

INTERDECADAL CHANGE IN REEF FISH POPULATIONS AT FRENCH FRIGATE SHOALS AND MIDWAY ATOLL, NORTHWESTERN HAWAIIAN ISLANDS: STATISTICAL POWER IN RETROSPECT

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ABSTRACT

Reef fish faunas were compared between surveys conducted more than a decade apart at each of two isolated and nearly pristine oceanic atolls (French Frigate Shoals [FFS] and Midway Atoll) in the northwestern Hawaiian Islands. Species composition, assemblage structure (density rankings), and population densities were compared to test the hypothesis that reef fishes had declined during a period of lower oceanic productivity in the central North Pacific. Within each of two principal habitats (barrier and patch reefs) at each atoll, species composition and rank densities differed little between sampling periods. Densities, however, generally declined by about one-third for many numerically dominant species and for taxa pooled into functional categories (trophic levels, feeding guilds). Patterns of temporal change were partly confounded by distributional shifts between barrier and patch reef habitats at FFS, perhaps reflecting indirect effects of storm disturbance on benthic algal habitat. Such effects, together with related changes in climate and oceanic productivity on an interdecadal time scale, might have been responsible for the apparent declines in reef fish densities at both atolls. Temporal patterns were clearer at Midway Atoll, where changes in benthic algae were not evident. Our observations indicate that the statistical power necessary to detect changes in the population densities of reef fish species that exhibit large temporal fluctuations in numbers, particularly on oceanic islands, is generally low. Power to detect twofold changes may be adequate, however, if taxa are pooled into functional categories.

Patterns of temporal change in the abundance of fishes on tropical coral reefs remain poorly understood despite a multitude of studies that have addressed several indirectly related issues. To date, most evaluations of temporal and spatial variation in reef fishes have been nonparametric comparisons of rank abundance (Jones and Thompson, 1978), multivariate characterizations of composition (Bortone et al., 1986), or comparisons of sampling methods (Bortone and Kimmel, 1991). Few studies (Thresher and Gunn, 1986; Lincoln Smith et al., 1991; Green and Shenker, 1993) have attempted to estimate the statistical power necessary to detect temporal or spatial differences in density or abundance, particularly at the species level. Yet the ability to estimate population size (or an adequate index of abundance) is clearly important for studies of stock dynamics. This would seem especially applicable to the majority of species with pelagic larval dispersal, whose temporally fluctuating local populations often, but not always (Sale, 1990), reflect variable recruitment (Doherty and Williams, 1988; Sale, 1991).

Most studies of reef fish assemblage and population structure have focused on the faunas of continental reefs. Time series abundance data are conspicuously lacking for fishes at isolated oceanic islands. Because of the relative isolation of such islands and the implications of isolation for planktonic dispersal, the faunas of archipelagos such as the Hawaiian Islands may be particularly subject to recruitment limitation (Hourigan and Reese, 1987). If so, the temporal patterns of isolated island faunas may be especially dynamic (Myers and Pepin, 1994).

For the above reasons, we conducted temporal comparisons of fishes in shallow-reef habitats at two isolated oceanic atolls (French Frigate Shoals [FFS] and

Midway Atoll) in the Northwestern Hawaiian Islands (NWHI). The main objective of the study was to determine if the abundances of reef fishes at these two sites, protected from fishery exploitation and other human impacts as U.S. Fish and Wildlife Refuges, had declined between the early 1980's and 1992–1993, in concert with population declines in lobsters, sea birds, and seals (Polovina et al., 1994) that resulted from regional decreases in oceanic productivity (Polovina et al., in press). The undisturbed shallow-reef fish populations at these two isolated atolls permit straightforward assessments of natural changes in productivity that are uncomplicated by human impacts. A secondary objective was to use these data to assess the statistical power needed to detect natural temporal changes in island reef fish populations whose numbers may fluctuate widely due to episodic recruitment.

METHODS

Trained observers conducted visual underwater surveys of fish faunas from 1980 to 1983 at a series of shallow reef stations at FFS, located in the middle of the Hawaiian Archipelago (24°N, 166°W). Identical surveys were conducted in 1980 at Midway Atoll (28°N, 177°W), about 700 nmi northwest of FFS. Because surveys of fish faunas were secondary to original study objectives (Norris and Parrish, 1988; Schroeder, 1985, 1987, 1989), the temporal distribution of sampling efforts varied among stations at an atoll, and the average level of effort differed between atolls. We hereafter refer to these surveys as “baseline.” Using methods identical to those used in the baseline surveys, the first and second authors and two other trained observers resurveyed the fish faunas at FFS in July 1992 and at Midway in August 1993. We refer to these surveys as “recent” surveys.

Stations and Surveys.—FFS. Baseline surveys were conducted on three trips (May–June 1980, October–November 1980, March 1983). Nine stations were sampled 2–4 times each on at least one of the trips, for a total of 43 visual tallies. Two shallow-reef habitats were surveyed: (1) the expansive barrier reef (BR) of the atoll (inside and outside the barrier) and (2) discrete patch reefs (PR), isolated at various distances from one another within the sandy-bottom lagoon. The two habitats were sampled with slightly unequal effort (four BR stations, five PR stations). Thirty-six samples (4 samples-station⁻¹; nine stations) were chosen a priori to represent baseline conditions. All nine stations were resampled during July 1992 with equal effort (4 samples-station⁻¹; nine stations).

Stations and Surveys.—MIDWAY. A variable number of baseline samples were collected on two trips conducted during March–April and August 1980. In August, each of nine stations (four BR, five PR) was surveyed twice, for a total of 18 visual tallies over the two habitats. In August 1993, fish faunas were resurveyed at eight of these nine historical stations and at three complementary ones—two stations that were sampled during March–April 1980 and another station whose location was approximate. For each historical and complementary station, a matched “reference” station, 100 to 300 m distant, was sampled in August 1993 in order to generalize historical station observations to a larger spatial scale. Altogether, a total of 44 tallies (11 pairs of stations; 2 samples-station⁻¹) were completed in August 1993. As at FFS, inside and outside BR habitats were evaluated together because data were too few to warrant further partitioning of microhabitats.

Habitat Descriptions.—At both atolls, “outside” barrier stations were composed of dead coral pavement (“spur-and-groove” ridges and swales) and exposed to open ocean swell at 5- to 8-m depths in expansive continuous habitat (0 to >20-m deep). At FFS, outside stations had one-fourth to one-third live *Porites lobata* cover. Outside stations at Midway had a sparse cover (<1%) of live *Pocillopora meandrina*. Inside stations at FFS (2–6 m depths) occupied an expansive, semi-exposed limestone bench (one-fourth to one-half live *P. lobata* cover) near the inside lip of the northwestern barrier reef. At Midway, inside stations consisted of *Montipora* spp. corals (one-third to three-fourths live coral cover), with coral rubble and sand, in similarly expansive but less exposed areas within the lip of the northern barrier reef at 1–3 m depths. Patch reefs at both atolls consisted of mounds of dead coral rock and unconsolidated coral rubble (<1-m to 3-m relief) on sand bottoms (4–10 m depth). Live coral cover on patch reefs was generally low (<5% *Porites* spp.) at Midway, but greater (one-half to three-fourths *Porites* spp.) at FFS and varied among reefs at an atoll, as did the types and amounts of algal cover. Major habitat features such as coral and algal cover were recorded on videotape at each station.

Sampling Design.—Identical sampling designs and counting protocols, including swimming speed on transects (Lincoln Smith, 1988) were used to characterize fish faunas during baseline and recent periods. Surveys were conducted only when horizontal underwater visibility exceeded 10 m. Divers

Table 1. French Frigate Shoals and Midway Atoll. Summary comparison of observer tallies, by atoll and sampling period, based on two criteria (species richness and numerical density [$N \cdot 10 \text{ m}^{-2}$] of total fishes). Bootstrapped means of paired differences between divers ("Mn diff" as Diver 1 minus Diver 2) are noted as percentages of grand means ("Pct GM"; all data pooled) for each site and period.

		N	Mn diff	LL _{95%} CI	UL _{95%} CI	Prob [Mn diff = 0]	Pct GM
Species richness							
FFS	baseline	9	-2.28	-7.11	2.27	0.69	7
	recent	9	0.60	2.64	1.42	0.79	2
Midway	baseline	8	0.02	-2.12	2.00	0.98	<1
	recent	22	1.09	-0.36	2.77	0.56	5
Total density							
FFS	baseline	9	-2.47	-5.90	1.09	0.26	17
	recent	9	-1.00	-2.99	0.78	0.26	8
Midway	baseline	8	0.75	-1.27	2.76	0.76	4
	recent	22	-0.10	-2.30	1.85	0.97	<1

visually counted all non-cryptic fishes present on belt transects (Brock, 1954) or within otherwise delimited (see below) areas of reef during daylight (0800–1700) hours. Tallies were limited to juvenile and adult fish larger than recent recruits (J.D.P., unpubl. data). A two-diver team always conducted simultaneous fish counts at a station; a minimum of one pair of counts was completed at each station during each sampling period. At FFS, 64% and 100% of the second pair of counts were repeated on the same day for baseline and recent surveys.

Belt transects of constant dimensions (50 m \times 10 m; 500-m² area) were surveyed in expansive BR habitats. A 50-m line divided the transect area into two contiguous and parallel 250-m² strips (each 50-m long \times 5-m wide, with outer boundaries delimited by unobtrusive markers placed about 10 min prior to beginning counts). The two observers simultaneously tallied opposite strips, and each observer's total count represented a single density estimate (number of fish-500-m²).

Most PR stations (and all test PR stations) were completely censused, including the fringing sand-rock ecotone. Each observer's count represented a single density estimate (number of fish-100–200 m²). On PR station censuses (as on BR station transects), fishes were tallied by species or lowest recognizable taxon, and tallies were recorded on waterproof data forms with printed names of major taxa. Tape measurements of average reef diameter were used to estimate the area of each patch reef, assuming a circular shape (reefs were roughly circular in outline). Areas were estimated for both baseline and recent surveys, because areas of emergent, consolidated substrates vary seasonally and annually on patch reefs in sandy-bottom lagoons of atolls such as Midway (Schroeder, 1989).

Data Analyses.—Analyses were directed toward answering three major questions: (1) Did fish species composition or density rankings differ between baseline and recent surveys? (2) Was there a change in the densities of fishes, including feeding guilds, trophic levels or any common and abundant species, between the two survey periods? (3) Were test stations representative of larger-scale spatial patterns that prevailed atoll-wide?

OBSERVER COMPARABILITY. Comparabilities of observer counts were assessed for baseline and recent surveys at each atoll. Species richness (number of taxa) and density estimates for total fishes (as measures of recording and density estimation skills, respectively) were compared between observers by atoll and sampling period, using bootstrapped means of paired (between-diver) differences, matched by station (Manly, 1991).

STATION REPRESENTATIVENESS. In an analysis preliminary to our primary comparisons at Midway, the August 1993 data were evaluated for effects of major habitat type (BR, PR) and station type (historical, reference) on density. The trophic categories listed below were evaluated by parametric two-way (Model I, fixed effects) ANOVA.

ASSEMBLAGES. Assemblage structure was evaluated using the relative abundance and ubiquity of taxa. Abundance rankings were derived from the relative densities of taxa on transects. Ubiquity was gauged by the frequency occurrence of taxa on individual transects. Only the top 20 taxa within rankings were evaluated to reduce inherent bias towards concordance (similarity among rankings) when rare, invariably low-ranked taxa are included in comparisons (Ebeling et al., 1990; Grossman et al., 1990). At Midway, some species were pooled within genera to match baseline with recent survey data. Analyses of assemblages included all available data; i.e., 9 stations at FFS; at Midway: 9 stations in 1980, and 22 stations (10 BR, 12 PR) in 1993.

TEMPORAL CHANGES. Potential temporal changes in the densities of total reef fishes were evaluated

Table 2. Midway Atoll. Summary results of 2-way fixed (Model I) ANOVAs evaluating the effects of habitat type (BR = barrier reef, PR = patch reef) and station type (Test, Ref = Reference) on density ($N \cdot 10 \text{ m}^{-2}$) for trophic groups of reef fishes observed on the August 1993 survey. Degrees of freedom for all F-ratio tests of main effects were 1,41. Habitat-by-station type interaction terms were insignificant in all cases ($P = 0.25\text{--}0.75$).^a

	Habitat type				Station type			
	F-ratio	Prob > F	$N \cdot 10 \text{ m}^{-2}$		F-ratio	Prob > F	$N \cdot 10 \text{ m}^{-2}$	
			BR	PR			Test	Ref
Total fishes	45.05	<0.001	8.0	17.3	0.14	0.71	12.0	12.5
Herbivores	9.52	<0.01	3.5	5.3	0.03	0.87	4.4	4.4
Secondary consumers	51.17	<0.001	4.3	11.6	0.15	0.70	7.2	7.6
Benthic carnivores	6.78	0.013	3.5	5.4	0.32	0.57	4.7	4.3
Planktivores	47.47	<0.001	0.1	4.1	0.33	0.57	0.7	0.9
Corallivores	7.93	<0.01	0.08	0.02	3.16	0.08	0.06	0.02
Piscivores	11.77	0.001	0.02	0.09	6.51	0.015	0.02	0.08

^a Significance levels ($\alpha_{2,cm} \leq 0.10$) were adjusted for multiple comparisons as follows: trophic levels ($\alpha_{2,cm} \leq 0.10/2 \leq 0.05$); carnivore guilds ($\alpha_{2,cm} \leq 0.10/4 \leq 0.025$).

across both major habitat types. We further explored whether temporal changes were detectable for either of the two major trophic levels ("primary consumers" or herbivores, "secondary consumers" or carnivores) that comprise total fishes, and for each of four foraging guilds included within the carnivore level (benthic invertebrate-feeders, hereafter referred to as "benthic carnivores"; "planktivores"; "corallivores"; and "piscivores"). Taxa were classified into trophic levels and foraging guilds according to Hobson (1974), Randall (1985), and Norris and Parrish (1988). Fishes with mixed diets were assigned to a single trophic level and guild corresponding to the type of food that dominated the diet. Analyses emphasized pooled categories because of likely poor statistical resolution at the species level (see Results).

Temporal density patterns were evaluated separately for FFS and Midway because the distributions and levels of sampling effort were unequal at the two atolls. A matched-pairs design was used for primary analysis, with the data matched by sampling station and paired by sampling period. Our primary test variable was the baseline minus recent period difference or "delta" in density. Within-day repeat counts did not represent true temporal replicates for tests of between-period differences. The means of a constant number of repeat counts (four at FFS; two at Midway) were used to represent the respective period-station estimates. Sample sizes thus reflected the number of test stations sampled (FFS: either four BR or five PR, or nine total; Midway: four BR plus four PR = eight total).

Because these period-station data were too few ($N = 4\text{--}9$) to evaluate normality meaningfully, deltas were bootstrapped to generate nonparametric probabilities in tests of the null hypothesis, H_0 : delta-bar (mean) = 0. Bootstraps were computed using a Microsoft Quick Basic 4.5 program written by D. Kobayashi (NMFIS, Honolulu Laboratory).

For the two-way ANOVAs, in which repeat counts were representative of short-term temporal and sampling variability, log-transformed counts sufficiently satisfied the additivity assumption and approximated normality adequately to permit parametric tests. ANOVAs were computed using PC SAS 6.03 (SAS Institute, 1988).

Two-tailed probabilities (α_2) were used except when a one-tailed test (α_1) of a specific prediction was more appropriate. Type I error was relaxed to 0.10 to increase statistical power (Cohen, 1988). Bonferroni's correction (Manly, 1991: 52) was used to adjust probability values for m multiple comparisons ($\alpha_{cm} \leq \alpha_{0.10}/m$) as necessary. Overall patterns of change at both atolls were evaluated by combining the probabilities associated with independent test results for each site (Sokal and Rohlf, 1981: 779).

Statistical power was estimated for density comparisons between periods using major taxa and functional groupings. Sample sizes required for detecting changes of defined magnitude also were estimated. Estimates were approximated for t -tests of normally distributed log-transformed data (Cohen, 1988).

RESULTS

Observer Comparability.—Species richness was indistinguishable between observers within baseline and recent dive teams at either site, differing at most by 7% between observers (Table 1). Estimated densities of total fishes likewise varied little (<10% on average between divers within teams; Table 1).

Table 3. French Frigate Shoals. Mean numerical densities ($N \cdot 10 \text{ m}^{-2}$) of major fish taxa on baseline (1980-83) and recent (July 1992) surveys. The top 30 taxa are ranked in descending order of their weighted grand means within each sampling period for both habitat types pooled. Trophic guild acronyms are: bc = benthic carnivores; h = herbivores; c = corallivores; zp = planktivores; pi = piscivores. A dashed horizontal line separates the top 30 baseline taxa from lower-ranked taxa that ranked within the top 30 on the recent survey.

Taxon	Baseline			Recent			
	Rank _b	D _{br}	D _{pr}	Rank _r	D _{br}	D _{pr}	D _{wh}
<i>Thalassoma duperrey</i> (bc)	1	2.11	1.87	1	1.98	1.72	1.35
Scaridae (h)	2	0.82	2.17	2	1.57	2.18	1.32
<i>Chromis ovalis</i> (zp)	3	0.36	2.12	22	1.33	0.17	0.11
<i>Mulloidichthys vanicolensis</i> (bc)	4	0.48	1.93	13	1.29	0.45	0.22
<i>Ctenochaetus strigosus</i> (h)	5	1.16	1.06	3	1.10	1.82	1.16
<i>Dascyllus albisella</i> (zp)	6	0.24	1.47	4	0.92	2.02	1.15
<i>Stegastes fasciatus</i> (h)	7	0.25	1.22	5	0.79	1.72	1.05
<i>Chaetodon miliaris</i> (zp)	8	0.20	0.86	6	0.56	1.74	0.98
<i>Priacanthus</i> spp. (zp)	9	0.02	0.85	78	0.48	abs	<0.01
<i>Neoniphon samarra</i> (bc)	10	0.04	0.52	10	0.31	0.59	0.30
<i>Stethojulis balteata</i> (bc)	11	0.15	0.40	17	0.29	0.25	0.16
<i>Acanthurus triostegus</i> (h)	12	0.13	0.39	8	0.28	0.75	0.56
<i>Centropyge potteri</i> (h)	13	0.17	0.35	12	0.27	0.36	0.23
<i>Labroides phthirophagus</i> (bc)	14	0.04	0.35	16	0.21	0.35	0.20
<i>Canthigaster jactator</i> (bc)	15	0.12	0.26	14	0.20	0.30	0.22
<i>Acanthurus</i> spp. ^a (h)	16	0.37	0.06	15	>0.19	0.09	0.21
<i>Chromis hanui</i> (zp)	17	0.27	0.12	20	0.19	0.21	0.15
<i>Chromis vanderbilti</i> (zp)	18	0.32	abs	7	0.16	abs	0.63
<i>Pervagor spilosoma</i> (c)	19	0.01	0.26	71	0.15	abs	<0.01
<i>Macropharyngodon geoffroy</i> (bc)	20	0.02	0.20	31	0.12	0.06	0.04
<i>Apogon</i> spp. (zp)	21	<0.01	0.29	abs	0.11	abs	n/a
<i>Chaetodon multilineatus</i> (c)	22	0.12	0.08	30	>0.10	0.05	0.04
<i>Naso unicornis</i> (h)	23	0.10	0.09	32	>0.09	0.06	<0.04
<i>Chaetodon fremblii</i> (bc)	24	0.10	0.09	24	>0.09	0.12	0.09
<i>Cheilinus unifasciatus</i> (pi)	25	0.04	0.13	25	<0.09	0.17	0.09
<i>Mulloidichthys flavolineatus</i> (bc)	26	0.18	0.02	9	<0.09	0.84	0.42
<i>Parupeneus multifasciatus</i> (bc)	27	0.04	0.12	19	<0.09	0.23	0.15
<i>Bodianus bilunulatus</i> (zp)	28	0.06	0.10	21	0.08	0.15	0.11
<i>Thalassoma ballieui</i> (bc)	29	0.14	0.04	18	0.08	0.18	0.15
<i>Plectroglyphidodon johnstonianus</i> (c)	30	0.12	0.03	28	0.07	0.06	0.04

Table 3. Continued.

Taxon	Baseline				Recent			
	Rank _b	D _{BR}	D _{PK}	D _{both}	Rank _c	D _{BR}	D _{PK}	D _{both}
Synodontidae (pi)	32	>0.01	0.11	0.06	26	<0.01	0.12	0.07
<i>Gomphosus varius</i> (bc)	34	0.05	0.05	0.05	23	<0.01	0.15	0.09
<i>Epibulus insidiator</i> (pi)	39	0.03	0.03	0.03	29	<0.01	0.07	0.04
<i>Zebrasoma flavescens</i> (h)	40	0.02	0.04	0.03	11	abs	0.45	0.26
<i>Parupeneus pleurostigma</i> (bc)	41	<0.01	0.05	0.03	27	<0.01	0.11	0.06
Top 30 taxa		7.9	17.3	13.2		4.3	16.4	11.0
Total fishes		9.1	18.5	14.3		4.7	18.1	12.1

**Acanthurus nigroris*, *A. nigrofasciatus*, *A. blochii*, *A. dussumieri*, and *A. olivaceus*.

Table 4. Midway Atoll. Mean numerical densities ($N \cdot 10 \text{ m}^{-2}$) of major fish taxa on August surveys in 1980 (baseline) and 1993 (recent). The top 30 taxa are ranked in descending order of their weighted grand means within each sampling period for both habitat types pooled. For trophic guild acronyms see Table 3 caption. A dashed horizontal line separates the top 30 baseline taxa from lower-ranked taxa that ranked within the top 30 on the recent survey.

Taxon	Baseline			Recent		
	Rank _b	D_{PR}	D_{sub}	Rank _r	D_{PR}	D_{sub}
<i>Siegestes fasciatus</i> (h)	1	2.30	3.02	1	2.41	3.09
<i>Dascyllus albisella</i> (zp)	2	0.01	2.51	4	abs	2.10
<i>Thalassoma duperrey</i> (bc)	3	2.33	2.44	2	2.33	2.04
<i>Chromis ovalis</i> (zp)	4	0.72	1.41	11	0.21	0.46
<i>Stethojulis balteata</i> (bc)	5	0.70	0.68	8	0.36	0.41
<i>Chromis hanui</i> (zp)	6	0.45	0.57	46	0.02	0.02
<i>Chaetodon miliaris</i> (zp)	7	0.12	0.55	12	<0.01	0.55
<i>Apogon</i> spp. (zp)	8	abs	0.45	3	<0.01	2.81
<i>Acanthurus triostegus</i> (h)	9	0.80	0.45	16	0.23	0.13
<i>Cirrhipetes</i> spp. (h)	10	0.77	0.44	40	0.05	abs
<i>Thalassoma ballieui</i> (bc)	11	0.55	0.26	7	0.40	0.47
<i>Ctenochaetus strigosus</i> (h)	12	0.16	0.42	21	0.11	0.12
<i>Labroides phillipphagus</i> (bc)	13	0.12	0.36	19	0.04	0.24
juvenile Scaridae (h)	14	0.33	0.29	5	0.05	1.83
<i>Kyphosus</i> sp. (h)	15	0.44	0.28	14	0.42	0.02
<i>Calotomus</i> spp. (h)	16	abs	0.28	15	<0.01	0.35
<i>Aulostomus chinensis</i> (pi)	17	<0.01	0.39	45	abs	0.04
<i>Paracirrhites forsteri</i> (bc)	18	0.02	0.17	23	0.01	0.14
<i>Bodianus bilunulatus</i> (pi)	19	0.04	0.17	22	0.08	0.14
<i>Abudefduf abdominalis</i> (zp)	20	0.24	0.15	10	0.29	0.47
<i>Scarus perspicillatus</i> (h)	21	0.15	0.14	28	0.11	0.02
<i>Chaetodon fremblii</i> (bc)	22	0.06	0.14	18	0.02	0.26
<i>Dendrochirus barberi</i> (pi)	23	abs	0.14	42	abs	0.05
<i>Cirrhitops fasciatus</i> (bc)	24	0.04	0.22	35	0.02	0.04
<i>Scorpaena</i> spp. ^a (pi)	25	abs	0.12	64	abs	<0.01
<i>Neoniphon sammara</i> (bc)	26	<0.01	0.11	43	<0.01	0.03
<i>Coris venusta</i> (bc)	27	0.07	0.11	9	0.07	0.66
<i>Acanthurus nigroris</i> (h)	28	0.21	0.10	20	0.22	0.05
<i>Gomphosus varius</i> (bc)	29	0.16	0.10	51	0.03	abs
<i>Acanthurus olivaceus</i> (h)	30	0.20	0.10	—	abs	abs
<hr style="border-top: 1px dashed black;"/>						
<i>Parupeneus pleurostigma</i> (bc)	59	0.01	<0.03	6	<0.01	0.86
		0.04				0.47

Table 4. Continued.

Taxon	Baseline			Recent		
	Rank _b	D _{PR}	D _{PR}	Rank _b	D _{PR}	D _{PR}
<i>Anampses cuvier</i> (bc)	50	0.03	0.05	13	0.09	0.37
<i>Cheilinus bimaculatus</i> (pi)	88	abs	<0.01	17	abs	0.32
<i>Plectroglyphidodon johnstonianus</i> (c)	38	0.04	0.12	24	0.12	0.05
Synodontidae (pi)	35	0.02	0.18	25	<0.01	0.13
<i>Canthigaster jactator</i> (bc)	33	0.03	0.17	26	<0.02	0.11
<i>Acanthurus leucopareus</i> (h)	61	0.05	abs	27	0.14	abs
<i>Acanthurus nigrofascus</i> (h)	abs	>0.00	abs	29	abs	0.12
<i>Parupeneus porphyreus</i> (bc)	66	<0.01	0.04	30	<0.01	0.09
Top 30 taxa		11.0	22.9		7.8	18.5
Total fishes		12.8	25.8		9.0	19.2
						13.4
						14.3

* *Scorpaena* spp. data on August 1980 survey matched with *Scorpaena contorta* data on August 1993 survey.

Spatial Comparisons at Midway.—For stations sampled on the August 1993 survey, the densities of all higher-level trophic groups clearly differed between habitat types (PR > BR; Table 2). However, the densities of all groups except piscivores were indistinguishable between historical and reference stations (Table 2), as were most of the major individual taxa comprising these groups, suggesting that historical stations were representative of larger scale patterns.

Species Presence-Absence.—FFS. Approximately 96 and 87 reef fish species were recorded on baseline and recent surveys. Of these, 11 conspicuous and easily recognizable species were seen during the baseline period but not during the recent survey (P → A; where "P" = present and "A" = absent), compared to seven species recorded in July 1992 but not seen in 1980–1983 (A → P; binomial test, accept H_0 : P → A = A → P; $P = 0.24$; Siegel and Castellan, 1988). About 80 species were observed during both of the periods.

Species Presence-Absence.—MIDWAY. Baseline and recent surveys each recorded 91 species. Nine conspicuous species were seen on the August 1980 survey but not in August 1993, compared to 11 species recorded in 1993 but not seen in 1980 (binomial test, accept H_0 : P → A = A → P; $P = 0.41$). About 77 species (85% of total) were observed on both surveys.

Assemblage Structure.—FFS. The abundance (density) rankings of major fishes at FFS during baseline and recent surveys are represented by the 30 most numerous fishes in 1980–1983, with analogous rankings for July 1992 (Table 3). Rankings are based on grand mean densities, using all within-period data for both habitat types (rankings within each major habitat type are also provided). For the 20 most numerous taxa, ranks of densities were similar between the two sampling periods and both major habitats (Kendall's $W = +0.53$, $P = 0.001$ [one-tailed]; Siegel and Castellan 1988). Density ranks (Rank_b and Rank_r, Table 3), pooled over habitat types, were correlated between sampling periods (Spearman's $r_s = +0.45$, $0.05 > P > 0.01$). Between-period correlations by habitat type were significant for patch ($r_s = +0.54$, $P < 0.01$) and barrier reefs ($r_s = +0.41$, $0.05 > P > 0.025$). Rankings were correlated between the two habitat types during baseline surveys ($r_s = +0.81$, $P < 0.001$), but less so during the recent period ($r_s = +0.34$, $0.10 > P > 0.05$; Table 3). Patterns in rank frequency of occurrence generally resembled those of density rankings; most abundant taxa were widespread and ubiquitous (patchily distributed, daytime resting schools of species like *Mulloidichthys* spp. were conspicuous exceptions).

Assemblage Structure.—MIDWAY. For the top 20 most numerous fish taxa at Midway, ranks of densities were similar between the two sampling periods and both major habitats (Kendall's $W = +0.44$, $k = 4$, $0.025 > P > 0.01$; Table 4). Density ranks (Rank_b and Rank_r, Table 4), pooled over habitat types, were correlated between sampling periods ($r_s = +0.63$, $P < 0.01$). Ranks of densities within habitat type also were correlated between sampling periods (BR: $r_s = +0.80$, $P < 0.01$, PR: $r_s = +0.64$, $P < 0.01$). Midway rankings diverged more between the two habitat types than at FFS, both in August 1980 ($r_s < 0.01$, $P > 0.45$) and in August 1993 ($r_s = +0.14$, $P > 0.30$; Table 4).

Habitat Effects.—Spatial differences in fish assemblage structure were evident between barrier and patch reefs at each atoll, and the general persistence of these spatial differences across surveys is apparent. For example, the damselfish *Dascyllus albisella* was consistently abundant on patch reefs but rare to absent on barrier reefs, both at FFS and at Midway (Tables 3, 4). The absence of time-by-

Table 5. French Frigate Shoals and Midway Atoll. Summary of nominal changes in density within the top 30 taxa of reef fishes, grouped by major trophic level and carnivore feeding guild. Parentheses indicate the numbers of individual taxa, included in the level or guild, whose density changed significantly^a between baseline and recent periods. Also noted are results for binomial tests of the relative number of nominal increases and decreases.

	French Frigate Shoals		Midway Atoll	
	Increase	Decrease	Increase	Decrease
Herbivores	3	3	2	8 (1)
Secondary consumers	7	17	5	15
Benthic carnivores	6	8 (2)	3	9 (4)
Planktivores	1	6 (3)	2	5 (3)
Corallivores	0	2 (1)	0	0
Piscivores	0	1	0	1
Total fishes	10	20	7	23
	H ₀ : # decreases = # increases			
	H _{a1} : # decreases > # increases			
	20/30 decreases		23/30 decreases	
	P = 0.05		P = 0.003	

^a Mean density differences (bootstrapped delta-bars) changed for 6/30 taxa at FFS (significance evaluated at $\alpha_{2,0.10} \leq 0.10/30 \leq 0.0033$). At Midway Atoll, 8/30 taxa changed based on alpha levels similarly adjusted for multiple comparisons.

habitat interactions, illustrated by the persistence of habitat-specific assemblages, in fact simplifies evaluation of temporal patterns. A detailed examination of species-habitat associations, presently recognized as generally important for coral reef fishes (McGehee, 1994 and references therein), is beyond the scope of this paper.

Temporal Density Comparisons.—FFS. Evaluation of temporal changes in density for specific taxa was limited to the 30 most numerous taxa, accounting for 90–96% of the total fishes present on transects, and focused on the top 10 within one or both habitats during either sampling period (Table 3). Most of the changes in densities between baseline and recent periods were decreases, with several notable exceptions among the herbivores (Table 3). Taxa with the greatest apparent declines between 1980–1983 and 1992 included several planktivores: bigeyes, *Priacanthus* spp. (a 50-fold or 50× decline) and the damselfish, *Chromis ovalis* (12×). Temporal changes were significant (at $\alpha_{2,0.10}/30 \leq 0.0033$) for only 6 of the top 30 taxa (Table 5); declines in these 6 taxa ranged from about 50% to >99% (Table 3).

A stronger pattern emerges if only directional (plus or minus) changes in taxa are evaluated: decreases significantly outnumbered increases (Table 5). In general, however, species-level data had low statistical power (see Discussion for “Power of Temporal Comparisons”).

Temporal patterns further emerge if taxa are pooled into functional categories. Atoll-wide density changes were detectable for one trophic level and some carnivore guilds (a 27% decrease in total carnivores; Table 6; Fig. 1). A similar, apparent decrease in benthic carnivores was not significant (Table 6). A 70% decrease in corallivores was significant (Table 6). The carnivore declines were general—47% on the barrier reef and 20% on patch reefs.

Herbivore numbers show a trivial net change if data for both habitats are pooled (Table 6; Fig. 1). Pooling, however, obscures a 38% increase on patch reefs, complemented by a 50% decrease on the barrier reef. Herbivore changes primarily reflected those of surgeonfishes (Acanthuridae; Table 6), the browser guild (Jones, 1968) and yellow tang (*Zebrasoma flavescens*) in particular. The latter species increased on patch reefs by >1,000% (Fig. 2).

The overall trophic representation of fishes differed between the two periods.

Table 6. French Frigate Shoals. Summary comparisons between baseline and recent densities (N-10 m⁻²), by habitat and across both major habitats, for major functional groupings of fishes. All tests were evaluated at $\alpha_{crit} \leq \alpha_{2,0.10}/m$, with $m = 2$ for parrotfish and surgeonfish included within herbivores; other m 's defined in Table 2 footnote. Standard errors are listed in parentheses for baseline means. Sample sizes are 4, 5 and 9 for BR, PR, and both habitats, respectively. (* indicates significance at $\leq \alpha_{2,0.10}/m$)

Trophic level/guild	Reef type	Baseline mean	% Total fishes	Change (%)	Prob[change] = 0
Total fishes	BR	9.1 (0.6)	100	-48	0.02 ns
	PR	18.5 (2.2)	100	-3	0.81
	both	14.3 (2.0)	100	-16	0.14
Herbivores	BR	3.2 (0.7)	35	-50	<0.001*
	PR	5.4 (0.5)	29	+38	<0.001*
	both	4.4 (0.6)	31	+10	—
Parrotfish	BR	0.8 (0.5)	9	-71	<0.001*
	PR	2.2 (0.3)	12	+<1	0.94
	both	1.6 (0.4)	11	-16	—
Surgeonfish	BR	1.8 (0.3)	20	-42	<0.001*
	PR	1.7 (0.2)	9	+92	<0.001*
	both	1.7 (0.2)	12	+29	—
Secondary consumers	BR	5.9 (0.9)	65	-47	0.006*
	PR	13.1 (2.0)	71	-20	0.15
	both	9.9 (1.7)	69	-27	0.022*
Benthic carnivores	BR	4.0 (0.4)	44	-60	<0.001*
	PR	6.8 (1.1)	37	-12	0.47
	both	5.6 (0.8)	39	-27	0.034 ns
Planktivores	BR	1.5 (0.7)	16	-3	0.78
	PR	5.7 (1.6)	31	-28	0.21
	both	3.8 (1.1)	27	-23	0.29
Corallivores	BR	0.29 (.15)	3	-76	<0.001*
	PR	0.40 (.06)	2	-66	<0.001*
	both	0.35 (.07)	2	-70	<0.001*
Piscivores	BR	0.10 (.07)	1	-92	<0.001*
	PR	0.18 (.07)	1	+8	0.75
	both	0.14 (.04)	1	-24	0.39

Herbivores contributed one-third, and carnivores about two-thirds, to total fish density in the two habitats during the baseline period. Estimates for recent surveys, however, were about one-tenth greater and one-fourth less for herbivores and carnivores.

Temporal Density Comparisons.—MIDWAY. Most apparent changes in the density of specific taxa between baseline and recent periods were declines (Table 4). Taxa with the greatest apparent declines between 1980 and 1993 included one benthic carnivore, the patch-reef squirrelfish *Neoniphon sammara* (8×) and several planktivores: the damselfish *Dascyllus albisella* (>2×) on patch reefs, *Chromis ovalis* in both habitats (4×), the barrier-reef damselfish *C. hanui* (30×), and the patch-reef butterflyfish *Chaetodon miliaris* (2×).

Counter to the major trend of lower numbers in 1993 (and unlike FFS), a few increases were apparent at Midway (Table 4). Foremost among these were two species on patch reefs: the goatfish *Parupeneus pleurostigma* (20×) and the labrid *Cheilinus bimaculatus* (30×), as well as two labrids that occurred in both habitats but increased more dramatically on patch reefs, *Coris venusta* (4×) and *Anampses cuvier* (6×).

Temporal changes were significant (at $\alpha_{2,0.10}/30 \leq 0.0033$), however, for only 8

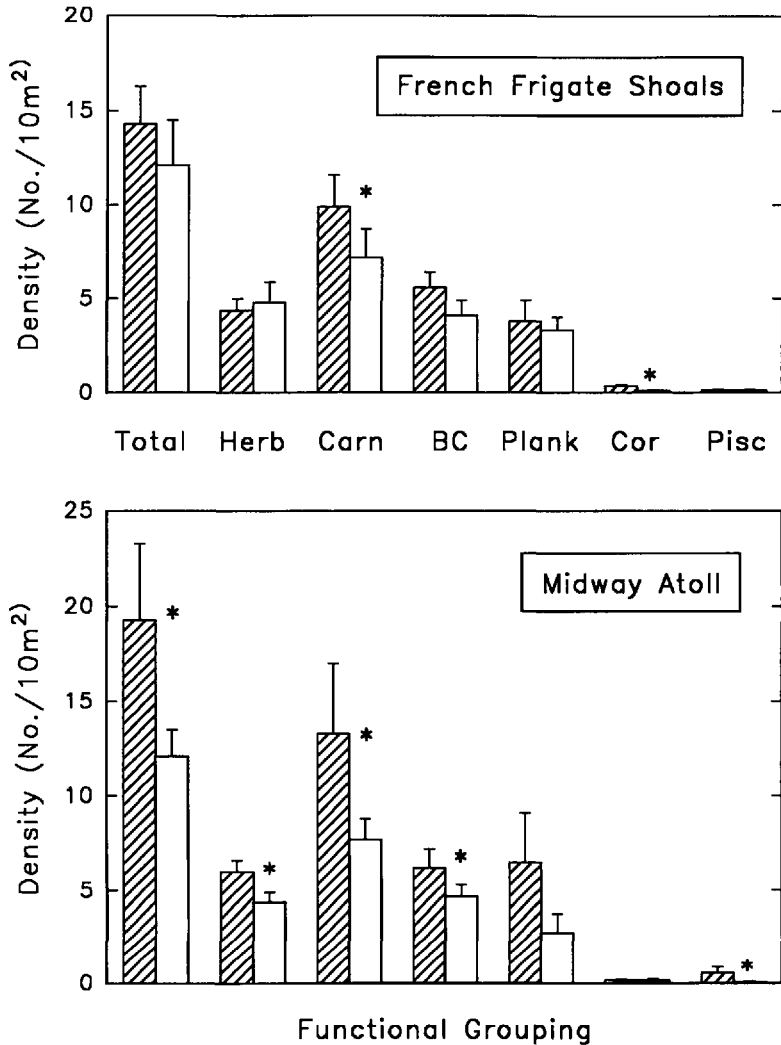


Figure 1. French Frigate Shoals (top) and Midway Atoll (bottom). Numerical densities ($N \cdot 10 \text{ m}^{-2}$) for total fishes, herbivores, all carnivores, benthic carnivores, planktivores, corallivores, and piscivores, during the respective baseline (cross-hatched) and recent (hollow) periods at each site. Estimates are unweighted grand means of the two major habitat types. Approximate standard errors are noted. (* indicates a significant baseline-recent difference [see Tables 6, 7].)

of the top 30 taxa (Table 5). Changes at historical stations ranged from a 97% decrease in *Chromis hanui* to a 20-fold increase in *Parupeneus pleurostigma* (both $P < 0.001$). A stronger pattern emerged if the direction of apparent change was evaluated for the top 30 taxa: nominal decreases outnumbered increases (Table 5). In general, species-level data provided poor resolution at Midway (as at FFS) because of large among-station variability in paired period differences.

Stronger temporal patterns again emerged when carnivore taxa were evaluated as functional categories. Density changes were detectable (within habitats) for most carnivore guilds. Benthic carnivores pooled across both habitats declined 24% (Table 7). Evidence for an apparent 57% decrease in pooled planktivores,

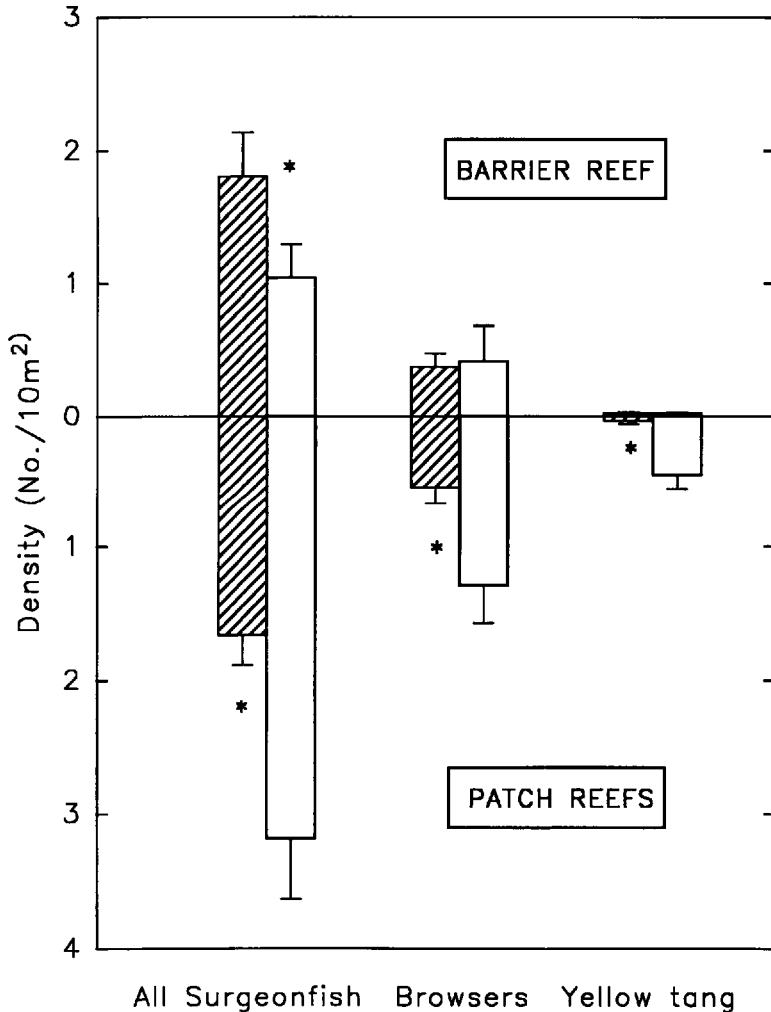


Figure 2. French Frigate Shoals. Estimated mean numerical densities ($N=10\text{ m}^{-2}$) on the barrier reef (above horizontal line) and on patch reefs (below horizontal line) for all surgeonfishes (Acanthuridae), the browsing surgeonfish guild (Jones, 1968), and the yellow tang *Zebrasoma flavescens* during baseline (cross-hatched) and recent (hollow) periods. Approximate standard errors are noted. (* as in Fig. 1.)

however, was weak ($P = 0.10$). An even larger (88%) decrease in pooled piscivore density was highly significant. Among carnivores, only corallivores clearly showed no evidence of temporal decline (Table 7).

Temporal declines became even more apparent when trophic levels were examined. Herbivores and carnivores exhibited 27% and 42% declines (Table 7). Herbivores contributed about one-third and carnivores about two-thirds to total fish counts (both habitats pooled) during August surveys in 1980 and 1993 (Table 7). Overall, the density of total fishes at Midway declined by about one-third across both major habitats (Table 7).

Spatially, the observed declines were extensive for both trophic levels and component carnivore guilds at Midway (Table 7). Herbivores declined an estimated 36% on the barrier reef and 18% on patch reefs. Analogous declines in

Table 7. Midway Atoll. Summary comparisons between baseline and recent densities ($N \cdot 10 \text{ m}^{-2}$), by habitat and across both major habitats, for major functional groupings of fishes. Sample sizes are 4, 4 and 8 for BR, PR, and both habitats, respectively. Other details are noted in Table 6 caption.

Trophic level/guild	Reef type	Baseline mean	% Total fishes	Change (%)	Prob[change] = 0
Total fishes	BR	12.8 (1.9)	100	-30	—
	PR	25.8 (6.6)	100	-41	—
	both	19.3 (4.0)	100	-37	0.006*
Herbivores	BR	6.0 (0.9)	47	-36	—
	PR	5.9 (1.1)	23	-18	—
	both	6.0 (0.6)	31	-27	0.006*
Secondary consumers	BR	6.8 (1.5)	53	-24	—
	PR	19.9 (5.8)	77	-48	—
	both	13.3 (3.7)	69	-42	0.036*
Benthic carnivores	BR	4.8 (0.4)	38	-15	—
	PR	7.6 (1.8)	29	-30	—
	both	6.2 (1.0)	32	-24	0.002*
Planktivores	BR	1.9 (1.2)	15	-57	—
	PR	11.0 (3.9)	43	-57	—
	both	6.5 (2.6)	34	-57	0.10 ns
Corallivores	BR	0.14 (.06)	1	+113	0.004*
	PR	0.17 (.10)	<1	-72	0.37
	both	0.15 (.06)	<1	+9	0.76
Piscivores	BR	0.05 (.02)	<1	-94	0.004*
	PR	1.01 (.57)	4	-88	<0.001*
	both	0.52 (.32)	<3	-88	0.002*

carnivores were 24% at barrier-reef and 48% at patch-reef stations. Declines in carnivore guilds (excluding the extremely variable corallivores) differed little (0–15%) between the two habitat types (Table 7).

In summary, the overall decreases in fish density we observed at Midway between the August 1980 and 1993 surveys included herbivores and carnivores, occurred in both major reef habitats, and constituted nominal decreases for numerous specific taxa (Tables 5, 7).

Temporal Density Comparisons.—BOTH ATOLLS. If independent test probabilities are combined (Sokal and Rohlf, 1981), density declines were significant across both reef habitats at both atolls for total fishes ($P < 0.01$) and pooled carnivores ($P < 0.01$), the latter including benthic carnivores ($P < 0.005$) and piscivores ($P < 0.01$) (Tables 6, 7).

DISCUSSION

Observer Comparability.—The magnitude of variability in fish counts (consistently <10%) among observers was clearly minor compared to levels of natural temporal change (about 30–40%). Although the subjective counts of observers did not compromise the findings of our studies, the potential for such effects should be examined on a case-by-case basis. A better solution, where feasible, is to avoid the problem altogether by using the same personnel (retrained at intervals, as necessary; Bortone and Kimmel, 1991) for the duration of study. Visual count data are inherently imprecise (Sale and Sharp, 1983), and rigorous application of census methods is necessary even if consistent personnel are used.

Historical Stations as Representative.—Densities of most higher level taxa were indistinguishable between historical and reference stations at Midway in August 1993, despite statistical resolution sufficient to detect two- to three-fold differences in abundance between habitat types for all seven higher functional groups. One factor that probably contributed to the equivalent fish densities at historical and reference patch reefs was the similarity in areas of these two types of stations (historical: mean = 116 m², CV = 43%; reference: mean = 112 m², CV = 57%). We conclude that test stations were generally representative of their respective major habitat type at Midway Atoll, and (by inference) at FFS.

Temporal Changes in Reef Areas.—It is possible that our temporal comparisons of fish densities on patch reefs would have been compromised if the sizes of the reefs differed systematically between baseline and recent surveys. Bias could result from the strong inverse relation between reef size and fish density on reefs (Schroeder, 1989), reflecting ecotone (perimeter-to-area) and areal dilution effects (Ambrose and Swarbrick, 1989; DeMartini et al., 1989). Temporal fluctuations in the size of an individual patch reef (Schroeder, 1989) in fact might result in greater differences in fish densities over time at one reef, than at different reefs estimated concurrently. For example, fish densities could have been underestimated at Midway in 1993 if reef areas then had been generally larger than in 1980 because the 1993 survey occurred by chance at a time of lesser sand burial. That both surveys were conducted in August makes seasonal effects less likely, at least at Midway. However, interannual differences in sand inundation have been observed for patch reefs in Welles Harbor at Midway (Schroeder, 1989). We evaluated whether areal changes might have confounded our analyses, using a simple bootstrap comparison of areas of the four test PR stations, measured in 1980 and again in 1993. The results suggested no pattern ($\Delta\bar{x} = +37$ m², accept H_0 ; $\Delta\bar{x} = 0$, $P = 0.30$).

Presence-Absence and Relative Abundance.—Species richness of the fish assemblages was similar for baseline and recent surveys at each atoll. Similar species richness undoubtedly reflects the equal efforts (areas searched) on both surveys. Equivalent richness for the baseline and recent surveys at Midway likely represent a balance between the more than twofold (22/9) number of 1993 stations and the finer taxonomic resolution with which certain taxa such as labrids were recorded on the 1980 survey.

In general at both FFS and Midway, greater similarity was observed over time within habitat type, compared to persistent differences in both the composition and relative densities of certain species between habitats. Few studies (Hobson, 1984; Randall et al., 1993) have characterized the fish faunas at either atoll. Randall et al.'s (1993) qualitative description of a persistent, but typically habitat-specific, assemblage of fishes at Midway agrees with our conclusions for this site. In general, there are few differences between our 1993 observations and Randall et al.'s (1993) observations made in 1989 and 1991–1992 with regard to the characteristic habitats of the common and abundant fishes at Midway. The habitat specificities of coral reef fishes are generally recognized (McGehee, 1994).

Temporal persistence in the assemblage structure of reef fishes at FFS and Midway is apparent at the spatial scale of recognizable subhabitats ("physiographic zones" of Sale et al., 1994). The persistence of assemblages at Midway superficially differs from observations made to date at individual patch reefs on the Australian Great Barrier Reef; the latter represents the bases for a continuing debate on whether reef fish assemblage structure differs at a local scale among surveys separated in time (Sale et al., 1994). Another equally interesting question

is what any real changes in reef fish abundances on larger spatial scales might represent. Do changes in abundance of some taxa merely represent chance differences in local recruitment success and subsequent year-class establishment, or might changes in general abundance levels also reflect large-scale ecosystem processes (Doherty and Williams, 1988; Doherty, 1991)?

The general nature of the observed declines at Midway (involving both herbivores and carnivores) suggests that ecosystem-level effects, beyond stochastic recruitment of particular species or groups, are involved at least to some extent. Most reef fishes are zooplanktivorous during their pelagic larval phase, regardless of their carnivorous or herbivorous nature after settlement onto reefs (Leis, 1991). If food resources ever limit reef fish population numbers, decreases in water-column productivity during the pelagic larval phase of reef fishes should have a greater influence than decreases in the diverse, reef-based forage bases (Norris and Parrish, 1988; Parrish, 1989) of resident reef fishes.

Temporal Declines in Abundance.—The declines in fish densities over a broad scale (herbivores and carnivores) at Midway in August 1993 contrast with the declines in carnivores, accompanied by distributional shifts in herbivores, at FFS in July 1992. The observed lack of change in overall herbivore densities at FFS resulted from a net increase at patch reefs canceling a net decrease on the barrier reef. Density estimates for herbivores at FFS in 1992 thus were complicated by strong shifts in the spatial distributions of many taxa (primarily surgeonfish) between barrier and patch reefs, so that densities did not adequately index overall abundances. Lower densities of carnivorous fishes at FFS in 1992 were not confounded by distributional shifts, suggesting decreases in abundance throughout both barrier and patch reef habitats. The decreases in carnivorous and herbivorous fishes we observed at Midway, as well as the decreases in carnivores at FFS, might represent responses to decreased levels of productivity.

A key issue, then, is why reef fish declines crossed trophic levels at Midway but were confounded by distributional shifts in herbivores only at FFS. Relationships between herbivorous fishes and algae at FFS suggest one possible explanation. Herbivores (primarily surgeonfishes) increased disproportionately on patch reefs at FFS in 1992, compared to 1980–1983, coincident with the percentage cover of one algal taxon (*Microdictyon* sp.) that is an important food resource for browsers of filamentous algae (Jones, 1968). The *Microdictyon* bloom recorded at FFS in 1992 (F. Parrish, unpubl. data) might have resulted from storm destruction of live coral habitat and subsequent proliferation of algae. An analogous case of increased primary production on and near coral reefs induced by storm disturbance was described by Delasalle et al. (1993). Apparently the effects of storm disturbance were weak or absent at Midway in 1993 although evident at FFS in 1992. Interestingly, corallivore densities at Midway were clearly unchanged between 1980 and 1993, which contrasts with the marked declines in corallivores at FFS between 1980–1983 and 1992. For whatever reasons, *Microdictyon* was generally rare on patch reefs (and the barrier reef) at Midway in 1993, as it was during 1980 and 1981–1985 (Schroeder, 1989; R. Schroeder, pers. comm.). The persistent low abundance of herbivores relative to carnivores on patch reefs at Midway could reflect the similarly low abundance of algae on patch reefs during both August surveys. Algal abundances that fluctuate asynchronously among adjacent reefs have recently been shown to exert strong localized effects on the growth and reproduction of residential herbivorous fishes (Clifton, 1995).

The general decreases in reef fish abundance that we observed at Midway and at FFS may have been influenced by interdecadal changes in ecosystem produc-

tivity in the central Pacific, at and above the latitudes of the NWHI (Polovina et al., 1994). From 1977 to 1988, many major storm events generated unusually turbulent conditions that increased nutrient availability within the photic zone of waters near Hawaii, and may have stimulated planktonic productivity by 50% (Polovina et al., 1995). This increase may have led to higher production of lobsters, seabirds, and monk seals at FFS and Midway during the 1980's. The "declines" observed at Midway and FFS after 1988 actually represent returns to more "normal," lower levels of productivity (Polovina et al., 1994). Thus, the lower densities in reef fishes that we observed on 1992–1993 surveys might reflect typical fish abundances. Some of the declines in the numbers of reef fishes at Midway and FFS may represent lagged responses to poor recruitment of a series of year-classes that resulted from lower productivity. We cannot rule out the possibility that the observed declines represent coincident multiyear recruitment failures that do not directly reflect decreases in productivity. We consider a more direct link with productivity as more likely, however. The diverse timing and long duration of spawning seasons of Hawaiian reef fishes (Walsh, 1987), although less protracted at Midway than in the main Hawaiian Islands (MHI) (Schroeder, 1989), should protect assemblages against long-term, multispecies failures in recruitment resulting from strictly physical advection of planktonic stages. Such could be viewed as an assemblage-level analogue of the "storage effect" (Warner and Chesson, 1985), whereby long-lived species are buffered by age structure against marked fluctuations in population numbers.

We caution that our argument for links between reef fish abundance and productivity does not imply that populations were at carrying capacity when productivity levels were higher in the early 1980's. Reef fishes may have persisted at levels that were constant or variable fractions of carrying capacities. Our best estimates of the overall recent declines in reef fish standing stocks (about one-third), corrected for a realistic average production-to-biomass ratio of 1.5 (Polovina, 1984), nonetheless approximate Polovina et al.'s (1995) estimates of recent decreases in planktonic production.

Comparative Time Series Data.—NWHI. Few quantitative data exist on within- or among-year variation in fish population abundances at Midway or other shallow NWHI reefs. Randall et al.'s (1993) overview of the Midway fish fauna, although an invaluable contribution, is largely qualitative. Hobson (1984) provides primarily presence-absence data for Midway, FFS and other NWHI reefs.

Schroeder (1989) provides the only quantitative data available that might help interpret the temporal patterns of numerical change we observed for Midway fishes. During a 51-month period from May 1981 to August 1985, he censused the abundances of recruit and resident fishes on numerous patch reefs, including some of the same stations, in Welles Harbor at Midway. At quarter-year intervals, a total of 19–21 censuses were conducted at each of four control (unmanipulated) patch reefs ranging in size from 10 to 150 m². Total counts (recruits plus residents of all species pooled) generally fluctuated less than one-third within reefs, except for brief but large summertime recruitment spikes. Variation in total counts among the five August surveys (1981–1985, inclusive) was somewhat greater (CV = 45%; Schroeder 1989; fig. 5.8). However, three species (the fantail filefish *Peruvagor spilosoma*, *Dascyllus albisella*, and *Apogon maculiferus*) together comprised nearly one-half of the 1981–1985 totals and accounted for much of the variation in total numbers among the five August surveys (Schroeder, p. 175, table 4.3). During the August surveys of 1980 and 1993, *P. spilosoma* was rare, and the pooled densities of *D. albisella* and apogonids differed little if at all (15%,

Table 4, this study). The magnitude of the declines in total fishes that we observed between the 1980 and 1993 August surveys (41% on PR; Table 7) thus slightly exceeds the average magnitude of seasonal variation, and clearly exceeds the variation among Schroeder's (1989) five August surveys during the presumed period of higher productivity and abundance. Although not conclusive in itself, this information tends to support our conclusion that the lower estimates of abundance observed in 1993 reflect real declines.

Comparative Time Series Data.—OTHER SYSTEMS. Few studies comparable to ours have been published for fishes on coral reefs elsewhere. Most studies of reef fish variability have focused on spatial differences, whether at single or multiple scales (reviewed by Doherty and Williams, 1988). Green and Shenker's (1993) recent 2-year study is typical, with a focus on spatial differences within and among reefs. Choat et al.'s (1988) 12-year study of the fishes on island (New Zealand) reefs reported variations as large as 15-fold for some species. Similarly, the few long-term studies of fish numbers on continental reefs (Ogden and Ebersole, 1981; Sale et al., 1994) also indicate order-of-magnitude or greater fluctuations for some species. At present, published time series data of reef fish abundances are insufficient to identify whether general patterns of variation exist, much less assess whether populations on continental and oceanic reefs have different fundamental patterns. We urge others to continue documenting temporal variation in fish numbers for isolated and interconnected reef systems.

Power of Temporal Comparisons.—Our baseline versus recent data provide one of the few long-term data sets available which can be used to estimate statistical power in tests of whether reef fish populations have changed over time.

The statistical power of both FFS and Midway data are either encouraging or discouraging, depending on the level of ecological organization. Clearly, sampling efforts similar to those conducted here are inadequate for detecting less than huge ($>10\times$) changes in the abundance of many species. Impractically large sample sizes would be required to detect declines of reasonably large magnitude (e.g., twofold differences; Skalski and McKenzie, 1982) for most species. For example, detecting twofold changes for 9 of the 10 most common and abundant species at FFS would require 30–190 samples (where each sample is a station, sampled before and after with four repeat counts). Detecting twofold changes for 7 of the top 10 species at Midway would require from 25 to several hundred samples (with each station sampled before and after with two repeat counts), depending on species. At FFS, only the saddleback wrasse, *Thalassoma duperrey*, Hawaii's most common and abundant shallow-reef fish (Hourigan and Reese, 1987), would likely (at power ≥ 0.80) require <15 samples (14 at $\alpha_2 = 0.05$; 11 at $\alpha_2 = 0.10$). At Midway, only three species (the Pacific gregory damselfish, *Stegastes fasciatus*; the belted wrasse, *Stethojulis balteata*; and the saddleback wrasse) would require about a dozen or fewer samples (<8 to 15 at $\alpha_2 = 0.05$; <8 to 12 at $\alpha_2 = 0.10$).

Inadequate power to detect twofold changes in density at the species level should not be surprising. Lincoln Smith et al. (1991), for example, were in many cases unable to detect even 10-fold differences in the densities of young-of-year recruits among New Zealand rocky reefs.

In our study, power to detect twofold changes at higher levels of organization was acceptable (≥ 0.80) at practical sample sizes (<8 –12 samples) for total fishes (both atolls), pooled carnivores (FFS) and each major trophic level (Midway), and for some (FFS) or most (Midway) carnivore guilds (Table 8). If the question asked is answerable at higher levels of organization such as trophic levels or

Table 8. French Frigate Shoals and Midway Atoll. Estimates of statistical power to detect a difference between baseline and recent periods in log-transformed densities of major fish groups (all test stations, both habitat types). Also estimated are the sample sizes (number of stations sampled four and two times each per period at FFS and Midway, respectively) necessary to detect a twofold change^a in density with a power of 0.80.

Variable	Site	Observed change (%)	Power to detect 2X change at		N needed to detect 2X change at	
			$\alpha_2 = 0.05$	$\alpha_2 = 0.10$	$\alpha_2 = 0.05$	$\alpha_2 = 0.10$
Total fishes	FFS	-16	>0.21	>0.33	12	9
	Midway	-32	>0.95	>0.95	<8	<8
Herbivores	FFS	+10	0.10	0.18	15	11
	Midway	-27	>0.95	>0.95	<8	<8
Secondary consumers	FFS	-27	0.32	0.47	15	11
	Midway	-32	0.81	0.91	<8	7
Benthic carnivores	FFS	-27	0.36	0.51	13	10
	Midway	-21	>0.95	>0.95	<8	<8
Planktivores	FFS	-23	0.16	0.27	>100	
	Midway	-60	0.21	0.32	44	34
Corallivores	FFS	-70	0.79	0.89	30	23
	Midway	+5	0.13	0.22	88	68
Piscivores	FFS	-24	—	—	>100	
	Midway	-79	0.51	0.65	16	12

^a For log-transformed variables, a twofold change (log 2) equals a halving (50% decline) or a doubling (100% increase).

feeding guilds, then using visual surveys to estimate reef fish densities is a reasonable task. On the other hand, if species-level discrimination is desired (Sale and Guy, 1992), impractically greater sampling effort will be required. Our comparisons between baseline and recent surveys at each atoll amply demonstrate that matched-pair sampling and analysis designs, in which permanent stations provide their own spatial controls, can appreciably improve statistical power to detect temporal changes and thus reduce sampling effort. We recommend that matched-pair designs be routinely employed when making such comparisons.

SUMMARY AND CONCLUSIONS

The fish assemblages at FFS and Midway Atoll differed little in terms of the presence-absence or rank abundance of major species between the two sampling periods, when viewed within the spatial scale of major habitat types. However, at both sites and during both periods, persistent differences in fish assemblage structure existed between barrier and patch reef habitats. Temporal changes in fish densities were evident depending on the level of ecological organization examined. Matched-pair comparisons indicated significant changes for only 6 and 8 of 30 species at FFS and Midway, respectively, but species-level differences were difficult to resolve because of low statistical power. Trends in pattern emerged at each atoll if the sign of nominal changes in densities was evaluated; then, apparent decreases significantly outnumbered increases at the species level. Temporal changes became more apparent when higher level trophic categories were examined. Patterns of decline were similar for major trophic levels (herbivores and carnivores), for most carnivore feeding guilds, and for total fishes. These patterns of temporal change were generally similar (i.e., overall declines between the early 1980's and early 1990's) at the two atolls. Matched-pair analysis designs provided sufficient statistical power to meaningfully evaluate most major groups (trophic levels, feeding guilds) of fish taxa.

Densities of FFS and Midway reef fishes estimated in 1992 and 1993 (about 12 fish \approx 1 kg·10 m⁻²), although lower than baseline levels, were still about twice as high as typical values for shallow fished reefs in the MHI (0.4–0.6 kg·10 m⁻²; R. Brock, Hawaii Inst. Mar. Biol., pers. comm. Sept. 1992; \approx 0.7 kg·10 m⁻²; Grigg, 1994). This difference may reflect the highly exploited state of reef fish stocks at present in the MHI, relative to populations on pristine reefs of the NWHI. This possibility deserves further investigation because of its importance in the development of management plans for coastal fisheries resources.

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