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Influence of instantaneous variation on estimates of coral reef fish populations and communities

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ABSTRACT: The magnitude of different sources of variation in coral reef fish abundance data needs to be known if temporal changes in population and community data are to be correctly estimated. A particularly important missing component of the variability is the 'instantaneous' change in fish, largely caused by the interaction between fish movement and observer recognition. This variation occurs at a time scale less than that influenced by the focus of previous studies, including time of day, tides, migration, or birth and death processes. Without this measure of variance, estimates of temporal change are confounded. To determine the magnitude of this instantaneous variance, belt-transect visual counts of damselfish, surgeonfish, and parrotfish were conducted during a short interval at midday during neap tides over consecutive days in the calm season and compared to similar samples in 1992 and 2003. Within-site, or our estimate of instantaneous variation, was the greatest source of variability for the whole assemblage and for the surgeonfish/parrotfish group but not for damselfish. Direct between-year comparisons produced estimates of population change over time that were twice as high as those derived by an indirect method where the instantaneous spatial component was subtracted from the total variation. Because the inherent spatial component of variability makes it difficult to detect site change over time, we recommend sampling designs that use random sampling and have greater statistical power to detect change. Furthermore, aggregate metrics, such as numbers of species or density at the family, community, or the functional group, will have greater potential to detect change for sample sizes typical of coral reef studies. Otherwise, when life history traits and species level change are important, high replication will be required.

KEY WORDS: Acanthuridae · Community composition · Marine protected areas · Pomacentridae · Population variation · Sampling methods · Scaridae

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INTRODUCTION

Detecting change in coral reef fish populations and communities is a challenging task because of differences in detectability among species and inherent variability in abundance (Samoilys & Carlos 2000, Willis 2001, Thompson & Mapstone 2002, Edgar et al. 2004, Tessier et al. 2005). Variation is caused by short-term changes associated with deterministic diurnal and tidal movements (Galzin 1987, Thompson & Map-

stone 2002) and birth and death process (Sale & Dybahl 1975, Williams 1983, Doherty & Williams 1988, Hixon & Carr 1997), but also through more stochastic processes such as movements and the difficulty of detecting and counting small, fast-moving, and often cryptic species (Brock 1982, Fowler 1987, Lincoln-Smith 1988, Greene & Alevizon 1989, Kulbicki & Sarramegna 1999). We refer to this as instantaneous variation, as it is caused by an interaction between the observer and fish movement that occurs on a time scale

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less than the behavioral and population processes that are the focus of many scientific field studies. This variability creates difficulties when attempting to detect patterns of change unless the sources of variation and error are quantified (Sale & Dybahl 1975, Sale & Douglas 1984, Bohnsack 1983, Sale et al. 1984, Sale & Steel 1989, Planes et al. 1993, Galzin et al. 1994). Variations arising from differences in sampling method, inter-observer differences, and species, density, and site-related factors are likely to affect conclusions about actual population variability.

Many studies have assessed the magnitude of temporal change in coral reef fish populations and communities in relation to factors such as protection from fishing (Russ & Alcala 2004, McClanahan & Graham 2005), impacts of disturbance (Syms & Jones 2000, Halford et al. 2004, Graham et al. 2006, Wilson et al. 2006), and their interaction (Jones et al. 2004). Problems of accuracy can confound estimates of change, because there are unavoidable constraints on accurate sampling at specific times and locations and spatial variation can confound temporal variation (Stewart-Oaten et al. 1995). Where spatial variation is high, direct comparisons of mean population densities and community composition over time will be inaccurate, and this is the case for many coral reef organisms (McClanahan 1998, Thompson & Mapstone 2002).

Mobile species are likely to be more challenging in this regard because of their mobility and related behaviors, such as aggregation, and due to movements related to diurnal, tidal, and seasonal drivers. Although variation may be expected to be less for more sedentary taxa, direct estimation of population differences over time may still be difficult by direct comparisons of means because spatial variation, often associated with social or habitat aggregations, can be large and constitutes an important confounding effect (Stewart-Oaten et al. 1995). For these reasons, estimates of population change actually require an indirect method, where the temporal variation is derived from the difference between the total and other sources of variation (Stewart-Oaten et al. 1995).

It is clearly important to have accurate estimates of instantaneous and other sources of variation when attempting to estimate population variability and to design studies that estimate and minimize these sources of variation to the extent that this is possible. Yet, apart from a notable study (Thompson & Mapstone 2002), previous studies have scarcely attempted to systematically partition the main sources of error. Estimates of variation in populations over time scales of a single day and tidal cycle test for variation at this scale without distinguishing this variation from background or instantaneous variability (Galzin et al. 1994, Thompson & Mapstone 2002, Willis et al. 2006). These

studies only seldom find significant patterns, perhaps because instantaneous variation is larger than the daily or tidal variation they are trying to detect. One notable exception is a study of reef fishes on Heron Island where variation over time was found, in most cases, to not differ from random walk predictions (Ault & Johnson 1998). When randomness and instantaneous change are accounted for, it is likely that the magnitude of temporal change will be reduced and become more predictable, varying among species and assemblages in relation to various life-history characteristics and fluctuations in recruitment, growth, and longevity and, thus, speed of population turnover, all of which can be related to body size (Ebeling et al. 1990, Rahel 1990, Jennings et al. 1999).

In this study, the sources of variation in observers, space, and time were examined for a variety of coral reef fish that are common in Kenya and differ in ecological and life-history characteristics related to body size, diet, population density, and movement. Species and community structure in 2 areas subjected to different levels of management (1 closed to fishing for 14 yr, the other heavily fished) were compared, which created a natural experimental manipulation of population density for target species and allowed us to determine the effect of reduced abundance on variance. We aimed to compare 2 different ways of estimating temporal variation and determine the sampling effort required to detect levels of change.

MATERIALS AND METHODS

Study sites. The study was conducted on the lagoonal side of the fringing reefs north of Mombasa, Kenya, in a heavily populated and urbanized area where a marine park and reserve were created in 1989 to reduce fishing. Study areas were subject to different levels of management. The first area was the Mombasa Marine National Park (MMNP), which has been effectively enforced as a strict no-fishing zone since 1991. The second area, located off Ras Iwatine (RAS) ~3 km from the southern boundary of the MMNP, was part of a marine reserve where most fishing activities (excluding beach seining) were allowed and where fishing intensity was high (McClanahan & Mangi 2001). Data from 1992, 2003, and 2004 are presented. We expected the MMNP to show signs of recovering from fishing, while RAS was not expected to exhibit such characteristics (McClanahan & Arthur 2001, McClanahan & Graham 2005).

The study areas were located on the shallow reef flat (<3 m depth at low tide), where benthic communities form a mosaic of algae and coral-dominated hard substratum, interspersed with patches of sea grass. Ben-

thic community structure differed between the study sites. Cover of living corals was higher in the MMNP than at RAS ($23.6 \pm 9.7\%$ and $5.5 \pm 3.6\%$, respectively, mean \pm SD) while that of frondose macroalgae showed the opposite pattern (MMNP $1.7 \pm 1.3\%$; RAS $22.5 \pm 9.0\%$; Cros & McClanahan 2003).

Fish censuses. In each area, 3 transect lines of 100 m length were installed. Fish censuses were carried out by snorkeling along the transect line and counting the number of individual fish by species (Lieske & Myers 1994) within 2.5 m of either side (area $100 \times 5 \text{ m} = 500 \text{ m}^2$). Fish were sampled in 3 families by discrete group sampling (DGS), whereby the Pomacentridae were sampled separately from the Acanthuridae and Scaridae (McClanahan 1994). The 500 m^2 belt was chosen, as this is close to the area where community variability stabilizes when comparing quadrats of different sizes (T. McClanahan, unpubl. data), and it is a commonly used belt area in this system (McClanahan 1994). Fish $< 3 \text{ cm}$ in length were not counted, as their small size and cryptic behavior decreases their detection and increases variability in counts (Fowler 1987). Transects were located in permanently marked locations. In 1 case, the transect line broke (Site 5), and, although we attempted to replace it as closely as possible to the original location, it may have moved (see 'Results').

We undertook a sampling program that was expected to reduce the number of possible variables influencing the fish populations, such that we measured the instantaneous within-site (transect) variability as closely as possible. Consequently, the surveys were conducted by experienced observers, during 1 season at the calmest time of year, on days with calm and sunny conditions and during midday neap tides. These factors have been hypothesized to influence survey results (Helfman 1986, Galzin 1987, Thompson & Mapstone 2002, Williams et al. 2006); therefore, methods and sampling design were specifically developed to minimize these potential effects. From 2 to 7 December 2004, fish censuses were conducted independently by 5 different observers (TRM, NAJG, PC, JHB, and NVCP), each observer completing 3 census passes of each transect. In most cases, consecutive passes of a transect were completed serially with only a few minutes between transects, such that the time between samples was approximately the time required to complete a transect (approximately 20 min). Thus, each transect was surveyed 15 times, 45 passes of transects were made per management area, and 90 passes were made in total during 2004 (Table 1). Identical censuses were carried out during October to December 1992 and February to May 2003 by TRM in 4 sites within each area.

Multivariate representation. Non-metric multidimensional scaling (MDS) was used to describe pat-

terns in fish community data for each transect among the 5 observers in 2004 and between the years 1992 and 2003 using the PRIMER-E v6 package (Clark & Warwick 2001). Data were square-root transformed to down-weight abundant species, and MDS plots were produced based on Bray-Curtis similarity matrices. Group-average cluster analysis was performed on the same similarity matrix, and slices through the cluster dendrograms at similarity levels of 50 and 60 were overlaid on the MDS plots to define patterns more clearly (Clark & Warwick 2001). Data were analyzed in this way at the level of the whole assemblage and at that of taxonomic groups, namely the more sedentary pomacentrids and the more mobile scarids and acanthurids. Unexpectedly, no scarids or acanthurids were seen for 2 passes and only 1 *Acanthurus dussumieri* was observed in another pass at the RAS study site during 2003; these data were therefore removed due to very low similarity (5–9%) to the other data. Consequently, it should be remembered that the variation in this group, year, and site is even greater than presented for visual purposes.

Spatial variation. We analyzed the 2004 fish population data from both areas for 4 components of variation and similarity; total, within transect, between transect, and between observer (Table 1). For each area, we calculated the population density and community similarities (based on Bray-Curtis) for 3 levels; each observer within transects ($n = 45$ paired comparisons, 5 observers \times 3 transects \times 3 passes), between transects ($n = 15$, 5 observers \times 3 passes), and between observers ($n = 9$, 3 transects \times 3 passes; Table 1). The mean and standard deviation of the respective components were calculated, and 1-way ANOVAs were performed to compare RAS and the MMNP. Due to problems meeting the assumptions of a continuous model, we ran an ordinal MANOVA with sites nested within management areas to determine the strength of the factors of observer, site, and management areas on estimates of the population density of the studied species.

We calculated variability based on the coefficients of variation (CV) of each species, within each transect, area, and both areas combined (Table 1). The total CV of the areas was calculated as the means and standard deviations of all passes in the area ($n = 45$). The within-transect CV compared individual passes in a transect, the between-transect CV compared the means of all passes within each transect and compared this to the means in the different sites, and the observer CV used the means of the 3 passes of the observer and compared observers using the means of the 3 transects ($n = 9$; Table 1).

In order to determine the levels of variation and utility of permanent transects versus random or haphazardly selected transects, we also calculated the CV for differences between paired transects, or repeated

Table 1. Equations used in the calculations of within-site, between-site, observer, Bray-Curtis index, and the indirect calculation of temporal variation

Equation description	Calculation steps	No.	Equation	n
Within site coefficient of variation, CV ₁	(I) Site mean (sm) s = site no = number of observers np = number of passes per site op = observation per person per site	1.0	$\bar{X}_s = \frac{\sum_{i=1}^{no} \left(\frac{\sum_{j=1}^{np} op_j}{np} \right)_i}{no}$	np = 3 no = 5
	(II) Coefficient of variation for each site s = site ns = number of sites per reef	1.1	$CV_{s_i} = \frac{(\sigma_{s_i} \times 100)}{\bar{X}_{s_i}}$	ns = 3
	(III) Coefficient of variation, CV ₁	1.2	$CV_1 = \frac{(\sum_{i=1}^{ns} CV_{s_i})}{ns}$	ns = 3
Between site coefficient of variation, CV ₂	(I) Average of the site means (SM = site mean)	2.0	$\bar{X}_{SM} = \frac{(\sum_{i=1}^{ns} \bar{X}_{s_i})}{ns}$	ns = 3
	(II) Coefficient of variation, CV ₂	2.1	$CV_2 = \frac{(\sigma_{\bar{X}_{SM}} \times 100)}{\bar{X}_{SM}}$	
Observer coefficient of variation, CV ₃	(I) Average per observer per site	3.0	$\bar{X}_{op} = \frac{(\sum_{i=1}^{np} op_i)}{np}$	np = 3
	(II) Site average based on observer mean per site (ops = site average)	3.1	$\bar{X}_{ops} = \frac{(\sum_{i=1}^{no} \bar{X}_{op_i})}{no}$	no = 5
	(III) Coefficient of variation per site	3.2	$CV_{ops_i} = \frac{(\sigma_{op_i} \times 100)}{\bar{X}_{ops_i}}$	
	(IV) Total observer coefficient of variation, CV ₃	3.3	$CV_3 = \frac{(\sum_{i=1}^{ns} CV_{ops_i})}{ns}$	ns = 3
Bray-Curtis similarity index	BSI = Bray-Curtis similarity index; Min = minimum; Obs = observer N = number of species Nr = number of reefs	4.0	$\bar{X}_{BSI} = \frac{\sum_{i=1}^{N \times ns \times np} [2 \times \min(Obs_{s_1}, Obs_{s_2}) / \sum (Obs_{s_1}, Obs_{s_2})]_i}{N \times ns \times np}$	N Mombasa = 45; N Rās = 36 N total = 50; ns = 3 np = 3 nr = 2
Temporal coefficient of variation	CV time	5.0	CV total – CV space	

passes of the same transect. We calculated means and standard deviations for differences in pairs between all 15 passes in each transect and for all 105 possible paired differences. The paired-difference CV for each species in each transect was calculated, and we plotted the CVs derived from paired and unpaired methods against the mean density of each species. Means for the 2 methods were compared with a single-factor ANOVA, and plots of the CV against species popula-

tion density were used to make a visual comparison of the paired differences versus mean densities as a function of population density.

Temporal variation. Samples collected in 1992 and 2003 from the MMNP and RAS were used to estimate the temporal variation in the fish numbers and community structure. Data were grouped into the 2 areas and 3 families (Acanthuridae, Scaridae, and Pomacentridae). Similarities of 64 paired combinations from RAS

and the MMNP in both time periods were calculated, and the mean similarity for each reef-time-pair combination was derived. CVs were then calculated for the total, spatial, and temporal variation.

Total variation was calculated from the mean and standard deviation of the 16 replicates in both areas in the 2 years. A mean and standard deviation of the 4 replicates in each area and year were also calculated. The coefficient of spatial variation was calculated from the average of these means and the standard deviations. The coefficient of temporal variation was estimated using 2 methods: (1) directly comparing means over time as above using the means for each area and year, and (2) subtracting the mean within spatial variation from the total variation (Eq. 5.0, Table 1). The first is a direct comparison of means over time and the second is an indirect method where the temporal variation is the variation remaining after the mean spatial variation has been subtracted from the total variation.

Power to detect differences. In order to establish the sample sizes required to detect given differences in reef fish assemblages and individual species, we carried out a power analysis in the MiniTab statistical package. From the variances of the 3 transects in each area surveyed in 2004 and using a 1-way ANOVA model, we calculated the percent change detectable at the 0.05 alpha level with a power of 80% for each species. We used an n of 4, 10, 20, and 30, which represents sample sizes often used at the scale of both site and study area in fish population studies (McClanahan 1994, Jennings et al. 1995, Samoilys & Carlos 2000, Graham et al. 2006).

RESULTS

There were no statistically significant differences between observers (MANOVA, $F = 5.1$), but the areas differed substantially (MANOVA, $F = 59.7$, $p < 0.0001$) while sites nested within areas also differed (MANOVA, $F = 15.9$, $p < 0.003$). These between-area differences and similarities among observers are highlighted by the MDS plot (Fig. 1).

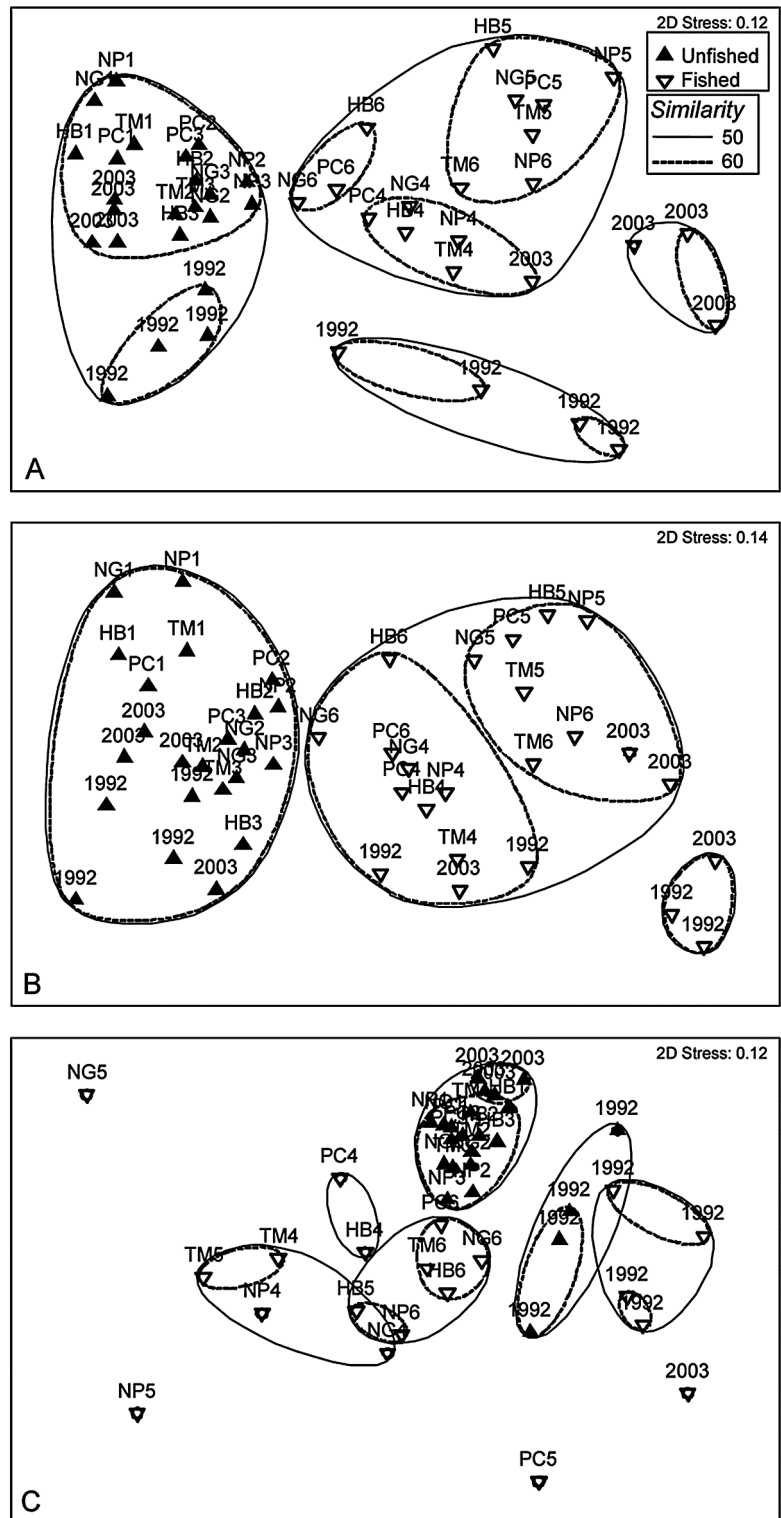


Fig 1. Multi-dimensional scaling (MDS) plots with similarity slices of 50 and 60 overlaid for the different passes of each transect within 2 different management areas for both temporal (1992 and 2003) data and multiple observer (initials identify observer) data. (A) Whole assemblage combined, (B) Pomacentrids and (C) scarids and acanthurids combined in both Ras Iwatine (RAS; fished) and the Mombasa Marine National Park (MMNP; unfished)

Table 2. Summary statistics for each sampled species in the 3 families and the total, observer, between-, and within-site coefficients of variation (CV)

Species	All sites					Fished					Unfished							
	Mean	SD	Total CV, %	Observer CV, %	Between-site CV, %	Mean	SD	Total CV, %	Observer CV, %	Between-site CV, %	Mean	SD	Total CV, %	Observer CV, %	Between-site CV, %	Within-site CV, %		
Acanthuridae																		
<i>Acanthurus nigrofasciatus</i>	8.3	7.9	95	85	93	86	2.2	3	152	129	146	147	14.4	6.2	43	36	40	16
<i>Ctenochaetus striatus</i>	4.6	6.1	134	64	72	118	1	1	146	95	107	88	8.1	6.9	85	43	48	71
<i>Acanthurus nigricauda</i>	1.3	2.1	163	131	206	120	0.1	0	495	224	387	100	2.5	2.4	96	70	85	48
<i>Acanthurus triostegus</i>	0.9	2.2	261	140	207	185	1.6	3	186	120	159	134	0.1	0.3	286	105	279	125
<i>Naso annulatus</i>	0.7	1.2	169	135	145	98	0.4	1	221	143	151	97	1	1.4	137	130	141	85
<i>Zebrasoma scopas</i>	0.6	0.9	145	71	105	102	0.1	0	303	109	158	173	1.1	1	89	148	204	87
<i>Naso unicornis</i>	0.6	1.5	271	148	204	155							1.1	2	179	59	88	42
<i>Acanthurus leucosternon</i>	0.4	0.7	174	63	118	139							0.8	0.8	101	63	118	68
<i>Zebrasoma veliferum</i>	0.3	0.6	203	120	168	104	0.2	1	294	120	152	173	0.4	0.6	154	119	173	76
<i>Acanthurus lineatus</i>	0.1	0.3	284	147	180	192							0.2	0.4	189	147	180	125
<i>Ctenochaetus strigosus</i>	0.1	0.3	346	104	205	175							0.2	0.4	236		241	108
<i>Acanthurus dussumieri</i>	0.1	0.2	415	164	279	192							0.1	0.3	286	105	279	125
<i>Acanthurus xanthopterus</i>	0.02	0.1	812	200	346	245							0	0.2	600		346	173
Pomacentridae																		
<i>Plectroglyphidodon lacrymatus</i>	41.5	44.5	107	32	34	97	16.8	5	32	37	30	10	66.2	52.3	79	37	38	72
<i>Chrysiptera unimaculata</i>	24.2	18.6	77	37	38	62	36	20	55	48	42	31	12.3	4.9	39	33	33	30
<i>Chromis weberi</i>	16.5	19.2	116	77	103	78	9.5	12	129	92	118	75	23.6	22.3	95	63	89	63
<i>Chromis dimidiata</i>	13.9	15.4	111	61	60	100	4.1	5	132	85	82	87	23.7	15.9	67	45	45	57
<i>Abudefduf sexfasciatus</i>	6.7	9.5	140	85	101	102	2.6	2	94	83	101	58	10.9	11.9	109	87	100	74
<i>Neopomacentrus azyron</i>	6.3	12.1	193	120	121	184	1	2	144	6	11	173	11.5	15.5	134	158	158	137
<i>Plectroglyphidodon dickii</i>	5.3	7.1	134	41	43	120							10.6	6.7	63	41	43	38
<i>Abudefduf vaiigiensis</i>	4.3	8.5	199	114	137	72	1.9	3	135	71	93	113	6.6	11.3	171	142	166	24
<i>Dascyllus trimaculatus</i>	4	5.9	148	82	103	129	7.1	7	97	70	86	82	0.8	1.1	137	100	128	139
<i>Pomacentrus caeruleus</i>	2.9	2.6	90	41	52	77	3.5	3	84	47	57	75	2.3	2.1	92	35	44	93
<i>Amphiprion allardi</i>	1.6	1.8	114	85	107	112	1.4	2	137	116	120	150	1.7	1.6	94	58	99	102
<i>Stegastes fasciatus</i>	1.5	1.6	111	117	147	77	1	1	153	152	206	83	2	1.7	83	80	87	67
<i>Abudefduf sparoides</i>	0.6	0.9	149	65	127	123	1.1	1	89	57	112	67	0.1	0.3	324	105	172	173
<i>Chromis nigrura</i>	0.5	1.2	234	139	186	123	0.1	0	378	149	207	173	1	1.6	162	131	179	64
<i>Amblyglyphidodon leucogaster</i>	0.5	2.8	542	224	207	245	1	4	379	224	207	173	0.2	0.5	305	104	205	108
<i>Chrysiptera leucopoma</i>	0.5	1	197	169	184	106	0.8	1	145	133	147	68	0.2	0.8	115	59	74	88
<i>Pomacentrus sulfureus</i>	0.4	0.7	185	114	179	149	0	0	671	224	387	173	0.6	0.8	136	107	141	59
<i>Pomacentrus baenschi</i>	0.3	0.6	215	107	141	133							0.6	0.8	136	107	141	59
<i>Pomacentrus pavo</i>	0.1	0.4	496	224	300	210	0.2	1	387	224	212	173	0	0.1	671		387	173
<i>Dascyllus aruanus</i>	0.1	0.4	481	224	297	206	0.2	1	334	214	297	138	0.1	0.3	495	224	326	100
<i>Chrysiptera annulata</i>	0.1	0.2	415	100	146	245	0.1	0	286	98	146	173	0.1	0.4	403		223	173
<i>Plectroglyphidodon johnstonius</i>	0.04	0.3	575	105	223	245	0	0	671	204	387	173	0.1	0.3	495	224	326	100
<i>Lepidozygus tapeinosoma</i>	0.04	0.3	575	224	334	182	0	0	378	149	207	173	0.1	0.3	495	224	326	100
<i>Chrysiptera biocellata</i>	0.03	0.2	542	149	207	245	0.1	0	378	149	207	173	0.1	0.3	495	224	326	100
<i>Stegastes nigricans</i>	0.01	0.1	949	224	387	245	0	0	671	224	387	173	0.1	0.3	495	224	326	100
Scaridae																		
<i>Scarus sordidus</i>	3.5	5.4	154	97	128	108	0.6	1	165	106	161	66	6.5	6.4	98	87	94	48

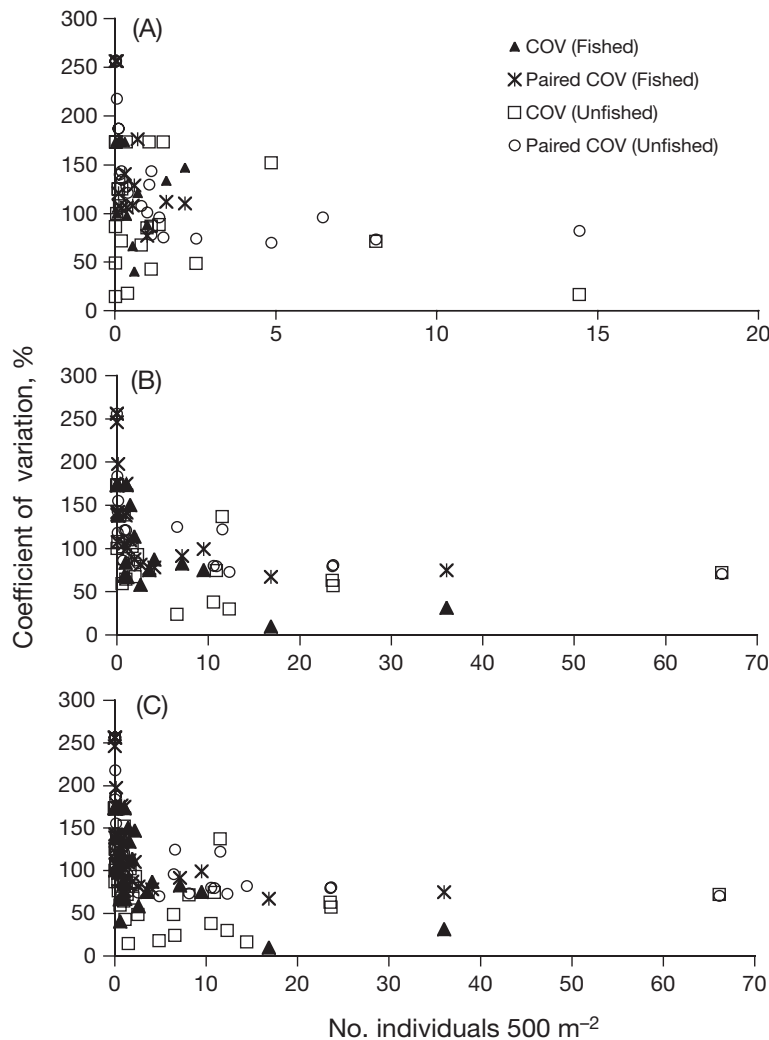


Fig. 2. Plots of coefficients of variation (CVs) against mean abundances for (A) the whole assemblage, (B) pomacentrids, and (C) the scarid and acanthurid groups for both variations around the mean and differences between paired transects in both RAS (fished) and MMNP (unfished)

there were fewer differences between the 2 areas (Table 4). Over ~10 yr, the maximum similarity for all fish was 37 and 58% when comparing RAS and the MMNP, respectively (Table 5). For the overall species assemblage and for acanthurids/scarids, there tended to be higher community similarity for the MMNP than for RAS for between-observer and within- and between-site comparisons (Table 4). The pomacentrid community similarity was higher among observers in the MMNP than at RAS, but there were no differences for between- and within-site comparisons (Table 4). For the whole assemblage and for the 2 taxonomic groups, the between-site community similarity was always lower than that between observers and within sites (Table 4). There was greater community similarity in the MMNP for acanthurids/scarids (43%) and pomacentrids (64%) than at

RAS (17% and 43% respectively) over the ~10 yr period (Table 5).

Most species required large sample sizes to detect small to modest changes in abundance data, with smaller changes being detectable in the MMNP than at RAS for most comparisons, although this varied with family and species (Table 6). At the family level, scarids required the least sampling to detect change, followed by the pomacentrids and the acanthurids at RAS. However, in the MMNP the pomacentrids required the least sampling. At the species level there were a few species in the MMNP that did not require extensive sampling to detect modest change. For example, *Acanthurus nigrofasciatus* and 2 parrotfish, *Calotomus carolinus* and *Scarus frenatus*, required only 4 transects to detect changes <50% (Table 6). At RAS, modest sample sizes of 10 transects could detect changes <50% for the 2 common damselfish *Plectroglyphidodon lacrymatus* and *Chrysiptera unimaculata*, but changes <100% are unlikely to be detected for any surgeonfish and only a few parrotfish at typical levels of sample replication.

Estimates of species variation over time were sensitive to the method of calculation, with the direct method of comparing means producing higher values than the indirect estimate derived by subtracting the mean spatial from the total variation (Table 7). In most cases the direct method indicated temporal variation to be about twice as great as the indirect method. Patterns with respect to family groups and area were consistent with the above measurements.

DISCUSSION

We set out to quantify various sources of population and community variability among coral reef fishes and the role of instantaneous variation on estimates of changes over time. The high instantaneous variation measured in this study indicates that this previously ignored factor is the largest source of variation for the populations of the species surveyed and can lead to difficulties in detecting differences between sampling methods, sites, management, and time (Samoilys & Carlos 2000). High within-site variability has been observed in other studies (Sale & Douglas 1984, Ault & Johnson 1998, Samoilys & Carlos 2000, Gust et al. 2001, Thompson & Mapstone 2002) and has been presented as evidence that fish assemblages are not in equilib-

Table 3. Summary of coefficients of variation of fish population density in all sites (=transect) and the fished and unfished reefs and ANOVA tests of significance. Tukey test for post hoc comparisons given, where ws = within sites, bs = between sites, and bo = between observers

	All sites	Fished	Unfished	Management 1-way ANOVA	
				F	p
Acanthuridae and Scaridae					
Total variation	354.0	300.2	256.7	0.3	0.56
Observer	134.9	139.8	112.1	1.9	0.17
Within site	209.8	204.5	199.7	0.0	0.94
Between sites	152.2	127.6	96.9	3.1	0.09
F ratio	5.0	4.2	7.4		
p	0.01	0.02	0.002		
Tukey test	ws>bs,bo	bs<ws,bo	bs<ws,bo		
Pomacentridae					
Total variation	284	254	92	1.3	0.27
Observer	118	123	89	2.8	0.10
Within site	159	166	137	0.8	0.38
Between sites	147	118	92	2.7	0.11
F ratio	1.9	1.6	2.2		
p	0.15	0.21	0.13		
Whole assemblage					
Total variation	320	267	224	1.1	0.31
Observer	127	128	101	4.0	0.05
Within site	185	178	170	0.1	0.73
Between sites	150	120	94	5.8	0.02
F ratio	7	4.44	9.36		
p	0.0	0.016	0.0002		
Tukey test	ws>bo	ws>bo,bs	ws>bo,bs		

rium with their resources (Sale & Douglas 1984). Our study shows, however, that as much as 15 to 25 % of this within-site community variation is essentially instantaneous or on a time scale considerably faster than reproductive and mortality processes that would potentially reflect population responses to resources.

The amount of variation in sampling is similar to the community similarity predictions of neutral theory, where neutral theory predicts that reef corals will have Bray-Curtis similarities between 70 and 85 %, whereas actual coral communities have considerably lower similarities, presumably due to non-random processes (Dornelas et al. 2006). Consequently, because a high percentage of the total variation is essentially instantaneous, estimating temporal variation and determining underlying population or ecological processes is difficult. Our 2 methods for calculating temporal variation produced considerably different estimates. For the analysis of individual populations, removing spatial variation from estimates of temporal change reduced the estimate of change by half. We suggest that temporal variation is often over-estimated because of the problems of instantaneous variation where estimated variation is confounded by variation at very small temporal scales. Therefore, we suggest that coral reef fish are more stable in terms of birth and death processes

than previous comparisons of means over time. Random walks have previously been used to account for temporal variability (Ault & Johnson 1998), and their use needs to be compared with our field-based method to determine their accuracy in estimating instantaneous variation.

High instantaneous variation will reduce the efficacy of estimating fish populations and communities, because real but minor changes will go undetected due to this inherent variability and the low to moderate sample sizes commonly used in coral reef fish studies. This is commonly observed in short-term efforts to quantify change over daily and tidal cycles (Mapstone & Thomson 2002, Willis et al. 2006). There may be cycles, but they are not strong enough to be distinguishable from population noise; therefore, efforts to quantify them are likely to produce false negatives. Future efforts to examine temporal patterns will need to quantify instantaneous variation or noise in order to estimate the strength of weak signals.

We attempted a paired test, which is a common method, to reduce variation and detect changes when between- is larger than within-sample variation. However, we found that it did not reduce variation, which can be attributed to the high within-site or instantaneous variation. The explicit intent of monitoring fixed sites over time as repeated or paired sampling of the same site is to reduce variation and increase the power to detect smaller change. The consequence, however, is that repetition of the same sites reduces the opportunity for replication in space, the associated degrees of freedom, and the generality of the findings. When within-site is equal or higher than between-site variation, as found for most of our studied species, monitoring programs would be better suited to increase the number of transects and sites rather than repetition of the same sites over time. This would also have the benefit of increasing the spatial generality of the findings.

Despite higher within-site population variability, we found higher community similarity within than between sites. Community similarity will be most influenced by dominant species, and because these dominants have the lowest instantaneous variation, community similarity will reflect this and produce lower within- than between-site variation. This suggests that change is more likely to be detected for dom-

Table 4. Mean percent similarities (Bray-Curtis index) between observer, within sites, and between sites in all sites, fished and unfished management areas. A 1-way comparison Tukey test for post hoc comparisons is given, where ws = within sites, bs = between sites, and bo = between observers

	— All sites —		— Fished —		— Unfished —		Management, 1-way ANOVA	
	Mean	SD	Mean	SD	Mean	SD	<i>F</i>	<i>p</i>
Acanthuridae and Scaridae								
Between observers	71.0	11.5	62.3	8.1	79.8	6.4	28.8	0.001
Between sites	52.7	24.1	35.2	22.0	68.1	8.1	33.3	0.001
Within site	59.7	28.4	43.5	23.8	75.9	3.4	43.2 ^a	0.001
<i>F</i> ratio	8.0		12.6 ^a		5.4			
Prob > <i>F</i>	0.001		0.001		0.01			
Tukey test	bo, ws > bs				ws, bo > bs			
Pomacentridae								
Between observers	84.4	4.3	81.8	4.0	87.1	2.8	11.7	0.003
Between sites	64.3	7.3	62.9	6.4	65.6	8.0	1.0	0.33
Within site	87.9	5.0	88.6	2.5	87.3	1.7	0.5	0.5
<i>F</i> ratio	135.4		136.0		89.4			
Prob > <i>F</i>	<0.0001		<0.0001		<0.0001			
Tukey test	ws > bo > bs		ws > bo > bs		bo, ws > bs			
Whole assemblage								
Between observers	80.8	5.1	77.3	4.4	84.3	2.7	18.4	0.0001
Between sites	62.6	7.7	57.8	5.7	67.4	6.5	18.1	0.0001
Within site	83.5	4.3	83.4	2.0	83.6	0.5	0.0	0.91
<i>F</i> ratio	97.2		136		91.0			
Prob > <i>F</i>	<0.0001		<0.0001		<0.0001			
Tukey test	bo, ws > bs		ws > bo > bs		bo, ws > bs			

^aWelch's ANOVA

Table 5. Mean percent similarities (Bray-Curtis index) of the studied reefs over 2 time periods

	Unfished 1992	Fished 1992	Unfished 2003
Acanthuridae and Scaridae			
Fished 1992	36.1		
Unfished 2003	42.5	35.4	
Fished 2003	9.8	16.5	6.9
Pomacentridae			
Fished 1992	35.9		
Unfished 2003	64.1	33.3	
Fished 2003	36.6	42.6	44.8
All assemblages			
Fished 1992	35.9		
Unfished 2003	57.7	34.1	
Fished 2003	33.1	37.4	33.5

inant species and community similarity when using repeated or paired sampling and low levels of replication. Similarly, pooling of species into family groups also reduced the CV, and other forms of pooled data, such as numbers of species per site or functional groupings, would be expected to detect change at smaller sample sizes (Rahel 1990). Consequently,

repeated-site monitoring programs will be most successful at detecting change for aggregate or pooled measures, including change for aggregate or pooled communities, family, or functional groups. Detecting change in many moderately common or rare coral reef fish species may be unrealistic at currently common sampling levels, and the lack of significantly measured change may often be due to lack of statistical power rather than lack of change. Aggregation, the size of the sample, the sampling area, and the size of the community sampled can influence conclusions about the role of deterministic versus stochastic processes in ecosystems (Rahel et al. 1984, Ebeling et al. 1990, Rahel 1990), and coral reef fishes appear to fit this general pattern.

Across species, CVs of abundance were more variable at low population densities, with variation often 2 or 3 times larger than the means. Fishing reduces population densities and therefore increases the patchiness of the distributions. Detection associated with greater flight distances or movement of fish in fished reefs can also be expected to increase population and community variation (Kulbicki 1998, Willis et al. 2006). However, it is not inevitable that lower population densities increase the CV, as we observed a number of species with both low population densities and CVs. CVs were simply more unpredictable at low popula-

Table 6. Percentage change detectable for each species surveyed and the 3 families within different management areas with sample sizes of 4, 10, 20, and 30. Calculated for a power of 0.8 and with an alpha level of 0.05

Species	Fished				Unfished			
	Percentage change detectable				Percentage change detectable			
	n = 4	n = 10	n = 20	n = 30	n = 4	n = 10	n = 20	n = 30
Acanthuridae								
<i>Acanthurus nigrofuscus</i>	384	216	148	120	43	24	16	13
<i>Ctenochaetus striatus</i>	231	130	89	72	187	105	72	58
<i>Acanthurus nigricauda</i>	263	148	101	82	126	71	49	39
<i>Acanthurus triostegus</i>	348	196	135	109	327	184	126	102
<i>Naso annulatus</i>	254	143	98	79	223	125	86	69
<i>Zebrasoma scopas</i>	454	254	175	141	227	127	87	71
<i>Naso unicornis</i>					111	62	43	35
<i>Acanthurus leucosternon</i>					177	99	68	55
<i>Zebrasoma veliferum</i>	453	254	175	141	200	112	77	62
<i>Acanthurus lineatus</i>					327	182	126	102
<i>Ctenochaetus strigosus</i>					283	159	109	88
<i>Acanthurus dussumieri</i>					327	184	126	102
<i>Acanthurus xanthopterus</i>					452	254	174	141
Pomacentridae								
<i>Plectroglyphidodon lacrymatus</i>	25	14	10	8	188	106	72	59
<i>Chrysiptera unimaculata</i>	82	46	32	26	78	44	30	24
<i>Chromis weberi</i>	195	110	75	61	165	92	63	51
<i>Chromis dimidiata</i>	227	128	88	71	149	84	57	46
<i>Abudefduf sexfasciatus</i>	151	85	58	47	195	109	75	61
<i>Neopomacentrus azyron</i>	453	254	175	141	358	201	138	112
<i>Plectroglyphidodon dickii</i>					99	56	38	31
<i>Abudefduf vaigiensis</i>	297	167	114	93	62	35	24	19
<i>Dascyllus trimaculatus</i>	215	121	83	67	363	204	140	113
<i>Pomacentrus caeruleus</i>	195	110	75	61	243	136	94	76
<i>Amphiprion allardi</i>	392	220	151	122	267	150	103	83
<i>Stegastes fasciolatus</i>	218	122	84	68	176	99	68	55
<i>Abudefduf sparoides</i>	175	98	67	54	453	254	175	141
<i>Chromis nigrura</i>	452	253	174	141	168	94	65	52
<i>Amblyglyphidodon leucogaster</i>	454	254	175	141				
<i>Chrysiptera leucopoma</i>	178	100	69	55	283	159	109	88
<i>Pomacentrus sulfureus</i>	448	251	172	140	230	129	89	72
<i>Pomacentrus baenschi</i>					155	87	60	48
<i>Pomacentrus pavo</i>	453	254	175	141	448	251	172	140
<i>Dascyllus aruanus</i>	361	202	139	112				
<i>Chrysiptera annulata</i>	452	254	174	141				
<i>Plectroglyphidodon johnstionus</i>					453	254	175	141
<i>Lepidozygus tapeinosoma</i>	448	251	172	140	263	148	101	82
<i>Chrysiptera biocellata</i>	452	253	174	141				
<i>Stegastes nigricans</i>	448	251	172	140				
Scaridae								
<i>Scarus sordidus</i>	173	97	67	54	127	71	49	40
<i>Calotomus carolinus</i>	452	254	174	141	47	26	18	15
<i>Scarus frenatus</i>	317	178	122	99	37	21	14	12
<i>Scarus psittacus</i>	105	59	40	33	188	106	72	59
<i>Leptoscarus vaigiensis</i>					398	223	153	124
<i>Scarus ghobban</i>	453	254	175	141	452	253	174	141
<i>Scarus rubroviolaceus</i>	448	251	172	140	232	130	89	72
<i>Scarus niger</i>					262	147	101	82
<i>Scarus atrilunula</i>					224	126	86	70
<i>Scarus spp.</i>					448	251	172	140
<i>Scarus falcipinnis</i>					448	251	172	140
<i>Scarus russelli</i>					448	251	172	140
Juveniles	213	120	82	66	137	77	53	43
Acanthuridae	280	157	108	87	101	57	39	31
Pomacentridae	66	37	25	21	48	27	18	15
Scaridae	29	16	11	9	70	40	27	22

Table 7. Average of the species coefficients of variation for the studied fish groups for comparisons of field sampling in 1992 and 2003 and for 2 methods for estimating temporal variation

	Temporal variation			
	Total	Space	Direct comparison of means	Indirect (Total–Space)
Unfished				
Acanthuridae and Scaridae	192.8	129.0	122.3	63.8
Pomacentridae	132.5	87.3	101.2	45.2
All fish	161.9	107.6	111.5	54.3
Fished				
Acanthuridae and Scaridae	217.7	144.3	138.1	73.4
Pomacentridae	201.0	146.2	111.2	54.8
All fish	206.9	145.5	120.8	61.4
All reefs				
Acanthuridae and Scaridae	202.6	118.2	168.7	84.5
Pomacentridae	187.2	113.5	148.3	73.8
All fish	194.7	115.6	157.5	79.2

tion densities. Consequently, determining population change in many rare species will be difficult without large replication.

In some cases, experienced observers have been shown to bias estimates of fish length, transect width, and the flight distance of fish (Kulbicki 1998, Edgar et al. 2004, Harvey et al. 2004). These biases may be sufficiently consistent between observers that the relative effects are small (Williams et al. 2006). Nonetheless, the bias could influence outcomes for important aspects of ecology where absolute measures are required, such as of fish biomass and derived estimates of consumption and energy requirements. Kulbicki (1998) suggested that comparisons of reserve and non-reserve sites are biased by the flight response of fish in environments with different levels of human use. Our study suggests, however, that differences between fished and unfished sites can be due to reduced densities and higher population variation in unfished reefs.

Variation will increase as the size of the sampled area is reduced. Compared to many studies that sampled areas of 250 m² or less (Jennings et al. 1995, English et al. 1997), we used a relatively large area. Consequently, methods using smaller areas will have higher variation and more difficulty detecting differences and change without large replication (Samoilys & Carlos 2000). However, greater replication required less effort for smaller sample sizes, and it is not clear without further work which combination of sample size unit and replication for a given effort will yield the least variation.

Life history, ecological, and behavioral characteristics of fish species will also influence the ability to detect change. Life history characteristics such as

growth, longevity, recruitment variability, and population turnover rates will all affect responses to natural perturbations or cessation from fishing (Connell & Sousa 1983, McClanahan & Graham 2005, Wilson et al. 2006), and species maximum attainable length is a useful surrogate for many of these characteristics (Jennings et al. 1999). Movement pattern, the extent of aggregation into schools, or preferred habitat can greatly influence spatial variance (Ault & Johnson 1998, Graham et al. 2003), and this is highlighted by the sample sizes needed to detect change in some of the schooling planktivorous damselfish species. Movements relating to tidal and diurnal rhythms, seasonality, and the home range size can vary between species and with local geography (Galzin 1987, Zeller 1997, Kramer & Chapman 1999, Thompson & Mapstone 2002) and require standardization when possible to improve the chances of detecting real change.

CONCLUSIONS

There is inherent and near-instant variation in fish communities that makes it difficult to detect temporal change in most coral reef fish species using common field methods. This is probably due to a combination of the high movement, the patchy spatial distribution of many coral reef species, and some observer differences. Detecting differences over time by repeated sampling of sites will be most feasible for only a few of the most abundant species and for pooled measures such as community-level analyses, numbers of species, taxonomic families, and functional groups. Detection of species-level changes will be difficult unless changes >100% occur, but would be more likely without repeated site sampling because of higher within-site than between-site variation and fewer degrees of freedom. Because spatial variation confounds direct estimates of temporal change, the magnitude of change in species numbers over time is probably about half the estimates of past methods that directly compared means. We did detect significant community change in the 2 reefs over a 10 yr period, but the study sites were both influenced by a cessation and continuation of fishing and the tendency of species assemblages to diverge over time (Bengtsson et al. 1997). Temporal-change estimates that eliminate spatial variation suggest that where fishing effects are small, coral reef fish

are more stable than previous estimates. Future work will need to estimate the instantaneous variation in their samples before making reasonable estimates of temporal population variation.

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