

Recruitment dynamics and first year growth of the coral reef surgeonfish *Ctenochaetus striatus*, with implications for acanthurid growth models

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Abstract Newly recruited *Ctenochaetus striatus* were monitored over a 16-month period in American Samoa, 2002–2003. During this period, a mass recruitment of age-0 *C. striatus* occurred in March 2002 with numbers reaching 22.9 recruits m^{-2} . This program provided an invaluable opportunity to (1) analyze the dynamics of a mass recruitment episode and to assess its significance with respect to more typical patterns of recruitment and (2) establish the pattern of recruit growth during their first year of life. Age-based analysis indicated that the mass recruitment generated about 90 % of annual recruitment, but recruit mortality was high; thus, most recruitment was provided by continuous settlement throughout the year. The mass event appeared to be a short-lived pulse with recruits residing on the reef an average of 14.1 d compared with 161.1 d for other recruits. Recruits grew rapidly, achieving 90 % of their adult size during their first year, and they formed their first otolith annulus after 1 yr, thereby providing a firm basis for otolith interpretation of

fish ages during the early life history phase of this species. The extensive age-based documentation of their first year growth in this study validates the distinctive “square” growth pattern exhibited by acanthurids as described in the literature (i.e., long life span with rapid initial growth that quickly reaches an asymptotic size), and it demonstrates the impact that the presence of age-0 fish has when generating growth parameters for populations exhibiting square growth. We found that the parameters from the re-parameterized von Bertalanffy growth function have preferred characteristics when modeling square growth in fish and that fixing age-at-length zero to pelagic larval duration is a preferable method to constrain growth models when lacking age-0 fish.

Keywords Acanthuridae · *Ctenochaetus striatus* · Early life history · Recruitment · Growth

Introduction

Coral reef surgeonfish (Acanthuridae) exhibit a distinctive “square” growth pattern during the course of their long lives (e.g., Choat and Robertson 2002). This growth pattern is characterized by a rapid growth spurt during the first year or two of the fish’s life followed by a quick cessation in somatic growth for the remaining decades of the fish’s life, yielding a nearly right-angled growth “curve.” This pattern has also been observed in some lutjanids and chaetodontids, as well as some other non-tropical reef species (e.g., Newman et al. 2000; Berumen 2005). Although the asymptotic leg of the square growth curve has been substantiated by numerous age-based studies, the rapid, nearly vertical growth of the first leg of the square growth curve warrants some scrutiny, because most published acanthurid

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growth curves are based on few, if any, age-0 fish. This generally occurs for logistical reasons because acanthurid recruits tend to be sporadically available, modest in number, and multiple sampling trips to remote sites may be necessary to acquire a full size range of fish during this period of rapid growth. The lack of demographic information about this early stage is especially important for two reasons. Are the young fish actually growing as fast as the models indicate (i.e., to nearly adult size in their first year)? Second, this early-growth period is critical in setting the values of the growth parameters for a fish species. The growth parameters of the commonly used von Bertalanffy growth function (VBGF) can swing 100 % depending on how many young fish anchor the growth equation, which explains some disparities in growth parameter values in the earlier literature.

The present study contributes to an understanding of these early demographic processes by tracking an unusually massive recruitment of the bristletooth surgeonfish *Ctenochaetus striatus* over a 16-month period. Two general issues are highlighted by this focus. Firstly, mass recruitments appear to be restricted mainly to members of the families Acanthuridae and Siganidae (Kami and Ikehara 1976; Pillai et al. 1983; Doherty et al. 2004; Priest et al. 2012). Mass recruitments are usually followed by rapid and very high mortality rates. The significance of these events is unclear with the possibility that mass recruitments represent a process to swamp high mortalities of recruits by predators (Doherty et al. 2004). Given the importance of mass recruiting species as food fishes, details of these events and their subsequent contribution to adult populations are important. Secondly, the study species shares the important characteristic of highly asymptotic growth patterns with a number of reef fishes with the consequence that age and size are decoupled. Changes in size distributions of targeted reef fish populations are considered to be the most consistent predictor of fishing pressure (Jennings et al. 1999; Dulvy et al. 2003). For species such as *C. striatus* in which size structure of adult populations cannot be used as an indicator of fishing pressure, additional information of initial growth rates and age structure is a high priority.

We first focus on this early life history period for *C. striatus*, and then show its linkage to the adult growth stage of this species described by Trip et al. (2008). The specific aims of this study are to (1) examine recruit dynamics following a mass recruitment event; (2) determine whether the growth rate of recruits during their first year supported the square growth concept; the latter point also involves validating the first annual ring on the otolith, which is critical in generating a growth curve with accurate parameters for species with square growth characteristics; and (3) evaluate the effects of age-0 recruits on acanthurid growth models.

Materials and methods

Study population and area

Ctenochaetus striatus is among the most abundant and widely distributed coral reef fishes in the Indo-Pacific region. It is common in American Samoa where it is harvested in the local subsistence fishery (Ponwith 1991; Green 2002; Brainard et al. 2007; Sabater and Tofaeono 2007; Craig et al. 2008; Ochavillo et al. 2011). This study was conducted at Ofu Island in the Samoan Archipelago (14°S and 170°W), which is a small volcanic island (7.5 km²) with a well-developed back reef moat (6.6 km long, 100–300 m wide, and 0.5–2 m deep at low tide, but flooded at high tide). The moat supports a high diversity of corals and fish (Craig et al. 2001; Green 2002; Birkeland et al. 2008). The study area consisted of three sampling sites (Pools 100, 200, and 400) within a 4.1-km section of the moat: Pool 100 was located on the western end of the moat in front of Ofu Village (14.17166°S, 169.67841°W, surface area ~30,000 m²); Pool 200 was located 2.4 km southeast of Pool 100) near the island airstrip (14.18457°S, 169.66611°W, surface area ~10,000 m²); Pool 400 was located 1.7 km eastward from Pool 200 in front of the locally known “Hurricane House” (14.17888°S, 169.65416°W, surface area ~30,000 m²). A further 2.5 km eastward from Pool 400 would be the end of the moat at the eastern end of Ofu Island. Recruits for age and growth analysis were collected at all three sites (usually at one site per sampling period), but quantitative measurements of recruit densities were taken only at Pools 200 and 400. Water temperature was recorded continuously in Pool 400. Diurnal water temperatures fluctuated 1–4 °C and mean temperatures were 2 °C warmer during November–May (30 °C) than June–September (28 °C).

Definition of recruits

Recruits were defined as a mixture of recently settled fish together with other age-0 fish that had settled over previous months. Virtually, all fish described herein were age-0 fish that recruited in 2002; thus, they are referred to as recruits to distinguish them from older *C. striatus* juveniles, a few of which may be adult sized and several years old (Ochavillo et al. 2011; P Craig unpub. data). For all aged fish, their recruitment date was defined as the first day after the settlement band mark on their otoliths (see below).

Initially, recruitment of *C. striatus* was operationally defined as the sighting of large numbers of small, uniquely colored, and newly recruited juveniles in their adult benthic habitat (e.g., Caley et al. 1996). Their sudden appearance throughout Ofu moat was designated Day 0 for subsequent quantitative counts of recruits over the next 16 months.

During this time, they soon adopted the brown coloration of adults and grew from 5 to 7 mm (fork length) to a nearly adult size of 150–170 mm; thus, a sliding scale was used to count and collect recruits through the study. This was not difficult because nearly all *C. striatus* in Ofu moat were either growing recruits or considerably larger adults (150–200 mm). It is possible that some larger recruits may have been excluded from early samples, but this omission would not greatly affect either density counts (because such larger recruits were relatively few in number) or age analyses (because larger recruits were sampled as the fish grew).

Recruitment dynamics

Recruitment dynamics were determined by quantitative field counts aided by analysis of recruit ages from separate collections (described below). Recruits were monitored by snorkel at two sites (Pools 200 and 400) at 1–3 month intervals from March 10, 2002 to July 10, 2003 (Table 1). At each site, average counts along five transects (3 m wide and 50 m long) were recorded. Transects had fixed starting points, but due to the shallow waters in the moat, the specific location of the 50-m transect lines was not well defined because they followed coral edges in the moat (not a depth profile) and thus might take slightly different courses in each survey. This is unlikely to introduce error because the recruits were highly mobile. It is acknowledged that recruit survival rates and potential movements within or out of the moat

may have affected these calculations, but were not assessed (see “Discussion”).

Age, growth, and maturity

To determine recruit age, growth, and maturity, random collections based on recruit availability were made almost monthly at typically one of three sites (Pools 100, 200, or 400), where large schools of new recruits had originally been observed on Day-0 (Table 1). Each monthly sample of 15–97 recruits (total 334 recruits) was caught by hand net for measurement of fork length (FL) to the nearest mm; 281 of these fish were further examined for weight to the nearest 0.1 g; sexual maturity was assessed by a visual inspection of the gonads; and otoliths were removed, cleaned, and stored dry. Age (in days) was estimated for a subsample of 82 fish that were randomly selected from each 5-mm FL size class within each monthly collection in order to subsample the complete size range present, while selecting a similar number of individuals across months. Note that this size selection produced a sampling bias for some aspects of this study because recruits were not aged in proportion to their recruitment abundance (see below).

Age estimates were based on sectioned sagittal otoliths (Choat and Axe 1996). Daily ring formation has previously been validated for juvenile acanthurids of the same genus (*Ctenochaetus binotatus*; Lou and Moltschaniwsky 1992). One sagitta of each pair of otoliths was weighed to the nearest 0.01 mg in order to establish the relationship between otolith weight and age, and to allow checking the

Table 1 Sampling summary for recruit density counts and collections of *Ctenochaetus striatus*

Density counts (at Pools 200 and 400 only)		Recruit collections							
Date	Day after mass recruitment	Date	Day after mass recruitment	Location Pool	N	size (mm)	Aging subsample		
							N	size (mm)	
10-Mar-02	0	13-Mar-02	4	100	97	56–73	6	57–70	
	(27)	5-Apr-02	27	100	47	59–72	6	59–71	
	(62)	10-May-02	62	100	21	65–77	6	65–78	
9-Jun-02	92	17–18-Jun-02	101	100	16	114–150	8	114–150	
8-Jul-02	121	8-Jul-02	121	100	12	69–82	5	69–82	
3-Oct-02	208	21–29-Sep-02	200	100 and 200	19	74–98	6	69–98	
9-Nov-02	245	2–4-Nov-02	239	100 and 200	24	78–105	7	78–101	
2-Jan-03	299	17-Dec-02	283	200	17	97–115	5	97–115	
16-Feb-03	344	3–18-Feb-03	339	200	24	94–162	10	94–162	
19-Apr-03	408	10-Apr-03	397	400	21	106–139	6	106–134	
16-May-03	435	13-May-03	430	400	15	128–175	10	128–175	
10-Jul-03	490	10-Jul-03	488	400	21	130–179	7	133–179	
					Total	334	56–179	82	57–179

Density days shown in parentheses were interpolated by equation. Mass recruitment of *C. striatus* occurred on March 10, 2002. Occasional small brown acanthurid recruits (*Acanthurus nigrofuscus*?) were excluded from samples

precision of the daily increments (Boehlert 1985; Choat and Axe 1996). A transverse section was obtained by grinding down both rostral and distal ends of the otoliths using 1,200 grade wet and dry sandpaper or lapping film, resulting in a thin section containing the nucleus (Trip et al. 2008). Each sectioned otolith was polished with lapping film and covered with clear Crystalbond thermoplastic cement (Aremco) for reading. Daily increments were counted under a high power microscope with transmitted light. Age was estimated as the mean count of two readings by the same reader (EDL Trip). If counts deviated by more than 10 %, a third count was performed or a second otolith was processed when available, or else the individual was not included in the age-based analyses. A settlement band on the otolith allowed the daily rings to be separated into pelagic larval and post-settlement phases (Wilson and McCormick 1999) in 80 of the 82 otoliths examined. This allowed calculations of birth date, pelagic larval duration (PLD), recruitment date, post-settlement days on the reef (PS), and total age (PLD + PS) for 80 fish, and birth date and total age for the remaining two fish. All size-at-age data were pooled to calculate their growth rate, and otoliths were examined for the establishment of an age-1 annulus. Size at recruitment (SS) was determined using the growth equation for PS recruits and settling time (x) at zero ($y = -0.0009x^2 + 0.6274x + 51.06$, $R^2 = 0.8774$). This allowed total fish growth rate to be separated into pelagic ($SS \text{ PLD}^{-1}$) and PS (through 1 yr) segments [(length at 1 yr—SS) (1 yr—PLD) $^{-1}$].

The 82 recruits aged were also combined with adult data from Trip et al. (2008) to model the growth of *C. striatus*. The VBGF and re-parameterized equation of the VBGF (rVBGF) were fitted as described by Trip et al. (2008). The VBGF is described as follows: $L(t) = L_\infty \{1 - \exp(-K(t - t_0))\}$, where $L(t)$ is estimated mean size-at-age t , L_∞ is mean asymptotic size, K is a curvature parameter, and t_0 is theoretical age-at-length zero. The rVBGF is a re-parameterization of the VBGF equation and is described as follows:

$$L(t) = L_\tau + \frac{(L_\mu - L_\tau) \left[1 - r^{2^{\frac{(t-\tau)}{(\mu-\tau)}}} \right]}{1 - r^2}, \quad \text{where}$$

$$r = \frac{L_\mu - L_\omega}{L_\omega - L_\tau}$$

$L(t)$ is predicted mean size-at-age t , parameters L_τ , L_ω , and L_μ are predicted mean size-at-ages τ , ω , and μ . Ages τ and μ are chosen arbitrarily within the age range of the data so as to represent the general form of growth, and age ω is the average of τ and μ (Francis 1988). Here, ages τ and μ were selected as ages 1 and 5 yrs, generating parameters of mean size-at-ages 1, 3, and 5 yrs (L_1 , L_3 , and L_5). The VBGF and rVBGF are two parameterizations of the same growth

function. Consequently, the VBGF and rVBGF generate the same growth curve (i.e., they describe growth in the same way), but differ in the nature of their parameters. One notable characteristic of the rVBGF is that of producing parameters that express mean size-at-age, a measure that is inherently biologically relevant and interpretable.

The VBGF and rVBGF were fitted to the size-at-age data from Trip et al. (2008) with and without the recruits aged in this study, to compare the parameter values generated by the two growth functions under different constraining methods with the parameter values found when including the recruits. Size-at-age data in Trip et al. (2008) included two recruits; thus, the two cases considered are hereafter referred to as “with 2 recruits” [Trip et al. (2008) data without the recruits aged in the present study] and “with 84 recruits” [Trip et al. (2008) data with the recruits aged in the present study]. The VBGF and rVBGF were fitted following five different methods: (1) with two recruits and without constraining the curve fitted; (2) with two recruits but constraining length-at-age zero (L_0) to mean size-at-settlement (estimated larval size at settlement $SS = 51.1 \text{ mm FL}$); (3) with two recruits but constraining age-at-length zero (t_0) to PLD which equaled 56.5 d; (4) with two recruits but constraining age-at-length zero (t_0) to zero; and (5) with 84 recruits and no constraints on the growth curves fitted. Confidence intervals (95 % CIs) were estimated for each parameter assuming a normal distribution of the residuals (Haddon 2001).

Use of aging to interpret recruitment dynamics

Otolith analyses were used to assist the interpretation of recruitment dynamics, but statistical limitations occurred for several reasons: Firstly, although these aged fish were randomly collected, they were subsampled by size group rather than in proportion to their field abundance; secondly, peak recruitment pulses may have been missed in months after the mass recruitment; and thirdly, individual sample sizes were small (Table 1). As a result, the ages represented monthly snapshots that were qualitatively used in three ways. First, the recruitment dates of the 80 aged recruits provided the minimum number of months that recruitment occurred through the study and second, to estimate the relative contribution of each month's recruits to total recruitment, a reconstruction was made by pairing density counts and collections of aged fish, when these two data sources were taken during similar time periods (the mean time difference between paired samples was 6.3 d, range 0–16 d; Table 1). A density baseline for this reconstruction was calculated by averaging densities at Pools 200 and 400 to expand the sample size and area of coverage ($y = 12.358x^{-0.831}$, $R^2 = 0.9851$). Each density count was partitioned according to the number of aged

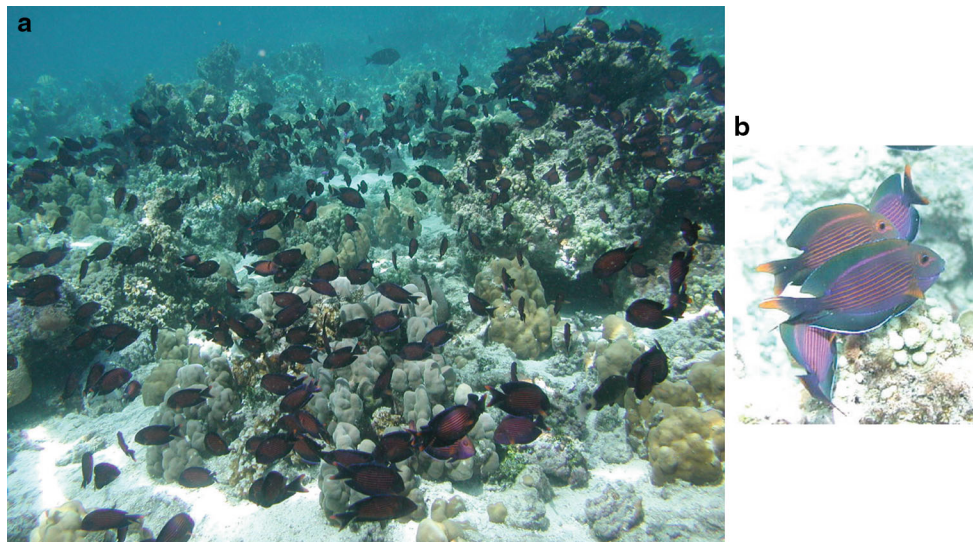


Fig. 1 **a** School of newly recruited *Ctenochaetus striatus* (mean size 64.3 mm fork length) in Ofu moat on March 10, 2002 and **b** their coloration. Photos by P Craig

recruits (in the paired sample) that were binned by recruitment month, and the sum of each month's reconstructed densities of aged fish (per bin) provided an approximation of their total density contribution. This was converted to percentages as an indicator of their relative contribution to total recruitment during the study period. On two collection days (Days 27 and 62), when comparable field density counts were not available for collection dates, densities were interpolated using the density equation. Third, to estimate how long each month's recruits remained in the study area, post-settlement ages of each month's number of aged fish were summed in subsequent samples after their recruitment month and then averaged (mean days \pm SD).

Results

A mass recruitment of *C. striatus* recruits occurred on Ofu's reefs in March 2002, first appearing in low densities on reef slopes about one week after the full moon (5–9 March), followed by massive numbers in shallow waters on 10 March (Day 0, Fig. 1a). Age data indicated that peak recruitment occurred during the two-week period, 8–24 March, with no recruitment during the month preceding this period or for one week afterward. Mean recruitment size at Day 4 after the mass event was 64.3 mm FL (range 56–70 mm, $n = 97$). Their initial coloration was a vivid purple–blue body with orange lateral stripes, an orange eye ring, and dark fins with orange-tipped caudal fin lobes (Fig. 1b). Within three to four weeks, their color faded to the brown color of adults, with light brown horizontal lines along their sides.

Recruitment dynamics

Recruits initially roved over the substrate in schools of about 50–5,000 fish. On Day 0, a large school of fish was encountered on transects in Pool 200, but not in Pool 400, resulting in a wide initial density range of 0.17–22.9 recruits m^{-2} (Fig. 2). By Day 15 (based on visual observations) and definitely by Day 92, when the next density survey was conducted, fish numbers in Pool 200 had declined sharply, thereafter becoming more widely dispersed and declining gradually in abundance. Calculations of survival rates based on Fig. 2 would be misleading, however, because age analysis revealed a more complex recruitment scenario. Rather than tracking a single mass recruitment event during the course of this study, nearly continuous recruitment occurred throughout 2002 (Fig. 3). Only 16 % of the aged recruits originated from the mass event. Others (10 %) had recruited 1–4 months prior to this event, and 74 % recruited 1–11 months after it. Altogether, the 80 aged recruits settled on 72 d over the 16-month period.

However, the low percentage of mass recruits in aged samples (16 %) was an artifact of the size-based method used to select otoliths to analyze. To put the mass event into a more realistic perspective, its contribution was qualitatively reconstructed as described in the Methods. This reconstruction, while approximate, indicated that the mass event accounted for 88 % of all recruits over the 16-month sample period, with each remaining month's cohort of recruits contributing 0.01–3.1 % of the total sample (Fig. 4). Nonetheless, the mass recruitment in Ofu moat appears to have been a short-lived affair (Fig. 5), as estimated by the time that each monthly cohort remained

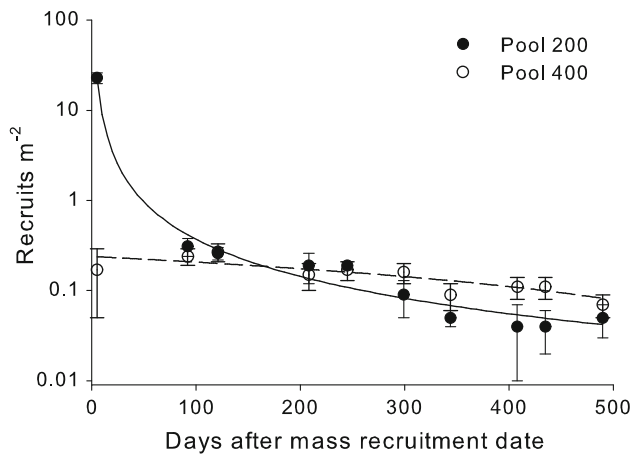


Fig. 2 Density of *Ctenochaetus striatus* recruits at two sites in Ofu moat beginning with a mass recruitment event on March 10, 2002 (Day 0). Standard deviation bars are indicated. Lines plotted are best-fit regressions (Pool 200: $y = 203.71x^{-1.37}$, $R^2 = 0.98$; Pool 400: $y = -0.0003x + 0.24$, $R^2 = 0.64$)



Fig. 3 Actual recruitment dates (pooled by month) for the 80 aged *Ctenochaetus striatus* recruits in this study. The mass recruitment event on March 10, 2002 is indicated (arrow), but is under-represented due to the subsampling method used (see “Discussion”)

on the reef (estimated as the mean post-settlement time of combined collections for each monthly cohort). Counter intuitively, the mass recruits spent far less time on the reef (mean 14.1 d and maximum 47 d) than most earlier and later monthly cohorts (even though sampling continued for an additional 1.2 yrs after the last mass recruit was collected). Recruits from November 2001 to February 2002 averaged 172.1 d (maximum 206 d) on the reef and those from June to January 2003 averaged 156.3 d (maximum 330 d).

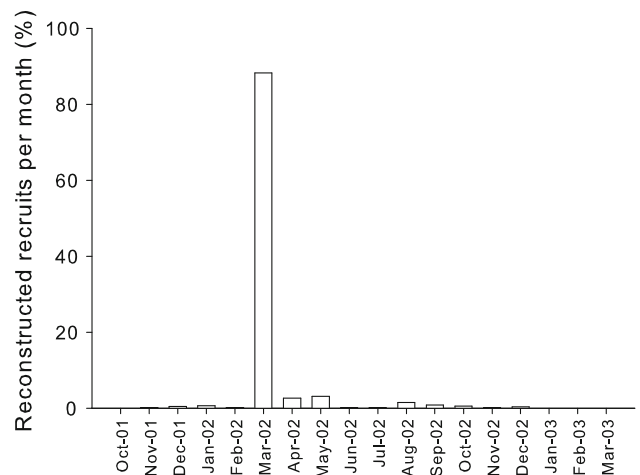


Fig. 4 Reconstructed proportions of each month's cohort of new recruits to total recruitment during the study period, as described in the “Methods”

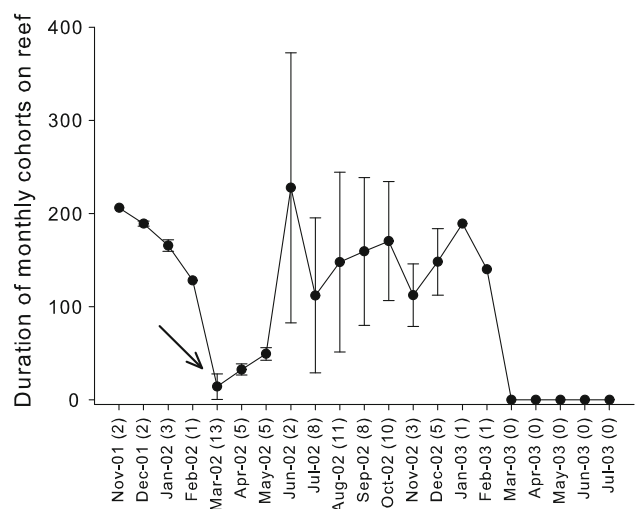


Fig. 5 Estimated residency time (mean days \pm SD) that each newly recruited cohort of fish (pooled by month) remained in Ofu moat as indicated by the total collection of recruits from each monthly cohort. The March 2002 mass cohort (arrow) and monthly sample sizes of aged fish are indicated in parentheses along the x-axis

Age, growth, and maturity

The 16-month period of recruit collections provided a detailed account of *C. striatus* age, growth, and maturity during their first year of life. Otolith weight varied significantly ($P < 0.0001$) with number of daily rings on the otoliths, thus supporting the age interpretation of these fish (Fig. 6). PLD averaged 56.5 d (SD = 4.7, range 47–69 d, $n = 80$) and was similar to that recorded for this species in

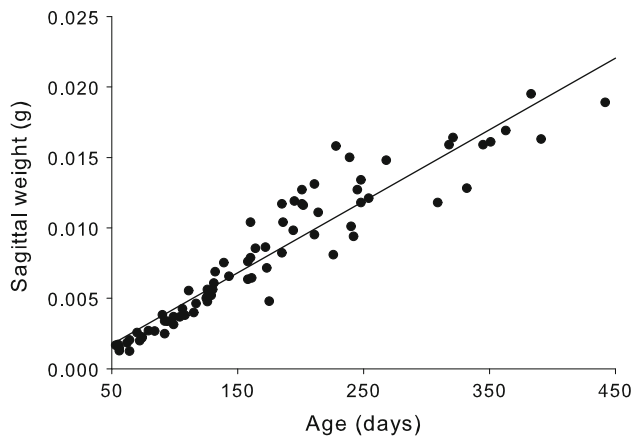


Fig. 6 Relationship between age (number of daily bands) and otolith weight. The linear regression is of the form: $y = 0.0001x - 0.0008$; $R^2 = 0.89$, $P < 0.0001$

the Great Barrier Reef (57.4 d; Wilson and McCormick 1999). PLD in Ofu was not statistically related to either mean water temperature during the larval period ($R^2 = 0.0017$, $P = 0.7$) or the date of recruitment ($R^2 = 0.0083$, $P = 0.4$).

Aged fish ranged 0–330 d in post-settlement age ($n = 80$; post-settlement age could not be estimated for the two oldest fish aged), 53–442 d in total age ($n = 82$), and 56–179 mm in fork length. Virtually, all were age-0 fish, and all were sexually immature with no apparent gonadal growth, even for the largest (179 mm) and oldest fish (442 d) analyzed. During their first year on the reef, their length–weight relationship was $w = 2.461(10^{-5}) \times L^{2.992}$ ($R^2 = 0.984$, $P < 0.0001$).

Of particular significance in this study was that by Day 365 (total age), their fork length was 157.7 mm (Fig. 7), which equated to 90 % of their adult asymptotic size of 175.6 mm (Trip et al. 2008). Net growth during this first year (total age) was 0.43 mm d^{-1} . Estimated larval size at settlement was 51.1 mm, which was used to separate net growth rates for the pelagic and PS phases: 0.90 and 0.35 mm d^{-1} , respectively. The four older age-1 fish in the sample formed their first otolith annulus at an average of 376 d (SE ± 14.5 d). Annulus formation occurred between April and June, which coincided with the end of the warmer season and beginning of the slightly cooler season. Back-calculated birth dates indicated that parental spawning in January 2002 produced the mass recruitment event observed in March 2002, and the broad spread of spawning dates for the complete collection of aged recruits (73 nights over 15 months) indicated year round spawning by this species.

Combining size-at-age of the recruits with data from Trip et al. (2008) revealed a square-shaped growth trajectory characteristic of acanthurid fishes, with *C. striatus* reaching 90 % of asymptotic (adult) body size by the age of 1 yr and spending >95 % of their life span at adult size

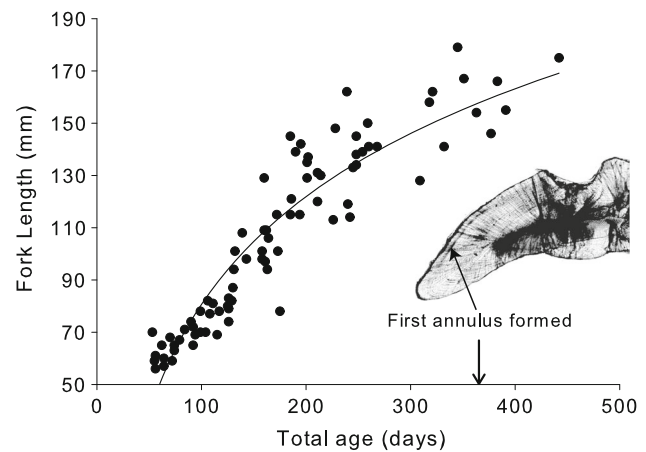


Fig. 7 Growth of *Ctenochaetus striatus* recruits over a 16-month period. Observed size-at-age data are fitted with best-fit regression: $y = 59.59 \times \ln(x) - 193.82$; $R^2 = 0.87$. The mean date of the first annulus formation on the otolith is indicated (arrow). Inset photograph shows the position of the year-1 annulus at approximately Day 364 on the sectioned sagittal otolith of a 390-day-old individual

(Fig. 8). Comparison of the growth parameter values under different constraining scenarios (Table 2) demonstrated that (1) not using a constraint when lacking age-0 fish generated parameter values that significantly differ from those obtained with the recruits for both the VBGF and rVBGF; (2) when using a constraint (any), the parameters describing the asymptotic leg of the curve (L_∞ in the VBGF, and L_3 and L_5 in the rVBGF) did not significantly differ from that found when using the recruits, suggesting that the parameters that were the most affected by the type of constraint used were those describing the ascending leg of the growth trajectory: K and t_0 (VBGF), and L_1 (rVBGF); and (3) the constraint that generated parameter values that were closest to those found when including the recruits were that of fixing theoretical age-at-length zero (t_0) to PLD [fixed as a negative value ($-PLD$) such that the growth trajectory intercepts the y axis], for both the VBGF and rVBGF (Table 2). The latter point was of particular interest as it showed that constraining t_0 to PLD provided the best growth parameter estimates over the fast growing, ascending leg of the growth curve. In addition, comparison of the confidence intervals around the parameter values showed a significantly greater spread in the values for the VBGF parameters, suggesting a comparatively higher stability in the rVBGF parameters (Table 2).

Discussion

Recruitment dynamics

Mass recruitment events of *C. striatus* occur occasionally in American Samoa—nine events have been reported at the

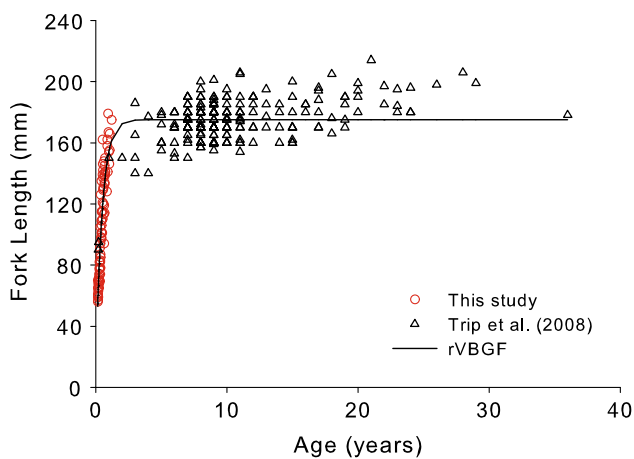


Fig. 8 Growth trajectory of *C. striatus* from Ofu where the age-0 fish from the present study have been combined with the older and larger fish reported by Trip et al. (2008). Combining the two datasets produced the following rVBGF (re-parameterized VBGF) parameters: $L_1 = 153.8$, $L_3 = 174.8$, $L_5 = 175.2$. Figure modified from Trip et al. (2008) with additional data from the present study

same time of year at various locations over the past 25 yrs (Birkeland et al. 1987; Green 2002; Brainard et al. 2007; personal observations by A Green, P Craig). Villagers harvest the new recruits when they are accessible (Craig et al. 2008). Based on modeling ocean currents and virtual

larval transport, Kendall et al. (2011, 2013) suggested that Ofu Island could be reliant on outside larval sources for fish recruitment and that for fish with longer PLDs similar to *C. striatus*, the main islands of Tutuila and Samoa could be significant larval sources. Self-seeding by larvae from Ofu is also a possibility (e.g., Jones et al. 2009). There have also been sightings of large recruitment pulses of *C. striatus* elsewhere in the South Pacific islands (e.g., Moorea: Doherty 2002; personal observations by P Craig in Nuie and Cook Islands), but this does not appear to be a consistent life history characteristic of this species throughout its range. *C. striatus* is common on the Great Barrier Reef, but recruits there are rare, and mass recruitment events have not been observed despite more than 20 yrs of observations (Doherty 2002; personal observations by JH Choat and K Clements)].

The 2002 recruitment event was widespread in American Samoa, but largest numbers were observed in Ofu moat (Green 2002). This site allowed access to the recruits over an extended period, and age-based analysis provided insight into how the recruitment event unfolded. Our expectation that we were monitoring the mass recruitment event from March 2002 was misleading. Although this group recruited abruptly in high densities, age analysis revealed that their residence time on the reef was brief,

Table 2 Parameter values of VBGF and rVBGF fitted to describe the growth of *Ctenochaetus striatus*

	VBGF parameters ($\pm 95\%$ CI)			rVBGF parameters ($\pm 95\%$ CI)		
	L_{inf}	K	t_0	L_1	L_3	L_5
With 2 recruits						
No constraint	181.4 [179.9–182.8] 183.7 fa	0.30 [(-1.20)–1.79] 1.74 fa	-2.99 [(-4.49)–(-1.50)] -1.84 fa	125.9 [124.4–127.4] 121.8 fa	150.7 [149.2–152.2] 146.0 fa	164.4 [162.9–165.9] 160.5 fa
Constraining L_0 to size at settlement	175.6 [174.0–177.6] 175.5 fa	1.38 [(-0.19)–2.96] 1.51 fa	-0.22 [(-1.80)–1.35] -0.21 fa	143.4 [141.8–144.9] 147.1 fa	173.6 [172.0–177.1] 174.1 fa	175.5 [173.9–177.1] 175.4 fa
Constraining t_0 to PLD	175.5 [173.9–177.1] 175.5 fa	1.80 [0.23–3.37] 1.83 fa	-0.15 [-0.15 fa]	153.6 [152.1–155.2] 154.5 fa	174.9 [173.3–176.4] 174.9 fa	175.5 [173.9–177.0] 175.4 fa
Constraining t_0 to zero	175.4 [173.8–177.0] 175.4 fa	3.32 [1.75–4.89] 3.41 fa	0 0 fa	157.8 [156.2–159.4] 157.8 fa	175.2 [173.6–176.8] 175.2 fa	175.4 [173.8–176.9] 175.4 fa
With 84 recruits						
No constraints	175.6 [174.2–177.0] 175.6 fa	2.08 [0.69–3.49] 2.09 fa	-0.02 [(-1.42)–1.37] -0.02 fa	153.8 [152.4–155.2] 154.3 fa	174.8 [173.4–176.2] 175.1 fa	175.2 [173.8–176.6] 175.5 fa

The VBGF and rVBGF were fitted using data from Trip et al. (2008) with and without the recruits aged in this study: (1) “With 2 recruits”: Trip et al. (2008) data only, and (2) “With 84 recruits”: Trip et al. (2008) data with the recruits aged in this study. The 95 % CI around each parameter value is presented in square brackets. Results are presented for the same set of analyses conducted using fractional ages (fa) for adults to reflect their month of capture (using a common theoretical birth date of January 1st) and align with the fractional age of recruits (estimated in days and then expressed as a fraction of years)

averaging only 14.1 d. In contrast, even though sampling started when the mass recruitment occurred, 84 % of the aged recruits sampled did not originate in that initial pulse, but were produced by year round spawning, and their residence time on the reef was much longer, averaging 161.1 d. Mortality due to artisanal fishing around both Ofu and neighboring Olosega islands briefly targeted the mass recruitment, but the total harvest was negligible in 2002 (143 kg; Craig et al. 2008). Predation of the mass cohort seems the most probable explanation for its short duration on the reef. Jacks, groupers, and trumpet fish were observed attacking the recruits on the reef front, but predation was not monitored in the study area, especially when the moat was flooded at high tide and afforded predators easy access to the recruits. A large-scale emigration of these fish seems less likely because (1) earlier and later recruits remained on the reef for much longer periods, and (2) although some ontogenetic habitat shift is conceivable, Lecchini and Galzin (2005) observed that *C. striatus* utilized most types of shallow-water habitat during both settlement and post-settlement stages.

The apparently low survival of the mass recruits in Pool 200 was consistent with that described in the literature for other coral reef fishes (e.g., Doherty et al. 2004; Almany and Webster 2006), and the age-based analysis indicated nearly all of this decline occurred within a few weeks after settlement. We conclude that the mass recruitment event itself may have contributed little to the overall recruitment of *C. striatus* in Ofu in 2002; thus, the role of mass recruitment events in the population maintenance of this species remains unclear.

Note that the numbers above contain a sampling bias that should be clarified. Because the recruits that were aged were not sampled in proportion to their abundance in the field, fish from the mass recruitment would be under-represented during the time of their peak abundance by our size-based subsampling methodology. But most of the mass recruits did not appear to survive long or remain in the moat; thus, their contribution to annual recruitment was negligible, at least in the moat.

Age and growth, with implications for acanthurid growth models

By combining the growth phase of the recruits with that of adults (from samples of larger and older *C. striatus* collected in Ofu by Trip et al. 2008), the present study clearly validates the square growth pattern of acanthurid fishes (Fig. 8). The recruits grew rapidly, achieving 90 % of their adult size in their first year, and their asymptotic size of 175.6 mm was reached soon thereafter. Somatic growth then essentially ceased although individuals continued to live for decades. Furthermore, the formation of the first

annulus on the otolith provides a firm basis for otolith interpretation of fish ages during the early life history phase of this species.

This growth pattern has significant implications for coral reef fish management. First, it confirms that, for all but the smallest individuals, a fish's size and age are not linked; thus, size is not useful for determining acanthurid age, maturity, fishing pressure, or fishing regulations. Second, it impacts estimates of growth parameters (described below), particularly those of the oft-used VBGF, unless selection criteria are standardized (e.g., Choat and Axe 1996; Craig et al. 1997; Craig 1999; Trip et al. 2008).

Trip et al. (2008, and citations therein) noted that the biological interpretation and statistical properties of the VBGF parameters K (growth coefficient), L_{inf} (asymptotic length), and t_0 (time when theoretical length would be zero) have often been questioned. The present study demonstrated that K was significantly affected by the presence and number of small fish (particularly age-0) in the sample. For example, when the aged recruits from this study were added to the previous Ofu growth data for older fish presented by Trip et al. (2008), K increased by 16–51 % or decreased by 37 %, depending on the constraint used to model growth (Table 2). We tested three different constraining methods: fixing length-at-age zero to size at settlement and to 0, and fixing age-at-length zero to PLD. All three methods generated K values that differed from the value of K found when growth was modeled using the recruits aged in this study. These results demonstrate two points. First, the presence of young fish affects the value of VBGF parameters, especially parameter K , a fact that has also been noted for several other fishes exhibiting the square growth characteristics (e.g., Craig et al. 1997; Berumen 2005). Second, using a constraint when fitting the VBGF, a method that is routinely used to take into account the lack of young individuals in a sample, does not generate a value of K that adequately represents early growth. This is most likely due to the fact that K is a curvature parameter (not a measure of growth rate) that varies with the age at which the growth curve reaches asymptotic size (L_{inf}) and thus varies directly with the presence and number of samples in the ascending arm of the growth curve.

In contrast, adding the aged new recruits from the present study to the previous Ofu growth data from Trip et al. (2008) had a smaller effect on the parameters of the re-parameterized equation of the VBGF (rVBGF; Francis 1988). That is, rVBGF parameters were comparatively more stable than the VBGF parameters. This was particularly evident for VBGF parameters K and t_0 , which showed 95 % CIs that span up to ten times the parameter values, whereas rVBGF parameter mean size-at-age 1 yr L_1 varied over a range of values that covered less than 0.05 times the parameter value. Additionally, the value of rVBGF parameter L_1 increased by only

seven to 22 % when adding the new recruits, depending on the constraining method used.

The constraining method that produced parameter values that were closest to those found when including the recruits (i.e., closest to the “true” values) was that of constraining age-at-length zero to PLD. This was true for both the VBGF and rVBGF. However, while both growth functions produced parameter values that were relatively close to the “true” values under this constraint, the VBGF and rVBGF differed significantly in the following aspect. There was a distinct difference between the two equations in terms of how close the constrained parameter values were found to be to the “true” values. While the values for rVBGF parameter L_1 with constraint versus recruits were nearly identical (153.6 mm when constrained versus 153.8 mm with the recruits, Table 2), there was a comparatively greater effect on VBGF parameter K , which varied from 1.80 under the constrained model to 2.08 with the recruits (Table 2). These results are significant as they suggest that the rVBGF produces parameter values that better represent growth, especially growth of the ascending leg of the growth trajectory. In turn, this indicates that the rVBGF parameters (especially parameter L_1) are not as sensitive to the presence or absence of young individuals in the sample as VBGF parameter K and that K is thus a poor descriptor of fish growth and should be avoided when comparing populations. A possible explanation for this difference in parameter stability between the two parameterizations of the VBGF may lie in the fact that rVBGF parameters are expressions of mean size-at-age, which may thus be inherently more stable than the curvature coefficient K .

Finally, we tested the potential effect of combining daily ages for recruits together with annual ages of older fish in parameter calculations by converting all annual ages to fractions of a year that reflect their month of capture, thus aligning the age of adult individuals with that of the recruits, which were estimated in days and later expressed as a fraction of years. In the present study, there was little difference in the parameter values between the two types of age calculation (except when the curves were unconstrained and without the aged recruits from the present study), and therefore the effect of using whole ages of older fish as opposed to fractional ages was negligible (Table 2). Given that the majority of demographic studies of coral reef fishes use whole ages, we believe that using whole ages for older fish may provide a better platform for comparison in future studies.

In conclusion, we advocate that (1) Francis' (1988) reparameterization of the VBGF (rVBGF) be preferentially used to model square growth in fish (over the traditional VBGF equation) and that (2) fixing age-at-length zero to PLD be used as the preferred method to constrain growth

models when lacking adequate numbers of age-0 fish (for both the VBGF and rVBGF). We believe these two recommendations are of particular significance when the aim is to produce estimates of growth rate (mean size-at-age instead of K) or to compare growth values between populations. As the rVBGF and VBGF are two parameterizations of the same growth function, the issues we address with these recommendations are that of biological interpretability and statistical properties of the growth parameters. Given the widespread use of the traditional VBGF parameters (in particular parameters K and L_∞) in fisheries modeling and related areas, however, we believe that the most sensible approach will be one of documenting the VBGF in combination with the rVBGF parameters, and selecting the function that will be most appropriate for the questions under analysis. Such factors are essential to an understanding of the biology of square growth coral reef fishes and to management efforts to assess or regulate their harvest.

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