

FEEDING HABITS OF YELLOWFIN TUNA ASSOCIATED WITH FISH AGGREGATION DEVICES IN AMERICAN SAMOA

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ABSTRACT

In American Samoa, Fish Aggregation Devices (FADs) provide target fishing locations with high catch rates, but little is known about their ecological impact. The effect on the diet of yellowfin tuna associating with FADs has been examined in the Philippines, French Polynesia and Hawaii, but results differ among the regions. Diel patterns of movement around FADs appear to be consistent among regions. The stomach contents of yellowfin tuna were compared from FADs, offshore banks, areas away from these features and from before FADs were deployed in American Samoa. Differences were minimal among these four groups of yellowfin tuna in the frequency of occurrence of important prey in their diets. Diurnal patterns in the stomach fullness and the frequency of occurrence of some prey in the diet indicate that these yellowfin tuna are not feeding at night and that they may prey on vertically migrating mesopelagic organisms during crepuscular periods. FAD- and bank-associated yellowfin tuna probably follow the diel movement patterns observed in other areas. The regional differences in the apparent effect of FAD association on the diet of yellowfin tuna are discussed and possible explanations are given.

Anchoring floating objects in deep water as Fish Aggregation Devices (FADs) has become common practice in the tropical and sub-tropical oceans of the world. In American Samoa, FADs have been successfully used to provide target fishing locations with high catch per unit of effort for pelagic species (Buckley et al., 1989); however, little is known about the ecological impacts on the aggregated fish communities.

Most studies that have examined the effects of FADs on the aggregated fish communities have focused on the yellowfin tuna (*Thunnus albacares*) because of its close association with FADs anchored in deep (>500 m) water and its importance as a commercial, sport and subsistence fish. The influence of FADs on the diet of yellowfin tuna has previously been studied in the Philippines (Yesaki, 1983a, 1983b; Barut, 1988), French Polynesia (Lehodey, 1990) and Hawaii (Brock, 1985).

In the Philippines, cannibalism by large yellowfin tuna (FL > 99 cm) is high at FADs (Yesaki, 1983a, 1983b; Barut, 1988), minimal away from FADs (Yesaki, 1983a) and was apparently low before FADs were used in deep water (Nakamura, 1936; Ronquillo, 1953). These FADs act as catalysts for yellowfin tuna cannibalism because large and very small tunas (FL < 30 cm) are aggregated (Yesaki, 1983a), and the large yellowfin tuna feed heavily on the aggregated fish community of which juvenile yellowfin tuna are a part (Yesaki, 1983a, 1983b; Barut, 1988). The large FAD-associated yellowfin tuna have considerably more food in their stomachs than large yellowfin tuna caught away from FADs (Yesaki, 1983a) and large yellowfin tuna studied in other areas (Yesaki, 1983a; Barut, 1988).

In French Polynesia, the breadth of the diet of yellowfin tuna at FADs and away from FADs is similar and does not include juvenile tunas (Scombridae), but yellowfin tuna eat more juvenile reef fishes at FADs than both away from FADs and at banks (Lehodey, 1990). FAD-associated yellowfin tuna (90 to 120 cm FL) less frequently have empty stomachs and have more food in their stomachs than non-FAD-associated and bank-associated yellowfin tuna.

No cannibalism by smaller yellowfin tuna (about 25 to 132 cm FL) is found at FADs in Hawaii, but their diet changes from the typical array of prey that is observed away from FADs to a species of vertically migrating shrimp that is otherwise only rarely eaten (Brock, 1985). FAD-associated yellowfin tuna more frequently have empty stomachs and are less full than non-FAD-associated yellowfin tuna which may be due to a depletion of locally available prey at the FADs by the aggregated predators. Brock (1985) suggests that this condition may cause the observed diet shift by FAD-associated yellowfin tuna.

Using biotelemetry in Hawaii, Holland et al. (1990) clearly show a pattern of diel movements for FAD-associated and island-associated yellowfin tuna consisting of diurnal association with FADs and island bathymetry, and nocturnal excursions away from these features to open water. In other biotelemetry studies, sample sizes are smaller (1 to 4), but some degree of diurnal FAD-association is evident among yellowfin tuna tracked in the western equatorial Pacific Ocean (Yonemori, 1982), French Polynesia (Cayré and Chabanne, 1986) and the Indian Ocean (Cayré, 1991). Some degree of island-association is also evident in the eastern Pacific Ocean (Carey and Olson, 1982) and the Indian Ocean (Cayré, 1991). Consequently, the patterns described by Holland et al. (1990) may be consistent among FAD- and island-associated yellowfin tuna in most areas, whereas changes in the diet of yellowfin tuna caused by FAD-association are regionally specific.

Holland et al. (1990) propose that the observed diel pattern is driven by an optimal foraging strategy. The diurnal association with an island may expose yellowfin tuna to a zone of enhanced prey density where both epipelagic and reef species co-occur, and the nocturnal excursions to deeper water may be foraging behavior targeting vertical migrators that inhabit the surface layers at night. The same diel pattern observed in FAD-associated yellowfin tuna suggests that they respond to FADs anchored in deep water as outliers of island bathymetry, but they are not exposed to the same zone of enhanced prey density as the island-associated yellowfin tuna.

In American Samoa, outliers of island bathymetry occur as offshore banks (Ralston and Goolsby, 1986) which are characterized as "natural fish aggregation devices" in Buckley et al. (1989) and which may influence the movements of yellowfin tuna in a manner similar to anchored FADs (Holland et al., 1990). The influence of FADs on the diet of yellowfin tuna in American Samoa was investigated by comparing the stomach contents of yellowfin tuna caught (1) prior to FAD deployment, (2) away from FADs and banks, (3) at FADs and (4) at offshore banks. In addition, the diurnal feeding patterns of these yellowfin tuna were examined in relation to the movement patterns observed around FADs and islands in other areas of the Pacific and Indian Oceans. Factors that may contribute to the different results among studies are discussed.

METHODS AND MATERIALS

Data Collection.—Stomachs of yellowfin tuna were sampled from FADs (February 1985 through May 1989), banks (January 1989 through May 1989) and non-FAD areas (June 1986 through June 1989), whenever conditions and circumstances allowed during a 4.5-year study-period. Yellowfin tuna were caught from sunrise to sunset (0600 to 1900) by trolling and occasionally other hook-and-line techniques. The date, time, area and other capture parameters were recorded for individual yellowfin tuna. They were inspected for evidence of stomach eversion and immediately submerged in an ice and saltwater brine. Yellowfin tuna showing signs of stomach eversion were not included in the analysis. After returning to port, yellowfin tuna were weighed to the nearest 0.1 kg, measured to the nearest mm FL, and their stomach contents were removed, labeled and preserved in buffered 10% formalin.

Yellowfin tuna were considered to be associated with a FAD if they were caught within 1.6 km of

a FAD buoy (Buckley et al., 1989). FAD-associated yellowfin tuna were sampled in four locations (A, B, C and G of fig. 1 in Buckley et al., 1989), 5 to 13 km from shore, where FADs were anchored in approximately 1,000 to 2,200 m depths (Itano and Buckley, 1987). In total, these FADs were on station 88% of the time (American Samoa's Department of Marine and Wildlife Resources (DMWR), unpubl. data) from their first deployments between December 1984 and March 1985 (Itano and Buckley, 1987) until the end of the sampling period for this study in June 1989.

Yellowfin tuna were identified as associated with an offshore bank if they were caught near a bank's 183 m isobath or shallower (Buckley et al., 1989). Bank-associated yellowfin tuna were sampled from three banks (Northeast, East and South Banks in Ralston and Goolsby, 1986) that are small pinnacles rising from depths of thousands of meters to within 100 m of the surface about 20 to 60 km from shore (Ralston and Goolsby, 1986; DMWR, unpubl. data). Yellowfin tuna were considered not to be associated with a FAD or bank if they were caught >1.6 km from a FAD buoy and over depths >183 m at an offshore bank (Buckley et al., 1989). These individuals were designated as non-FAD-associated yellowfin tuna, and include fish caught near islands, near flotsam and in open water. Situations where there was a question about a yellowfin tuna's association with a FAD or bank were typically absent.

Before FADs were deployed, the stomach contents of yellowfin tuna were recorded from the Samoan region by Hida (1973) and the South Pacific Commission (selected raw data from Argue et al., 1983). The prey of these 49 (19 empty) yellowfin tuna (36 to 74 cm FL) were combined to describe the pre-FAD food habits of yellowfin tuna. In addition, the larger, undigested prey were described from 34 yellowfin tuna caught almost exclusively in the area now occupied by FADs (DMWR, unpubl. data) before FADs were deployed.

In the laboratory, stomach contents were rinsed in water and the prey items were identified to the lowest taxonomic category practical, then counted, blotted and weighed to the nearest 0.01 g. Prey items were assigned to one of six categories based on their degree of digestion (0–5%, 6–20%, 21–35%, 36–50%, 51–90% and 91–100% digested). The fullness of individual yellowfin tuna was represented by the ratio of their stomach contents weight (g) to their pre-eviscerated body weight (kg).

Three measures were used to express the importance of each prey taxon to the diets of non-FAD-, FAD- and bank-associated yellowfin tuna: (1) the frequency of occurrence in the non-empty stomach samples, (2) the number eaten, and (3) the percentage of the total weight of all prey. Only the frequency of occurrence of each prey taxon could be determined for the pre-FAD yellowfin tuna.

The Kruskal-Wallis test and non-parametric multiple comparisons for unequal sample sizes (Zar, 1984) were used to test the mean length and fullness of yellowfin tuna for statistical differences among the non-FAD-, FAD- and bank-associated groups.

Diet Comparisons.—The food habits of the four groups of yellowfin tuna were compared using "important" fish families and invertebrate taxa. Important prey taxa were those that occurred in $\geq 10\%$ of the non-empty stomachs or comprised $\geq 2\%$ of the weight or number of the prey in at least one of the four groups of yellowfin tuna. Nine invertebrate taxa and 16 fish families met these criteria.

There is a high degree of correlation among the frequency of occurrence, number and weight of a prey type in the diet (Macdonald and Green, 1983). We felt that the frequency of occurrence was the most appropriate diet information to compare among the groups of yellowfin tuna because it reflects the uniformity with which the group preys upon a prey type (Bowen, 1983). The frequency of occurrence is less susceptible to influence by rare episodes of gorging than is the number of a prey type, and is less susceptible to influence by the occasional occurrence of large individuals than is the weight of a prey type.

The diet of pre-FAD yellowfin tuna could only be compared to the diets of non-FAD-, FAD- and bank-associated yellowfin tuna using the frequency of occurrence of each prey taxon. Comparisons were made using the chi-square test for more than two proportions (Zar, 1984) for each prey taxon. Because 25 prey taxa are compared between the four groups of yellowfin tuna, the null hypothesis (that the frequency of occurrence of the prey is equal in all four groups) may be rejected, when it is in fact true, more often than the level of significance that is used. However, this is acceptable for exploring the potential differences in the frequency of occurrence of each prey. Where a statistically significant difference was found, the multiple comparisons for proportions with unequal sample sizes test (Zar, 1984) was used to determine which groups consumed that prey type at a different frequency than which others. Each chi-square test for more than two proportions and each multiple comparisons test were performed at a significance level of 0.10.

Small differences among the diets of non-FAD-, FAD- and bank-associated yellowfin tuna may be due to differences in prey availability in each environment. The least digested prey in a stomach are the most likely to have been eaten in the vicinity of the capture location. Therefore, prey that were more than half digested were excluded from the diet comparison among non-FAD-, FAD- and bank-associated yellowfin tuna. The number, percent weight and frequency of occurrence of fish families and invertebrate taxa were calculated using only those prey items that met this criterion. Yellowfin tuna stomachs that contained only prey that were greater than half digested were considered as empty. For each prey taxon, differences among the frequency of occurrence in the diets of non-FAD-, FAD-

and bank-associated yellowfin tuna were compared using the chi-square test for more than two proportions and the multiple comparisons test, as described above, with a significance level of 0.10.

In addition, we believed that the number of a prey type eaten per occurrence might reflect the abundance of that prey relative to the abundance of the predators at the time the sample was caught. The mean number per occurrence was statistically compared for each prey taxon among the diets of non-FAD-, FAD- and bank-associated yellowfin tuna using the Kruskal-Wallis test and non-parametric multiple comparisons for unequal sample sizes (Zar, 1984) with a significance level of 0.10. The power of these tests is dependent upon the number of occurrences of the prey type in each group (i.e., n_i for the tests). Ranking the numbers of a prey type occurring in the stomachs reduces the influence of gorging episodes unless they consistently occur.

Diel Patterns.—The data were examined for possible diel feeding patterns using the degree of correlation between fullness and time of day and using the frequency of occurrence of selected prey taxa in non-FAD-, FAD-, and bank-associated yellowfin tuna. Spearman's rank correlation procedure (Zar, 1984) was performed on the fullness of individual yellowfin tuna and the time of capture. The frequency of occurrence of euphausiids and squid (prey taxa composed at least partially of vertical migrators) were compared to the frequency of occurrence of the two most frequently occurring crustacea and fishes (that were probably consistently available throughout the day) in four time intervals. Time intervals are early morning (0600–0859), late morning (0900–1159), afternoon (1200–1459) and evening (1500–1900). Prey that were greater than half digested were not included in the calculations of frequency of occurrence for each time interval.

RESULTS

In this study, 228 yellowfin tuna caught in American Samoa were analyzed. The 97 yellowfin tuna caught at FADs had a mean length of 63 cm FL (30 to 148 cm FL), the 66 bank-associated yellowfin tuna had a mean length of 75 cm FL (49 to 111 cm FL), and the 65 non-FAD-associated yellowfin tuna had a mean length of 64 cm FL (33 to 115 cm FL). The number of yellowfin tuna sampled in this study was too low to allow meaningful comparisons between years, among FADs, among banks and among non-FAD areas. The mean length of the bank-associated yellowfin tuna was significantly different from the mean lengths of the FAD-associated ($P < 0.001$, $Q = 5.2$) and the non-FAD-associated ($P < 0.001$, $Q = 4.4$) yellowfin tuna, but no significant difference was found between the FAD-associated and non-FAD-associated yellowfin tuna ($P > 0.5$, $Q = 0.5$).

Prey items or their remains were found in nearly all yellowfin tuna examined. No bank-associated yellowfin tuna were empty, one FAD-associated yellowfin tuna was empty (1.0%), and one non-FAD-associated yellowfin tuna was empty (1.5%). The bank-associated yellowfin tuna were significantly less full (mean = $1.08 \text{ g}\cdot\text{kg}^{-1}$) than both the FAD-associated ($P < 0.001$, $Q = 4.8$) and the non-FAD-associated ($0.005 < P < 0.01$, $Q = 3.0$) yellowfin tuna. Stomach fullness of FAD-associated (mean = $4.85 \text{ g}\cdot\text{kg}^{-1}$) and non-FAD-associated (mean = $4.99 \text{ g}\cdot\text{kg}^{-1}$) yellowfin tuna was not significantly different ($0.2 < P < 0.5$, $Q = 1.5$).

Crustacea and fishes each occurred in greater than 90% of the non-FAD-, FAD- and bank-associated yellowfin tuna with prey remains. Crustacea and fishes were also numerically dominant from all three areas. Fishes comprised a larger portion of the weight in the diet of FAD-associated yellowfin tuna (90.8%) than in the diets of non-FAD- (75.8%) and bank-associated (56.6%) yellowfin tuna. By weight, crustacea and molluscs represented, respectively, 5.5% and 3.1% of the FAD-associated, 4.7% and 17.4% of the non-FAD-associated, and 23.7% and 17.7% of the bank-associated yellowfin tuna diets.

Diet Comparisons.—A significant difference in the frequency of occurrence was found for 14 of the 25 important prey taxa among the diets of pre-FAD, non-FAD-, FAD- and bank-associated yellowfin tuna (Table 1). The frequency of occurrence for eight of the nine invertebrate taxa was significantly lower in the pre-FAD yellowfin tuna than in the three groups of yellowfin tuna examined in this

Table 1. The percent frequency of occurrence of important prey in the diets of pre-FAD, non-FAD-, FAD- and bank-associated yellowfin tuna (PRE, NON, FAD and BANK, respectively). The asterisks indicate a significant difference (* = 0.10, ** = 0.05, *** < 0.01) among the frequencies of occurrence of that prey taxon in each of the diets. The underlined percent frequencies of occurrence are statistically different ($\alpha = 0.10$) than the frequency of occurrence for that prey taxon in the diet of pre-FAD yellowfin tuna; other statistical similarities or dissimilarities are not implied.

	Percent frequency of occurrence			
	PRE	NON	FAD	BANK
Crustacea	43.3	95.3	94.8	97.0
Hyperiidæ	3.3	31.3	18.8	43.9 ***
Euphausiidæ	0.0	10.9	9.4	16.7 *
Stomatopoda	33.3	<u>78.1</u>	<u>88.5</u>	<u>78.8</u> ***
Shrimp	6.7	32.8	26.0	28.8 **
Crab megalopæ	16.7	<u>76.6</u>	<u>71.9</u>	<u>59.1</u> ***
Phyllosomes	3.3	7.8	10.4	<u>28.8</u> ***
Mollusca	26.7	60.9	70.8	74.2
Octopoda	10.0	35.9	31.3	27.3 **
Squid	16.7	<u>53.1</u>	<u>61.5</u>	<u>66.7</u> ***
Other inverts.	0.0	<u>32.8</u>	<u>41.7</u>	<u>56.1</u> ***
Fishes	80.0	90.6	94.8	93.9
Engraulidæ	20.0	4.7	11.5	1.5 ***
Carapidæ	0.0	4.7	6.3	3.0
Holocentridæ	20.0	20.3	12.5	12.1
Fistularidæ	10.0	3.1	4.2	1.5
Dactylopteridæ	3.3	10.9	7.3	10.6
Priacanthidæ	3.3	1.6	2.1	1.5
Carangidæ	3.3	4.7	13.5	4.5 **
Mullidæ	0.0	1.6	6.3	6.1
Chaetodontidæ	13.3	12.5	19.8	10.6
Acanthuridæ	36.7	26.6	37.5	24.2
Scombridæ	13.3	12.5	13.5	3.0 *
Balistidæ	23.3	23.4	32.3	<u>24.2</u>
Monacanthidæ	16.7	12.5	19.8	4.5 **
Ostraciidæ	13.3	14.1	15.6	<u>39.4</u> ***
Tetraodontidæ	10.0	7.8	7.3	<u>13.6</u>
Diodontidæ	10.0	4.7	0.0	1.5 **
	Sample Size			
	30	64	96	66

study. However, the frequency of occurrence for each family of fish in the diet of the pre-FAD yellowfin tuna was similar to the frequency of occurrence in at least one of the other groups of yellowfin tuna. The frequency of occurrence of carangids (jacks) in the diet of yellowfin tuna caught by the DMWR (unpubl. data) prior to the deployment of FADs was 26.5%.

For prey not greater than half digested, a significant difference in the frequency of occurrence was found for eight of the 25 important prey taxa among the diets of non-FAD-, FAD- and bank-associated yellowfin tuna (Table 2). The number per occurrence was significantly different among the three groups of yellowfin tuna for crab megalopæ, phyllosomes (larval lobsters), octopods and engraulids (anchovies) (Table 2). However, the non-parametric multiple comparisons test of the number of phyllosomes per occurrence was not able to detect which yellowfin tuna groups were different from which others.

Seven of the 11 prey taxa with significant differences in the frequency of occurrence or the number per occurrence among the diets of the three groups of

Table 2. The percent frequency of occurrence, the number and the percent weight of important prey in the diets of non-FAD-, FAD- and bank-associated yellowfin tuna (NON, FAD and BANK, respectively). The asterisks indicate a significant difference (* = 0.10, ** = 0.05, *** < 0.01) among the yellowfin tuna groups in the percent frequency of occurrence or the number per occurrence for that prey taxon. The underlined percent frequency of occurrence is statistically different (alpha = 0.10) from the frequencies of occurrence for that prey taxon in the other two groups of yellowfin tuna. The underlined number for a prey taxon indicates that the number per occurrence for that prey taxon is statistically different (alpha = 0.1) from the other two groups of yellowfin tuna.

	% Occurrence			Number			% Weight		
	NON	FAD	BANK	NON	FAD	BANK	NON	FAD	BANK
Crustacea	92.2	90.5	93.9	795	1,424	750	3.9	5.2	22.9
Hyperiidea	26.6	6.3	24.2	*** 31	7	27	0.1	<0.1	0.3
Euphausiidae	9.4	<u>7.4</u>	12.1	27	85	147	0.1	0.2	1.9
Stomatopoda	67.2	79.0	65.2	253	387	323	2.1	3.0	17.5
Shrimp	31.3	21.1	22.7	42	591	41	0.1	0.8	0.4
Crab megalopae	75.0	67.4	57.6	433	317	138	*** 1.3	1.1	1.5
Phyllosomes	3.1	5.3	<u>25.8</u>	*** 2	6	<u>56</u>	** <0.1	<0.1	1.0
Mollusca	48.4	37.9	47.0	101	92	93	18.4	2.8	19.4
Octopoda	29.7	25.3	19.7	35	50	16	* 2.6	0.3	0.7
Squid	34.4	<u>19.0</u>	34.9	** 62	38	<u>60</u>	15.9	2.5	18.7
Other inverts.	28.1	28.4	43.9	52	55	66	0.2	0.2	1.1
Fishes	68.8	85.3	84.8	1,157	1,085	349	77.5	91.8	56.6
Engraulidae	4.7	9.5	1.5	* 627	188	1	* 17.5	3.7	<0.1
Carapidae	4.7	<u>5.3</u>	3.0	3	5	<u>3</u>	0.4	0.4	3.2
Holocentridae	18.8	12.6	12.1	52	40	26	5.0	2.6	8.9
Fistularidae	1.6	3.2	1.5	37	36	1	1.9	0.9	<0.1
Dactylopteridae	10.9	7.4	6.1	11	15	17	0.8	0.7	1.1
Priacanthidae	1.6	2.1	1.5	6	3	20	<0.1	<0.1	3.0
Carangidae	4.7	13.7	4.6	* 3	25	7	0.9	18.5	6.6
Mullidae	1.6	<u>4.2</u>	4.6	1	11	4	<0.1	1.1	2.5
Chaetodontidae	12.5	16.8	9.1	18	22	9	0.4	0.3	1.0
Acanthuridae	25.0	32.6	19.7	60	262	31	4.6	17.3	6.1
Scombridae	12.5	10.5	1.5	** 9	17	2	35.6	36.2	0.1
Balistidae	20.3	26.3	<u>18.2</u>	19	43	17	1.7	1.5	1.2
Monacanthidae	10.9	14.7	3.0	* 32	48	28	2.7	4.3	0.9
Ostraciidae	12.5	10.5	<u>30.3</u>	*** 10	15	43	0.3	0.2	2.2
Tetraodontidae	7.8	7.4	<u>12.1</u>	7	8	13	0.7	0.3	6.0
Diodontidae	3.1	0.0	1.5	2	0	5	0.1	0.0	4.0
	Sample size			Total number			Total weight		
	64	95	66	2,105	2,656	1,248	1,858	1,978	522

yellowfin tuna were found to be different in the diet of bank-associated yellowfin tuna (Table 2). The fish families Engraulidae, Scombridae (mackerels) and Monacanthidae (filefishes) were conspicuously rare in frequency of occurrence or number. Their combined weight was only 1% of the diet of bank-associated yellowfin tuna, but was 56% and 44% of the diets of non-FAD- and FAD-associated yellowfin tuna, respectively. Crab megalopae and octopods were eaten in significantly lower numbers per occurrence by bank-associated yellowfin tuna, but contributed similar proportions to the weight of the diets of non-FAD-, FAD- and bank-associated yellowfin tuna because bank-associated yellowfin tuna were less full. Prey that occurred more frequently in the diet of bank-associated yellowfin tuna than the diets of non-FAD- and FAD-associated yellowfin tuna were small prey, phyllosomes and ostraciids (trunkfishes), which contributed little weight to the diet.

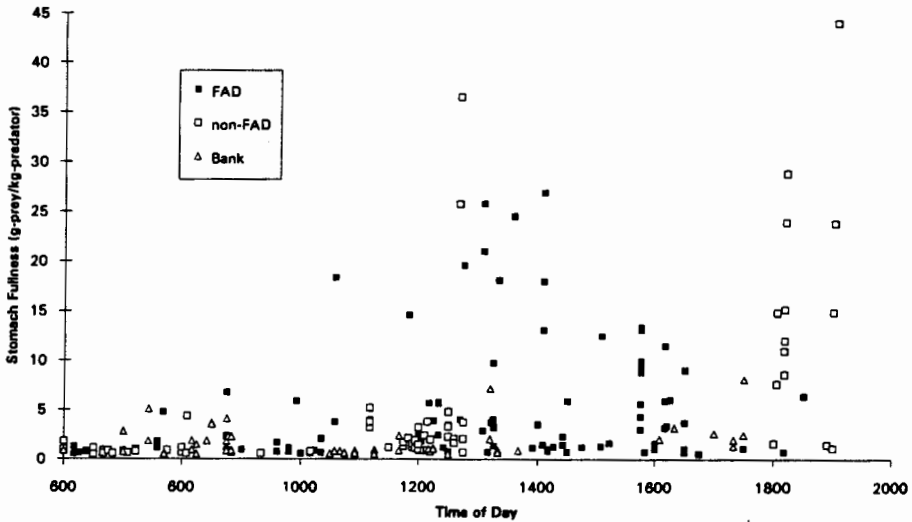


Figure 1. The stomach fullness ($\text{g}\cdot\text{kg}^{-1}$) of individual tuna plotted against their time of capture for FAD-, non-FAD- and bank-associated yellowfin tuna.

phyllosomes and ostraciids (trunkfishes), which contributed little weight to the diet.

Engraulids and carangids occurred at a significantly higher frequency in the diet of FAD-associated yellowfin tuna than in the diets of non-FAD- and bank-associated yellowfin tuna, while squid and hyperiid amphipods occurred significantly less frequently (Table 2). Differences in the number per occurrence of all prey taxa were not significant between the diets of FAD-associated and non-FAD-associated yellowfin tuna (Table 2).

Shrimp and acanthurids (surgeonfishes) were consumed in much greater numbers by FAD-associated yellowfin tuna than by non-FAD- and bank-associated yellowfin tuna, but they were not found to be significantly different in frequency of occurrence or in average number per occurrence among the three groups of yellowfin tuna (Table 2). For each prey taxon, a single instance of gorging was sampled with some of the individual prey more than half digested. The stomach of one FAD-associated yellowfin tuna contained 917 small (0.1 g) caridean shrimp. The stomach of another FAD-associated yellowfin tuna contained 325 juvenile stages of the acanthurid, *Ctenochaetus striatus*.

Diel Patterns.—In general, there was a trend of increasing stomach fullness during the daylight hours for the 65 non-FAD-, the 93 FAD- and the 58 bank-associated yellowfin tuna for which the time of capture is known, although many nearly empty stomachs were encountered throughout the day (Fig. 1). The Spearman rank correlation coefficients, evaluating the relationship between time of day and fullness of FAD-associated ($r_s = 0.232$) and non-FAD-associated ($r_s = 0.723$) yellowfin tuna, were significant ($0.05 < P < 0.02$ and $P \ll 0.001$, respectively). However, the correlation between time of day and fullness of bank-associated yellowfin tuna was not significant ($0.2 < P < 0.5$) as indicated by the Spearman rank correlation coefficient ($r_s = 0.102$).

The diel trends in the frequency of occurrence of larval stomatopods, crab megalopae, acanthurids, balistids (triggerfishes), euphausiids and squid exhibited some similarities among non-FAD-, FAD- and bank-associated yellowfin tuna,

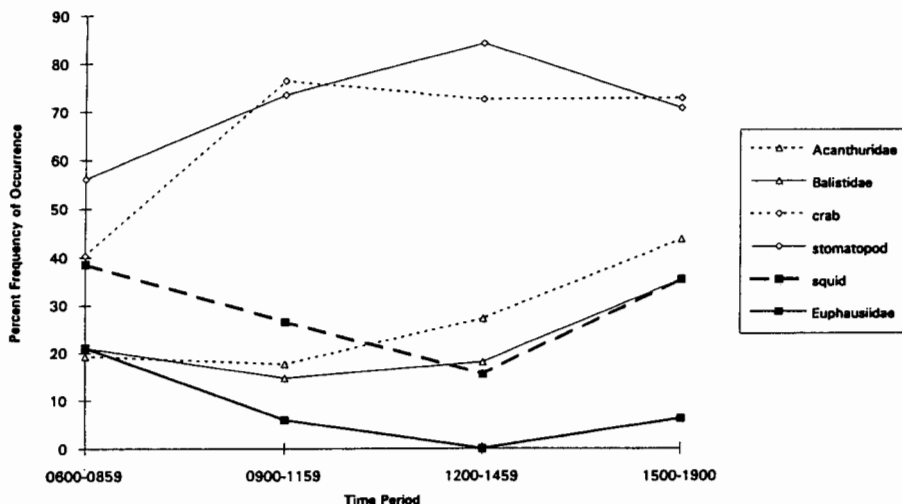


Figure 2. The frequency of occurrence of the two most frequently eaten fishes (Acanthuridae and Balistidae), the two most frequently eaten crustacea (crab megalopae and stomatopods), and two prey taxa partially composed of vertically migrating species (squid and euphausiidae) in the combined diet of FAD-, non-FAD- and bank-associated yellowfin tuna. The sample sizes corresponding to each time period are 57 (0600-0859), 34 (0900-1159), 77 (1200-1459), and 48 (1500-1900).

but some trends were erratic, probably due to small sample sizes in each time interval. The data were pooled to clarify the general diel trends in the frequency of occurrence of the prey observed among the non-FAD-, FAD- and bank-associated yellowfin tuna. Generally, there was an increase in the frequency of occurrence of larval stomatopods, crab megalopae, acanthurids and balistids from the early morning hours into the evening hours (Fig. 2). The trend in the frequency of occurrence of squid and euphausiids was a decrease from the early morning hours to a low in the afternoon hours and a return to higher levels in the evening (Fig. 2). For euphausiids, this pattern was consistent among the non-FAD-, FAD- and bank-associated yellowfin tuna, but, for squid, this pattern was clear only in the bank-associated yellowfin tuna.

DISCUSSION

The proportions of fishes, crustacea and molluscs, by weight, in the non-FAD- and bank-associated yellowfin tuna diets in American Samoa are within the range found among other studies examining yellowfin tuna of similar size and not associated with FADs in the western Pacific (Alverson, 1963), the central Pacific (Reintjes and King, 1953; Tester and Nakamura, 1957; Brock, 1985; Lehodey, 1990), the western Pacific (Borodulina, 1981; Myers, 1984) the Atlantic (Dragovich, 1970), and the Indian Ocean (Thomas, 1964). By weight or volume, fishes are 26 to 75%, crustacea are 5 to 45%, and molluscs (primarily cephalopods) are 2 to 67% of the diet of yellowfin tuna in these studies and in this one.

The difference in mean length between the bank-associated and the FAD- and non-FAD-associated yellowfin tuna is expected because bank-associated yellowfin tuna are typically larger than FAD- and log-associated yellowfin tuna (Lewis and Hampton, 1992), and the non-FAD-associated yellowfin tuna in this study include some log-associated individuals. We do not believe the difference in mean length

precludes direct comparisons among these groups of yellowfin tuna, especially in light of the extensive overlap in the length distribution among the groups.

Diet Comparisons.—The contrast in the frequency of occurrence of invertebrate prey between the diet of pre-FAD yellowfin tuna and the diets of non-FAD-, FAD- and bank-associated yellowfin tuna in this study may be an artifact of different methods of stomach content analysis. The relatively large number of fish families identified in the diet of pre-FAD yellowfin tuna indicates that careful identification methods were employed for larger prey. However, it is likely that smaller invertebrates or their remaining parts were overlooked in some of the samples. The strong similarities in the frequency of occurrence of important fish families among the diets of pre-FAD, non-FAD-, FAD-, and to a lesser extent the bank-associated yellowfin tuna, indicate that the influence of FADs on the diet of yellowfin tuna in American Samoa did not manifest itself as clearly as in the Philippines or in Hawaii.

Excluding the prey that were more than half digested from the diet comparison among non-FAD-, FAD- and bank-associated yellowfin tuna removed the influence of retained hard parts and well digested prey on the results. These prey were probably consumed a considerable time prior to the yellowfin tuna's capture and possibly a considerable distance away from the location of capture.

The lower frequency of occurrence or number per occurrence of prey taxa in the diet of bank-associated yellowfin tuna may be caused primarily by the greater distance from islands of these tuna than the FAD- and non-FAD-associated yellowfin tuna. Larval and pelagic juvenile stages of prey (crab megalopae and some octopods, scombrids and monacanthids) may be entrained in large eddies created by the islands (IATTC, 1988) and typically neritic, semipelagic prey (some scombrids) are more available nearer the islands. In addition, many pelagic juveniles and pelagic species (some monacanthids and scombrids) are known to aggregate at floating objects, whether drifting or anchored (Hunter and Mitchell, 1967, 1968; Itano and Buckley, 1987; Fedoryako, 1989), and the bank-associated yellowfin tuna do not include any individuals that were caught near floating objects.

The higher frequency of occurrence of phyllosomes and the lower number per occurrence of engraulids in the diet of bank-associated yellowfin tuna than in the diets of FAD- and non-FAD-associated yellowfin tuna may be artifacts of the data. However, it is possible that the planktonic phyllosomes are able to maintain their position at the banks and the engraulids are able to avoid the banks where predators are aggregated. While island proximity may be a factor in the availability of engraulids, they are also frequently eaten by pelagic predators at great distances from land (Hida, 1973). The higher frequency of occurrence of ostraciids in bank-associated yellowfin tuna is due in part to *Lactoria diaphana*, which is also commonly found in yellowfin tuna diets in Guam (Myers, 1984). This species is able to live an entirely pelagic existence (Myers, 1989), and perhaps preferentially aggregates, or is more vulnerable, at offshore banks than other areas. *Lactoria diaphana* is not previously recorded from Samoa (Wass, 1984).

In the diet of FAD-associated yellowfin tuna, hyperiid amphipods and squid occurred less frequently than in the diets of non-FAD- and bank-associated yellowfin tuna. If the differences are not artifacts of the data, it is possible that these prey are generally less available to yellowfin tuna associated with FADs because yellowfin tuna spend more time near the surface when at FADs than when away from FADs (Holland et al., 1990).

The higher frequency of occurrence for engraulids and carangids in the diet of FAD-associated yellowfin tuna than in the diets of non-FAD- and bank-associated

yellowfin tuna appear to be within normal limits. Engraulids have not been observed to aggregate at the FADs (Itano and Buckley, 1987), and their frequency of occurrence in the diet of FAD-associated yellowfin tuna does not exceed that found in the diet of pre-FAD yellowfin tuna. Carangids do aggregate at FADs in American Samoa (Itano and Buckley, 1987) as well as other areas (Hunter and Mitchell, 1967; Klima and Wickham, 1971; Wickham et al., 1973; Matsumoto et al., 1981; Frusher, 1986; Rountree, 1989; Fedoryako, 1989; Myers, 1989). However, carangids occurred nearly twice as frequently in the diet of yellowfin tuna caught by the DMWR (unpubl. data) prior to FAD deployment as in the diet of FAD-associated yellowfin tuna.

It is not likely that the large number of shrimp and acanthurids eaten by FAD-associated yellowfin tuna in this study represent a change in the diet caused by FADs. Similar instances of gorging on small caridean shrimp by yellowfin tuna and skipjack tuna (*Katsuwonus pelamis*) have previously been reported by Bryan (1978) about 1,000 km northwest of the Samoan Islands, near Funafuti. Also, a kawakawa (*Euthynnus affinis*), a neritic tuna, was caught "chuck full of tiny shrimp" in American Samoa (raw data from Hida, 1973) before FADs were deployed. The episode of gorging on *C. striatus* coincided with an unusually massive settlement event by the same species onto the reefs in American Samoa (DMWR, 1985).

Diel Patterns.—Yellowfin tuna with nearly empty stomachs occurred throughout the day, suggesting that yellowfin tuna are almost always in search of prey. Most stomach content analyses of yellowfin tuna yield a high percentage of empty or near empty stomachs (e.g., Reintjes and King, 1953). It is possible that the occurrence of nearly empty stomachs is exaggerated by undetected regurgitation and by gear selection of yellowfin tuna that are actively searching for food or feeding in the upper water column.

Feeding on prey available in deeper water at night has been proposed as the incentive for yellowfin tuna to leave the zone of enhanced prey they occupy during the day around islands (Holland et al., 1990). However, it does not appear that yellowfin tuna in American Samoa frequently feed at night, based on the absence of full stomachs in the early morning. Several other studies also concluded that yellowfin tuna are primarily diurnal predators based on the patterns of stomach fullness (Reintjes and King, 1953; Yamaguchi, 1969; Grudinin, 1989), the absence of deeper mesopelagic prey in the diet (King and Iversen, 1962; Talbot and Penrith, 1963; Legand et al., 1972; Perrin et al., 1973; Borodulina, 1981), the lower numbers of live yellowfin tuna on longlines retrieved at night (Watanabe, 1958; Yamaguchi, 1969), and the poor success of longlining for yellowfin tuna at night (King and Iversen, 1962; Talbot and Penrith, 1963; Legand et al., 1972; Grudinin, 1989).

Roger and Grandperrin (1976) propose that yellowfin tuna may sometimes feed on vertically migrating mesopelagic organisms during the morning and evening hours when there is sufficient light for feeding and the vertically migrating mesopelagic organisms are at vulnerable depths. The pattern in the occurrence of euphausiids and squid in the diet of yellowfin tuna in this study is consistent with this proposal, although these broad taxa are not composed exclusively of vertically migrating mesopelagic species.

Bank-associated yellowfin tuna show very little increase in fullness during the day, suggesting that the ratio of the prey biomass to the predator biomass is very low, or that the prey recruitment rate relative to the prey removal rate is very low. The continued association with offshore banks, in spite of having less food

lowfin tuna were small compared to the differences between the diets of the FAD-associated and non-FAD-associated yellowfin tuna in Hawaii.

The diurnal patterns in the diet of yellowfin tuna do not indicate different diel patterns of movement than those observed via biotelemetry in other areas. However, successful foraging by yellowfin tuna appears to take place primarily during the day, suggesting that the incentive to depart islands, banks and FADs at night is not related to nocturnal feeding. Feeding on vertically migrating prey during crepuscular periods (Roger and Grandperrin, 1976) would explain a portion of this behavior, but it does not explain the long distances, up to 45 km (Holland et al., 1990), covered each night. If yellowfin tuna are actively disassociating from shallow bathymetry at night but they are not feeding, then the motivation for this behavior is less clear. Perhaps yellowfin tuna, especially small individuals, are more vulnerable to injury or predation by nocturnal predators when in the immediate vicinity of stationary objects, such as islands, banks and FADs, at night. If so, then remaining dispersed from these fixed points of reference would reduce their chances of being located.

Regional Comparisons.—The very high proportion of fish, by weight, in the diet of FAD-associated yellowfin tuna in American Samoa is similar to that found in the Philippines (95%—Yesaki, 1983a; 96%—Barut, 1988), but unlike that found in French Polynesia (39%—Lehodey, 1990) and Hawaii (15%—Brock, 1985). Scombrids, carangids and acanthurids were the greatest contributors to the weight of fish in the diet of FAD-associated yellowfin tuna and they are highly variable as prey of yellowfin tuna. In some studies, acanthurids do not occur as prey of yellowfin tuna (Borodulina, 1981), but in others, acanthurids rank high in number, frequency of occurrence, and weight (Reintjes and King, 1953), or they are considered the single most important prey (Ronquillo, 1953). In this study, the unusual episode of gorging on *C. striatus* contributed considerably to the weight of fish in the diet of FAD-associated yellowfin tuna. Scombrids and carangids are gravimetrically important prey in many studies because of their relatively large size (Reintjes and King, 1953), but their occurrence in the diet of yellowfin tuna can vary considerably between years in the same area (Nakamura, 1936; Matthews et al., 1977). In this study, scombrids and carangids were not extremely abundant in the diet of FAD-associated yellowfin tuna. Another factor contributing to the high percentage of fish in the diet of FAD-associated yellowfin tuna is the significantly low frequency of occurrence, and hence low weight, of squid.

Considering the measures of stomach fullness and frequency of empty stomachs, more prey are available to FAD-associated than to non-FAD-associated yellowfin tuna in the Philippines (Yesaki, 1983a) and French Polynesia (Lehodey, 1990), while the converse is true in Hawaii (Brock, 1985). In American Samoa, the amount of prey available to yellowfin tuna appears to be similar for individuals in these two groups. The resulting regional differences in the availability of yellowfin tuna prey at FADs relative to non-FAD areas may depend on the sizes of the yellowfin tuna sampled, the design and location of the FADs, the regional differences in the species composition of the potential prey, and the sampling methods.

The sizes of the yellowfin tuna sampled from FADs in the Philippines and French Polynesia are considerably larger than those sampled in Hawaii and in this study. Larger yellowfin tuna can consume a wider size range of prey than smaller individuals, and depending on the strength of the currents flowing by the FAD, potential prey for the smaller yellowfin tuna may not be able to maintain their position at the FAD (Kihara, 1981; Rountree, 1989). If potential prey are

not able to aggregate at the FADs, or if the aggregated prey are depleted (Brock, 1985), then the diet of smaller FAD-associated yellowfin tuna will consist mostly of current-borne organisms eaten while the yellowfin tuna maintain their position upcurrent from the FAD (Holland et al., 1990) where they are protected from potential predators (Rountree, 1989).

The FAD design and location influence both the predator and prey aggregation rate and the prey's vulnerability to predation. Generally, there is a positive relationship between the attractiveness of a FAD and the size and complexity of its subsurface structures (Hunter and Mitchell, 1967, 1968; Klima and Wickham, 1971; Matsumoto et al., 1981; de San, 1982; Feigenbaum et al., 1989; Rountree, 1989). There is also a positive relationship between protection from predation and the size of the subsurface structures (Rountree, 1989). The location of a FAD will determine many other influential factors, including the water depth (Matsumoto et al., 1981; de San, 1982; Preston, 1982; Frusher, 1986) and the distance from the nearest island or FAD (Hilborn and Medley, 1989; Holland et al., 1990; Cayré, 1991).

The species composition of the potential prey for yellowfin tuna differs among regions, and the affinity for FADs differs among potential prey species. Therefore, the aggregation rate of potential prey to FADs can be expected to differ among regions depending on the species composition of the potential prey. In the Philippines, where very small tunas with a high affinity for FADs are plentiful, a large portion of the potential prey biomass for large yellowfin tuna is aggregated to the FADs. The potential prey for large yellowfin tuna appear to be more vulnerable to predation at the FADs than away from the FADs, and more vulnerable than before FADs were deployed (Yesaki, 1983a; Barut, 1988). In American Samoa, carangids may be analogous to very small tunas in the Philippines in the respect that their distribution as potential prey is altered by the presence of FADs, although they do not appear to be more vulnerable to predation at the FADs than before FADs were deployed.

Some of the increased vulnerability of very small tunas to predation by large yellowfin tuna when associated with the FADs in the Philippines may not be directly caused by the FADs. The size of FAD-associated tunas generally increases with depth (Kihara, 1981; Matsumoto et al., 1981; Yesaki, 1983a; Barut, 1988; Lehodey, 1990) and with horizontal distance from the FAD (Matsumoto et al., 1981). The natural stratification by size may be disrupted by the fishing method used to sample the large yellowfin tuna examined by Yesaki (1983a, 1983b) and Barut (1988), which requires large amounts of chum to pass through the water column. The stomach contents of the large FAD-associated yellowfin tuna sampled at the FADs contain, on average, 47% to 68% chum by weight (Barut, 1988; Yesaki, 1983a, 1983b; respectively). In addition, bright lights are frequently used to intensify the aggregation of tunas at FADs for several consecutive nights (Kihara, 1981; de San, 1982) before setting with a purse-seine. This practice may compress the natural size stratification and increase predation on very small tunas at night when the yellowfin and other tunas would otherwise leave (Holland et al., 1990; Cayré, 1991).

The change in the diet of yellowfin tuna observed in Hawaii that is attributed to association with FADs (Brock, 1985) may be, in part, caused by the relatively close proximity of the FADs to the island. Reid et al. (1991) show that the species of shrimp dominating the diet of FAD-associated yellowfin tuna, *Oplophorus gracilirostris*, is part of a vertically migrating "mesopelagic-boundary community" that occurs primarily within the 700 m isobath of the islands. The average anchor depth for Hawaiian FADs is 830 m (Brock, 1985) and the FAD- and island-

associated yellowfin tuna are frequently near or within the 700 m isobath (Holland et al., 1990). Few of the non-FAD-associated yellowfin tuna sampled in Hawaii were thought to be associated with the island (R. E. Brock, pers. comm.). In addition to feeding in a zone of enhanced prey density during the day (Holland et al., 1990), island-associated yellowfin tuna may feed on *O. gracilirostris* during crepuscular periods (Roger and Grandperrin, 1976) or at night (Holland et al., 1990) in Hawaii. If this is true, then the dominance of *O. gracilirostris* in the diet of FAD-associated yellowfin tuna is to be expected when other prey is depleted.

In summary, very little difference was observed among the diets of pre-FAD, non-FAD- and FAD-associated yellowfin tuna in American Samoa. However, the diet of bank-associated yellowfin tuna was somewhat different, and may be the combined result of a greater distance from islands and a lack of structure near the surface to aggregate prey. The yellowfin tuna sampled in this study did not feed much at night, but may feed on vertically migrating prey during crepuscular periods. It is likely that yellowfin tuna in American Samoa follow the pattern of diurnal association and nocturnal disassociation with FADs and islands as observed in other areas. However, if the yellowfin tuna are not feeding at night, then perhaps they are avoiding fixed points of reference such as islands and FADs, where nocturnal predators may easily find them. Differing results among studies examining the effect of FAD association on the diet of yellowfin tuna may be caused by differences in 1) the size of the yellowfin tuna examined, 2) the design and placement of the FADs, 3) the species composition of the potential prey, and 4) the sampling methods employed.

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