

Seasonal trends and fish-habitat associations around Pari Island, Indonesia: setting a baseline for environmental monitoring

Hawis H. Madduppa · Sebastian C. A. Ferse ·
Unggul Aktani · Harry W. Palm

Received: 11 April 2011 / Accepted: 9 April 2012 / Published online: 28 April 2012
© Springer Science+Business Media B.V. 2012

Abstract Indonesia is the world's richest country regarding reef fish diversity. Nevertheless, the reef ichthyofauna of the Indonesian Archipelago remains poorly known, primarily due to a lack of sampling. Coral reefs in the Kepulauan Seribu Marine National Park close to the Indonesian capital Jakarta are under threat by many destructive activities that trigger a loss of

habitat and species diversity. This communication: (1) describes the reef fish community structure from three distinct reef habitats in the Pari Island group dominated by *Acropora* branching corals (ACB), foliose corals (CF) and massive corals (CM), using a number of community properties such as numerical abundance, species richness, diversity, and multivariate similarity; (2) examines the temporal variation of the fish community from the three habitats; and (3) discusses possible implications for the monitoring of qualitative changes in coral reef systems on small islands. During this study, a total of 13 536 individual fishes were counted, representing 205 species belonging to 36 families. In terms of species richness, Pomacentridae was the dominant fish family in ACB and CF sites (40 % and 48.6 %, respectively), and Labridae (27.4 %) was the dominant family in the CM plots. The most species-rich habitat was ACB with 125 species (with *Amblyglyphidodon curacao* as the most characteristic species), followed by CM and CF with 117 (*Thalassoma lunare*) and 79 species (*Pomacentrus alexanderae*), respectively. Average Shannon-Wiener diversity (ln basis) ranged from 2.0–2.9 (ACB), 2.4–3.1 (CF), and 2.1–3.0 (CM), with no significant difference between growth forms. Abundance, species richness and diversity showed significant seasonal variability, but the effects differed between habitats. Multivariate analysis of the reef fish community was able to detect significant differences between species composition and diversity of the reef fish community between sites with different coral growth forms at Pari Island, both when based on species abundances and

H. H. Madduppa (✉)
Marine Biological Laboratory,
Department of Marine Science and Technology (ITK),
Faculty of Fisheries and Marine Sciences,
Bogor Agricultural University (IPB),
Jl. Agatis No. 1,
Bogor 16680, Indonesia
e-mail: madduppa@daad-alumni.de

H. H. Madduppa
e-mail: madduppa@yahoo.com

S. C. A. Ferse
Leibniz Center for Tropical Marine Ecology (ZMT),
Fahrenheitstrasse 6,
28359 Bremen, Germany

U. Aktani
Department of Waters Resources Management (MSP),
Bogor Agricultural University (IPB),
Bogor 16680, Indonesia

H. W. Palm
Aquaculture and Sea-ranching,
Faculty of Agricultural and Environmental Sciences,
University Rostock,
Justus-von-Liebing Weg 6,
18059 Rostock, Germany

when aggregated according to trophic categories. It thus constitutes a useful tool to detect qualitative differences of the species-rich Indonesian coral reef ecosystems.

Keywords Biodiversity · Habitat preference · Trophic level · Coral triangle · Multivariate analysis · Fish-habitat association

Introduction

Coral reefs are tropical ecosystems that display high biodiversity, belong to the most attractive shallow-water ecosystems in the world. Fishes reach their greatest biodiversity in coral reef ecosystems (Allen and Werner 2002), particularly in Indonesia. Coral reefs in Indonesia harbour approximately 590 species of corals (Veron 2002) and over 2000 species of reef fish (Allen and Adrim 2003). While the reefs of Indonesia harbour one of the richest fish assemblages on the planet and sustain the livelihoods of millions of people, they are also among the most threatened by anthropogenic factors (Burke et al. 2011).

The coral reef structure and its complexity resulting from a high diversity of coral growth forms provide a variety of habitats for thousands of fishes (Luckhurst and Luckhurst 1978; Beukers and Jones 1998; Bellwood et al. 2005). Each coral species has different life-forms, closely related to the hydrological regime and sunlight exposure at the respective locality (Baker and Weber 1975; Pandolfi and Greenstein 1997), and coral reefs thus display a high spatial variability in terms of species composition and topographic complexity. Reef fish often cluster on specific corals, form distinct communities (Adrim and Hutomo 1989; Chabanet et al. 1997; Friedlander and Parrish 1998), and generally have limited movement compared to other marine vertebrates of the same size (Kramer and Chapman 1999). They utilize corals as a territory (Waldner and Robertson 1980; Patton 1994), source of food (Reese 1981), place of refuge (Carr and Hixon 1995), and reproduction (Almany et al. 2007).

Changes in the abundance of particular groups of fish or of fish community composition have been used as indicators for reef habitat quality (e.g. Hourigan et al. 1988; Reese 1993; Roberts et al. 1988). Spatial variability and complexity of coral reefs affect the trophic structure of the fish community. For instance, depletion in coral reefs has a direct effect to the

abundance of fishes which exclusively feed on coral (Halford et al. 2004). However, only few of the species found in a coral reef ecosystem depend specifically on scleractinian corals (Munday et al. 2007). On the other hand, a reduction of coral cover, either by natural or by anthropogenic factors, is often accompanied by increases in algal abundance (Diaz-Pulido and McCook 2002), which may trigger the appearance of herbivorous fishes (Wilson et al. 2006). Consequently, the presence or absence of specific indicator species can detect environmental impact and change. Due to their territorial behaviour, close association with the benthic habitat in reefs, conspicuousness, and abundance in reef fish communities, wrasses (Labridae), butterflyfishes (Chaetodontidae) and damselfishes (Pomacentridae) are considered the most useful indicator species for the assessment of coral reef conditions (e.g. Crosby and Reese 1996; Ormond et al. 1996; Lewis 1997a). Additional information can be derived from groups particularly susceptible to fishing pressure, such as groupers (Serranidae), or fulfilling key functional roles, e.g. parrotfishes (Scaridae) (Hodgson 1999). Several species live in close association with the colonies of branching corals (Patton 1994; Chabanet et al. 1997), e.g. *Chaetodon* (Pratchett et al. 2006), *Chromis* (Graham et al. 2006), *Dascyllus* (Lieberman et al. 1995), *Thalassoma* (Itzkowitz 1979), and *Pomacentrus* spp. (Bergman et al. 2000). Some members of other fish taxa show a similar strong association with the reef habitat. For example, Scaridae are generally associated with massive corals (Chabanet et al. 1997), as they feed on epilithic algae growing on flat calcareous surfaces (Bellwood and Choat 1990). Especially the availability of shelter sites of appropriate sizes is important for the distribution of coral reef fish (Friedlander and Parrish 1998).

The relationships between different fish species and their required habitats have been studied in great detail (e.g. Done 1982; Roberts and Ormond 1987; Chabanet et al. 1997; Friedlander and Parrish 1998). However, caused by difficulties to establish long-term observations that cover multiple years and/or long-term anthropogenic change, the effects that changes in the composition of coral habitats have on the structure of reef fish communities are less known. This is particularly true for Indonesia, where systematic, long-term coral reef monitoring efforts are largely absent. Sale (1977) has predicted that reef fish communities have an unstable structure at the species level, which

implies that species composition at a certain site may not return to its original state following natural or anthropogenic disturbance. While some later studies have observed reef fish communities to be largely resilient to moderate levels of habitat disturbance (Sano 2000; Booth and Beretta 2002), others found that gradual declines in habitat quality or major disturbances such as the widespread coral bleaching in 1998 can lead to considerable shifts in fish community composition (Jones et al. 2004; Bellwood et al. 2006). A thorough understanding of the coral reef ecosystems, especially of the associated fish fauna and its link to the benthic community, is thus critical for an improved management of these vital resources. So far, the reef fish community in the Indonesian Archipelago remains poorly studied compared to coral reef areas in neighboring countries, such as the Great Barrier Reef (Tomascik et al. 1997). This communication: (1) describes the reef fish community structure from three distinct Indonesian reef habitats in the Pari Island group (part of Kepulauan Seribu) dominated by *Acropora* branching corals (ACB), foliose corals (CF) and massive corals (CM), by using a number of community properties such as numerical abundance, species richness, diversity, evenness, multivariate composition and relative abundance of trophic categories; (2) examines the temporal variation of the fish community from these habitats; and (3) discusses possible implications of using fish community data for an improved monitoring of changes in coral reef habitat quality on small tropical islands. As few studies of the reef fish community from the area are available to date, the present study also sets a baseline for future monitoring efforts.

Material and methods

Study sites

Pari Island together with four other coral cays (Burung, Tikus, Kongsu, and Tengah Island) forms the Pari Island group in the southernmost part of the Kepulauan Seribu complex. It is located about 35 km north-northwest of Jakarta and 18 km from mainland Java (05°51'S and 106°37'E), with an approximate circumference of 4 km (Fig. 1). Pari Island is considered a fringing reef. While some studies of the coral community of Pari Island have been carried out in the 1980s (Brown and Suharsono

1990; Hoeksema 1991), the fish community of the area remains poorly studied. The platform on which the Pari Island group is situated has two large reef flat lagoons with a depth of approximately 6 m (Tomascik et al. 1997). Seaweed farming by local people is carried out in these lagoons. In the past, Kepulauan Seribu has experienced considerable impacts from blast fishing (Aktani 2003). Between 1920–2005, its coral composition has decreased due to long-term natural and anthropogenic stress (van der Meij et al. 2010). Bleaching resulting from ENSO (El Niño Southern Oscillation) events in Pari Island, followed by the death mainly of branching species of the genera *Acropora* and *Pocillopora*, was observed as early as the 1980s (Brown and Suharsono 1990). During the northwest monsoon from November to March, Pari Island experiences a 'wet' season which is characterized by a lot of rain, rough waves and wind, and a 'dry' season during the southeast monsoon (June to September) (Rees et al. 1999). Transitional seasons usually occur in October/November and April/May.

Data collection

The locations of the study sites were determined initially by manta tow and snorkelling, and observing the coral reef conditions of the representative areas (3–7 m depth). The study sites were selected based on size allowing 3 replicates and the predominance of distinct coral life-form categories (*Acropora* branching corals (ACB), foliose corals (CF) and massive corals (CM), Fig. 2). All sites were located along the southern reef edge of the Pari Island group (Fig. 1). At each sampling site, three replicate 5 × 5 m permanent quadrats were established, marked by a buoy, and their location recorded using GPS. The perimeter of each quadrat was marked permanently using stakes and nylon string. Replicate plots were approximately 10 m apart. The quadrats were placed parallel to the coastline at the selected sampling sites (ACB, CM, or CF).

During the first sampling period, the Permanent Quadrat method (PQ) was used to assess the sessile benthic fauna at the study sites. This method is a detailed observation method for quantitative and qualitative benthic sampling (English et al. 1997). Coral life-form categories were verified following English et al. (1997). To describe benthic cover, each quadrat (5 × 5 m) was divided into 25 individual 1 × 1 m units using string PVC quadrats, which yielded a total of

Fig. 1 Location of the Pari Island group, north of Jakarta, Java Island, Indonesia. The map below shows the position of Pari Island group relative to Jakarta. The location within Indonesia is shown in the inset on the lower left. The sampling sites will be referred to by their initials throughout the rest of the text (ACB, CM, and CF)

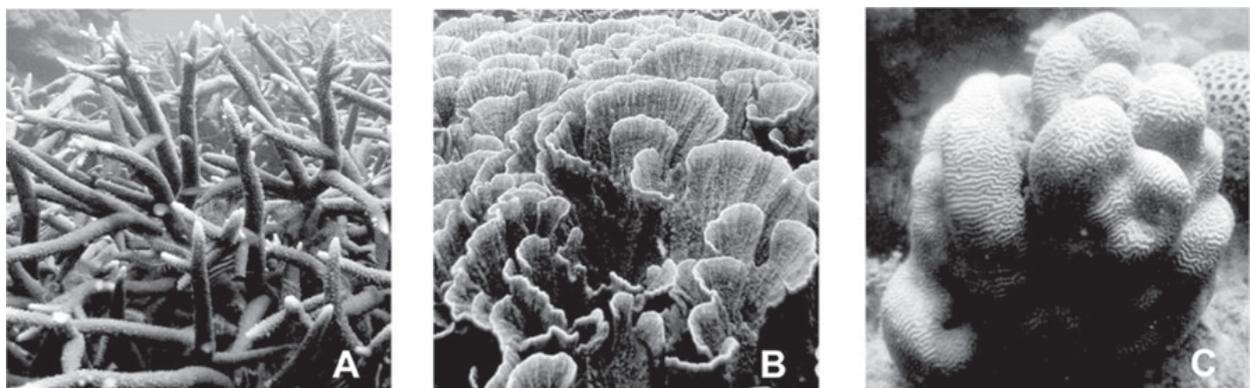
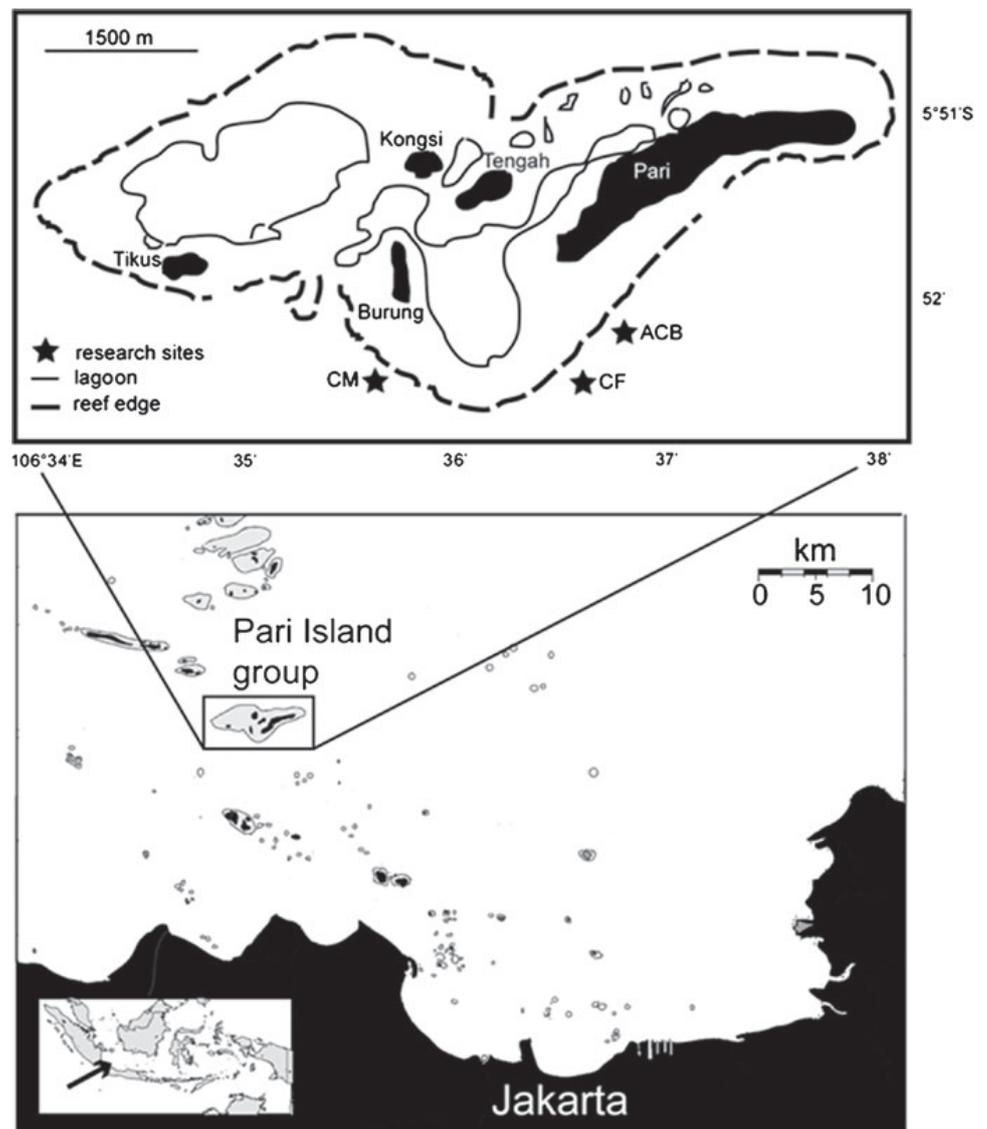


Fig. 2 Three categories of coral life-forms at the sampling area: (a) branching *Acropora* coral (ACB), (b) foliose coral (CF), and (c) massive coral (CM)

225 1×1 m units across the three replicates within each of the three habitat types. Each subunit was photographed using a Nikonos 5 underwater camera (20 mm lens). All images were processed with the software ImageJ (Abramoff et al. 2004). Photographic assessment of the habitat composition was conducted only once at the beginning of the study. However, no singular event that would have affected only particular transects (e.g. corallivore outbreak, anchor damage) was observed throughout the study. Based on visual estimation of the habitat during each underwater census, benthic cover was assumed to not have changed significantly throughout the study period.

Reef fish communities were assessed by underwater visual census (UVC) (English et al. 1997). In an attempt to reduce daily variability of fish density data (caused by differences in nocturnal and diurnal behaviour), sampling excluded the high activity periods of early morning and late afternoon (Colton and Alevizon 1981; English et al. 1997). Sampling was carried out consecutively at the different sites between 09:00 and 16:30 from August 2003 to May 2004. Each quadrat was surveyed once during each sampling time. During each census, the observer waited for at least 10 min before beginning with the record of fish data inside the PQT in order to allow the fishes to resume normal behaviour (Brock 1982; Halford and Thompson 1994). Fish counts were stationary, with the observer taking a position at the edge of the quadrat (consistent over consecutive samplings) that allowed for the best overview of the quadrat for counting. Only individuals within the quadrat, up to a height of 4 m above the substrate, were counted. The approximate duration of one fish census was limited to 15–20 min by using a watch for each transect. Each individual (cryptic and large pelagic species were excluded) was counted and identified to species level. Fish recruits up to a size of 3–5 cm (depending on species) were excluded from the counts. To study seasonal variability, a total of six observations were made during the late dry season (13.–14.08.2003, 19.–20.09.2003, 23.–24.10.2003), the rainy season (30.–31.12.2003, 5.–6.03.2004), and the early dry season (11.–12.05.2004). After data collection, reef fish identification was confirmed by using standard fish identification books (i.e. Randall et al. 1990; Kuitert 1992; Allen 2000). The trophic level of fish species was classified into one of five categories (carnivores, planktivores, omnivores, herbivores, and corallivores) using FishBase (Froese and Pauly 2010).

Data analysis

The average proportion of live coral cover at the three sites was compared using Pearson's chi-square statistic with the program JMP 7.0 (SAS Institute 2007). The community Shannon-Wiener diversity index H' was calculated on a ln basis (Shannon and Weaver 1949; Magurran 1988). Abundance, species richness and community diversity were compared among sites using repeated-measures ANOVA in the statistical package STATISTICA 7.0. All data met assumptions of normality (Kolmogorov – Smirnov test) and homogeneity of variances (HOV, Brown Forsythe test). In order to assess seasonal effects, general linear models with Standard Least Squares fitting were constructed in JMP. The parameters abundance, species richness and species diversity were included as response variables. Separate models were constructed for each site and parameter. The uneven number of sampling times per season precluded using a single categorical variable to account for effects of 'season'. As independent variables, the models thus contained two continuous binary dummy variables to account for seasons, and five binary dummy variables to account for individual sampling times. Due to the unbalanced design, individual effect tests could not be conducted, and the values from the model parameter estimation were used as indicators of significant effects.

Multivariate analysis of the fish community data was conducted using the program PRIMER 5.2.9 (Kruskal 1964; Clarke and Gorley 2001). Fish abundance and trophic category data were fourth-root transformed prior to analysis to reduce the influence of some overly abundant species and give more weight to rare species while retaining the information value of relative abundances, an approach frequently used in the multivariate analysis of community data (Field et al. 1982; Clarke and Green 1988). Multivariate analysis of similarity (ANOSIM) based on both the entire fish community and on trophic categories was used to determine differences between sites. A two-way crossed design with the factors treatment and sampling month was used to limit permutations to take place within the same treatment (for time effects) and sampling month (for treatment effects). The maximum number of permutations was set at 999.

SIMPER (similarity percentages – species contribution) was used to determine fish species characteristic for each growth form (Clarke 1993). Data were

standardized and fourth-root transformed (see above). The cut-off percentage used was 90 %.

Non-metric Multidimensional Scaling (MDS) was performed to visualize differences in fish communities from the different coral life forms (Shepard 1962; Kruskal 1964). MDS was based on Bray-Curtis similarities, and 100 restarts were used for the calculations.

Results

Reef fish community structure in different habitats

The average benthic community composition at the three sampling sites is shown in Table 1. *Acropora* branching corals covered 68.5 ± 8.7 % of the ACB plots, while the coverage of foliose and massive corals in the CF and CM plots was 70.0 ± 2.0 % and 47.1 ± 11.3 %, respectively. The coverage with other live hard corals was low at all sites, but dead corals made up almost one quarter of the substrate in the CM plots. The relative amount of live coral compared to other substrate differed significantly between the three sites (Pearson chi-square, $\chi^2 = 13.31$, $p = 0.0013$, $df = 2$).

A total of 13 536 individual fishes were counted, belonging to 205 species and 36 families. For the *Acropora*-branching coral plots, a total of 125 fish species was recorded, while a total of 79 fish species was observed in the foliose coral plots, and a total of 117 fish species was recorded from the massive coral

Table 1 Benthic community cover per life-form category (in % \pm SE, ACB Branching *Acropora* Coral, CF Foliose Coral, CM Massive Coral, HC Hard Corals, DC Dead Corals, DCA Dead Coral with Algae, SP Sponge, SC Soft Corals, OT Others)

CATEGORIES	ACB	CF	CM
ACB ^a	68.5 \pm 8.7	–	–
CF ^a	–	70.0 \pm 2.0	–
CM ^a	–	–	47.1 \pm 11.3
Other HC	7.2 \pm 1.5	8.2 \pm 2.2	4.3 \pm 0.3
DC	1.1 \pm 0.5	0.6 \pm 0.4	13.7 \pm 4.5
DCA	4.0 \pm 2.4	6.5 \pm 1.1	13.7 \pm 5.5
SP	0.3 \pm 0.2	0 \pm 0	0 \pm 0
SC	0 \pm 0	0.8 \pm 0.5	1.8 \pm 0.3
OT	0.9 \pm 0.1	0.5 \pm 0.4	2.7 \pm 1.2
Abiotic	18.0 \pm 7.3	13.3 \pm 2.7	16.7 \pm 7.4

^a only shown for the plots in which this growth form dominated

plots. The composition of the 5 most diverse fish families that were observed in the ACB, CF, and CM plots is given in Table 2. The most abundant families in the ACB plots were the Pomacentridae (damselfishes), followed by the Labridae (wrasses). The most abundant family in the CF plots again were the Pomacentridae (damselfishes), followed by Labridae (wrasses) and Chaetodontidae (butterflyfishes). The most abundant family in the CM plots were the Labridae (wrasses), followed by Pomacentridae (damselfishes) and Scaridae (parrotfishes). Overall, the most common families were the Pomacentridae and Labridae, a pattern also observed at other locations in Indonesia (Ferse 2008).

No significant differences in fish abundance, diversity or species richness were found between the habitat types (Table 3). Fish abundance ranged from 139 ± 7 to 490 ± 67 ind/25 m², the diversity index (H') ranged between 2.04 ± 0.22 and 3.07 ± 0.04 , and species richness ranged from 16.3 ± 1.2 to 31.7 ± 1.5 species/25 m² over the entire study period.

Temporal variation of the fish community from different habitats

The temporal variation in Shannon-Wiener diversity indices of the fish communities, average species richness, and average fish abundance is shown in Fig. 3. Fish abundance, species richness and diversity all varied significantly over the study period, and the effect of time on abundance and species richness differed between habitats (Table 3). The increase from the wet to the early dry season was significant for all three parameters in the *Acropora*-branching coral plots (Table 4). There were two sampling times with a slight increase in species richness, in late dry season 2003 and early dry season 2004 (transition periods). The different sampling periods can be characterized as follows. In all plots, fish abundance, species richness and diversity value were high in the early dry season, while in the rainy season, they were low (Table 5). In the massive coral plots, season did not have a significant effect on fish abundance (Table 4), but species richness and diversity were significantly lower during the wet than during the dry seasons (Table 5). In terms of trophic groups, the CF plots showed little changes throughout the year, while the other two sites exhibited more temporal variability (Fig. 4).

Table 2 Composition of the 5 most diverse fish families at the three study sites

Fish Family	Common Name	ACB		CF		CM	
		Species	% of total species	Species	% of total species	Species	% of total species
Pomacentridae	Damselfishes	42	40.0	36	48.6	21	22.1
Labridae	Wrasses	23	21.9	20	27.0	26	27.4
Apogonidae	Cardinalfishes	10	9.5				
Chaetodontidae	Butterflyfishes	8	7.6	4	5.4		
Scaridae	Parrotfishes					16	16.8
Serranidae	Groupers					10	10.5
Lutjanidae	Snappers			4	5.4	5	5.3
Nemipteridae	Spinecheeks	5	4.8	3	4.1		

Multivariate analysis based on fish abundance and trophic categories

Fish community composition differed significantly between the three habitat types (Table 6). A significant effect was found both in terms of species composition and in terms of trophic categories. Three species living in close association with *Acropora* corals, *Amblyglyphidodon curacao*, *Chromis analis* and *Abudefduf sexfasciatus* (Pomacentridae), were most characteristic for this habitat (Table 7). *Pomacentrus alexanderae* (Pomacentridae), *Amblyglyphidodon curacao* (Pomacentridae) and *Labroides dimidiatus* (Labridae) were the species most characteristic for coral foliose habitat, while in the massive coral habitat, *Thalassoma lunare* (Labridae), *Caesio cuning* (Caesionidae) and *Scarus chameleon* (Scaridae) were the most characteristic species (Table 7).

Table 3 Results of repeated-measures ANOVA for abundance, species richness, and diversity of fish assemblages (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, n.s. not significant)

Variable	Factor	F	Df	p
Abundance	Site	0.3442	2	n.s.
	Month	9.9530	5	***
	Month*Site	2.7922	10	*
Species Richness	Site	2.0749	2	n.s.
	Month	11.9314	5	***
	Month*Site	3.4401	10	**
Shannon-Wiener index (H')	Site	3.18	2	n.s.
	Month	5.73	5	***
	Month*Site	1.62	10	n.s.

In terms of trophic groups, the ACB and CF plots were initially relatively similar (Fig. 4). In the CF plot, omnivores were the most dominant group throughout the year. In the ACB plots, omnivores dominated initially, but were replaced by carnivores as the most dominant group from January on. In the CM plots, herbivores were relatively more abundant than in the other plots, and trophic composition was more variable throughout the year (Fig. 4).

The significant differences in fish communities between habitat types in terms of species abundance and trophic composition detected by the ANOSIM (Table 5) are visible in the MDS plots (Fig. 5). The community samples from CM clearly separate from the ACB and CF samples, while the latter are clustered more closely together. However, this pattern was more pronounced for fish abundance, while community composition based on trophic categories showed a less clear separation, reflecting the lower ρ value of the ANOSIM for this parameter (Table 6).

Discussion

Reef fish community structure

The present study describes the reef fish community at a small island ecosystem close to the Kepulauan Seribu Marine National Park in Indonesia. The present study data confirm the high species richness of coral reef fishes in the Indonesian part of the coral triangle. Species richness at Pari Island (205 species) is in a range similar to that observed for other Indonesian localities, such as the Togean Islands and Weh Island (Allen and

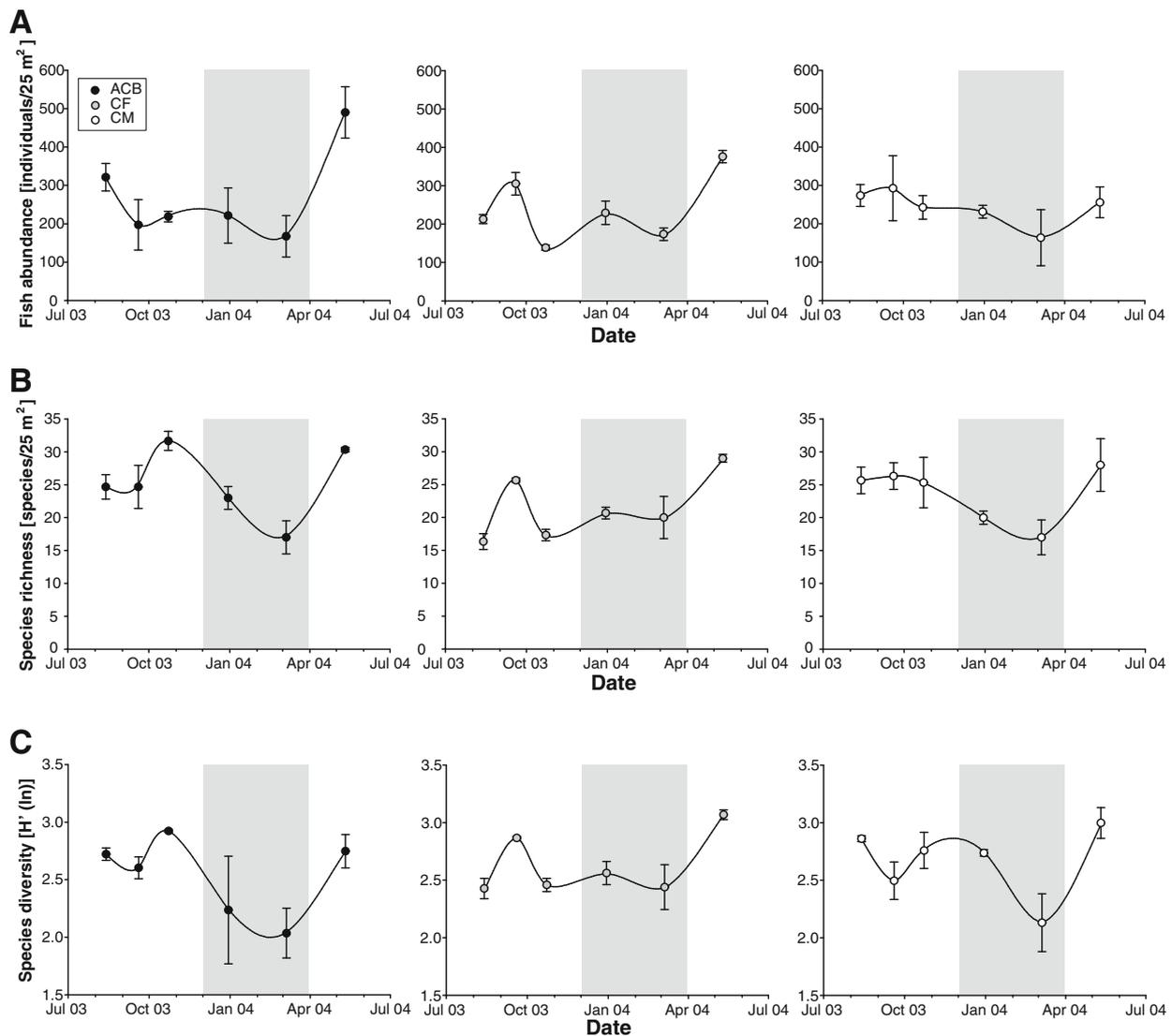


Fig. 3 Fluctuation of the average value of (a) fish abundance, (b) species richness, and (c) species diversity (Shannon-Wiener Index; ln basis) of fish assemblages at the sampling sites. The

shaded areas indicate the months of the rainy season. Polynomial trend lines are fitted to the data to indicate trends over time

Werner 2002). However, these values are distinctly higher than those reported from other marine tropical ecosystems, such as the Marshall Islands (178) or the Caribbean (122) (Gladfelter et al. 1980), and the Gulf of Aqaba in the Red Sea (121) (Khalaf and Kochzius 2002). The presence of a high biodiversity of corals around Pari Island, combined with a complete tropical coastal ecosystem in the area (consisting of mangroves, seagrass beds and associated coral reefs), helps to explain the general high species richness in the study area.

At the level of the experimental plots, habitat appears to have played a different role with regard to the fish community. The growth form of corals influences the structural complexity of the benthic habitat,

which in turn can influence the associated fish community (Gratwicke and Speight 2005a). A positive correlation with the structural complexity of a coral reef habitat has been reported for fish abundance (e.g. Friedlander et al. 2003; Chittaro 2004; Walker et al. 2009), the number of species (e.g. Gratwicke and Speight 2005b; Dominici-Arosemena and Wolff 2006; Wilson et al. 2007), biomass (e.g. Friedlander et al. 2003), and species diversity (e.g. Molles 1978; McCormick 1994; Öhman and Rajasuriya 1998). However, in the present study, no differences were found in abundance, species richness and diversity between the more structurally complex habitat dominated by branching *Acropora* corals, and the foliose

Table 4 Results of the general linear model testing for seasonal effect on fish assemblages in the three habitats. Significant differences are indicated by an asterisk

Parameter	Season	ACB		CF		CM	
		<i>t</i> -ratio	<i>p</i>	<i>t</i> -ratio	<i>p</i>	<i>t</i> -ratio	<i>p</i>
Abundance	late dry vs. wet	1.97	0.0723	1.36	0.1983	1.50	0.1599
	late dry vs. early dry	2.16	0.0519	5.64	0.0001*	0.24	0.8139
	wet vs. early dry	4.13	0.0014*	7.00	<0.0001*	1.26	0.2325
Species richness	late dry vs. wet	2.62	0.0226*	1.71	0.1128	2.19	0.0490*
	late dry vs. early dry	1.93	0.0772	5.91	<0.0001*	0.59	0.5665
	wet vs. early dry	4.55	0.0007*	4.20	0.0012*	2.78	0.0167*
Diversity	late dry vs. wet	2.17	0.0505	0.08	0.9361	3.46	0.0047*
	late dry vs. early dry	0.08	0.9354	4.50	0.0007*	0.64	0.5312
	wet vs. early dry	2.26	0.0435*	4.41	0.0008*	4.11	0.0015*

and massive coral plots. Although the three habitat types arguably differed in terms of their structural complexity (branching corals offering more microhabitats than massive corals), this difference was not reflected in the univariate fish community parameters. Niche availability or habitat diversity thus does not appear to have played a role at the scale of the experimental plots. Similarly, the differences in the amount of live coral cover between the three sites did not have a manifest impact on any of the univariate parameters. Their usefulness as indicators for habitat quality thus appears limited when derived from plots of the size used in this study. Furthermore, it indicates that at the level of the study plots, the fish communities were not structured by habitat-mediated factors such as predation impact or available space, but that different factors such as recruitment or migration were playing a stronger role.

On the other hand, specific fish families were particularly associated with certain habitat types. As shown, Scaridae and Lutjanidae were found mainly in the massive coral site, while Lutjanidae and Apogonidae were observed only in the foliose and branching *Acropora* coral sites, respectively. Habitat quality, rather than availability of space and shelter, resulted in a different composition of the community in the three habitat types. Thus, differences in the type of coral coverage may not be detected by an assessment of fish diversity or abundance, while they may at the same time be visible in terms of the community composition. Habitat fidelity appears to have been highest in the CF plots, which had low variability in abundance and species richness during each census, and lowest in the ACB plots, where variability was highest. However, this may at least partially be a result of higher small-scale heterogeneity in the ACB plots – in this case,

Table 5 Seasonal values of fish abundance, species richness and diversity (mean ± SE)

Habitat	Season	Abundance (ind/25 m ²)	Species richness (species/25 m ²)	Diversity (H')
ACB	Late dry	245.67±38.36	27.00±2.20	2.75±0.05
	Rainy	194.33±62.84	20.00±2.12	2.14±0.34
	Early dry	490.00±66.91	30.33±0.33	2.75±0.14
CF	Late dry	219.00±16.07	19.78±0.81	2.58±0.05
	Rainy	201.50±23.40	20.33±2.05	2.50±0.15
	Early dry	376.00±16.07	29.00±0.58	3.07±0.04
CM	Late dry	269.78±48.05	25.78±2.63	2.71±0.12
	Rainy	197.50±44.90	18.50±1.82	2.43±0.14
	Early dry	256.00±39.95	28.00±4.00	3.00±0.13

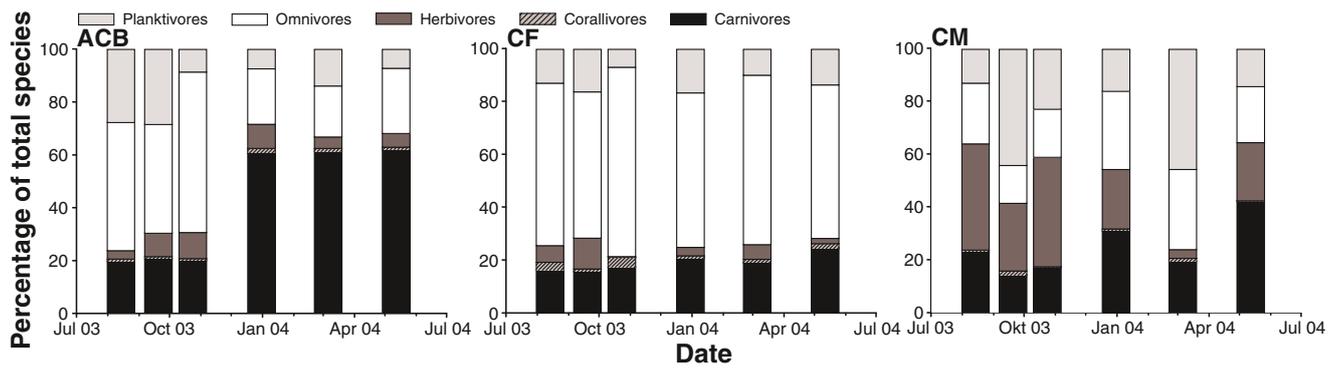


Fig. 4 Distribution and mean composition of reef fish at the sampling sites based on trophic categories

using plots larger than $5 \times 5 \text{ m}^2$ may have resulted in less instantaneous variability. However, as shown by the similar seasonal trends in all plots and the high seasonal compared to instantaneous variation, the effect of plot size seems small compared to temporal and site-specific effects.

A significant correlation was found between the community composition and coral habitat type. The

specialization of fish according to the coral growth form is of great interest for coral reef ecologists, especially concerning the connection between the fishes and their feeding habit (Randall 1974; Hourigan et al. 1988; Cox 1994). Feeding specialization among coral fishes can reduce competition within a reef (Gladfelter and Johnson 1983; Ross 1986), thus enabling higher species diversity, and plays an important

Table 6 Results of a crossed two-way ANOSIM within sites based on abundance of all species and trophic categories ($*p < 0.05$, $**p < 0.01$, *n.s.* not significant)

Relative abundance					Trophic categories				
Test	Factor	Test pairs	ρ	p (ρ)	Test	Factor	Test pairs	ρ	p (ρ)
Global pairwise	Site		0.612	**	Global pairwise	Site		0.325	**
		ACB, CF	0.383	**			ACB, CF	0.278	**
		ACB, CM	0.778	**			ACB, CM	0.315	**
		CF, CM	0.691	**			CF, CM	0.444	**
Global pairwise	Time		0.252	**	Global pairwise	Time		0.175	**
		Aug, Sep	0.580	**			Aug, Sep	0.099	<i>n.s.</i>
		Aug, Oct	0.358	*			Aug, Oct	0.309	<i>n.s.</i>
		Aug, Dec	0.580	**			Aug, Dec	0.284	**
		Aug, Mar	0.642	**			Aug, Mar	0.358	*
		Aug, May	0.235	<i>n.s.</i>			Aug, May	0.469	**
		Sep, Oct	0.358	*			Sep, Oct	0.062	<i>n.s.</i>
		Sep, Dec	0.111	<i>n.s.</i>			Sep, Dec	0.000	<i>n.s.</i>
		Sep, Mar	0.346	*			Sep, Mar	0.086	<i>n.s.</i>
		Sep, May	0.025	<i>n.s.</i>			Sep, May	0.284	*
		Oct, Dec	-0.148	<i>n.s.</i>			Oct, Dec	0.062	<i>n.s.</i>
		Oct, Mar	0.481	**			Oct, Mar	0.346	*
		Oct, May	0.185	<i>n.s.</i>			Oct, May	0.346	*
Dec, Mar	0.272	<i>n.s.</i>	Dec, Mar	0.099	<i>n.s.</i>				
Dec, May	-0.099	<i>n.s.</i>	Dec, May	0.049	<i>n.s.</i>				
Mar, May	0.148	<i>n.s.</i>	Mar, May	0.346	**				

Table 7 Composition of 10 most high species contribution within each sampling site using SIMPER (Similarity Percentages – Species contribution)

Species per site	Av. Abundance	Av. Similarity	% Contribution	Cumulative %
ACB, average similarity: 27.46				
<i>Amblyglyphidodon curacao</i>	14.61	2.88	10.5	10.5
<i>Chromis analis</i>	13.89	2.27	8.27	18.77
<i>Abudefduf sexfasciatus</i>	15.22	1.95	7.11	25.88
<i>Scolopsis bilineatus</i>	4.5	1.41	5.15	31.03
<i>Thalassoma lunare</i>	4.83	1.21	4.42	35.45
<i>Chaetodon octofasciatus</i>	2.72	1.19	4.35	39.8
<i>Labroides dimidiatus</i>	2.89	1.11	4.05	43.85
<i>Chromis atripectoralis</i>	5.89	1.08	3.92	47.78
<i>Abudefduf vaigiensis</i>	9.06	0.87	3.15	50.93
<i>Chaetodontoplus mesoleucus</i>	2.06	0.84	3.05	53.98
CF, average similarity: 40.37				
<i>Pomacentrus alexanderae</i>	38.56	6	14.86	14.86
<i>Amblyglyphidodon curacao</i>	19.89	4.84	11.99	26.85
<i>Labroides dimidiatus</i>	4.83	3.48	8.62	35.47
<i>Abudefduf sexfasciatus</i>	16.44	2.91	7.22	42.69
<i>Chaetodon octofasciatus</i>	4.39	2.36	5.85	48.53
<i>Thalassoma lunare</i>	6.39	1.72	4.26	52.79
<i>Halichoeres purpurascens</i>	5.56	1.55	3.83	56.63
<i>Neoglyphidodon thoracotaeniatus</i>	6.89	1.4	3.46	60.09
<i>Chromis atripectoralis</i>	8.28	1.37	3.38	63.47
<i>Dischistodus prosopotaenia</i>	5.39	1.24	3.06	66.54
CM, average similarity: 28.47				
<i>Thalassoma lunare</i>	6.17	2.66	9.33	9.33
<i>Caesio cuning</i>	22.39	2.48	8.71	18.04
<i>Scarus chameleon</i>	7.72	1.79	6.29	24.33
<i>Scarus forsteni</i>	11	1.63	5.73	30.05
<i>Chaetodon octofasciatus</i>	2	1.27	4.48	34.53
<i>Amblyglyphidodon curacao</i>	6.17	1.23	4.32	38.85
<i>Pomacentrus alexanderae</i>	8.22	1.21	4.26	43.11
<i>Abudefduf sexfasciatus</i>	7.22	1.18	4.15	47.26
<i>Labroides dimidiatus</i>	2.56	1.16	4.09	51.35
<i>Scolopsis bilineatus</i>	3.83	1.06	3.71	55.07

role for the structure of the fish community. A positive relationship has been described for species that depend on coral for food or shelter, such as corallivorous chaetodonts (Cox 1994), with other groups being more related to variables such as water depth or algal abundance (Nanami et al. 2005; Feary et al. 2007a). While the fish diversity was high at all sampled sites, there was a clear difference in species composition according to the trophic categories. Most similar were the

sites ACB and CF, which had relatively similar structural complexity, where the fish community mainly consisted of carnivorous, omnivorous and planktivorous fish. At CM, a high number of herbivorous and planktivorous fish was observed. This would characterize the ACB site as a refuge for mainly carnivorous fish, CF as habitat of omnivorous fish, and CM for herbivorous and planktivorous fish, with some migration among habitats. The present high composition of

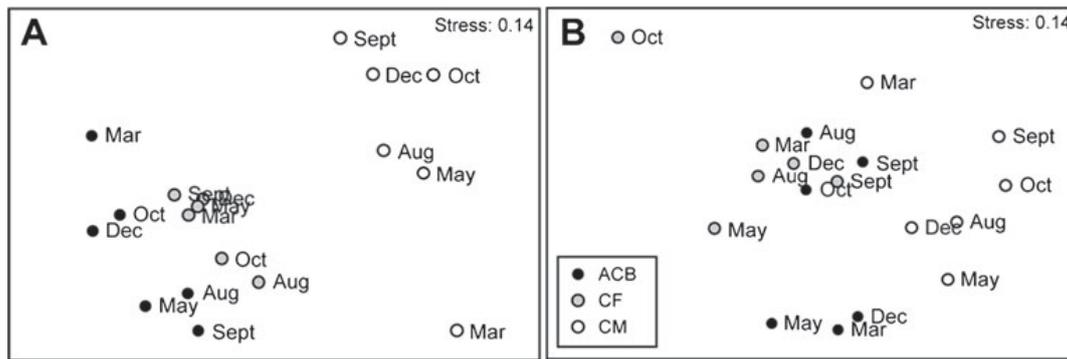


Fig. 5 MDS plot of fish communities at the Pari Island, showing pattern of association among 205 species based on abundance (a) and trophic categories (b) during the entire study period among sites

herbivorous fishes in the CM plots might be explained by the high percentage of dead coral and algae, attracting herbivores such as parrotfish. Similarly, reef zooplankton shows an affinity for particular substrate types (Allredge and King 1977), which could explain the differences in the relative abundance of planktivores between sites. However, while there was a correlation between habitat types and fish community, it is difficult to infer causality from this, as all plots from one site were of the same habitat type. Factors such as water currents and visibility may influence both the coral species composition (Jokiel 1978) as well as the associated fish fauna (Williams 1991). The fish fauna in the CM habitat mainly consisted of species that are associated with reefs within a high energy (i.e. currents and wave exposure) environment. As shown by the ANOSIM and MDS plots, the highest difference in community composition was between this site and the ACB and CF sites, both of which were located within a relatively low energy environment. Thus, both habitat and fish communities in this study may be the result of environmental factors acting at the respective sites. However, as shown in studies simultaneously covering a range of environmental variables and habitat types, benthic community composition plays a significant role in shaping the associated fish community (e.g., Nguyen and Phan 2008), and it is thus likely that habitat played a similar strong role in shaping the fish community here.

Temporal variation of the fish community from different habitats

Although the assessed univariate community parameters could not clearly distinguish between the three sampling sites, clear differences were observed

between the dry and the rainy season. Fish communities can vary considerably according to seasonal variation (Aktani 2003; Chittaro and Sale 2003). The high species richness and abundance of reef fishes in October 2003 and May 2004 might be caused by the transitional monsoon, which features moderate physical environmental conditions in comparison to the Northwest/Southeast Monsoon (dry season). By contrast, species richness and diversity as well as abundance decreased during the West Monsoon (rainy season), when environmental conditions were rougher. Within the dry season and in the transition period preceding and following it, more fishes and fish species were observed on all sites. At Pari Island, the rainy season causes heavy winds and waves that cause high turbidity at the sampling sites, while the dry season is dominated by weak currents and clear water.

Several factors may have contributed to the observed seasonal patterns. The observed increases in periods of higher visibility may have partially been an observer-induced bias. Sale and Douglas (1981) concluded that the higher number of species and individuals recorded in some of their censuses was at least partially caused by increased water clarity. However, Bohnsack and Bannerot (1986) did not observe any significant effects of visibility on abundance or species richness. Thus, the observed variation might be caused by seasonal migration of some species (such as Acanthuridae and Carangidae) that are not limited to a specific territory or habitat, resulting in different species numbers and abundances of the fish community. Chittaro and Sale (2003) found substantial seasonal changes in fish abundance in an Australian fish community, caused mainly by temporal variation in herbivorous and carnivorous species. However, Acanthuridae were only observed during the October

and December census in the ACB and CM plots. Similarly, Carangidae were only observed in October in the CM plots. These two groups may be classified as transitional species, or migrating species. Yet, they do not account for the high abundance and species richness observed in June. Rather, this peak may have been the result of recruitment pulses and post-settlement migration. Post-settlement movements can play a significant role in temporal patterns in community composition (Lewis 1997b). Even though small recruits were not included in the counts, seasonal recruitment pulses are still likely to introduce temporal patterns in the abundance of particular species. In a study in Sulawesi/Indonesia, strong recruitment pulses of labrids and pomacentrids were observed in May/June (Ferse 2008). Juveniles of many fish species utilize the shelter provided by live coral, and are often associated with more heterogeneous coral growth forms (e.g., Feary et al. 2007b). An indicator for seasonal recruitment is found in the fact that abundance differed between seasons in the branching and foliose coral habitat, while differences were not significant in the massive coral site, which also featured a higher amount of dead coral.

Implications for an improved monitoring of environmental change on small tropical islands

Coral reef fishes have been used as an indicator for environmental degradation and influence in different tropical ecosystems (Bortone and Davis 1994; Harmelin et al. 1995; Jones and Kaly 1996; Öhman and Rajasuriya 1998; Chovanec et al. 2003). In the present study, a number of fish species exhibited a strong relation to a particular habitat type, i.e. to branching Acroporids (e.g., *Chromis analis*), massive corals (e.g., *Scarus chameleon*, *Scarus forsteni*), and foliose corals (e.g., *Pomacentrus alexanderae*). This could have implications for an improved monitoring of environmental change in the region. The use of corallivorous species as bioindicators could be considered to monitor the health of coral reefs. For instance, *Chaetodon octofasciatus*, which in the present study occurred in all of the study plots, has been shown to be highly correlated with reefs dominated by live *Acropora* in other parts of the Kepulauan Seribu Marine National Park (Madduppa 2006). Pratchett et al. (2006) could demonstrate that extensive coral depletion can have a major effect on the abundance of butterflyfishes, which rely on hard

corals for food and are limited in their ability to utilize alternate prey types. Even though the percentage of corallivorous species is small in proportion to the total fish community (Findley and Findley 2001), members of this family have been considered by many authors as biological indicator for coral reef health (e.g. Crosby and Reese 1996; Öhman et al. 1998a; Kulbicki et al. 2005). The appearance of scarids in only the massive coral plots, which had the lowest amount of live coral but the highest amount of dead coral and algae, would make them a candidate as an indicator species of environmental degradation. On the other hand, due to their grazing activity, parrotfishes are an important group for reef resilience (Bellwood et al. 2004), and they can be particularly vulnerable to overfishing (e.g., McClanahan 1994). Thus, the use of parrotfish as environmental indicators should be treated highly context-specific. However, by using a multivariate approach that combines assessments of a number of key groups that fulfil important ecological functions and are associated with a particular type of habitat, fish community data can serve as a valuable tool in judging habitat quality. Chovanec et al. (2003) suggested that associated coral reef organisms such as fishes are a crucial indicator of the ecological integrity of the ecosystems at different scales due to their complex habitat requirements. Furthermore, Raymundo et al. (2009) were able to show that functionally diverse fish communities are able to increase the resilience of the coral reef ecosystem e.g. in terms of susceptibility to disease. Therefore, using fishes as bioindicators represents a good monitoring tool especially with regard to anthropogenic factors.

The multivariate analysis of the reef fish community was able to detect differences between the composition of the coral reef fish community associated with different habitat types at Pari Island, both when based on species abundances and when aggregated according to trophic categories. On the other hand, traditional univariate measures, such as fish abundance and species diversity, were able to show seasonal changes that were not consistently detected by multivariate analysis, underlining the importance of selecting appropriate variables and tools depending on the factor to be assessed. In conclusion, the present results from Pari Island demonstrate that the fish community constitutes a useful bioindicator for environmental change in small island coral reef ecosystems. While the detection of high functional diversity of the fish community, a factor important for reef resilience (Bellwood et al. 2004), requires a more thorough

assessment, resource constraints may necessitate focusing the census protocol on fewer selected species. Based on the present study results, labrids and pomacentrids, together with serranids, chaetodonts and scarids, are suggested to be included in monitoring programs in the region as indicator species, as they combine species closely associated with particular substrate types, fulfilling important ecological functions, and being susceptible to fishing pressure. The reef environments of Indonesia are facing increasing anthropogenic pressures, as well as a multitude of management interventions and restoration efforts. The results of the current study should be seen as a baseline study for the reef environment of the Kepulauan Seribu, since it is the first detailed study in the region. The results furthermore emphasize that future studies are critical to test what species are the best indicators of coral reef health in the Pari Island group. Future monitoring should be repeated at least twice per year to cover seasonal changes. In addition, more studies of reef fish communities and habitat characteristics throughout the region are needed to document environmental changes over time and assess the effectiveness of management and restoration measures.

Acknowledgments We wish to thank the following institutions and people for their assistance and help during this study. Marine Biological Laboratory – IPB for the logistic support, members of Fisheries Diving Club – IPB (Beginer Subhan, Mikael Prastowo, Malvin, Rd Ade Komaruddin, Marlen and Fahad) and Agdalena for all their help in the field work. We thank Adriani Sunuddin for fruitful discussion, and Werner Wosniok for statistical advice. The study was supported by the Faculty of Fisheries and Marine Sciences, Bogor Agricultural University (HHM, Marine Science Special Training Course/MST), and the German Academic Exchange Service (DAAD) Guest Lectureship Program (HWP).

References

- Abramoff MD, Magelhaes PJ, Ram SJ (2004) Image Processing with ImageJ. *Biophoton Int* 11:36–42
- Adrim M, Hutomo M (1989) Species composition, distribution and abundance of Chaetodontidae along reef transects in the Flores Sea. *Neth J Sea Res* 23:85–93
- Aktani U (2003) Fish communities as related to substrate characteristics in the coral reefs of Kepulauan Seribu Marine National Park, Indonesia, five years after stopping blast fishing. Dissertation, University of Bremen, Bremen, Germany
- Allredge AL, King JM (1977) Distribution, abundance, and substrate preferences of demersal reef zooplankton at Lizard Island Lagoon, Great Barrier Reef. *Mar Biol* 41:317–333
- Allen GR (2000) Marine fishes of South-East Asia. Periplus Editions (HK) Ltd, Singapore
- Allen GR, Adrim M (2003) Coral reef fishes of Indonesia. *Zool Stud* 42:1–72
- Allen GR, Werner TB (2002) Coral reef fish assessment in the ‘coral triangle’ of Southeastern Asia. *Environ Biol Fish* 65:209–214
- Almany GR, Berumen ML, Thorrold SR, Planes S, Jones GP (2007) Local replenishment of coral reef fish populations in a marine reserve. *Science* 316:742–744
- Baker PA, Weber JN (1975) Coral growth rate: variation with depth. *Earth Planet Sci Lett* 27:57–61
- Bellwood DR, Choat JH (1990) A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. *Environ Biol Fish* 28:189–214
- Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. *Nature* 429:827–833
- Bellwood DR, Hughes TP, Connolly SR, Tanner J (2005) Environmental and geometric constraints on Indo-Pacific coral reef biodiversity. *Ecol Lett* 8:643–651
- Bellwood DR, Hoey AS, Ackerman JL, Depczynski M (2006) Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. *Glob Change Biol* 12:1587–1594
- Bergman KC, Öhman MC, Svensson S (2000) Influence of habitat structure on *Pomacentrus sulfureus*, A Western Indian Ocean reef fish. *Environ Biol Fish* 59:243–252
- Beukers JS, Jones GP (1998) Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia* 114:50–59
- Bohnsack JA, Bannerot SP (1986) A stationary visual census technique for quantitatively assessing community structure of coral reef fishes, NOAA Technical Report NMFS 41. National Marine Fisheries Service, National Oceanic and Atmospheric Administration (NOAA)
- Booth DJ, Beretta GA (2002) Changes in a fish assemblage after a coral bleaching event. *Mar Ecol Prog Ser* 245:205–212
- Bortone SA, Davis WP (1994) Fish intersexuality as indicator of environmental stress. *BioScience* 44:165–172
- Brock RE (1982) A critique of the visual census method for assessing coral reef fish populations. *Bul Mar Sci* 32:269–276
- Brown BE, Suharsono (1990) Damage and recovery of coral reefs affected by El Niño related seawater warming in the Thousand Islands, Indonesia. *Coral Reefs* 8:163–170
- Burke L, Reynter K, Spalding M, Perry A (2011) Reefs at risk revisited. World Resources Institute (WRI), Washington, DC
- Carr M, Hixon M (1995) Predation effects on early post-settlement survivorship of coral-reef fishes. *Mar Ecol Prog Ser* 124:31–42
- Chabanet P, Ralambondrainy H, Amanieu M, Faure G, Galzin R (1997) Relationships between coral reef substrata and fish. *Coral Reefs* 16:93–102
- Chittaro PM (2004) Fish-habitat associations across multiple spatial scales. *Coral Reefs* 23:235–244
- Chittaro PM, Sale PF (2003) Structure of patch-reef fish assemblages at St. Croix, U.S. Virgin Islands, and One Tree Reef, Australia. *Mar Ecol Prog Ser* 249:277–287
- Chovanec A, Hofer R, Schiemer FBA, Markert AMB, Zechmeister HG (2003) Chapter 18 Fish as bioindicators, Trace Metals and other Contaminants in the Environment. Elsevier, pp 639–676
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Aust J Ecol* 18:117–143

- Clarke KR, Gorley NR (2001) PRIMER v5: Unser manual/tutorial. PRIMER-E Ltd., Plymouth
- Clarke KR, Green RH (1988) Statistical design and analysis for a 'biological effects' study. *Mar Ecol Prog Ser* 46:213–226
- Colton DE, Alevizon WS (1981) Diurnal variability in a fish assemblage of a Bahamian coral reef. *Environ Biol Fish* 6:341–345
- Cox EF (1994) Resource use by Corallivorous Butterflyfishes (Family Chaetodontidae) in Hawaii. *Bul Mar Sci* 54:535–545
- Crosby MP, Reese ES (1996) A manual for monitoring coral reefs with indicator species: butterflyfishes as indicators of change on Indo-Pacific reefs. Office of Ocean and Coastal Resource, pp 44–47
- Diaz-Pulido G, McCook LJ (2002) The fate of bleached corals: patterns and dynamics of algal recruitment. *Mar Ecol Prog Ser* 232:115–128
- Dominici-Arosemena A, Wolff M (2006) Reef fish community structure in the Tropical Eastern Pacific (Panamá): living on a relatively stable rocky reef environment. *Helgoland Mar Res* 60:287–305
- Done TJ (1982) Patterns in the distribution of coral communities across the central Great Barrier Reef. *Coral Reefs* 1:95–107
- English S, Wilkinson C, Baker V (1997) Survey manual for tropical marine resources. Australian Institute of Marine Science (AIMS), Townsville
- Feary DA, Almany GR, Jones GP, McCormick MI (2007a) Coral degradation and the structure of tropical reef fish communities. *Mar Ecol Prog Ser* 333:243–248
- Feary DA, Almany GR, McCormick MI, Jones GP (2007b) Habitat choice, recruitment and the response of coral reef fishes to coral degradation. *Oecologia* 153:727–737
- Ferse SCA (2008) Artificial reef structures and coral transplantation: fish community responses and effects on coral recruitment in North Sulawesi/Indonesia. Dissertation. University of Bremen, Bremen, Germany
- Field JG, Clarke KR, Warwick RM (1982) A practical strategy for analysing multispecies distribution patterns. *Mar Ecol Prog Ser* 8:37–52
- Findley JS, Findley MT (2001) Global, regional, and local patterns in species richness and abundance of butterflyfishes. *Ecol Monogr* 71:69–91
- Friedlander AM, Parrish JD (1998) Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *J Exp Mar Biol Ecol* 224:1–30
- Friedlander AM, Brown EK, Jokiel PL, Smith WR, Rodgers KS (2003) Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs* 22:291–305
- Froese R, Pauly D (2010) "FishBase. World Wide Web electronic publication. www.fishbase.org"
- Gladfelter WB, Johnson WS (1983) Feeding niche separation in a guild of tropical reef fishes (Holocentridae). *Ecol* 64:552–563
- Gladfelter WB, Ogden JC, Gladfelter EH (1980) Similarity and diversity among coral reef fish communities: a comparison between tropical Western Atlantic (Virgin Islands) and tropical central Pacific (Marshall Islands) Patch reefs. *Ecol* 61:1156–1168
- Graham NA, Wilson SK, Jennings S, Polunin NV, Bijoux JP, Robinson J (2006) Dynamic fragility of oceanic coral reef ecosystems. *Proc Natl Acad Sci USA* 103:8425–8429
- Gratwicke B, Speight MR (2005a) The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *J Fish Biol* 66:650–667
- Gratwicke B, Speight MR (2005b) Effects of habitat complexity on Caribbean marine fish assemblages. *Mar Ecol Prog Ser* 292:301–310
- Halford AR, Thompson AA (1994) Visual census surveys of reef fish. Long-term monitoring of the Great Barrier Reef. Australian Institute of Marine Science (AIMS), Townsville
- Halford A, Cheal AJ, Ryan D, Williams DM (2004) Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. *Ecol* 85:1892–1905
- Harmelin JG, Bachet F, Garcia F (1995) Mediterranean marine reserves: fish indices as tests of protection efficiency. *Mar Ecol* 16:233–250
- Hodgson G (1999) A global assessment of human effects on coral reefs. *Mar Pol Bul* 38:345–355
- Hoeksema BW (1991) Control of bleaching in mushroom coral populations (Scleractinia: Fungiidae) in the Java Sea: stress tolerance and interference by life history strategy. *Mar Ecol Prog Ser* 74:225–237
- Hourigan TF, Tricas TC, Reese ES (1988) Coral reef fishes as indicators of environmental stress in coral reefs. In: Soule DF, Kleppel GS (eds) *Marine organisms as indicators*. Springer, New York City, pp 107–135
- Itzkowitz M (1979) The feeding strategies of a facultative cleanerfish, *Thalassoma bifasciatum* (Pisces: Labridae). *J Zool* 187:403–413
- Jokiel PL (1978) Effects of water motion on reef corals. *J Exp Mar Biol Ecol* 35:87–97
- Jones GP, Kaly UL (1996) Criteria for selecting marine organisms in biomonitoring studies. Academic, San Diego and London
- Jones GP, McCormick MI, Srinivasan M, Eagle JV (2004) Coral decline threatens fish biodiversity in marine reserves. *Proc Natl Acad Sci USA* 101:8251–8253
- Khalaf MA, Kochzius M (2002) Changes in trophic community structure of shore fishes at an industrial site in the Gulf of Aqaba, Red Sea. *Mar Ecol Prog Ser* 239:287–299
- Kramer DL, Chapman MR (1999) Implications of fish home range size and relocation for marine reserve function. *Environ Biol Fish* 55:65–79
- Kruskal JB (1964) Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29:1–27
- Kuiter RH (1992) Tropical reef-fishes of the Western Pacific, Indonesia and adjacent waters. PT. Gramedia Pustaka Utama, Jakarta
- Kulbicki M, Bozec YM, Green A (2005) Implications of biogeography in the use of butterflyfishes (Chaetodontidae) as indicators for Western and Central Pacific areas. *Aquat Conserv Mar Freshwat Ecosyst* 15:S109–S126
- Lewis AR (1997a) Effects of experimental coral disturbance on the structure of fish communities on large patch reefs. *Mar Ecol Prog Ser* 161:37–50
- Lewis AR (1997b) Recruitment and post-recruitment immigration affect the local population size of coral reef fishes. *Coral Reefs* 16:139–149
- Liberman T, Genin A, Loya Y (1995) Effects on growth and reproduction of the coral *Stylophora pistillata* by the mutualistic damselfish *Dascyllus marginatus*. *Mar Biol* 121:741–746

- Luckhurst BE, Luckhurst K (1978) Analysis of the influence of substrate variables on coral reef fish communities. *Mar Biol* 49:317–323
- Madduppa HH (2006) Bioecological study on eightband butterflyfish (*Chaetodon octofasciatus*, Bloch 1787) to detect condition of coral reef ecosystem in East Petondan Island, Seribu Islands, Jakarta. MSc Thesis. Bogor Agricultural University, Bogor
- Magurran AE (1988) Ecological diversity and its measurement. Princeton University Press, Princeton
- McClanahan TR (1994) Kenyan coral reef lagoon fish: effects of fishing, substrate complexity, and sea urchins. *Coral Reefs* 13:231–241
- McCormick MI (1994) Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage. *Mar Ecol Prog Ser* 112:87–96
- Molles MC Jr (1978) Fish species diversity on model and natural reef patches: experimental insular biogeography. *Ecol Monogr* 48:289–305
- Munday PL, Jones GP, Sheaves M, Williams AJ, Goby G (2007) Vulnerability of fishes on the Great Barrier Reef to climate change. In: Johnson J, Marshall P (eds) Climate change and the Great Barrier Reef. Great Barrier Reef Marine Park Authority, Townsville, pp 357–391
- Nanami A, Nishihira M, Suzuki T, Yokochi H (2005) Species-specific habitat distribution of coral reef fish assemblages in relation to habitat characteristics in an Okinawan coral reef. *Environ Biol Fish* 72:55–65
- Nguyen LV, Phan HK (2008) Distribution and factors influencing on structure of reef fish communities in Nha Trang Bay Marine Protected Area, South-Central Vietnam. *Environ Biol Fish* 82:309–324
- Öhman MC, Rajasuriya A (1998) Relationships between habitat structure and fish communities on coral. *Environ Biol Fish* 53:19–31
- Öhman MC, Rajasuriya A, Svensson S (1998) The Use of Butterflyfishes (Chaetodontidae) as Bio-indicators of Habitat Structure and Human Disturbance. *Ambio* 27:708–716
- Ormond RFG, Roberts JM, Jan RQ (1996) Behavioural differences in microhabitat use by damselfishes (Pomacentridae): implications for reef fish biodiversity. *J Exp Mar Biol Ecol* 202:85–95
- Pandolfi JM, Greenstein BJ (1997) Taphonomic alteration of reef corals: effects of reef environment and coral growth form. I. The Great Barrier Reef. *Palaios* 12:27–42
- Patton WK (1994) Distribution and ecology of animals associated with branching corals (*Acropora* Spp.) from the Great Barrier Reef, Australia. *Bul Mar Sci* 55:193–211
- Pratchett MS, Wilson SK, Baird AH (2006) Declines in the abundance of *Chaetodon* butterflyfishes following extensive coral depletion. *J Fish Biol* 69:1269–1280
- Randall JE (1974) The effect of fishes on coral reefs. *Second Int Coral Reef Symp* 1:159–166
- Randall JE, Allen GR, Steene RC (1990) Fishes of the Great Barrier Reef and Coral Sea. Crawford House, Bathurst
- Raymundo LJ, Halford AR, Maypa AP, Kerr AM (2009) Functionally diverse reef-fish communities ameliorate coral disease. *Proc Natl Acad Sci USA* 106:17067–17070
- Rees JG, Setiapermana D, Sharp VA, Weeks JM, Williams TM (1999) Evaluation of the impacts of land-based contaminants on the benthic faunas of Jakarta Bay, Indonesia. *Oceanol Acta* 22:627–640
- Reese ES (1981) Predation on corals by fishes of the family Chaetodontidae: implications for conservation and management of coral reef ecosystems. *Bul Mar Sci* 31:594–604
- Reese ES (1993) Reef fishes as indicators of conditions on coral reefs. International Society for Reef Studies, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Florida, USA
- Roberts CM, Ormond RFG (1987) Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Mar Ecol Prog Ser* 41:1–8
- Roberts CM, Ormond RFG, Dawson SAR (1988) The usefulness of butterflyfishes as environmental indicators on coral reefs. 6th International Coral Reef Symposium, pp 331–336
- Ross ST (1986) Resource partitioning in fish assemblages: a review of field studies. *Copeia* 1986:352–388
- Sale PF (1977) Maintenance of high diversity in coral reef fish communities. *Am Nat* 111:337–359
- Sale PF, Douglas WA (1981) Precision and accuracy of visual census technique for fish assemblages on coral patch reefs. *Environ Biol Fish* 6:333–339
- Sano M (2000) Stability of reef fish assemblages: responses to coral recovery after catastrophic predation by *Acanthaster planci*. *Mar Ecol Prog Ser* 198:121–130
- SAS Institute (2007) JMP statistics and graphics guide, Release 7. SAS Institute Inc., Cary
- Shannon CE, Weaver W (1949) The mathematical theory of communication. University of Illinois Press, Urbana
- Shepard R (1962) The analysis of proximities: multidimensional scaling with an unknown distance function. II. *Psychometrika* 27:219–246
- Tomascik T, Mah AJ, Nontji A, Moosa MK (1997) The ecology of the Indonesian seas, Part One and Two. Periplus Editions, HK
- Van der Meij SET, Suharsono, Hoeksema BW (2010) Long-term changes in coral assemblages under natural and anthropogenic stress in Jakarta Bay (1920–2005). *Mar Pol Bull* 60:1442–1454
- Veron JEN (2002) Reef corals of the Raja Ampat Islands, Papua Province, Indonesia. Part I. Overview of Scleractinia. In: McKenna SA, Allen GR, Suryadi S (Eds.), A Marine Rapid Assessment of the Raja Ampat Islands, Papua Province, Indonesia. Conservation International, Center for Applied Biodiversity Science, Department of Conservation Biology, Washington, DC, USA, pp 26–28
- Waldner RE, Robertson DR (1980) Patterns of habitat partitioning by eight species of territorial Caribbean damselfishes (Pisces: Pomacentridae). *Bul Mar Sci* 30:171–186
- Walker BK, Jordan LKB, Spieler RE (2009) Relationship of reef fish assemblages and topographic complexity on South-eastern Florida coral reef habitats. *J Coast Res* 53:39–48
- Williams DM (1991) Patterns and processes in the distribution of coral reef fishes. In: Sale PF (ed) The ecology of fishes on Coral Reefs. Academic, San Diego and London, pp 437–474
- Wilson SK, Graham NAJ, Pratchett MS, Jones GP, Polunin NVC (2006) Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Glob Change Biol* 12:2220–2234
- Wilson S, Graham N, Polunin N (2007) Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Mar Biol* 151:1069–1076