(t-t_0)})$ where L_t is the length at age t; L_∞ is the asymptotic length, K the yearly growth constant and t_0 the theoretical age at length zero) was fitted to the available length-at-age data using the ELEFAN I program (Pauly 1987). Growth rates of males and females were determined separately and the results compared. FISAT (FAO-ICLARM 1997), a computer aided software, was used for the determination of von Bertalanffy growth equations and for comparison of growth between the sexes. Sizes of males and females were compared using χ^2 tests.

Results

Relationships between body mass and length for both sexes and for males and females are given in Table 1. Comparisons of the results for males and females showed no size variation between the two sexes ($P > 0.05$).

Age and growth estimates using otolith bands

The total length of the fish sample ranged from 3.2 to 11.9 cm. Out of 180 specimens, 62 were males, 71 were

Table 1 Relationships between mass and length measurements for *C. larvatus* males, females and both sexes combined

	Both sexes	Males	Females
n	612	290	322
BM	3.10 $TL^{-3.66}$	3.09 $TL^{-3.64}$	3.11 $TL^{-3.68}$

BM body mass, *TL* total lengthCorrelation coefficients (*r*) for all relations are >0.95

females, ten were juveniles (<6.7 cm) and the remaining 37 were not sexed.

All polished otoliths of adult fishes had concentric alternating opaque and hyaline bands. The non-transparent opaque bands were wider than the translucent hyaline ones. Observations of the marginal increments of samples taken throughout the year revealed that opaque bands were deposited during the colder winter months while hyaline bands were formed during the warm summer period (Fig. 2). This suggests the annual deposition of one opaque and one hyaline band. In 174 otoliths, the seasonal bands were clearly visible; in six this was not the case. Daily rings could be counted under higher magnification in the otoliths of juveniles of less than 1 year. The number of daily growth rings ranged from 44 to 117. No validation has been done to confirm the periodicity of ring formation. Daily deposition of rings is assumed following the work of Fowler (1989).

Seasonal bands of the otoliths were counted twice with an interval of at least 8 weeks by the same person. The outcome was identical in 146 cases. There was a difference of one in the counts of 23 otoliths. We decided to take the value of the last count in these cases. The difference was larger than one in the remaining five cases, which were considered unreliable and were not taken into account.

The ages of the fishes in the sample varied from a few months to 14 years (Fig. 3). Eight individuals were smaller than 6.0 cm and they were less than 1 year old. Thirteen 1 year-old fishes ranged in size from 6.0 to 10.0 cm. The remaining 148 individuals were larger than 8.0 cm and their ages ranged from 2 to 14 years. This result shows that size is a good predictor of age for individuals smaller than 8.0 cm but that it is not possible to estimate the age from the size of larger fish.

The von Bertalanffy growth model was fitted to the length-at-age data for the male and females separately. The maximum length (L_∞) values obtained for males and females are 10.6 and 10.7 cm, respectively, and the corresponding growth constant (K) values are 1.04 and 1.10 $year^{-1}$. Statistical comparisons show no variation in growth between the two sexes (Table 2). Length-at-age data from both sexes were analysed using FISAT and the resulting growth parameters were used to draw the growth curve in Fig. 3. The result shows that *C. larvatus* grows very fast during the first 2 years after which growth slows down. Fishes older than 3 years do not change in size noticeably.

Otolith mass and otolith length measurements were compared with the age of the fish in Fig. 4. Regression equations reveal a strong correlation between the size parameters and age. Otolith mass increases linearly with age. The length parameters are related to age following logarithmic curves. All these relationships are highly significant ($P<0.01$).

In summary: the body length of *C. larvatus* reaches an asymptotic maximum at an age of about 3 years. However, both mass and size of the otoliths continue to grow at highly steady rates throughout the life of the fish.

Estimates of growth rates using length frequency data

The distribution of juvenile *C. larvatus* is restricted to pockets covered by branching coral but adults are

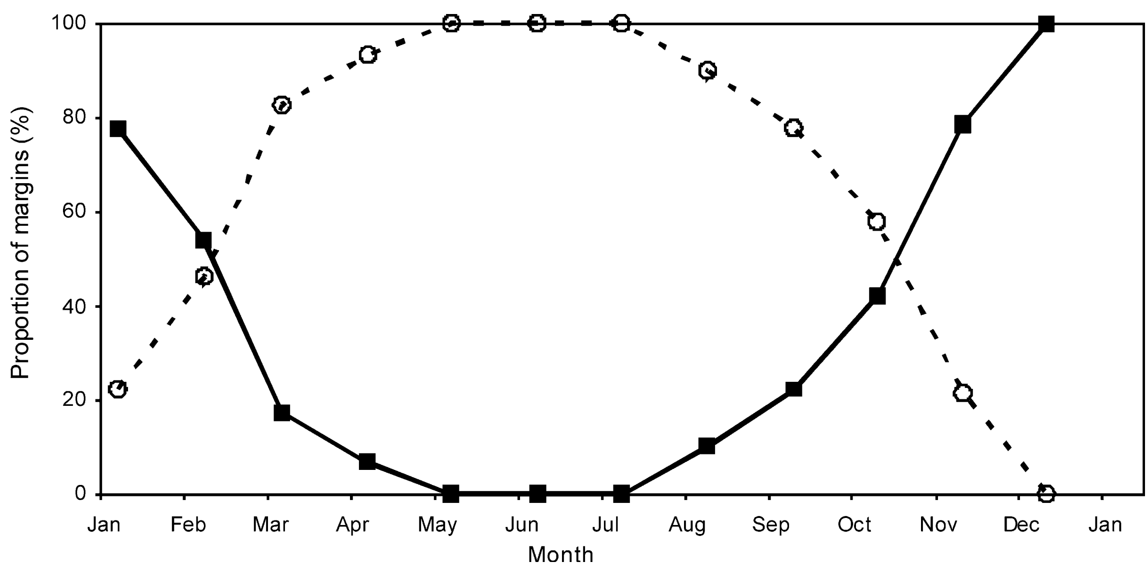


Fig. 2 Monthly changes in the appearance of the margins of *C. larvatus* otoliths. (*filled square*) opaque and (*open circle*) hyaline bands

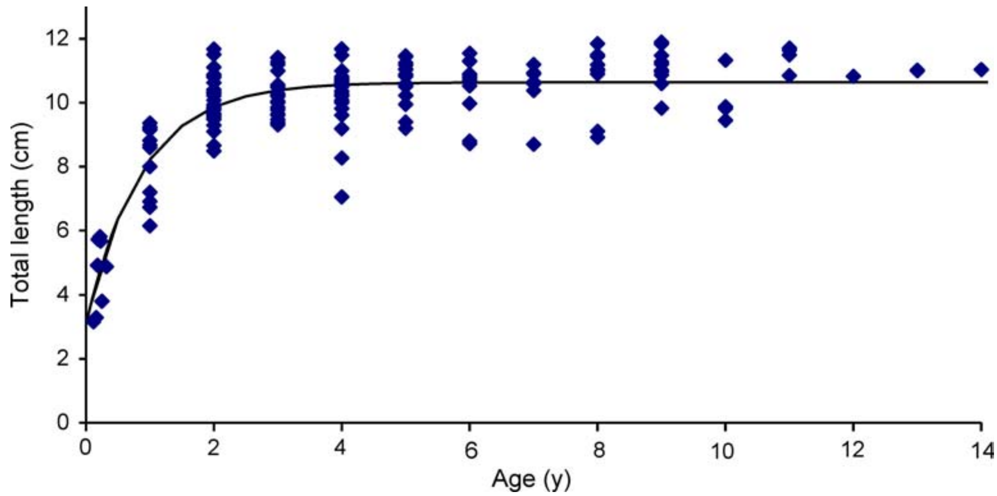


Fig. 3 Growth curve for *C. larvatus* in the Red Sea. The von Bertalanffy growth curve $L_t = 10.64(1 - e^{-1.14(t+0.30)})$ was fitted to the length-at-age data

Table 2 Estimates of the von Bertalanffy growth parameters for *C. larvatus* (with the lower and upper boundary values of 95% confidence intervals between brackets)

	n	L_∞ (cm)	K (year^{-1})	t_0 (year)
Sexes combined	164	10.64 (10.55–10.72)	1.14 (1.03–1.24)	−0.30 (−0.37 to −0.23)
Males	62	10.64 (10.49–10.74)	1.04 (0.90–1.19)	−0.34 (−0.44 to −0.24)
Females	71	10.71 (10.58–10.85)	1.10 (0.95–1.24)	−0.31 (−0.39 to −0.22)

abundant all over the reef. Length frequency distribution of adult fish was monitored for twelve consecutive months (Fig. 5). Most of the adult fish recorded from the sites were less than 9.5 cm long and densities fluctuated around 60 individuals 1,000 m^{-2} with no apparent seasonal pattern. Neither the size of adult fish nor the density changed during the study period.

A cohort of juvenile fish joined the adult population in October 1999 at an average size of 6.5 cm. The length of the cohort increased from 6.5 to 8.5 cm in 8 months. At the same time the density of the young fish decreased gradually from 280 to 30 individuals 1,000 m^{-2} (Fig. 5).

Juvenile length increase is shown in Fig. 6. Recruitment of *C. larvatus* occurred in June and July. Most of the recruits remained at the recruitment site until October. During this time, their average size increased from 4.5 to 6.5 cm. Fewer juvenile fishes remained in the recruitment site from November to January. These reached an average size of 8.5 cm in January. From January onwards, the number of young fish remaining in the recruitment sites was so small that it was difficult to follow the growth of the cohort.

In Fig. 7 the first part of the Von Bertalanffy growth curve of Fig. 4 is compared with the average sizes recorded during the visual surveys. Growth estimates ob-

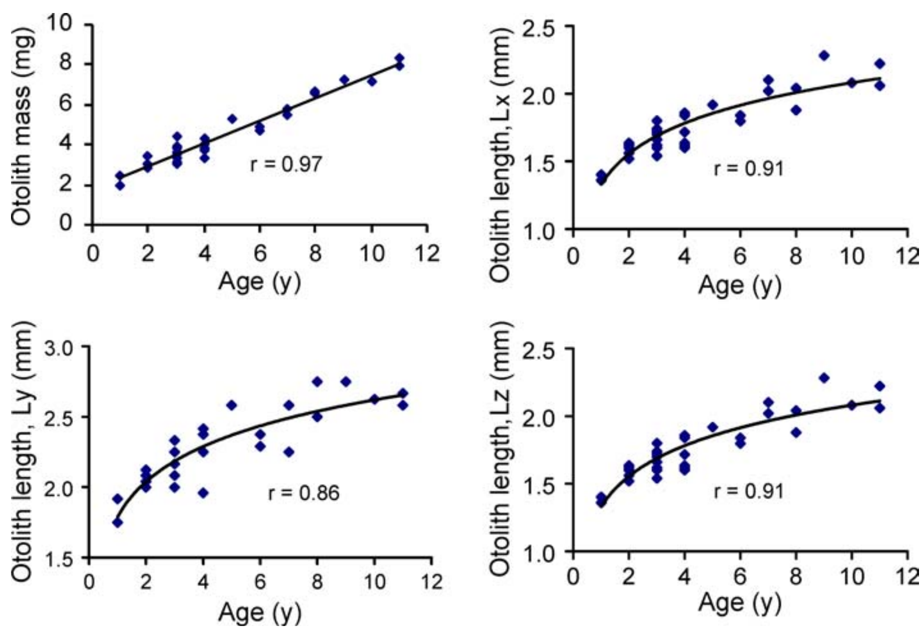


Fig. 4 Relationships between length and mass measurements of otoliths and fish age for *C. larvatus*. The regression lines (with P values <0.01 in each case) are: Age = 0.57 mass + 1.75 Age = 0.51 ln (L_x) + 2.65 Age = 0.36 ln (L_y) + 1.79 Age = 0.32 ln (L_z) + 1.33

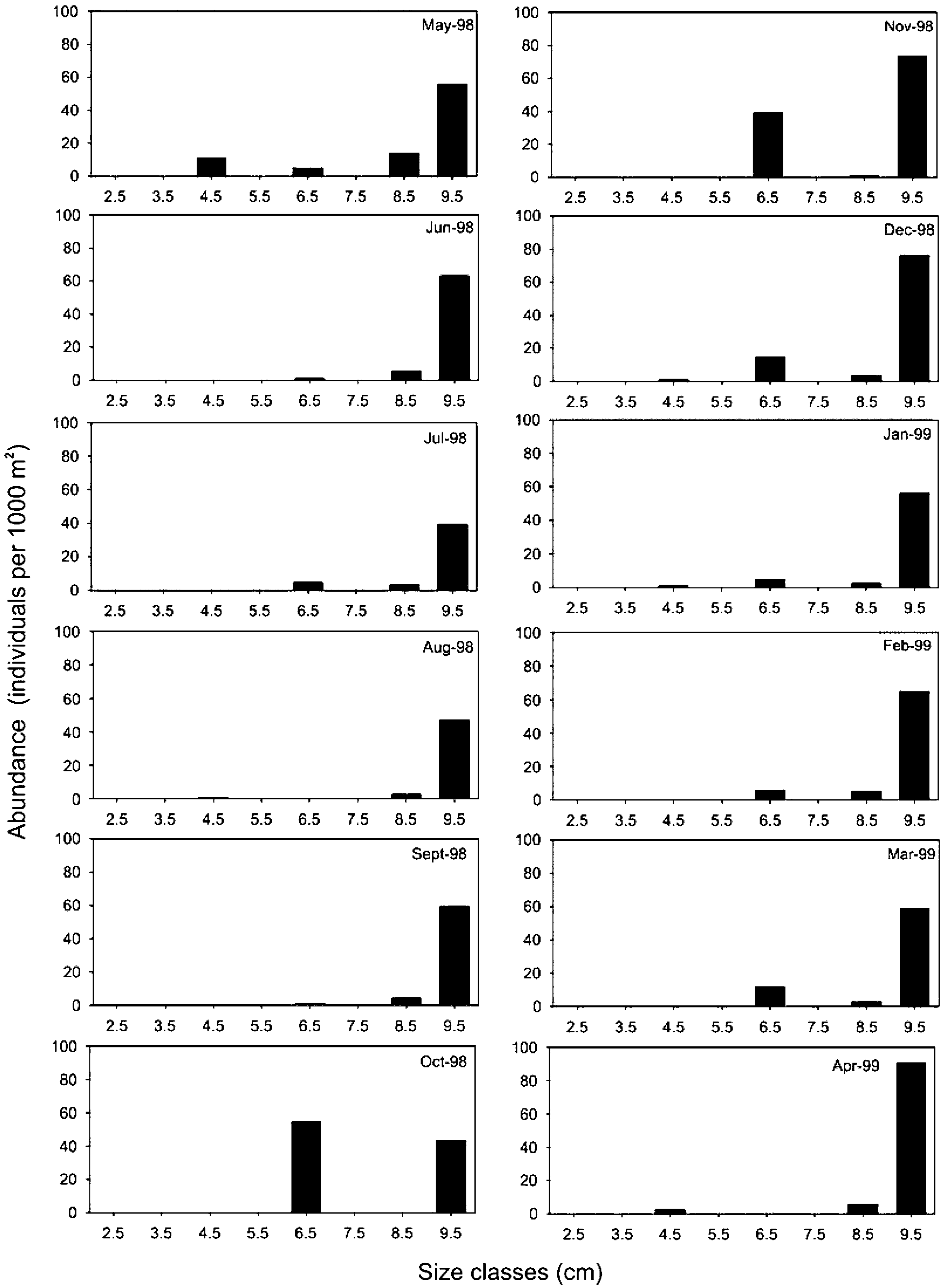


Fig. 5 Monthly changes in size and abundance of adult *C. larvatus* in the southern Red Sea

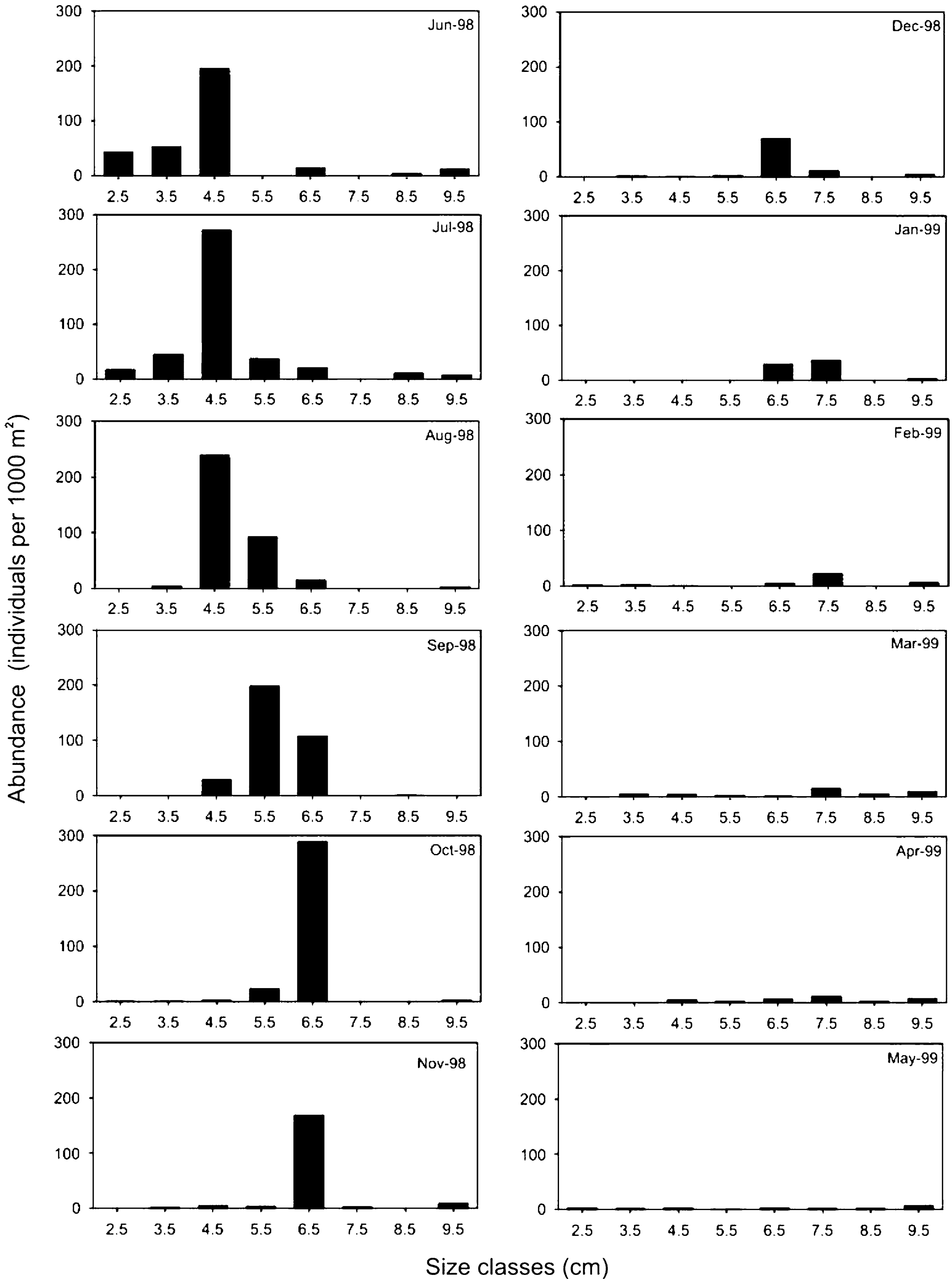


Fig. 6 Monthly changes in the size and abundance of juvenile *C. larvatus* in the southern Red Sea

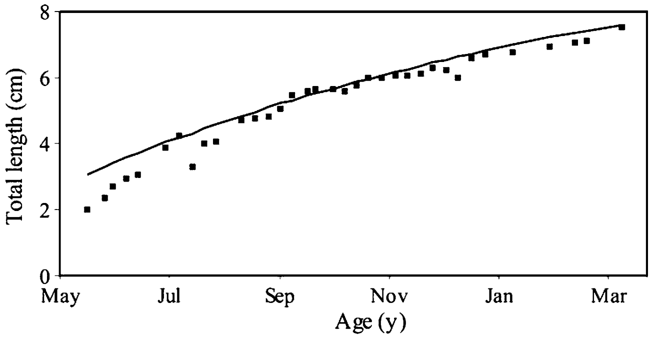


Fig. 7 Comparison between the von Bertalanffy growth curve obtained from length-at-age data (*solid line*) and length frequency data (*scatter plot*) of juvenile *C. larvatus*

tained from the two independent methods are remarkably similar. In both cases young fishes grow fast during the first 8 months. The rate was very fast from June to October but slowed down from October onwards.

Changes in the density of juvenile *C. larvatus* through the first 10 months are depicted in Fig. 8. The numbers decreased gently from June to August but from August to October the abundance decreased sharply. The average size of the juvenile fishes in October was 6.5 cm. At this size the fishes were too big to hide among *Montipora* branches and probably leave the recruitment site to seek shelter among larger corals. A steady decrease in the density of young fishes at the recruitment sites was recorded from October to January.

Discussion

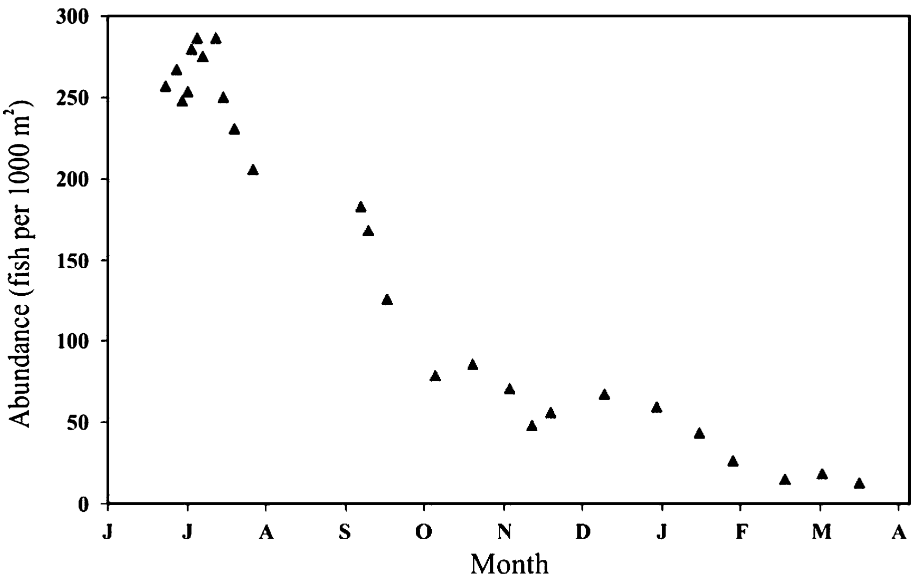
Growth estimates of tropical fishes have been considered problematic due to the supposed lack of annual bands in the hard parts and because of the believe in the absence of a distinct spawning season (Morales-Nin and Ralston 1990). However, Longhurst and Pauly (1987) pointed out that the opinion had no scientific basis. Recent studies have shown that it is indeed possible to determine the age of tropical fishes by reading growth bands in the otoliths (Ntiba and Jaccarini 1988; Fowler 1989; Brown and Sumpton 1998; Morales-Nin and Ralston 1990). Results from the present study revealed the presence of distinct growth bands in the otoliths of *C. larvatus*. This is the first study where otoliths have been used to determine the age of fish in the Red Sea.

Alternative bands of opaque and hyaline bands are deposited yearly in the otoliths of *C. larvatus*. Opaque bands are formed during the colder season while deposition of hyaline bands takes place during the summer. This result indicates the annual periodicity of band deposition. Annual deposition of an opaque and a hyaline band in the otoliths of tropical fishes has been recorded for *Lutjanus kasmira* (Morales-Nin and Ralston 1990), surgeonfishes and parrotfishes (Choat and Axe 1996).

Seasonal growth cycles in tropical fish might be related to physiological changes induced by the influence of temperature, feeding regime and reproductive cycle. Morales-Nin and Ralston (1990) pointed out that a seasonal temperature difference of 2–3°C might be sufficient to cause band formation in fish otoliths. In the study area the water temperature ranges between 27.5 and 33°C and reproduction in *C. larvatus* shows a clear seasonal cycle (Zekeria 2003).

Many workers have reported the deposition of opaque bands in summer (Fowler 1990 Choat and Axe 1996; Cazorla 2000). The present work, however, shows that opaque bands were deposited in the colder season. Results from the present work suggest that adult *C. larvatus* grow faster in the colder season. Although high temperature is known to enhance growth, the extreme high water temperature in summer months (>32°C) could inhibit growth in adult *C. larvatus*. Moreover,

Fig. 8 Changes in the density of juvenile *C. larvatus* during the first 10 months after recruitment



bleached corals, which are common in the study area during the summer (personal observation), could have less nutritional value than healthy corals found during the cold season.

The mass and the size of otoliths show strong correlation with the age of the fish. Unlike the length of the fish, which reaches asymptotic values after about 3 years, the otoliths increase in mass and size with increasing age. Hence, otolith growth is not synchronous with the growth of the fish itself. Positive correlation between the length and masses of otoliths was recorded for acanthurids and scarids (Choat et al. 1996), macrourid fishes (Lobropoulou and Papaconstantinou 2000), damselfish (Fowler 1990), and bay anchovy (Leak 1986). The very strong relationships between the mass and size of the otolith create the possibility of ageing *C. larvatus* using otolith mass or length.

A very fast growth was recorded for juvenile fish during the summer. Preliminary investigation of feeding rates showed that juvenile fishes take 50% more bites per unit time than adults. The observed fast growth of juvenile fishes could be due to consumption of more food. In their experimental studies on the growth of juvenile sablefish (*Anoplopoma fimbra*), Sogard and Olla (2001) observed faster growth of the fish at higher temperature. They pointed out that the rapid growth rate at higher temperatures was due to increased food consumption.

Rapid growth of juveniles was recorded in a number of butterflyfish species. *C. Miliaris* grew to over 8 cm within the first month (Ralston 1976). Similarly, *C. rainfordi* and *C. plebius* grew to about 6.0 and 6.5 cm, respectively, in 1 year time (Fowler 1989). Ralston (1976) pointed out that the rapid growth of juvenile butterflyfish is an adaptation to predator pressure. Predation on adult butterflyfishes is very low because predators are discouraged from consuming the compressed, spiny adult fishes, which may lodge in a predator's mouth. In contrast, juveniles are poor swimmers and they are easily handled by predators, which make them easy targets for heavy predation (Neudecker 1989).

The length frequency data provided a means to check results obtained from otolith band counts. Recruitment in *C. larvatus* is seasonal in the southern Red Sea where juvenile fishes settle on branching corals in June and July (Zekeria 2003). These young fish form a distinct cohort whose growth is easy to follow by monitoring changes in fish size. In the present study, the growth pattern estimated from otolith bands is similar to results obtained using length frequency data. Both methods show fast growth of young fish during the first few months of the fish life.

In the present study otoliths have been used to age the butterflyfish *C. larvatus*. The length-frequency analyses gave similar results for juvenile fishes but not for adults. The fast growth of young butterflyfish could indicate fast recovery rates of exploited populations. Compared with other coral reef fishes the brown face butterflyfishes seem to be short lived. Further studies are required to obtain information about the longevity of other butterflyfishes.

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