



Population structure of *Ctenochaetus striatus* (Acanthuridae) in Tutuila, American Samoa: The use of size-at-age data in multi-scale population size surveys

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ABSTRACT

We combined size-at-age and underwater survey (UVS) data to investigate the spatio-temporal distribution of life-history stages of the bristletooth surgeonfish, *Ctenochaetus striatus*, around Tutuila Island, American Samoa. Three age-based size categories (recruits, juveniles and adults) were determined by examining the relationship between size, age and gonad maturity. The results from combining size-at-age with UVS density data showed varying densities at the scales examined (years, exposure, sector, and habitat) on the fore-reef slopes of Tutuila Is. While recruit densities were uniform, juvenile densities varied by year, exposure and sector, and adult densities were significantly higher at topographic sites that were comparatively more exposed to water motion than inside bays. Densities of recruits were positively correlated with habitat (rubble) illustrating the importance of this substratum for the survivorship of early life history stages. Densities of adults were positively correlated with coralline algae, which may suggest co-occurrence responding to similar physical environment of adult habitat that is possibly indirectly correlated to feeding. However, densities of juveniles were negatively correlated with food source although the variance accounted for was low. We hypothesize that some other substratum may possibly be important for juveniles. There was a negative correlation between recruit and adult densities, indicating the presence of ontogenetic shifts in habitat with age and size. It is proposed that ecosystem-based fishery management of *C. striatus* in Tutuila Is should consider the high abundance of adults in exposed topographic habitats in the establishment of marine protected areas. We have shown that size-at-age data when combined with underwater fish surveys significantly expands its utility in the study of the population structure of a coral reef fish thus allowing the identification of areas characterized by high abundance of particular life stages for management.

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1. Introduction

The study of population structure is fundamental in understanding population dynamics (Cole, 1954; Stearns, 1992). In particular, estimation of population size and age structure provides a basis for deriving information on population growth, mortality and recruitment rates. These parameters are critical in determining population productivity and the impact of fisheries (Beverton and Holt, 1957; Ricker, 1975; Roff, 1984; Beverton, 1992; Robertson et al., 2005). Population structure information is also necessary in understanding and predicting the effect of disturbances (including fishing), and these data are essential in estimating sustainable levels for various fisheries (e.g. Ault et al., 2008).

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Some authors suggest that coral reef fish species exist as metapopulations (e.g. Sale, 1998; Swearer et al., 2000; Jones et al., 2000) and spatially segregated populations. This could result in differences in recruitment, reproductive output, growth, mortality and survivorship, leading to variations in population structure. Geographical variation in population size and age structure has been shown for a number of coral reef fish species (Gillanders, 1995; Meekan et al., 2001; Gust et al., 2002; Robertson et al., 2005; Trip et al., 2008), and demographic parameter differences have been used as indicators for delineating stocks (defined as closed interbreeding units) and for defining appropriate scales in fisheries assessment and management (e.g. Begg et al., 1999). Identification of these 'unit stocks' is important for fisheries management because potential yields might vary among sub-populations (Caddy, 1975). The scale of the population structure variability can also be used to determine the 'spacing' of marine reserve sites forming a network of protected areas. However, the lack of stock structure information and connectivity among adult populations has limited the fishery implications in the design of Marine Protected Areas (MPAs) (Walters and Bonfi, 1999). Therefore, understanding the distribu-

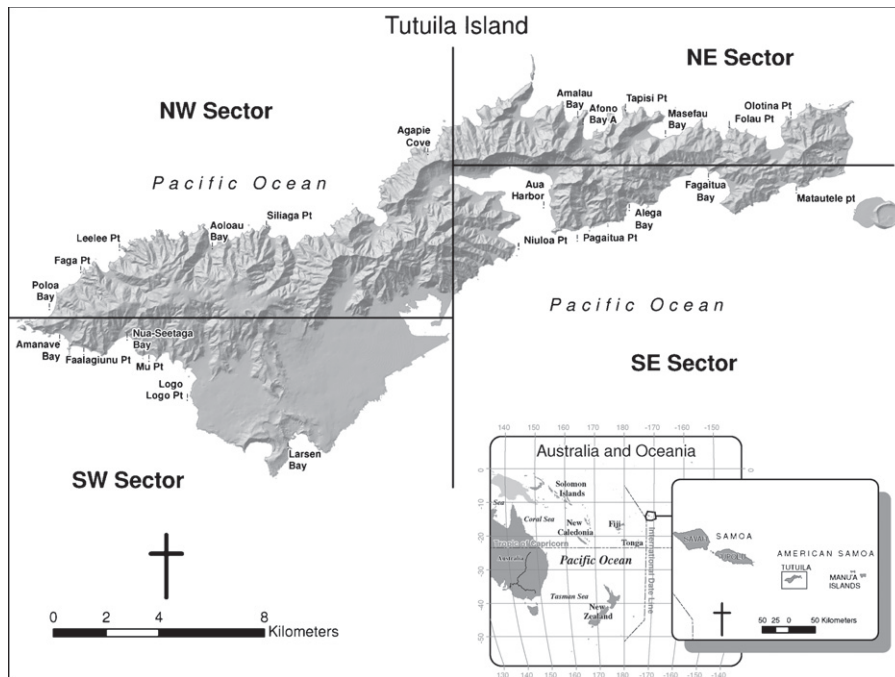


Fig. 1. Map of Tutuila Island, American Samoa, showing the sectors and population survey sites.

tion and potential spatial relationships between the different life history stages within a population, in particular between spawning and newly recruiting individuals, will provide essential information for the establishment and management of MPAs.

Ontogenetic shifts in habitat are common among reef fishes, and these are often size and age-based (reviewed in Williams, 1991; Mumby, 2006; Lecchini, 2006; Pratchett et al., 2008). However, the use of body size to explore distributional patterns across life history stages could be incomplete without age data since some life history milestones may be age-based (e.g. recruitment, sexual maturation). On the other hand, the collection of otolith-based age data is often slow and limited in spatial and temporal scope, although it provides a much higher resolution of population structure. Here, we propose to use a combination of size-at-age information with large-scale population survey data to derive insights on the population size and age structure of a widely distributed coral reef fish. Size-at-age data provides additional life history information to size-based surveys and we propose that this approach can provide a significantly higher resolution to routine size surveys. We have chosen the striated bristletooth surgeonfish *Ctenochaetus striatus* as the model species for this study. Size and age structures of *C. striatus* have been shown to vary across geographically separated populations and are hypothesized to vary primarily with local habitat conditions. In addition, its age structures have been shown to vary significantly across longitudinal and latitudinal gradients (Trip et al., 2008). Lastly, *C. striatus* is the dominant species in terms of density and biomass in American Samoa (Sabater and Tofaono, 2007), and is targeted by various fishing gears and constitutes a significant part of the over-all fisheries. Therefore, data on the population structure of this fish is important for local fisheries management. Additional information is also available on the diet, behavior, and habitat preferences for this species (Choat et al., 2002, 2004).

The main objectives of this study were: (1) to determine the spatial and temporal patterns of variation in the distribution of the various post-settlement stages of the study species; and (2) to identify substrata and intra-population co-variables to their distributions. We determined the relationship between size, age and sexual maturity, and established age-based size categories for size-based underwater survey data in order to derive a finer resolution

and perhaps a different perspective of the temporal and spatial distribution of *C. striatus*.

2. Materials and methods

2.1. Physical setting

The study was conducted in the island of Tutuila, American Samoa (Fig. 1). American Samoa is an unincorporated territory of the United States. It is approximately 4200 km south of Hawai'i, in the central South Pacific Ocean and directly east of the Independent State of Samoa. American Samoa is comprised of five volcanic islands (Tutuila, Aunu'u, Ofu, Olosega, and Ta'u) and two coral atolls (Swains Island and Rose Atoll). Tutuila is a highly eroded volcanic structure bounded by very narrow reef flats, narrow and steep reef slopes and banks that extend more than 3 km from its shore. It is the largest and most populated island in American Samoa.

The northern and southern sections of Tutuila Island are exposed to varying levels of wave intensity from swells generated by the trade winds following studies conducted in Hawaii by Friedlander et al. (2003). Northern Tutuila is exposed to more intense wave action generated by winds from the northwesterly trades from January to March. Storm-generated waves during the hurricane season reach 4–5 m in height. The southeasterly trade winds occur from July to December. There is a calm period between April and June at both sides of the island. This period is characterized by a continuous low-intensity wind that generates moderate wave action. The subdivisions by eastern and western sectors take into account the longitudinal variations in exposure and the island's topographic and geomorphic characteristics. It has been postulated that the varying hydrodynamic and geomorphic characteristics around Tutuila are driving the differences in coral reef substrata cover (see analyses below).

2.2. Determination of age, sexual maturity, growth and age-based size categories

We aimed to examine the relationship between size and age of *C. striatus* in order to establish age-based size categories represen-

tative of the life history of our study species. To achieve this, 263 samples of *C. striatus* were collected using spear fishing on the fringing reefs around Tutuila from 2003 to 2004. For each individual, fork length (FL) was measured to the nearest centimeter. The sagittal pair of otoliths was removed from each fish in the laboratory, cleaned of residues, and weighed to the nearest 0.1 mg. Otoliths were sectioned and increments were counted following Choat and Axe (1996), and Choat et al. (2003). Sexual identity and maturity of the gonads (immature, mature female, mature male) were recorded macroscopically. Size-at-age of newly recruited and young-of-the-year individuals (aged less than one year) was based on size-at-age data from additional collections of the bristletooth surgeonfish in nearby islands in American Samoa.

The Von Bertalanffy Growth Function (VBGF) was fitted to size-at-age data by minimizing the sum of squared residuals between observed and expected size-at-age. The VBGF is of the form: $L_t = L_\infty [1 - e^{-K(t-t_0)}]$, where L_t is the mean length at age t , L_∞ is mean asymptotic length, K is the curvature parameter and t_0 is theoretical age at which length is zero. The best-fit VBGF was estimated by constraining the model to size and age at settlement (Kritzer et al., 2001; Berumen, 2005), with fish expected to settle at 4.7 cm FL and 0.164 years (60 days), based on previous data for this species (Stobutzky and Bellwood, 1997). A Likelihood Ratio Test (LRT) was performed to test for differences in growth between the sexes (Kimura, 1980; Haddon, 2001; Welsford and Lyle, 2005).

Age-based size categories were determined by examining the age and size of individuals displaying immature, mature female and mature male gonads, with the aim of distinguishing between the following three life history stages: recruits, immature and reproductively mature (Craig et al., 1997). All individuals aged less than one year were taken as recruits or young of the year. In order to establish the age range of immature and mature individuals, the timing of reproductive maturity was estimated from the proportion of immature and mature individuals present in each age class, with age-at-maturity the age at which 50% or more individuals displayed mature gonads. This allowed estimating the age range of immature and mature individuals, respectively, with immature individuals ranging from 1 year to age-at-50% maturity and mature individuals ranging from age-at-50% maturity to maximum age. Estimates of age-at-maturity were also compared to that found for *C. striatus* at Lizard Island in the northern Great Barrier Reef (Australia; R. Jones and J.H. Choat, personal communication) and to published information on growth rate, body size and longevity for this species in both Tutuila and Lizard Is (Trip et al., 2008). Secondly, the range of body sizes (FL, in cm) for each of the three age-based life history categories identified (recruits, immature and mature) were estimated from expected mean size-at-age as estimated by the best-fit VBGF at the upper and lower margins of each age-based category, respectively.

2.3. Spatial and temporal distribution of bristletooth surgeonfish densities

The density data of the bristletooth surgeonfish was derived from Sabater and Tofaeono (2007). Here, we combine the relationship between size and age and density patterns to determine variation in patterns of three age-based size categories (1) between years, and (2) across spatial scales around Tutuila Island (Fig. 1). Briefly the sampling design in Sabater and Tofaeono (2007) involved subdividing Tutuila Island into two sections (northern and southern) as a function of wave exposure, each exposure further subdivided into two strata (eastern and western sectors) to accommodate longitudinal variation in habitat distribution and each sector further subdivided into two habitat types (embayments and topographic points).

A re-analysis of the arc-sine transformed benthic cover data of the major substrata categories collected (live coral, rubble, algae and coralline algae) in Sabater and Tofaeono (2007) using a general linear model multivariate factorial analysis of variance indicated significant differences between north and south Tutuila and between east and west Tutuila (Wilk's test: $\lambda = 0.87$, $df = 4$, exposure effect = $p < 0.05$; Wilk's test: $\lambda = 0.72$, $df = 4$, sector effect = $p < 0.001$; with no significant interaction: Wilk's test: $\lambda = 0.9$, $df = 4$, $p > 0.05$). Algal cover was significantly higher to the north of Tutuila while coralline algal cover was significantly higher in the south. Both algal and coralline algal cover were significantly higher in east Tutuila while live coral cover was higher in west Tutuila. These spatial differences in substrata cover are the basis for the analysis of variance design for the density of age-based size categories of *C. striatus* in this study.

A total of 16 reef sites were surveyed in 2005: 8 in the north and 8 in the south representing equal sampling effort for each sector and habitat. A total of 15 reef sites were surveyed in 2006: 8 in the north and 7 in the south. The survey was planned as a balanced design for the statistical analysis but some sites could not be resurveyed because of rough sea conditions. In 2006, a 'point' reef site in the southeast sector could not be re-surveyed and a 'transect' in the southwest sector could not be completed. This imbalance in sampling is addressed in the statistical analyses below. Thirteen of these sites were semi-permanent with re-surveys conducted around the general vicinity of the reef. Point habitats are reefs located at topographic tips of bays around the island. These reefs are considered to be more exposed than embayments that are found inside the bays.

The bristletooth surgeonfish was surveyed along with other 162 reef fish species that are targeted for subsistence and recreational fishing. The underwater surveys were conducted from July to December. These months were chosen so as to include the majority of spawning and recruitment events. The surveys were done between 0900 and 1400 h in 10 to 13-m depths in the middle fore-reef slopes. These depth ranges were chosen because reconnaissance surveys indicated that most reef fish families at the fore-reef slopes are found at these depths. Three replicate 30-m by 5-m belt transects (2.5 m on each side of the transect line) with 10 m gaps in between were surveyed on the reef slope. For each replicate transect, the total length (nearest centimeter) and the number of individuals of the target species observed inside the belt transects were recorded. All the surveys were undertaken by the same experienced diver to avoid bias and minimize variability in the estimation of fish size. The total length data were converted to fork length using length relationships for *C. striatus* in FishBase (www.fishbase.org) to coincide with the size-at-age data. Fish lengths were then used deterministically to assign each individual fish to one of the three age-based size categories (recruits: size < 10 cm; juveniles: 10 cm ≤ size < 15 cm; adults: ≥ 15 cm).

2.4. Reef substrata

Benthic community surveys were also conducted to determine possible fish density and reef benthos correlations. The second diver swam slowly (7 min per 30-m transect) and recorded the substrate and associated benthos using an underwater video camera. Footages were taken 0.5 m above and perpendicular to the reef substratum. Footages were digitized using Pinnacle Studio v.8.3.17 (Pinnacle Systems, 2002). Fifty frames were grabbed from each transect footage using VirtualDub 1.6.0 (Lee, 2002). Percentage cover data were extracted from the grabbed frames using Coral Point Count with Excel Extensions v.3.0 (CPCe) (Kohler and Gill, 2006). General reef substrata were categorized as live coral, algae (turf and macroalgae), coralline algae, and rubble. Rubble is defined here as loose fragments of dead corals. These four categories comprise the majority of the coral reef substrata in Tutuila and are more

recognizable in the video transect surveys. Coralline algae constitute a major substratum in American Samoan reefs. Turf algae were included as a category since *C. striatus* has been noted to feed and browse on epilithic algal complex (Crossman et al., 2005). The epilithic algal complex (EAC) not only consists of filamentous or turf algae, but also aggregates of detritus and sediment particles, microbes and meiofauna (reviewed in Crossman et al., 2005). This complex constitutes the major diet of the bristletooth surgeonfish (Crossman et al., 2005). The life-form categories were identified based on 12 random points that were automatically generated by the program CPCe in each frame. The cover data of live coral, algae, coralline algae and rubble was averaged per 50 frames of each transect.

2.5. Statistical analyses

In the analysis, we posed the following questions: (1) Does the density of individuals of *C. striatus* within each of the size categories differ between years and across spatial scales sampled? and (2) Within each size category, is there a relationship between density and substratum type, and with the density of other life history stages?

The density data for the size categories of *C. striatus* were averaged from the three transects from each reef site and transformed by taking the fourth root of the data point plus one. To attain a balanced sampling design, the average densities of the size categories in a southeast point site were used for a replicate reef site in 2006. In addition, the average densities of the size categories from two transects were also used for the third transect for the same site in 2006, an approach following Quinn and Keough (2002). Homogeneity of variances was analyzed using Hartley F-max, Cochran C and Bartlett tests and the probability plots and the plots of means versus residuals visually inspected. Density data were analyzed for each size category separately using a general linear model (GLM) multi-way factorial analysis of variance with year, exposure (north–south), sector (east–west), and habitat (embayment vs. points) as factors to examine patterns between years sampled and across spatial scales.

A general linear model for forward stepwise multiple regression analysis was used for each of the size categories (dependent variable) and the reef substrata (independent variable) to explore the relationship between substratum type and densities. The reef substrata analyzed were percent cover of live hard coral, algae, coralline algae and rubble. Substrata cover was arc-sine transformed for the analyses. Spearman Rank Order correlation analyses were used to explore the relationships among the densities of size categories. All statistical analyses were performed in STATISTICA 8.0 (StatSoft and Inc., 2007).

3. Results

3.1. Growth and longevity

The 263 fish collected ranged in size from 8 cm to 21 cm in fork length. The ages of these fish ranged from 1 to 34 years old. The growth curvature parameter K for the best fit VBGF through the size-at-age data was estimated at 0.9 and mean asymptotic size L_{∞} was estimated at 17 cm (FL) (Fig. 2a). Growth is fast, fish achieving 87% of their maximum size within two years of age. Growth rate became asymptotic at 5 years of age, and size and age were decoupled after this period. There was no significant difference in growth between the sexes (Likelihood Ratio Test; $\chi^2 = 7.81$; $df = 3$; $p = 0.88$).

3.2. Age-based size categories

Seventy-seven and 60% of individuals sampled displayed reproductively immature gonads at the ages of one and two years,

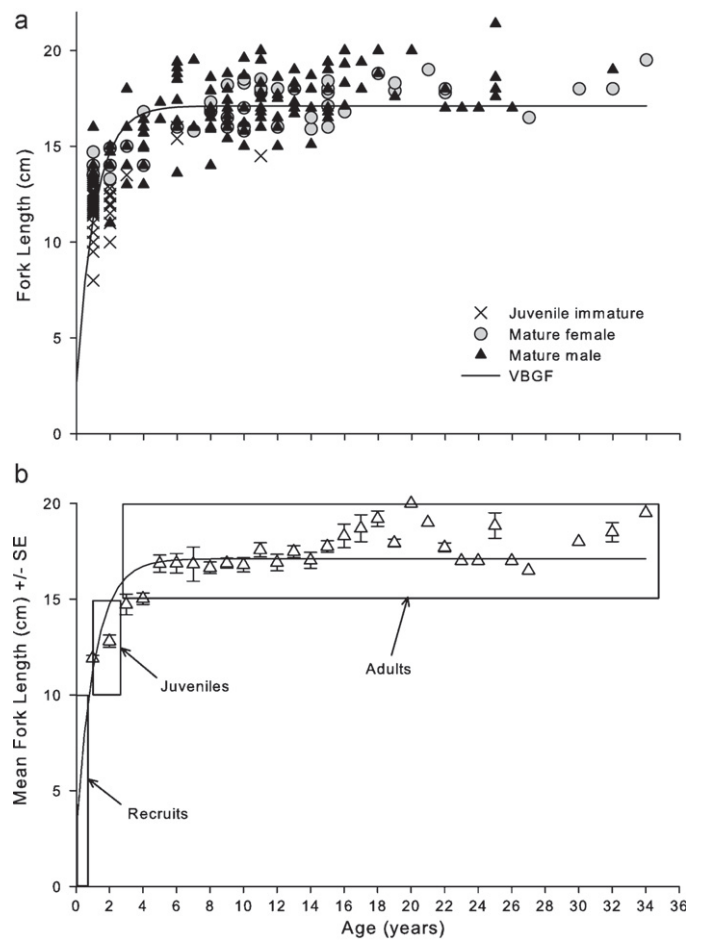


Fig. 2. Growth of *Ctenochaetus striatus* in Tutuila Is (American Samoa). (a) Sex-specific size-at-age of immature individuals (crosses), males (black triangles) and females (grey circles) is shown with best-fit Von Bertalanffy Growth Function ($n = 263$, $K = 0.9$, $L_{\infty} = 17$ cm (FL), $t_0 = 0.2$, $r^2 = 0.72$). (b) Average size-at-age (\pm standard error) across ages sampled, illustrating the age and size range of individuals for each of the three age-based size categories used in this study (recruits, juveniles, and adults).

respectively. In contrast, 89% of individuals aged three years displayed mature ovaries or testes, suggesting that sexual maturity of *C. striatus* occurred between the ages of two and three years in Tutuila Is, with close to 90% of males and females being mature by the age of three. Comparison with results from an independent histological analysis of *C. striatus* gonad material from Lizard Island (northern Great Barrier Reef, Australia; R. Jones and J. H. Choat, unpublished data) indicated that 95% of females at Lizard Is were sexually mature by the age of two years (R. Jones and J. H. Choat, personal communication); however, *C. striatus* from Tutuila have been shown to grow slower and achieve a smaller adult size than those living at Lizard Island (Trip et al., 2008) and slower growth is often associated with delayed maturity (Berrigan and Charnov, 1994), suggesting that *C. striatus* from Tutuila is likely to mature later than individuals from Lizard Island and that the present estimate of age-at-maturity between the ages of two and three years is realistic. Moreover, Craig et al. (1997) established size categories based on coloration and behavior for the blue-lined surgeonfish *Acanthurus lineatus*, a related fish, in American Samoa. They categorized *A. lineatus* as 2.5–5 cm as newly settled, 6–14 cm as immature juveniles, and 15 cm and larger as adults. The age-based size categories derived here for *C. striatus* approximate those established for *A. lineatus*.

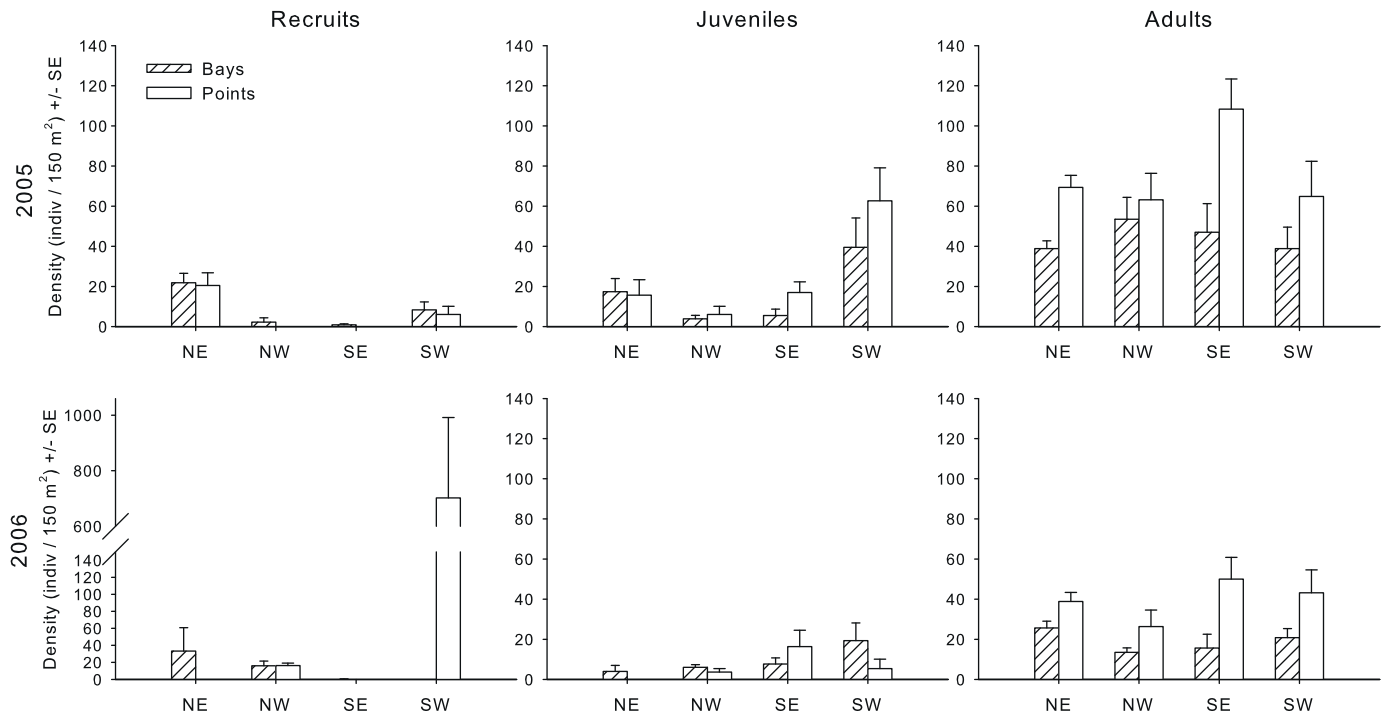


Fig. 3. Spatial and temporal variation in density of new recruits, juveniles, and adults of *Ctenochaetus striatus* around Tutuila Is (NE: North-East, NW: North-West, SE: South-East, SW: South-West). Mean density (individuals per 150 m²) is presented with standard error bars. Note difference in the scale bar on graph of recruit density in 2006.

Three age-based categories were identified: <1, 1–2, and 3+ years, respectively, and the following age-based size categories were established:

- (i) Recruits: < 10 cm (no otolith ring formed yet; aged <1 year);
- (ii) Juveniles (immature): 10–14 cm (fish aged one to two years);
- (iii) Adults (mature): 15 cm and larger (fish aged three years and older).

The groupings of the age-based size categories “recruits”, “juveniles”, and “adults” are presented in Fig. 2b.

3.3. Spatial and temporal distribution of size categories

Variation in the densities of the three life-history stages at the scales sampled is shown in Fig. 3. A total of 9429 bristletooth surgeonfish were recorded during the surveys in Tutuila. The probability plots, the means versus residual plots and the Hartley F-max, Cochran C and Bartlett tests indicated homogeneity of variances ($p > 0.05$) of *C. striatus* density among the three size categories.

Recruits. There were no significant differences in the distribution of recruits in all levels in the multi-way factorial analysis of variance (Table 1a). Although no significance difference in the density of recruits could be detected across exposure levels, sectors, habitats and years, a comparatively larger number of new recruits could be observed in the southwest sector on topographic points in 2006 (Fig. 3).

Juveniles. There were significant differences in the distribution of juveniles between years and between north and south Tutuila (i.e. with exposure) (Table 1b). Furthermore, there was a significant interaction among years, exposure and sector. An inspection of the interaction plots indicated that both sectors had higher density of juveniles in south Tutuila except in 2005.

Adults. There were significant differences in the distribution of adult *C. striatus* between years and habitats (Table 1c). There were more adults observed in 2005 and they were more abundant in topographic points of bays.

The general linear model for forward stepwise multiple regression analyses showed varying relationships between the size categories and the coral reef substrata. Rubble was positively correlated with the density of recruits ($R^2 = 0.12$; $F = 8.7$; $p < 0.01$) (Table 2a). Algal cover was negatively correlated with juvenile densities ($R^2 = 0.07$; $F = 5.7$; $p < 0.05$) (Table 2b). Coralline algal cover was positively correlated with adult densities ($R^2 = 0.07$; $F = 6.0$; $p < 0.05$) (Table 2c). The probability plots of substrata cover data showed normal distributions. However, only coralline algal cover data was normally distributed based on the Kolmogorov–Smirnov test ($d = 0.09$, $p > 0.05$).

There was a significant negative correlation in the density of recruits and adults of *C. striatus* (Table 3).

4. Discussion

This study shows that size-at-age data when combined with population size surveys at various spatial and temporal scales can provide useful insights into fish population structure and distribution. The use of age-based size categories expanded the utility of size-based survey data and enhanced the resolution of a population survey. These age-based life history categories allowed for an expansion of a multi-scale survey to different life-history stages and to contribute to the understanding of the dynamics of a reef fish population.

The analyses of age-based size categories in the multi-scale population surveys showed significant variability in the distribution patterns of the different post-settlement life-history stages of the bristletooth surgeonfish. There were no significant temporal and spatial differences in the intensities of recruitment between the years, exposures, sectors and habitats, although a comparatively higher density of new recruits could be observed in southwest Tutuila in one of the two years surveyed. This apparent uniformity in the recruitment pattern observed for *C. striatus* is not consistent with numerous studies showing disproportionate temporal and spatial distribution of early life stages of coral reef fish (e.g. Doherty and

Table 1

Variation in the density of (a) recruits, (b) juvenile, (c) adult *Ctenochaetus striatus* across temporal and spatial scales in Tutuila Is (American Samoa). Separate analyses of variance (ANOVAs) were performed for each age-based size category. Sector represents East–West areas within each North and South exposure; and habitat represents sheltered (bay) vs. exposed (points) locations sampled within each sector. Density data were (fourth-root of data +1) transformed. Significant results are highlighted in bold.

	SS	df	MS	F	p
(a) Recruits					
Year	0.32	1	0.32	0.37	0.55
Exposure	0.35	1	0.35	0.40	0.53
Sector	0.70	1	0.70	0.80	0.38
Habitat	0.10	1	0.10	0.11	0.75
Year × Exposure	0.04	1	0.04	0.05	0.83
Year × Sector	2.16	1	2.16	2.48	0.14
Exposure × Sector	2.61	1	2.61	3.00	0.10
Year × Habitat	0.46	1	0.46	0.53	0.48
Exposure × Habitat	1.54	1	1.54	1.77	0.20
Sector × Habitat	1.64	1	1.64	1.88	0.19
Year × Exposure × Sector	0.35	1	0.35	0.40	0.54
Year × Exposure × Habitat	1.22	1	1.22	1.39	0.26
Year × Sector × Habitat	1.72	1	1.72	1.97	0.18
Exposure × Sector × Habitat	0.32	1	0.32	0.37	0.55
Year × Exposure × Sector × Habitat	0.14	1	0.14	0.16	0.70
(b) Juveniles					
Year	1.23	1	1.23	7.64	<0.05
Exposure	1.54	1	1.54	9.57	<0.01
Sector	0.09	1	0.09	0.58	0.46
Habitat	0.01	1	0.01	0.03	0.87
Year × Exposure	0.01	1	0.01	0.04	0.84
Year × Sector	0.03	1	0.03	0.19	0.67
Exposure × Sector	0.37	1	0.37	2.32	0.15
Year × Habitat	0.39	1	0.39	2.38	0.14
Exposure × Habitat	0.22	1	0.22	1.36	0.26
Sector × Habitat	0.07	1	0.07	0.43	0.52
Year × Exposure × Sector	1.42	1	1.42	8.79	<0.01
Year × Exposure × Habitat	0.01	1	0.01	0.07	0.80
Year × Sector × Habitat	0.09	1	0.09	0.53	0.48
Exposure × Sector × Habitat	0.31	1	0.31	1.92	0.19
Year × Exposure × Sector × Habitat	0.08	1	0.08	0.48	0.50
(c) Adults					
Year	1.66	1	1.66	20.61	<0.001
Exposure	0.03	1	0.03	0.39	0.54
Sector	0.06	1	0.06	0.78	0.39
Habitat	1.39	1	1.39	17.18	<0.001
Year × Exposure	0	1	0	0.02	0.88
Year × Sector	0	1	0	0.02	0.89
Exposure × Sector	0	1	0	0.04	0.85
Year × Habitat	0	1	0	0.05	0.82
Exposure × Habitat	0.16	1	0.16	2.03	0.17
Sector × Habitat	0.08	1	0.08	0.97	0.34
Year × Exposure × Sector	0.18	1	0.18	2.17	0.16
Year × Exposure × Habitat	0	1	0	0.02	0.90
Year × Sector × Habitat	0.02	1	0.02	0.24	0.63
Exposure × Sector × Habitat	0.03	1	0.03	0.39	0.54
Year × Exposure × Sector × Habitat	0.01	1	0.01	0.15	0.70

Table 2

Relationship between the abundance of (a) recruits, (b) juvenile, (c) adult *Ctenochaetus striatus* and percent cover of each substratum type in Tutuila Is (American Samoa). Separate forward stepwise multiple regression analyses were performed for each size category. Significant results are highlighted in bold. Substrata cover was arc-sine transformed.

	Substratum	Regression coefficient (β)	p
(a) Recruits	Rubble	0.32	<0.01
(b) Juveniles	Algae	−0.26	<0.05
(c) Adults	Coralline algae	0.27	<0.05

Table 3

Spearman rank correlation analysis of the *Ctenochaetus striatus* size categories. Significant correlations are highlighted in bold ($p < 0.05$).

	Recruits	Juveniles	Adults
Recruits	–		
Juveniles	0.17	–	
Adults	−0.23	−0.03	–

Williams, 1988; Doherty, 1991; Doherty and Fowler, 1994; Booth et al., 2000). This variability in recruitment patterns of coral reef fishes has been attributed to their bipartite life cycle (e.g. Roughgarden et al., 1988), with stages that live in distinct habitats that have a variety of interacting factors that affect abundance: spawning activities and reproductive behaviors (as reviewed in Doherty, 1991), larval growth and survivorship (e.g. Bergenius et al., 2002), oceanographic patterns (Siegel et al., 2008) and predation at settlement (Shulman and Ogden, 1987; Eckert, 1987; Leis and Carson-Ewart, 1998; Webster, 2002). There are two possible explanations for the uniformity of recruitment patterns in the fore-reef slopes of Tutuila Island for *C. striatus*: (1) the absence of the variability in the effect of the various factors mentioned acting at the scales sampled, and (2) the possibility of the surveys missing some of the recruitment habitats. The second explanation is possibly the most parsimonious as Craig et al. (1997) showed that recruitment of the related blue-lined surgeonfish occurs in the shallow areas. We are currently conducting more reef flat surveys as initial observations indicate that recruitment of other coral reef fishes occurs in this habitat as well.

We recorded significantly higher densities of adult *C. striatus* in points of bays in Tutuila. In an earlier study, Sabater and Tofaono (2007) showed significant higher densities of all sizes of *C. striatus* in points of Tutuila. Here, we show that this is mostly due to adult densities (3 years and older). The higher densities of adults in points may be attributed to the higher cover of coralline algae, the importance of high water motion sites in broadcasting spawning gametes and as feeding sites. There seems to be no apparent relationship between adult *C. striatus* and coralline algae although turf algae (where they are observed to browse for feeding) can sometimes grow over this benthos. Randall and Randall (1963) were the first to hypothesize that reef fishes choose spawning sites that maximize the probability of dispersal and topographic points are examples of such sites. But it is also highly probable that both adult *C. striatus* and coralline algae prefer areas of high water motion. Coralline algae are known to thrive best in coral reef environments that regularly flush sediments (Fabricius and De'ath, 2001). On the other hand, adult *C. striatus* may use these topographic points as feeding sites for detritus and particulate matter. Planktivores and detritivores such as *C. striatus* have been shown to have similar dietary macronutrient profiles (Crossman et al., 2005). Overall, these results imply that the topographic points of bays will need to be considered when establishing protected areas around the island.

Various studies have shown similar correlation of fish distribution and coral reef habitats and characteristics (reviewed in Williams, 1991). Sabater and Tofaono (2007), in a study of reef fish assemblages in Tutuila Island, showed that the abundance of herbivores was significantly correlated with macroalgae. In this study, we have shown finer details and somewhat different perspective for the relationships of various *C. striatus* size categories and coral reef substrata. The density of recruits was positively correlated with rubble. The density of adult *C. striatus* was correlated with the presence of coralline algae indicating a possible indirect relationship between adults and the food source (detritus and particulate matter associated with high water motion environments). Surprisingly, the density of juveniles was negatively correlated with turf and macroalgae (food source) although the variance accounted for was low. These results suggest that various aspects of the study species' habitat will differentially affect the density (and survival) of the different stages of the life history. Likely explanations are that (i) rubble will provide settlement habitat and shelter from predators for new recruits, (ii) abundance of food source will be essential during the reproductive life of adult individuals, and (iii) possibly the importance of other coral reef substratum for juveniles. The results also suggest that shelter availability may override that of food resources during recruitment. In this case, we may expect

extrinsic mortality rates of early life history stages to generate high selective pressures on the choice of habitat at settlement. The significant negative correlation between recruit and adult densities may imply an ontogenetic shift of habitat with adults moving to more exposed sites on the reef slopes. We hypothesize that recruitment for this surgeonfish will occur preferentially on reef flats, as reported with the related blue-lined surgeonfish (Craig et al., 1997).

5. Conclusion and recommendations

In summary, we have shown that combined size-at-age data and multi-scale population surveys can be useful tools for the demographic analysis of the population structure of the bristletooth surgeonfish. The age-based size categories provided additional information to the population structure of this widely distributed coral reef fish. Using both tools, we established the distribution patterns of the various life-history stages across spatial and temporal scales. Based on available data, we show that recruitment is uniform in the deep fore-reef slopes and that there are fine scale spatial differences in the distribution of the adults as more of them are found on the comparatively more exposed topographic points of bays. We hypothesize that *C. striatus* larvae arrive in the shallow reefs and move to deeper fore reef slopes as they grow in size and age in Tutuila. Survivorship of recruits in the deeper reef slopes is enhanced by shelter availability and that of adults by food availability. We hypothesize that some other coral reef substratum may be important for the survival of juveniles. Future studies will have to determine the importance of these known factors on the recruitment and subsequent densities of the later stages of *C. striatus* in Tutuila Island. From a fisheries management perspective, our results suggest that the topographic points of bays around Tutuila Island are areas of high abundance of spawners and represent critical areas for the maintenance of population levels of the study species. Applying similar survey and size-age approaches to other reef fish species in Tutuila Island will contribute to establishing the role of these specific sites, and may serve as a future basis for the creation of MPAs in the region.

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