Abstract.—The herbivorous bluebanded surgeonfish. Acanthurus lineatus, was a major species harvested on coral reefs in American Samoa, accounting for 39% by weight of artisanal catches in 1994. Spawning occurred year-round but peaked during the austral spring and summer (October-February). A dense pulse of recruits (0.4-0.6 recruits/m²) settled onto the outer reef flat in March-April. Apparent survival was low during the first year but increased thereafter (80%/year). The fish were strongly site-attached on a daily basis, but an estimated 60% of the adults switched territories at least once during a 3-year period, thereby negating attempts to estimate mortality through attrition rates of marked individuals. Estimates of fish condition changed through the year, generally paralleling seasonal changes in a suite of environmental factors. The fish grew rapidly, attaining 70-80% of their total growth during their first year, followed by slow growth and long life (up to 18 years), characteristics that confounded standard growth analyses by producing age-specific growth parameters. Growth was best described by a two-phase von Bertalanffy growth curve for ages 0-3 (K=1.1) and ages 4- $18 (K=0.12, L_{m}=22.1 \text{ cm})$, with the separation based on the age at which 50% of the population reached maturity. Indicators of fishing pressure over a 9year period were equivocal but did not

point to significant overfishing.

Manuscript accepted 4 April 1997. Fishery Bulletin 95:680-693 (1997).

Population biology and harvest of the coral reef surgeonfish Acanthurus lineatus in American Samoa

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Coral reef fishes are harvested for food throughout the South Pacific islands (Wright, 1993; Dalzell et al.¹). In American Samoa, well over 100 species are caught in artisanal and subsistence fisheries, but biological information about these species and their responses to exploitation is sparse. Moreover, these fish are often treated as taxonomic groupings rather than as individual species, and the information that is available often pertains to geographic areas distant from and dissimilar to isolated oceanic islands such as American Samoa.

The purposes of this study were to examine life history characteristics and harvest of one of the most abundant species caught in Samoa, the bluebanded surgeonfish, *Acanthurus lineatus*. This species is one component of a multispecies subsistence fishery that has declined in total catch in recent years for unclear reasons (Craig et al., 1993; Ponwith²; Saucerman³). Thus, we also examined whether overfishing accounted for declines in catches.

The herbivorous A. lineatus is broadly distributed throughout the Indo-Pacific and Indian Ocean regions and has been the subject of several studies on behavioral ecology (Robertson et al., 1979; Robertson and Polunin, 1981; Robertson, 1983 and 1985; Choat and Bellwood, 1985; Polunin and Klumpp, 1989; Choat, 1991; Craig, 1996). On the Great Barrier Reef of Australia, this species is long-lived; some fish live

¹ Dalzell, P., T. Adams, and N. Polunin. 1995. Coastal fisheries of the South Pacific. Workshop on management of South Pacific Inshore Fisheries, New Caledonia, 26 June–7 July 1995. Joint Forum Fisheries Agency—South Pacific Commission, Biol. Paper 30, 151 p.

² Ponwith, B. 1991. The shoreline fishery of American Samoa: a 12-year comparison. Dep. Mar. and Wildl. Res., American Samoa, Biol. Rep. Ser. 23, 51 p.

³ Saucerman, S. 1995. The inshore fishery of American Samoa, 1991 to 1994. Dep. Mar. and Wildl. Res., American Samoa, Biol. Rep. Ser. 77, 45 p.

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as long as 44 years (Choat and Axe, 1996). In Samoa, A. *lineatus* occurs in high densities on coral reefs $(0.4 \text{ fish/m}^2; \text{Craig}, 1996)$. It maintains feeding territories in shallow waters during the daytime but spends nights in deeper-water crevices where it is harvested by spear fishermen.

The fisheries

American Samoa has several small-scale fisheries for nearshore and offshore fishes and invertebrates (Craig et al., 1993). In 1994, the first year when all components of these fisheries were monitored, A. *lineatus* ranked second only to skipjack tuna (*Kat: wonus pelamis*) among all species harvested, accounting for 10% of the total catch of 295 metric tons (t) (DMWR⁴).

Acanthurus lineatus, a small fish averaging 18 cm fork length (FL) and 170 g, was caught in two interrelated coral reef fisheries: artisanal and subsistence harvests. Multispecies landings in these two fisheries were 76 and 86 t, respectively, in 1994 (Saucerman³). The artisanal fishery consisted of 56 nighttime spear divers, among whom 15 fished regularly (about 15 days per month) by free diving and scuba diving. At 28 t, A. lineatus accounted for 39% by weight of artisanal catches (Fig. 1). The subsistence fishery was more diverse: fish were captured by gill nets, throw nets, rod-and-reels, handlines, and by spear fishing; invertebrates were captured by hand picking and spearing. Many species were taken; A. lineatus

⁴ DMWR (Dep. Marine and Wildlife Resources), PO Box 3730, Pago Pago, American Samoa 96799. Unpubl. data.



Catch composition (by weight) of fish families in the 1994 artisanal fishery in American Samoa. Redrawn from Saucerman (see Footnote 3 in the text). accounted for only 1-3% of subsistence catches. In both artisanal and subsistence fisheries, use of destructive fishing practices (dynamite, poison) was infrequent.

Materials and methods

Tutuila Island in American Samoa (14°S, 171°W) is a steep volcanic island (142 km²) with 55 km of fringing coral reef. It has two seasons, a wet summer (Oct-May) and a slightly drier and cooler season (Jun-Sep) characterized by 2.5°C cooler nearshore water temperatures and increased SE trade winds. Nearshore water temperature (taken seaward of the reef flat at 0.3 m depth) ranged from 27°C to 31°C (n=295 daily measurements). Additional details about physical variables are presented below as they relate to changes in fish condition. Rainfall and wind data were obtained from NOAA.⁵

Data were collected from 1) field studies conducted by snorkeling in shallow waters (1-4 m) on the coral reefs fronting the villages of Afao, Leone, and Matu'u (Fig. 2) and from 2) market samples of the artisanal fishery. Reef flats at the study sites were narrow (100-250 m), dropped abruptly to a depth of 3-6 m, and descended gradually thereafter to 20 m. The outer reef flat inhabited by *A. lineatus* consisted of consolidated limestone, encrusting coralline algae,

⁵ NOAA (National Oceanic and Atmospheric Administration). 1994. Local climatological data, annual summary with comparative data, Pago Pago, American Samoa. National Climatic Data Center, Asheville, North Carolina, ISSN 0198-4357, 8 p.



Figure 2

Tutuila Island, showing locations of study sites at the villages of Afao, Leone, and Matu'u. The main study reef at Afao (see enlargement at right) shows the spawning site of *A. lineatus* in the outer reef channel (\times), the nighttime rest region (R) for *A. lineatus* using the study area, and the reef flat edge (dashed line).

and only 3.5% live coral cover (Craig, 1996). Spawning and nocturnal rest sites at Afao are shown in Figure 2 for those *A. lineatus* that maintained daytime feeding territories in the study area.

Length, weight, sex, and maturity

Length frequencies of fish in the artisanal catch were measured at 54 occasional intervals from 1987 to 1995. During 1991–94, fish were purchased at local markets to determine fork length (to the nearest mm), weight (to 0.1 g), sex, and maturity. Pooled monthly samples for these years consisted of 18-33 mature females, 18-49 mature males, and 9-116 immature fish, for a total of 1,139 fish. Maturity was assessed by visual inspection of gonads and by gonadosomatic index (GSI = $10^2 \times \text{gonad weight}/$ whole body weight). To determine maturity-at-size, immature fish whose sex could not be determined (13% of total sample) were assigned in equal proportions to numbers of identified males and females because the sex ratio of identified males and females was equal. Limited samples of rotenone-treated fish were collected at several nearshore sites in August 1990 to compare with sizes of fish taken in the artisanal fishery.

Spawning

Seasonal spawning patterns were determined from GSI trends and by conducting monthly visual surveys in the outer reef channel at the Afao site, 1993– 94. Confirmation of spawning was determined by an upward rush of fish with the production of visible milt clouds.

Settlement of young onto reef

At each of the three study sites, newly settled fish in five 2×20 m permanent transects along the outer edge of the reef flat were censused monthly, approximately one week after the new moon. A repeated-measures multivariate analysis-of-variance (MANOVA with Pillai's trace test statistic) was used to test for significant differences in settlement time among the three sites and to accommodate autocorrelation of counts among observed times (Tabachnick and Fidell, 1989).

Condition factor (CF)

We used two measures of fish condition: 1) as $10^5 \times$ body weight/length³, and 2) as the weight of the paired postabdominal fat bodies found in surgeonfishes (Fishelson et al., 1985). To examine seasonal changes, monthly mean CF values and fat body

weights were compared with trends in five environmental factors that might affect fish growth: 1) nearshore water temperature, 2) available feeding hours, 3) calm surf conditions, 4) rainfall, and 5) daylength. Available feeding hours were calculated as the number of feeding hours per month during the fish's daily peak feeding period (1000–1800: Craig, 1996), minus losses of feeding time during the cooler season due to earlier sunsets and increased occurrence of spring low tides that prevented access to the fish's intertidal feeding territories. An index of calm surf conditions was calculated as the inverse of wind speed, because seasonally strong winds increase turbulence in the surf zone, thereby decreasing feeding opportunities for A. lineatus (Craig, 1996). Rainfall was used as a possible indicator of the amount of nutrient input into coastal waters that might, in turn, enhance growth of the algae that the fish eat. Similarly, daylength might affect algal production. Monthly means of these five factors were calculated for the years 1991-94 and presented as percentages of the maximum monthly value that occurred during this period, which were water temperature (29.6°C), available feeding period (225 h), wind speed (27 km/h), rainfall (72 cm), and daylength (13.0 h).

Growth

Growth data were fitted to the von Bertalanffy growth function (VBGF):

$$l_t = L_{\infty} [1 - e^{-K(t-t_0)}],$$

where $l_t = \text{length at age } t$;

 \dot{L}_{∞} = asymptotic length;

K =growth coefficient; and

 $t_0 =$ time when length would theoretically be zero.

Two independent estimates of fish growth were made. In the first method, sagittal otoliths were used to estimate ages of 94 fish selected to span the widest size range possible (5.3–22.9 cm FL from pooled locations) with the methods described by Choat and Axe (1996), who aged the same species (by including tetracycline verification) from the Great Barrier Reef. Estimates of L_{∞} and K were derived from a Ford-Walford regression of the age-length relation (Pauly, 1983). Estimates of t_0 were made with Pauly's (1979) empirical equation:

 $\log(-t_0) = -0.392 - 0.275 \log L_{\infty} - 1.038 \log K.$

Additionally, one of each otolith pair was weighed to 10^{-4} g for comparison with fish age.

In the second method, individual growth rates were calculated for a subset of the naturally marked fish described in the field mortality study (see next section). The 57 fish selected were those for whom a time series of 4–20 size estimates was available for each fish. Lengths were estimated visually underwater; a comparison of visual estimates with actual sizes of the same fish when caught by spear indicated that the average error was $8.1 \pm 1.5\%$ (mean and SE throughout text, n=19, 6–20 cm FL).

The fish were initially selected from three general size classes according to their size at settlement onto the reef (2.5–5 cm) and approximate state of maturity based on dissection data (juveniles 6–14 cm, adults 15–23 cm). Sample sizes were 11 newly settled fish (monitored 1.7 ± 0.3 mo), 28 juveniles (5.2 ± 0.6 mo), and 18 adults (14.1 ± 1.0 mo). These fish were grouped into eight size classes of 2.5-cm intervals on the basis of their initial sizes. By using the mean growth rate of each size class, we calculated the time needed to grow to the next size class. These growth increments were plotted sequentially, forming a single growth curve for the population. A Gulland-Holt (1959) plot of growth increments of individual fish produced estimates of L_{∞} and K.

Mortality

Total mortality (Z), which equals natural mortality (M) plus mortality caused by fishing (F), was estimated by monitoring the gradual loss of 145 marked fish for three years at the Afao site and by analyzing the length and age composition of fish taken in the artisanal fishery.

Field mortality Earlier work had shown that A. lineatus was highly site-attached (Craig, 1996); thus we initially assumed that a fish had died if it failed to re-occupy its territory or nearby area. Individual adults (n=45) and juveniles (n=50) were recognized by distinctive line patterns behind the eye and on the cheek. Sexual dimorphism was not apparent, thus males and females were not distinguished in the field. Newly settled fish (n=50) were identified by a combination of their specific location, size, color phase,⁶ and line pattern when discernible. Because newly settled fish were selected on the basis of identifiability rather than first appearance in the study area, the time elapsed since settlement was not known. However, surveys were conducted frequently; therefore most newly settled fish had probably arrived within the previous week or two.

On average, about 35 fish were monitored at any one time; new individuals were added when others either outgrew their size class or were not relocated after three successive surveys. Small fish were inspected at least twice each week, larger fish about once per week. All three size groups were intermixed on the outer reef flat.

To calculate mortality, all fish within a size group were aligned to a common starting date. For each size class, mortality at any given time equalled 1 -(no. fish alive + no. fish outgrowing size class)/(initial no. fish in that size class). This approach 1) underestimated mortality for newly settled fish if there had been high mortality during the first days of settlement before observations began, or 2) overestimated mortality if observed fish emigrated from the study area. Total mortality (Z) was calculated as the slope of the descending limb of the "catch curve" (a plot of the natural logarithm of fish remaining each year versus relative age). Annual mortality was estimated as $1 - e^{-Z}$ (Ricker, 1975).

Total mortality Total mortality for harvested fish was estimated in several ways: 1) length-converted catch curves (Pauly, 1983); 2) the relation between Z and mean length of fish in the catch:

$$Z = K(L_{\infty} - L_c)/(L_c - L'),$$

- where L_c = the average length of fish greater than length L'; and
 - L' = the size at which fish are assumed to be fully recruited to the fishery (Beverton and Holt, 1957);

and 3) Hoenig's (1983) empirical relation between Z and a population's longevity:

$$\ln(Z) = 1.46 - 1.01 \ln(t_{max}),$$

where t_{max} = maximum age.

Natural mortality Natural mortality (M) was estimated with two empirical equations:

$$\log M = 0.007 - 0.279 \log L_{\infty} + 0.654 \log K + 0.463 \log T (Pauly, 1980), \quad (1)$$

where T = the average monthly water temperature in the study area (28.6°C), and

$$\ln(M/K) = 0.30 \ln(T) - 0.22$$
(Longhurst and Pauly, 1987). (2)

⁶ Color phases of newly settled A. lineatus are not described in the literature. The "light" phase is that of adult coloration; the "dark" phase is light-to-dark gray (overlying a faint adult color pattern) and the caudal fin is orange (differentiated from dark newly settled Ctenochaetus striatus which have orange only on caudal fin tips).

Biological characteristics of harvest

Length-based estimates of maturity and age were calculated for artisanal catches. Additionally, in 1994–95 we measured the catches of 19 groups of 1–4 fishermen (n=43) who had fished together, to determine their average catch per unit of effort (CPUE: kg/h per person). The principal method was spear fishing by free diving; data are presented for that gear only.

Results

Length, weight, sex, and maturity

A complete size range of newly settled, juvenile and adult A. *lineatus* was present in rotenone-treated samples from shallow nearshore waters <2 m deep (Fig. 3), but large fish were underrepresented because some avoided capture. Night spear fishermen harvested the larger fish, generally 15–21 cm FL.

Males and females taken in the fishery were of similar length (t=0.26, df=993, P=0.8) and the sex ratio was nearly equal (1 male:1.1 females, n=995). Length-weight relations for the sexes did not differ significantly (ANOVA, F=0.07, P=0.79); thus all fish were pooled, including smaller unsexed fish: log weight (g) = -1.60 + 3.03 log length (FL in cm)(r^2 =0.99, n=1,047). The relation between FL and standard length in cm was SL=0.86(FL) - 0.38 (r^2 =0.99, n=94).

Mature fish of both sexes generally had well-developed gonads (6.2 \pm 0.2 g, n=529) or gonads that appeared to be partly or wholly spawned out (1.2 \pm



0.1 g, n=108). Immature fish had little gonad development (0.2 \pm 0.01 g, n=502). Fish reached sexual maturity at 15–21 cm FL (Fig. 4), with males maturing at a slightly smaller size than females. Half of both sexes were mature at about 18 cm, i.e. at approximately 4 years of age.

Spawning

The gonadosomatic index (GSI) was highest during October-February (Fig. 5) and was strongly correlated with daylength and feeding hours (Table 1). Spawning also occurred throughout the year. During all months, groups of 50-200 fish were observed spawning at dawn in the outer portion of the outer reef channel at Afao (see Fig. 2). Additional details are provided elsewhere (Craig, in press).

Settlement of young onto reef

Newly settled fish (n=575) exhibited both light (79%) and dark (21%) color phases.⁶ Settlement peaked in March–April with densities of 0.4–0.6 recruits/m² on



the outer reef flat (Fig. 6). The settlement pulse occurred one month earlier at Matu'u as indicated by the significant site-time interaction detected by the repeated-measures MANOVA (P=0.03, F=4.67, numerator df=22, denominator df=6). In previous years, similar large pulses occurred in earlier months (Nov-Mar; senior author, pers. obs.).

Seasonal changes in fish condition

Fish condition factor (CF) peaked in summer and declined rapidly thereafter (Fig. 7). For mature fish, a decline in CF after the spawning season was expected, but a similar decline was evident among immature fish. Postabdominal fat bodies also declined



Table 1

Correlation coefficients between monthly averages for physical and biological variables: gonadosomatic index (GSI), condition factor (CF), and paired fat bodies of A. lineatus. P = probability value.

	Water temperature	Daylength	Calm surf index	Rainfall	Feeding hours
GSI: mature fish	0.034	0.906	0.418	0.36	0.817
	<i>P</i> >0.1	<i>P</i> <0.001	<i>P</i> >0.1	<i>P</i> >0.1	<i>P</i> <0.01
GSI: immature fish	0.347	0.129	0.252	0.335	0.311
	<i>P</i> >0.1	<i>P</i> >0.1	<i>P</i> >0.1	<i>P</i> >0.1	<i>P</i> >0.1
CF: mature fish	0.495	0.703	0.65	0.667	0.511
	<i>P</i> >0.1	<i>P</i> <0.02	P<0.05	<i>P</i> <0.02	P<0.1
CF: immature fish	0.846	0.546	0.925	0.706	0.343
	<i>P</i> <0.001	<i>P</i> <0.1	<i>P</i> <0.001	<i>P</i> <0.02	P>0.1
Fat bodies: mature fish	0.77	0.228	0.702	0.491	0.036
	<i>P</i> <0.01	<i>P</i> >0.1	P<0.02	<i>P</i> >0.1	P>0.1



steadily from early summer through the cooler season (Fig. 8). These losses resulted in CF values that were about 10% below peak summer levels and in fat bodies that were about two thirds below peak levels.

Seasonal changes in five environmental factors paralleled changes in fish condition (Fig. 8). During the cooler season, nearshore water temperatures dropped below maximum summer values (-9%), as did available feeding hours (-14%), calm water conditions (-44%), rainfall (-76%), and daylength (-13%). Most physical factors were significantly autocorrelated (7 out of 10 comparisons), indicating that there is a distinctive seasonal signal in the nearshore environment, despite Samoa's open-ocean location near the equator. Monthly CF values for immature and mature fish were significantly correlated with 3 of the 5 physical factors (Table 1). It seems clear that the fish were responding to a seasonal change, but causative factors are not known.

Growth

Otolith-based ages and size determinations of naturally marked fish provided two estimates of A. *lineatus* growth. Otolith weight was highly correlated with the number of annular bands in an otolith (Fig. 9). The fish grew rapidly, attaining 70–80% of their total growth by the end of their first year, and they were long-lived up to 18 years (Fig. 10). Field estimates of fish growth confirmed the rapid early growth but underestimated later growth in comparison with the otolith-based determinations. Similar values of K and L_m were derived from both the otolith-based age-length relation (Ford-Walford regression: K=0.7, $L_{\infty}=20.3$ cm, $r^2=0.93$) and from size increments of marked fish (Gulland-Holt plot: K=0.8, $L_{\infty}=21.0$ cm, $r^2=0.58$).

However, L_{∞} and K were highly dependent on the age range of fishes examined (Fig. 11). Iterative Ford-Walford regressions of the smoothed mean size at age showed that K dropped progressively from 0.8 for the whole sample (ages 0-12) to 0.1 when juvenile fish ages 0-3 were excluded. Asymptotic length (L_{\perp}) increased in a similarly systematic manner from about 20 cm to 22 cm. Therefore, separate VBGF growth curves were generated for the juvenile phase (ages 0-3, K=1.1, $t_0 = -0.2$, [L_{∞}=18.3 cm]) and adult phase (ages 4–12, K=0.12, $L_{\infty}=22.1$ cm, $t_{0}=-15.6$), a separation based on the age at which 50% of the population was mature (age 4, Fig. 4). The two-phase curve captured the precocious growth and attained a larger, more realistic L_{∞} that approached the maximum size of fish taken in the fishery (see Fig. 3). Using the relation that longevity is approximated by 3/K (Pauly, 1983) and the adult K-value derived for ages 4-12, we predicted that the maximum age would be 25 years, which compared favorably with the observed maximum age of 18 years.

Mortality

Mortality indices differed among the three size classes of naturally marked fish at the Afao site (Fig. 12). Only 2% of the newly settled fish and 34% of the juveniles appeared to survive and grow into the next



larger size class. At these rates, only $1\% (2\% \times 34\%)$ of the population would survive their first year on the reef. Thereafter numbers of marked adults declined rapidly at a loss of 48%/yr (Z=0.65). At these rates, the life span of combined life history stages would only be about 4–5 years. However, longevity, as revealed by otolith analysis, indicated that field mortality of marked fish was greatly overestimated. Mean ages of artisanal catches were 4–6 years (see below) and some fish lived up to 18 years. It is therefore likely that some marked fish emigrated from the study area rather than died (see "Discussion" section). To obtain a more realistic estimate of adult mortality, the annual loss of fish in each age class of the 1994–95 fishery was examined by length-converted catch curves calculated in two ways: 1) after conversion with the VBGF parameters for adult fish (Pauly, 1983), and 2) after graphical conversion of lengths to ages based on the weighted length-age relation derived by otolith analysis. The latter was included because of the variability of the VBGF parameters shown in Figure 11. For fish that were assumed to be fully recruited to the fishery, total mortality was low in both cases (Z=0.24 and 0.23; Fig. 13), equating to an annual loss of about 20%. Similar values were obtained with Hoenig's equation (Z=0.23) and Beverton and Holts' relation between Z and mean length of fish in the catch (Z=0.19, K=0.12, $L_{x}=22.1$ cm, $L_{z}=19.6$, L'=18 cm).

Natural mortality (\dot{M}) was estimated to be 0.2 and 0.45 with the empirical equations of Longhurst and Pauly (1987) and Pauly (1980), respectively, and with the adult values of K and L_{∞} . The lower value indicated that M is equivalent to Z; the latter value was spurious given that it exceeded Z.

Biological characteristics of harvest

The flattened growth curve exhibited by older A. *lineatus* limited analyses based on length-converted ages, but the conversion did indicate that most fish taken in the fishery were relatively young (Fig.

14). During the 9-year period 1987–95, annual catches varied moderately in mean age (3.6-6.2 years), mean length (17.5-19.3 cm FL), proportions of immature fish taken (29-60%), and total mortality (0.16-0.31)(Table 2). No trends in these variables were apparent, with one exception: the maximum size of fish decreased. Maximum sizes of fish in 1987–88, however, seem unrealistically high (Fig. 14), and in any case, mean sizes in later years (1994-95) were significantly larger than in earlier years (1987-88)(t=9.7, df=5088, P<0.001).







Although the more detailed 1994–95 market data spanned a relatively short period (Fig. 15), available data indicated no decrease in fish size (r=0.28, df=17, P>0.1) or CPUE over time (r=0.41, df=17, P=0.085), and no relation between fish size and CPUE at various island-wide fishing sites, i.e. sites with low CPUE did not have smaller fish (r=0.28, df=17 P>0.1).



Age-length relations for A. *lineatus*. The solid line indicates a two-phase von Bertalanffy curve for ages 0-3 and 4-18; the dashed line indicates the growth of naturally marked fish based on visual estimates of fish size over time.



Discussion

The life history traits exhibited by *A. lineatus* are common among coral reef fishes (e.g. Sale, 1991): it is a territorial fish that spawns year-round but primarily during the austral summer, its pelagic young settle onto the reef in a dense pulse and suffer high mortality, survivors are sedentary but occasionally relocate to new sites, and the fish grow rapidly, have relatively low mortality rates after their first year and may live for many years. Of particular interest in this study was the opportunity to examine fishing pressure on a coral reef species. In this instance, the possibility of emigration rates of a "highly site-attached species" and the rapid initial growth pattern provide a useful context for examining the fisheries data. Additionally, because



another data set is available for this species, we were able to compare locality-specific demographic traits.

Emigration

Acanthurus lineatus is strongly site-attached (adult fish have a 99.9%/day return rate to the same site: Craig, 1996), but it occasionally switches territories. After 3 years of monitoring, 6 of the 45 marked adults remained on site (Fig. 12), whereas 23 adults would have been present with an annual mortality rate of 20% as determined by catch curve. The difference (17/45) indicates that 38% of the adults that disappeared had probably emigrated to other sites. Craig

	1987	1988	1990	1994	1995
Mean FL (cm)	18.2	17.6	18.9	19.3	18.
SE	0.04	0.1	1.0	0.5	0.
Maximum FL (cm)	27.7	28.9	22.4	23.0	23.
Mean length-converted age	4.6	3.6	5.7	6.2	4.
Percent immature	46	60	37	29	5
Total mortality (\mathbf{Z}_1)	0.22	0.23	0.19	0.23	0.2
(\mathbf{Z}_{2})	0.25	0.16	0.31	0.23	0.2
n	2,499	1,126	329	720	74

 $Z_1 = Z$ derived from a catch curve based on length-converted ages with "adult" VBGF parameters.

 $Z_2^{i} = Z$ derived from a catch curve based on graphical conversion of length to age with the age-length relation.



(1996) also monitored the same marked fish described in the present study and reported that an additional 22% of the adults changed territories to nearby locations and were relocated (for the purpose of calculating mortality, these fish were not of course considered deaths). Altogether then, about 60% of the adults changed territories at some point during the 3-year period of observation. This analysis is not thought to be complicated by the loss of fish due to fishing mortality (F), because the 20% mortality rate incorporated F. Further, Afao was a lightly fished area (senior author, unpubl. data).

Emigration probably also accounted for the loss of many juveniles and newly settled recruits shown in Figure 12. Although the annual input of recruits to the reef was high, the observed "survival" rate of these fish during their first year (1%) could not maintain the standing stock of adult fish. To illustrate, the adult density of 40 fish/ $100m^2$ (Craig, 1996) would lose 8 fish/ $100m^2$ per year at an annual loss of 20%. To replace those fish with newly settled fish (with an annual input rate of 100 recruits/ $100m^2$ per year), a survival rate of 8% would be required during their first year.

Growth pattern

The rapid growth of young A. lineatus was so pronounced that initial VBGF analyses produced age-



dependent estimates of L_{∞} and K. The fish attained most of their adult size during their first year, even though the species was long-lived. There is increasing evidence that this growth pattern is common among coral reef fishes (Choat and Axe, 1996; Hart and Russ, 1996; Newman et al., 1996; Williams et al.⁷). Standard applications of growth models may be inappropriate for populations exhibiting these growth characteristics. Use of a two-phase von Bertalanffy growth curve (e.g. Soriano et al., 1992; Ross et al., 1995) is a possible solution, although care must be taken to establish consistent procedures for separating the two phases of the curve.

⁷ Williams, D., S. Newman, M. Cappo, and P. Doherty. 1995. Recent advances in the ageing of coral reef fishes. Workshop on management of South Pacific Inshore Fisheries, New Caledonia, 26 June-7 July 1995. Joint Forum Fisheries Agency-South Pacific Comm., Biol. Paper 74, 5 p.



Comparison of Samoan and Great Barrier Reef (GBR) populations

There are noteworthy differences between A. *lineatus* populations off Samoa and those on the GBR. Fish grow larger and live up to twice as long on the Great Barrier Reef than those off Samoa (Fig. 16); they are also more sparsely distributed and have lower recruitment rates of newly settled young (Choat and Bellwood, 1985; Choat and Axe, 1996; Craig, 1996; Choat, unpubl. data). Reasons for these differences are speculative and may be complicated by the existence of a fishery in Samoa (see section below).

Perhaps A. *lineatus* in Samoa is comparatively shortlived and maintains its abundance by a high annual input of newly settled young. Why there should be a greater abundance of newly settled fish in Samoa, an oceanic island, than in the extensive reef network of the GBR is unclear.

Fishing pressure

For at least the past 18 years, the catch composition of fish taken by night spear divers has not changed greatly, particularly with respect to the prominent catch of surgeonfishes (Fig. 17). Although Wass⁸ did not identify the species composition of the 1977–80 subsistence catch, local residents report that *A. lineatus* has always been a plentiful and popular food fish.

Indicators of current levels of fishing pressure were ambiguous. Some evidence indicated that overall fishing pressure was low: 1) survival rates of fish age 1 year and older were high (80% per year), 2)estimates of total mortality and the mean size of fish in the fishery changed little over a 9-year period. 3) there was no relation between fish size and CPUE, and 4) an estimate of natural mortality was similar to that of total mortality. However, some of these points are not overly persuasive. First, estimates of natural mortality were derived from empirical equations that embody considerable variability (Gulland, 1984). Second, trends based on fish size are of uncertain value as indicators of fishing pressure due to fish behavior. At night, when A. lineatus is harvested, there is an apparent spatial separation of small and large fish. Fish less than about 14 cm are not often encountered in the areas fished (senior author, pers. obs.), perhaps because they remain in shallower areas or hide within smaller crevices during the night. Thus the larger sizes of fish taken by the spear fishermen represent those that were available to them, i.e. there was little opportunity for size selection. Consequently, the mean size of fish harvested could remain relatively stable under increasing levels of fishing pressure until there were no more fish left to catch.

Indications that fishing pressure was affecting the population included 1) decreases in maximum size of fish over a 9-year period, 2) the absence of very old fish in the Samoan population compared with the GBR population, as might be expected in a fished population, and 3) a possible decrease in CPUE. These points, too, are less than compelling. First, the

⁸ Wass, R. 1981. The shoreline fishery of American Samoa, past and present. In J. Munro (ed.), Marine and coastal processes in the Pacific: ecological aspects of coastal zone management: proceedings of the UNESCO seminar at Motupore Island Research Center, 1980, p. 51-63. United Nations Education, Scientific and Cultural Organization, Paris.

decrease in maximum size was counterbalanced by a significant increase in the mean size of the catch during the same period (Fig. 14). Second, the comparison with GBR may not be valid, because natural longevities of the two populations may differ. The two populations are nearly 5,000 km apart and they dwell in different water temperature regimes; thus some geographic variation is likely. Third, the possible CPUE decline was not statistically significant and was also compromised by occasions when fishermen targeted species other than A. *lineatus*. One





group of fishermen we interviewed had been told before diving that the fish buyer already had enough *A. lineatus*, thus some low CPUE values may indicate a saturated market rather than a depleted stock.

Given the indefinite nature of these indicators, it remains unclear whether fishing pressure is having a significant effect on the demographics of *A. lineatus*, but the composite picture does not indicate substantial overfishing. We acknowledge, however, that localized overfishing is a distinct possibility. Villagers often complained that the night spear fishermen had depleted fish stocks along their village coastline. Although the artisanal fishermen generally rotated areas fished to maximize their CPUE, the villagers living near the area fished might be left with a diminished resource for a period of time.

An additional concern is that an increase in fishing efficiency was in progress in 1995, with a conversion from free diving to scuba diving. Catch-perunit-of-effort for scuba diving was more than twice that of free diving (3.8 vs. 10.5 kg/h for all species combined). A further concern is that the human population of American Samoa, like that on many other South Pacific islands, is increasing rapidly; thus the demand on nearshore resources seems likely to increase (Craig⁹).

The lack of overt signs of fishing stress for A. lineatus in the artisanal fishery is at odds with observed declines in the subsistence fishery on the same coral reefs. Multispecies subsistence catches dropped from 265 and 311 t in 1979 and 1991 (Ponwith²; Wass⁸), to 48 t 1995 (Saucerman³). Catches of A. lineatus, a minor component in this fishery, dropped

from 8 t in 1991 to 1 t in 1995. Although some of this decline may be attributed to reduced fishing effort, CPUE for most gear types declined as well (Saucerman³).

Causes of reduced subsistence catches are not clear but may include a variety of factors such as fishing for selected species, a reduced reliance on subsistence fishing, and habitat degradation (Craig et al.¹⁰). Coral reefs in American Samoa have been severely damaged in the past 15 years by three hurricanes, an *Acanthaster* starfish invasion, temperature rises that resulted in mass coral bleaching, and sedimentation from land. Whether these en-

⁹ Craig, P. 1995. Are tropical nearshore fisheries manageable in view of projected population increases? Workshop on management of South Pacific Inshore Fish., New Caledonia, 26 June-7 July 1995. Joint Forum Fisheries Agency—South Pacific Comm., Biol. Paper 1, 6 p.

¹⁰ Craig, P., A. Green, and S. Saucerman. 1995. Coral reef troubles in American Samoa. South Pacific Comm., New Caledonia, Fish. Newsletter 72:33-34.

vironmental disturbances have affected fish catches is not known, but it seems possible that these changes may have contributed to the current abundance of *A. lineatus* by creating expansive areas of denuded habitat suitable for the growth of turf algae that *A. lineatus* eats (Craig, 1996). As previously mentioned, live coral covered only 3.5% of the outer reef flat zone inhabited by this species, i.e. over 90% of the habitat seemed ideal for turf algae and *A. lineatus*. As the reefs recover, we speculate that *A. lineatus* may decrease in abundance and become less dominant in artisanal catches.

Acknowledgments

Support for this study was provided by the Federal Aid in Fish Restoration Act and an ARC major grant to J. H. C. We thank Julian Caley, Paul Dalzell, Alison Green, Gary Russ, and Tanielu Su'a for review comments.

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