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Intertidal territoriality and time-budget of the surgeonfish, *Acanthurus lineatus*, in American Samoa

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Synopsis

The herbivorous surgeonfish *Acanthurus lineatus* aggressively maintained feeding territories in the surf zone of the outer reef flat in American Samoa. Intertidal territories were re-established each morning, as well as after displacement by low tides or rough surf. Day-to-day site fidelity of recognizable individuals was high: 99.9% return rate per day for adults (15–20 cm), 99.6% for juveniles (8–13 cm), and 97.2% for recruits (2.5–5 cm). Fish fed on turf algae primarily in the afternoon (80% of available time), and spent 10% of their time on active territorial defense and 2–13% of their time on forays from their territory. On average, a fish defended its territory 1900 times daily and took 17 000 bites (= 7400 bites m^{-2} d^{-1}), but rough surf reduced feeding by 60% and defense by 75%. High territorial defense requirements significantly reduced feeding rates. Although the distribution and behavior of this species in Samoa was in large part similar to that reported for it elsewhere (Australia, Indian Ocean), there were notable differences: in Samoa *A. lineatus* densities within colonies were greater (0.4 fish m^{-2}), territory size was smaller (2.3 m^2), and defense rate against intruders was greater (2.5 attacks min^{-1}). These differences in Samoa may be related to their smaller body size, greater abundance or increased food supply caused by hurricane damage to reefs which has enhanced the algal turfs that *A. lineatus* feeds upon.

Introduction

In a recent review of domestic fisheries in American Samoa, Craig et al. (1993) showed that nearshore coral reef fishes account for 50% or more of all fish harvested by villagers. Although a large variety of species was taken, the surgeonfish *Acanthurus lineatus* was an important component of the year-round harvest, averaging 34% of reef fish sales at local markets (S. Saucerman personal communication). This species is a herbivorous browser that forms large, dense colonies of territories in the surf zone on the outer reef flat and upper reef slope.

Published reports on the behavior of this species are available from distant sites, primarily the Great Barrier Reef and Indian Ocean (Robertson et al. 1979, Robertson & Polunin 1981, Robertson 1983, Choat & Bellwood 1985, Davis 1985, Edward 1986, Polunin & Klumpp 1989, Choat 1991), but comparative data from the central South Pacific Ocean are lacking. The objectives of this study were to examine the territorial and time-budget behavior of this species in Samoa, and to compare the results of this study with those in other geographical areas. While territoriality is a common and well-documented behavioral pattern among coral reef fishes (reviewed by Horn 1989, Shapiro 1991), *A. lineatus* presents an opportunity to examine territorial behavior in a

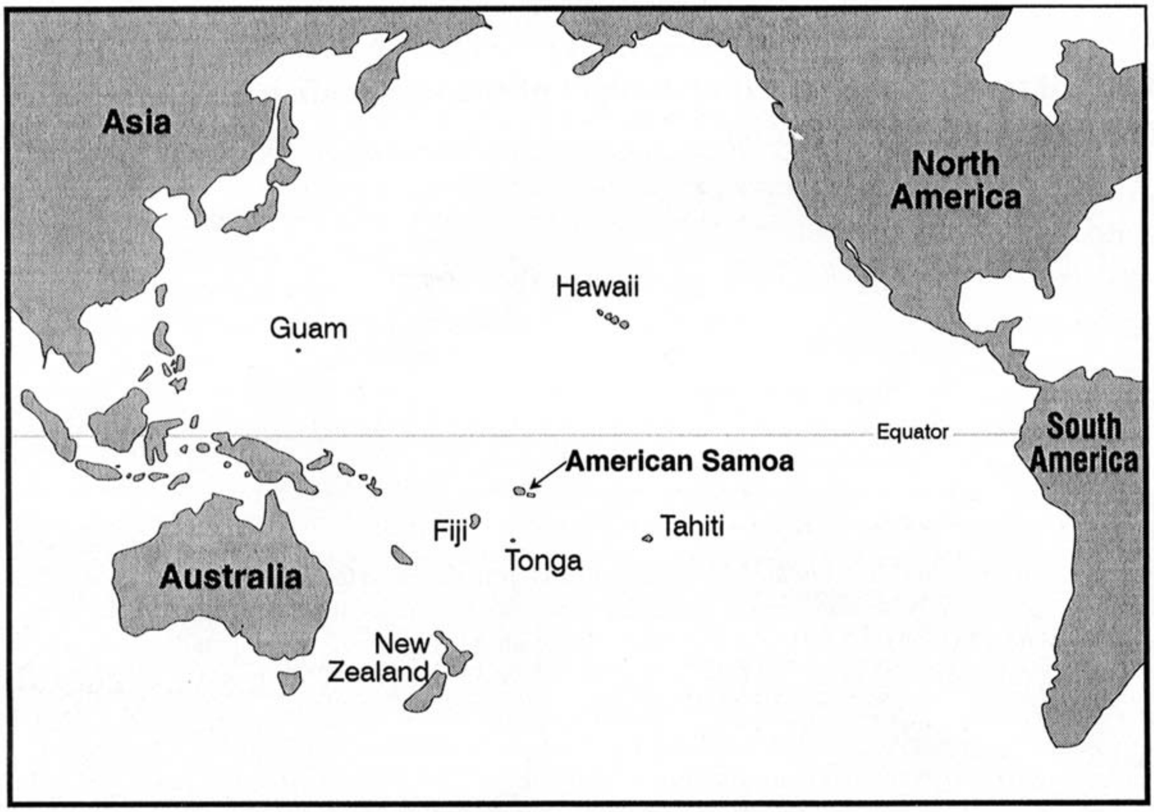

Fig. 1. Location of American Samoa (14° S, 170° W) in the South Pacific Ocean.

high-energy intertidal habitat where territories must be re-established daily, as well as after low tides and frequent dislocations due to wave surge.

Methods

This study was conducted at three locations (Afao, Amaluia, Matu'u) on the intertidal fringing reefs on the south side of Tutuila Island, American Samoa (Fig. 1). Sites were separated by 1.5–19 km. Reef flats at these sites were narrow (100–250 m), dropped abruptly to a depth of 3–4 m, and descended gradually thereafter. The surf zone inhabited by *A. lineatus* was characterized by consolidated limestone pavement, encrusting coralline algae, and low-profile and encrusting corals. Live coral coverage, calculated as the mean lineal extent of live corals along five 20 m line transects at each study area, averaged only 3.5 ± 1.4% (mean and SE, throughout paper). Most other substrates were covered by a thin layer of algal turf that was eaten by *A. lineatus*. Tidal range was 1 m, and water temperatures ranged 26.7–30.7° C along the reef slope at 0.3 m below the water surface.

Field observations of *A. lineatus* were performed using snorkeling gear from 1991–1994. Three size classes of fish were recognized based on their size at settlement onto the reef (recruits 2.5–5 cm) or approximate state of maturity (juveniles 8–13 cm, adults 15–21 cm; Craig unpublished data). Site fidelity was determined by monitoring 145 individually recognized fish at about weekly intervals for up to 2.3 years at the Afao site. Adults (n = 45) and juveniles (n = 50) were recognized by distinctive line patterns behind the eye and on the cheek. Secondary sexual characteristics were not apparent, so males and females could not be identified in the field. New recruits (n = 50) were identified by a combination of their specific location, size, color phase, and line pattern when discernable. Because surveys were conducted weekly, most recruits had probably arrived within the previous 2 weeks. Sizes of fish were estimated visually. A comparison of field estimates and actual sizes of the same 19 fish (6–20 cm) when caught by spear, indicated that the average discrepancy of visual estimates was 1.1 ± 0.2 cm ($r^2 = 0.90$).

Fish densities within a large colony (approximately 20 000 m^2 in size) at Afao were estimated by marking six reeftop plots (21.3 ± 2.0 m^2) with string at low tide and returning at high tide to count the number of territorial fish inside each plot. The sizes of 20 feeding territories were determined by observing individual adult fish for 15–40 minutes, mapping where feeding bites were taken, and then measuring the boundaries with a tape measure. The plot was drawn to scale on graph paper and a planimeter was used to determine its area.

To determine a time-budget, adult and juvenile *A. lineatus* from all three sites were observed on the intertidal reeftop during daylight hours when the tide was moderate to high and water depth was 0.6–1 m. Ten territorial fish and 10 non-territorial fish, selected haphazardly at each site, were observed during each 2 h interval from dawn to dusk (6:00 to 18:00 h, and for one hour from 18:00–18:59 h), and observations were recorded at different locations throughout a large colony. For each fish observed, an underwater slate was used to record numbers of (1) feeding bites, (2) attacks against other fish, (3) attacks received from other fish, (4) exits from territory. Water temperature and estimated fish size were also recorded. Attacks against other fish were primarily chases but included occasional feints (directed movements as if beginning to chase the intruder). Fish were observed at a distance of 2–3 m; any that were obviously affected by the viewer were excluded.

Due to wave turbulence in the surf zone, it was often difficult to observe an individual fish continuously for an extended period of time, thus a target observation time of 5 min was selected. Each territorial fish was observed 5.2 ± 0.04 min. Non-territorial fish were observed only 1.5 min ± 0.1 because they usually left the viewing area. A repeated-measures MANOVA was used to test for significant differences in bite rate and attack rate among study sites and time of day. Repeated measures were calculated using multivariate analysis-of-variance procedures (and Pillai's Trace test statistic) to accommodate for autocorrelation of counts among observation times (Tabachnick & Fidell 1989). Additional 5 min observations (n = 77 fish) were made on an opportunistic basis to quantify infrequent fish behavior (e.g., exits from territory).

Because I was unable to record simultaneously to identity of each fish attacked during the 5 min observation periods described above, a composite picture of species attacked was obtained separately by observing *A. lineatus* at various sites and recording all fishes attacked (n = 2215).

Additional behavioral observations were made when territorial fish experienced rough water conditions (n = 6 fish viewed and timed intermittently as visibility permitted, for a mean observation time of 5.2 ± 0.2 min), and in deeper water when the fish vacated their reeftop territories at low tide (n = 32, 2.8 ± 0.2 min) to determine whether they continued feeding elsewhere. For comparison, low-tide observations were also made of *A. lineatus* that permanently maintained subtidal territories (n = 33, 5.1 ± 0.01 min).

Results

A. lineatus formed large, dense colonies (0.4 ± 0.4 fish m^{-2}, excluding recruits) with feeding territories that were contiguous and saturated much of the outer reef flat. Most fish of all sizes were territorial; each adult defended a feeding area averaging 2.3 ± 0.2 m^2 (range 1.1–4.7 m, n = 20). The fish spent most of their day feeding within their territories, leaving only as noted below. In contrast, non-territorial fish wandered through the colony singly or in small groups. Non-territorial individuals were significantly smaller (13.2 ± 0.1 cm) than territorial fish (17.5 ± 0.1 cm; $t = 23.4$, $df = 471$, $p < 0.001$) and consisted of fewer sexually mature fish (approximately 3% versus 60%, based on size-at-maturity data: Craig unpublished data).

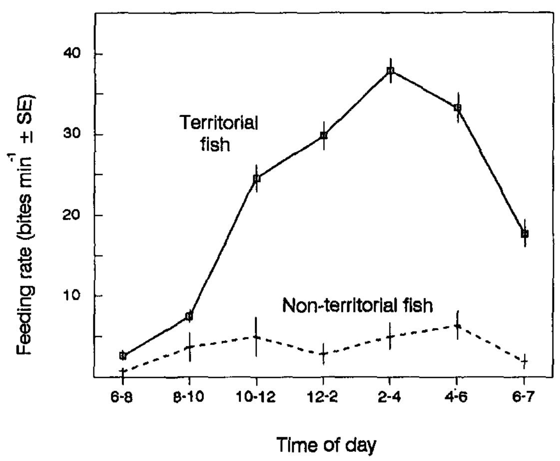

Fig. 2. Hourly feeding rates of territorial and non-territorial *A. lineatus* throughout the day. N = 30–47 fish for each data point.

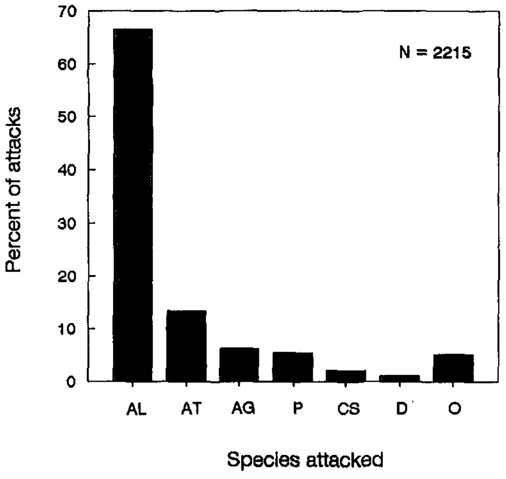

Fig. 3. Percent of attacks by territorial *A. lineatus* against intruding fish species: AL = *A. lineatus*, AT = *A. triostegus*, AG = *A. guttatus*, P = parrotfishes, CS = *Ctenochaetus striatus*, D = damselfishes, O = other. N = 2215 attacks observed at varied locations and dates.

Site fidelity

Each morning, *A. lineatus* returned to the reef flat from nighttime refuges. All exhibited strong day-to-day site fidelity, but the return rate varied according to fish size. Adults exhibited a return rate of 99.9% per day (n = 45), although the exact boundaries of some territories shifted, often abruptly, up to 1 m over time. At least 10 adults (22%) switched

Table 1. Two repeated-measure MANOVAs for determining relationships between time-of-day (7 periods) and site (3 reefs) on the feeding and attack rates of *A. lineatus*.

Variable	df[a]	F	p	Num[b] df	Den[c] df	F	Pillai's trace
Feeding rate							
a. Between-subject effects:							
-site	2	1.87	0.1738				
-error	27						
b. Within-subject effects:							
-hour				6	22	101.82	0.0001
-hour × site				12	46	1.47	0.1694
Attack rate							
a. Between-subject effects:							
-site	2	1.85	0.1771				
-error	27						
b. Within-subject effects:							
-hour				6	22	3.84	0.0090
-hour × site				12	46	2.19	0.0287

[a] Degrees of freedom.
[b] Numerator.
[c] Denominator.

residence to an adjacent or nearby territory during the course of this 2.3-year study.

Smaller *A. lineatus* were somewhat less site-tenacious (or suffered greater mortality). Juveniles had a return rate of 99.6% per day (n = 50), and recruits returned at a rate of 97.2% per day (n = 50). Even with these high return rates, however, turnover of the smaller *A. lineatus* on the reeftop was rapid: 84% mo^{-1} loss of recruits (i.e., 2.8% loss day^{-1} × 30 days), 12% mo^{-1} loss of juveniles, and 3% mo^{-1} loss of adults (Craig unpublished data). The median duration that the fish returned to the same territory was (after observations began): 7 days (recruits), 3.8 mo (juveniles), and 1.0 years (adults).

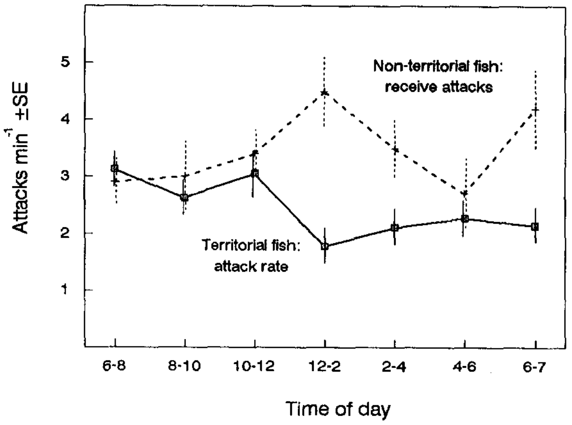

Fig. 4. Hourly attack rate by territorial *A. lineatus* and the hourly rate at which attacks were received by non-territorial *A. lineatus*. N = 30–47 fish for each data point.

Feeding activity

A repeated-measures MANOVA indicated that feeding patterns of territorial fish at the three study sites differed significantly for time-of-day but not for site or interaction between time and site (Table 1), thus sites were combined. The fish fed primarily during afternoon hours on turf algae within their territories (Fig. 2). They prevented non-territorial individuals from obtaining access to the food within their territories, as indicated by their six-fold greater feeding rate compared to non-territorial fish.

During the peak feeding period (14:00–17:59 h), feeding rates of territorial fish were not correlated with water temperature ($r^2 = 0.004$, $p > 0.1$, n = 68), fish size ($r^2 = -0.015$, $p > 0.1$, n = 68), or between the

Table 2. Summary of *A. lineatus* feeding and aggressive activities. All data refer to fish in the intertidal reeftop zone, except as noted.

Sample	N	Bites min^{-1}			Attacks min^{-1}					
		Mean	SE	P[b]	To others			Received		
					Mean	SE	P[b]	Mean	SE	P[b]
Total reeftop sample[a]										
Territorial fish	281	21.2	0.9	< 0.001	2.5	0.1	< 0.001	0.0	0.0	< 0.001
Non-territorial fish	216	3.6	0.6		0.1	0.0		3.5	0.2	
Territory location[c]										
Intertidal residents[a]	113	33.2	1.1	< 0.8	2.1	0.2	< 0.001	0.1	0.0	< 0.001
Subtidal residents	33	33.0	1.4		1.0	0.3		0.0	0.0	
Surf condition[c]										
Calm/moderate surf	113	33.2	1.1	< 0.005	2.1	0.2	< 0.05	0.1	0.0	< 0.001
Rough surf	6	19.1	6.7		0.7	0.3		0.0	0.0	
Low tide condition[c]										
Displaced intertidal residents	32	0.3	0.2	< 0.001	0.0	0.0	< 0.001	0.2	0.0	< 0.01
Subtidal residents	33	33.0	1.4		1.0	0.3		0.0	0.0	

[a] Excludes low tide periods.

[b] Student's t test.

[c] During afternoon feeding period (1200–1759).

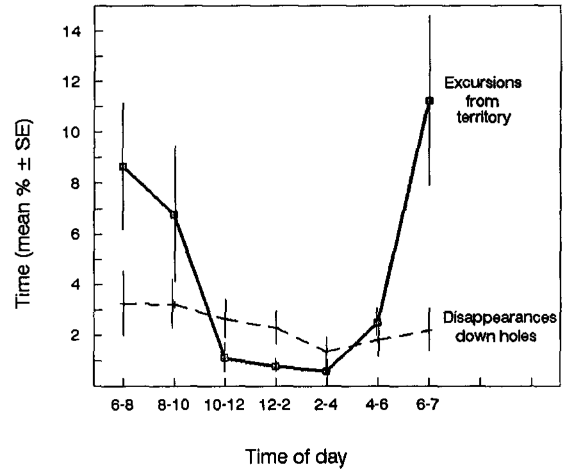

Fig. 5. Proportion of time spent away from their territories by a – excursions (usually participating in blackfin behavior), and b – disappearing down holes within or adjacent to their territories. N = 30–47 fish for each data point.

intertidal and subtidal locations of their territories (Table 2, $p > 0.8$). However, frequent defense of territories (see next section) resulted in significantly lower foraging rates during the peak feeding period ($r^2 = -0.333$, $p < 0.001$, $n = 70$).

Territorial defense

Agonistic activities included: (1) territorial defenses to prevent intruders from feeding within territories, (2) maintenance of territory borders, and (3) challenges to determine territory ownership. A repeated-measures MANOVA of attack rates indicated a significant interaction between time-of-day and study site (Table 1) which reflects variability in the occurrence of intruders. For the purposes of this paper, however, overall site differences were slight (Afao 1.9 ± 0.24 attacks min^{-1}, Amaluia 2.5 ± 0.22, Matu'u 2.7 ± 0.27) and thus were combined.

Attacks against intruders

Territorial individuals chased virtually all herbivorous fish that entered their territory, except small co-resident damselfish and blennies. Most attacks were directed toward wandering conspecifics (Fig. 3), but other herbivores were vigorously chased, particularly *A. triostegus*, *A. guttatus*, and *Scarus* spp.

Territorial fish were highly aggressive throughout the day (Fig. 4), attacking intruders at an average rate of 2.5 attacks min^{-1} (Table 2). They were far more aggressive ($p < 0.001$) and received far fewer attacks than non-territorial fish ($p < 0.001$).

Maintenance of territory borders

Although there were occasional encounters between adjacent territory-holders, a territorial fish more commonly maintained its territorial boundary by positioning itself along the territory's border and feeding there, especially whenever a neighbor was also feeding near that border. Such movements were not included in tabulations of attacks.

Territorial challenges

More intensive territorial challenges involved a distinctive display of aggressive behavior between two or more territorial fish, coupled with a rapid change in fish coloration. The fish darkened from an overall yellowish color to one with a black dorsal fin and blackened portions of its head and tail (termed 'blackfin' coloration and behavior). Pairs of blackfin *A. lineatus* swam rapidly and aggressively parallel to each other and in S-shaped configurations, as described by Nursall (1974). Small groups of 2–10 blackfin fish interacted on the reeftop in this fashion at distances of 0–20 m from their territories. Blackfin events usually consisted of brief interactions, 64% lasting 20 sec or less but up to 11 min (mean 40.5 ± 7 sec, n = 160), followed by varying periods of non-aggression and normal body coloration.

Intensive and prolonged blackfin behavior was observed on four occasions, each apparently lasting 2–3 days. For one pair, the fish occupying the territory reversed on two consecutive days, after which the challenger disappeared. Some escalated territorial challenges also involved one fish repetitively chasing another in loops extending about 30 m from the contested territory.

Territorial defense often resulted in wounds, presumably inflicted by the sharp caudal knife of conspecifics, although the possibility that some of these wounds resulted from life in the turbulent surf zone cannot be ruled out. For 79 juvenile and adult fish observed at least 1 month, 72% received cuts, scrapes, or split fins at some time. Most wounds healed rapidly within several days.

Excursions from territory

A. lineatus vacated their territories with some regularity, particularly during early morning and late afternoon (Fig. 5). At least 46% of these excursions involved blackfin behavior with other *A. lineatus*.

Additional types of territorial excursions occurred. First, 26% of the territorial fish briefly vacated their territory by swimming down nearby holes in the reeftop or, if their territory was adjacent to the reeftop dropoff, they swam over the reef edge. These were considered voluntary excursions because the movements did not appear to be responses to any biological or physical factor (e.g., escape from predators or rough water). For those engaging in this activity, it averaged 9% of their time throughout the day, but for the sample as a whole, this was a minor activity, amounting to only 2–3% of hourly activities. Second, at dawn some *A. lineatus* left their territories to group-spawn at a specific site in the reef outlet channel located about 100 m from the study area. Third, a temporary suspension of agonistic behavior occurred when surge-related water movements swept a group of fish off their territories and then swept them back again a few seconds later with the reverse flow. Surge-related movements were not tabulated as excursions from the fish's territory.

Modifications to general behavioral patterns

Disruptive physical conditions

The foregoing results were obtained during calm to moderate wave conditions, but heavy surf conditions frequently prevailed in the study areas. The fish must contend with strong currents, turbulence, periodic zero visibility due to bubbles, and a habitat that may be momentarily 'dry' between large waves. I tried, therefore, to record the activities of 6 *A. lineatus* during hazardous surf conditions.

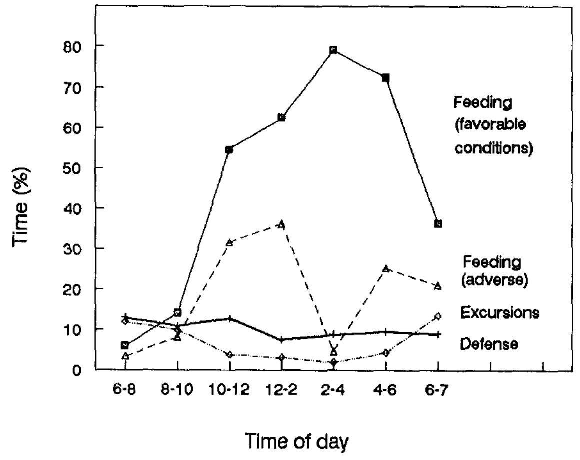

Fig. 6. Time budget for territorial *A. lineatus* during favorable wave and tide conditions, showing the proportion of time spent feeding, defending territory, and voluntarily leaving territory. Also shown is the reduced proportion of time spent feeding when the fish are confronted by adverse wave and tide conditions.

As expected, the fish's activities were strongly affected by the turbulence. They fed 42% less frequently (Table 2, $p < 0.005$), vacated their territories 8 times longer (47% vs. 6% of available time, $p < 0.0005$), and made 68% fewer attacks against intruders ($p < 0.05$).

Low-tide behavior

During spring low tides when the reeftop was exposed or nearly so, *A. lineatus* possessing intertidal territories were forced into deeper water. The fish then milled around the reeftop edge and generally ceased feeding (Table 2) even when the low tide occurred during their afternoon feeding period. The low attack rates by both displaced fish and those with permanent subtidal territories also indicated that the displaced fish were not attempting to raid subtidal territories. Subtidal *A. lineatus*, however, continued to feed during such times.

Activity time-budget

To calculate a time-budget for territorial fish, the mean time spent accomplishing one unit for each principal activity was determined: chasing another fish (and returning) in defense of a territory, 2.5 ± 0.3 sec attack^{-1} (n = 30), and being chased by another fish, 0.8 ± 0.1 sec attack^{-1} (n = 30). Total times for these activities equalled the unit time multiplied by the number of times the activity occurred each hour. A feeding unit of time was more complex to estimate because *A. lineatus* moved continuously within its territory as it fed, taking a series of bites in rapid succession (consisting of 5.4 ± 0.5 bites lasting 2.9 ± 0.3 sec, n = 30), followed by a brief pause as the fish moved to another site and resumed feeding. Portions of these movements and pauses were considered to be part of feeding activities, so the total feeding unit time was calculated to include an arbitrary 2-sec period before and after every bite series. The number of feeding units that occurred each hour of the day was calculated by dividing the total number of feeding bites h^{-1} (Fig. 2) by the mean number of bites per series. Total feeding time then equalled the number of feeding units h^{-1} multiplied by the unit time. A time budget was not calculated for non-territorial fish because their time spent in the viewing area probably did not reflect their complete range of activities (i.e. they presumably fed elsewhere).

Territorial *A. lineatus* spent up to 80% of their time engaged in feeding activities, primarily during afternoon hours (Fig. 6). About 10% of their time was spent actively defending their territory throughout the day, and another 2–13% of their time was spent away from their territory. During all remaining time, particularly during the morning hours, the fish remained 'on station' guarding their territories.

Under these conditions, an 'average' fish defended its territory 1900 times per day and took 17 000 bites of turf algae within its territory (= 7400 bites m^{-2} d^{-1}). Such rates were greatly curtailed, however, during rough surf and/or alow tide that forced the fish off their intertidal territories during their afternoon feeding period. When these adverse conditions are superimposed on Fig. 6, there was a 60% reduction in feeding (6800 bites d^{-1}) and a 75% drop in aggressive activities (500 attacks d^{-1}) (Table 2).

Discussion

The important role of herbivorous fishes in coral reef ecosystems is well established (e.g., reviews by Horn 1989, Choat 1991, Hay 1991). Herbivorous fishes (particularly damselfishes, surgeonfishes, and parrotfishes) often occur in high densities and consume large amounts of algae, presumably due to the low nutrient value of this food source (Horn 1989). Herbivorous fishes influence the species composition of benthic algae and invertebrates, contribute to erosion and sedimentation of tropical reefs, and through territoriality affect the distribution of other fishes (Lewis 1986, Robertson & Gaines 1986, Horn 1989).

A. lineatus is an abundant herbivorous fish on American Samoa's reefs. For the most part, its distribution and behavior here are similar to that described for this species in Australia and the Indian Ocean (Nursall 1974, Robertson et al. 1979, Robertson & Polunin 1981, Choat & Bellwood 1985, Robertson & Gaines 1986, Polunin & Klumpp 1989). At those locations, *A. lineatus* also forms colonies along the reef crest and upper slope, most individuals are territorial, territories are occupied diurnally and defended by single individuals, feeding on turf algae occurs primarily in the afternoon, aggression toward most other herbivores is high, and occasional excursions from its territory occur.

Some noteworthy differences are that *A. lineatus* territories in Samoa are much smaller (2.3 versus 7 m^2 in the Indian Ocean [Robertson et al. 1979]), densities within colonies are much greater (0.4 versus 0.05 fish m^{-2} in the Great Barrier Reef [Choat & Bellwood 1985]), territorial defense rates against intruders are much higher (2.5 versus 0.2 attacks min^{-1} in the Great Barrier Reef [Choat & Bellwood 1985] and 0.3 attacks min^{-1} in the Indian Ocean [Robertson et al. 1979]) and that most attacks were directed at conspecifics rather than other herbivorous species (67% versus 32% in the Great Barrier Reef [Choat & Bellwood 1985]).

Three readily identifiable factors may contribute to these differences: fish size, food abundance and competitor density (e.g., Norman & Jones 1984). First, territorial *A. lineatus* in Samoa may be smaller (and thus require smaller territories or are less able to defend larger territories) than *A. lineatus* at the other locations. For example, *A. lineatus* in Samoa's artisanal harvest in 1994 averaged 19.3 cm fork length (n = 720) compared 22.0 cm for a sample of 19 territorial fish from the Great Barrier Reef (H. Choat personal communication). Second, food may be more widely available in Samoa, where reefs have been damaged extensively by an *Acanthaster* invasion in the late 1970s and by hurricanes in 1990 and 1991, resulting in proportionally more habitat suitable for algal turf than might otherwise be available. Live coral coverage in the study areas was only 3.5% compared to 21–32% at the Great Barrier Reef (Choat & Bellwood 1985). Thus differences between regions might indicate that preferred food was more abundant on the Samoan reef flat, allowing a reduction in territory size which, in turn, resulted in higher fish densities within the colony and consequently more agonistic encounters with crowded conspecifics. Alternatively, higher densities of *A. lineatus* in Samoa increased defense requirements, causing a reduction in territory size. Large-scale manipulative experiments would be required to examine these possibilities.

Among surgeonfishes, *A. lineatus* aggressively dominates most other species (Robertson & Gaines 1986). Its tenacity in maintaining a territory in a high-energy surf environment is impressive. Beginning at settlement onto the reef and continuing thereafter, most *A. lineatus* exhibit strong territoriality. Overall defense requirements can be extensive, involving some 500–1900 chases of intruders daily. Additionally, (a) their physical presence is required for several hours in the early morning (prior to feeding) to guard their territory, and (b) a continuous but unquantified effort is expended to maintain territorial boundaries by positioning themselves opposite neighbors who approach a common boundary. Challenges for territorial possession are of a far more serious nature, often occupying up to 100% of a fish's time.

Given this large energy investment in territorial defense, it seems unusual that the fish would voluntarily vacate their territory with regularity. Some *A. lineatus* spent 9% of their time down reef holes or over the reeftop dropoff. Rarely, however, were intruders able to use this opportunity to feed in the unguarded territory, probably because the average disappearance time of the territory-holder was only 6 sec.

Other fish that participated in blackfin forays were absent from their territory 20–25% of their time in early morning and late evening. This behavior was not directly related to spawning, which occurred elsewhere at dawn. Blackfin behavior was clearly involved in territorial defence, but its function when groups of blackfin fish interacted away from their territories was less clear. Perhaps it was a way to assess whether better sites were available (e.g., Bartels 1984), or it represented ritualized fighting when a new site became available. I have observed considerable blackfin activity among fish at newly vacated sites. In view of these multiple forays by territorial fish, at least some of the fish identified as being 'non-territorial' in this study were probably territorial fish on forays from other areas.

In addition to territorial defense, low tides and rough surf impinged on foraging time. It was therefore unexpected that displaced intertidal *A. lineatus* did not continue feeding subtidally when the tide was low. Instead, they merely milled about until they were able to return to their intertidal territories 1–3 hours later. Meanwhile, permanently subtidal *A. lineatus* continued to feed during the low tide period and thus would seem to have superior feeding opportunities if food was of the same quality and quantity.

Circumstantial evidence suggests the opposite, however. Territorial fish, including the largest dominant individuals, appeared to be more abundant on the outer reef flat than in subtidal areas where there appeared to be a surplus of suitable space available. Also, one marked individual was observed to abandon its subtidal territory and challenge another one on the intertidal reef flat.

A possible factor contributing to usage of the intertidal reef flat is the availability of shelters or quick escape routes to deep water. Despite its flat appearance, deep holes and crevices occur in the outer reef flat which the fish use to escape from predators or crashing waves. This ready access may account for the absence of 'stampeding' behavior as described by Robertson et al. (1979). They reported that *A. lineatus* frequently rushed into deeper waters when threatened by predators (2.8 stampedes h^{-1}). This was not observed in the study area except occasionally when the fish fled from a nearby spear fisherman. Alternatively, fewer natural predators may exist on Samoa's reefs due perhaps to fishing pressure.

A final comment is that the aggression of *A. lineatus* is effective but not impenetrable. As noted by others (Robertson & Polunin 1981, Robertson 1984, Robertson & Gaines 1986), small algivores (damselfishes, blennies, miscellaneous invertebrates) and non-competitors (e.g., the detritivore *Ctenochaetus striatus* and carnivorous wrasses) are tolerated within the territory, and roving schools of herbivorous fishes can descend on an *A. lineatus* territory en masse and overwhelm the resident fish in Samoa (personal observation) as elsewhere.

Acknowledgements

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