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An analysis of fish-habitat associations on disturbed coral reefs: chaetodontid fishes in New Caledonia

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A concordance analysis was used to study the simultaneous influence of several environmental data sets on chaetodontid (butterflyfish) distributions. This multivariate and multitable method enabled the correlation of three types of benthic characteristics (mineral substratum, coverage of structural species and large echinoderms) with butterflyfish abundances in two bays of the urban centre of Nouméa (New Caledonia). The first concordance axis was related to a gradient in the coverage of branching corals. This disturbance gradient compared damaged reef areas dominated by long-spined sea urchins to areas with an extensive coverage of branching corals. The abundance of corallivorous chaetodontids was related to this gradient, supporting the view of corals as a food and shelter source for these fishes. The second concordance axis was interpreted as a gradient of heterogeneity in the coverage of benthic life-forms. The abundance of omnivorous chaetodontids was related to this gradient. Thus, the concordance axes defined two key components of habitat structure that were related to the entire fish community structure.

Key words: butterflyfishes; concordance analysis; coral cover; habitat disturbance; reef fish community; topographic complexity.

INTRODUCTION

Spatial patterns of coral reef fishes are influenced by a number of biological processes, such as recruitment (Doherty & Williams, 1988), competition (Jones, 1991) and predation (Hixon, 1991; Hixon & Beets, 1993). The balance between these interacting processes is in turn mediated by the reef habitat structure which provides refuges and resources for fishes (Hixon & Beets, 1993; Beukers & Jones, 1997). On coral reefs, habitat structure is shaped by the spatial arrangement of sessile organisms (Connell *et al.*, 1997). Among them, the reef-building corals are important 'structural species' for the construction of the reef architecture (Connell *et al.*, 1997; Jones & Syms, 1998). Therefore, the reef habitat structure is very vulnerable to disturbances due to its biological nature. As a result, human-induced disturbances often lead to a decrease in live coral

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cover and its associated fine-scale topographic complexity (Rogers, 1990; Wittenberg & Hunte, 1992; Hughes, 1994), which may in turn change the structure of coral reef fish assemblages (Jones & Syms, 1998).

In this context, to what extent are coral reef fish assemblages affected by the degradation of structural species such as the reef-building corals? Studies on relationships between live coral cover and fishes have produced contrasting results (Jones & Syms, 1998). It appears, however, that such a relationship tends to be higher with strongly site-attached fish species than with species having a wider home range (Roberts & Ormond, 1987). Indeed, butterflyfishes (Chaetodontidae) and live coral cover have demonstrated the most consistent patterns of habitat association. Chaetodontids have received far more attention than other coral reef fish species, and much information on their relationships with habitat structure has been gathered over the world (Great Barrier Reef: Fowler, 1990; Hawaii: Cox, 1994; French Polynesia: Bouchon-Navaro, 1986; Japan: Cadoret *et al.*, 1999; Sri Lanka: Öhman *et al.*, 1998; Red Sea: Roberts & Ormond, 1987). Most studies found that abundance and species richness of chaetodontids were highly correlated with live coral cover. Close association is partly explained by feeding habits since several chaetodontid species are obligate coral feeders (Harmelin-Vivien & Bouchon-Navaro, 1983; Harmelin-Vivien, 1989) but most studies failed to separate the effects of live coral cover from source of shelters and food source at the butterflyfish community level.

The present study investigated the species-environment relationships in a butterflyfish community from the fringing reefs of two urban bays in New Caledonia. The hypothesis was that disturbed reefs are likely to present a wide range of variations in habitat structure, especially live coral cover. Therefore, the intention was to substantiate the relationships between butterflyfishes and habitat structure on fringing reefs. This goal was achieved by: (1) describing the spatial distribution of butterflyfish species and habitat characteristics in terms of mineral substratum, coverage of structural species and abundance of large echinoderms, (2) identifying synthetic gradients in the reef habitat structure and in the composition of chaetodontid assemblages, and (3) analysing the relations between habitat structure and chaetodontid community variables, with special attention to food and shelter availability. Relationships between the entire fish community and habitat structure were used as a baseline for assessing the strength of chaetodontid-habitat associations.

MATERIAL AND METHODS

STUDY AREA

The present study was carried out on the fringing reefs of two bays of the Nouméa peninsula, namely Grande Rade and Sainte-Marie Bays (Fig. 1). The surrounding South-west lagoon is very large (2500 km²) and strongly influenced by ocean currents. As a result, urban and industrial influences are relatively low, except in the urban centre of Nouméa (*c.* 120 000 inhabitants), where significant impacts occur (Labrosse *et al.*, 2000). The two bays are similar in size, but have different exposure to tradewinds and lagoonal water circulation (Douillet *et al.*, 2001), that can affect differently the rate of water renewal in the bays (P. Douillet, pers. comm.).

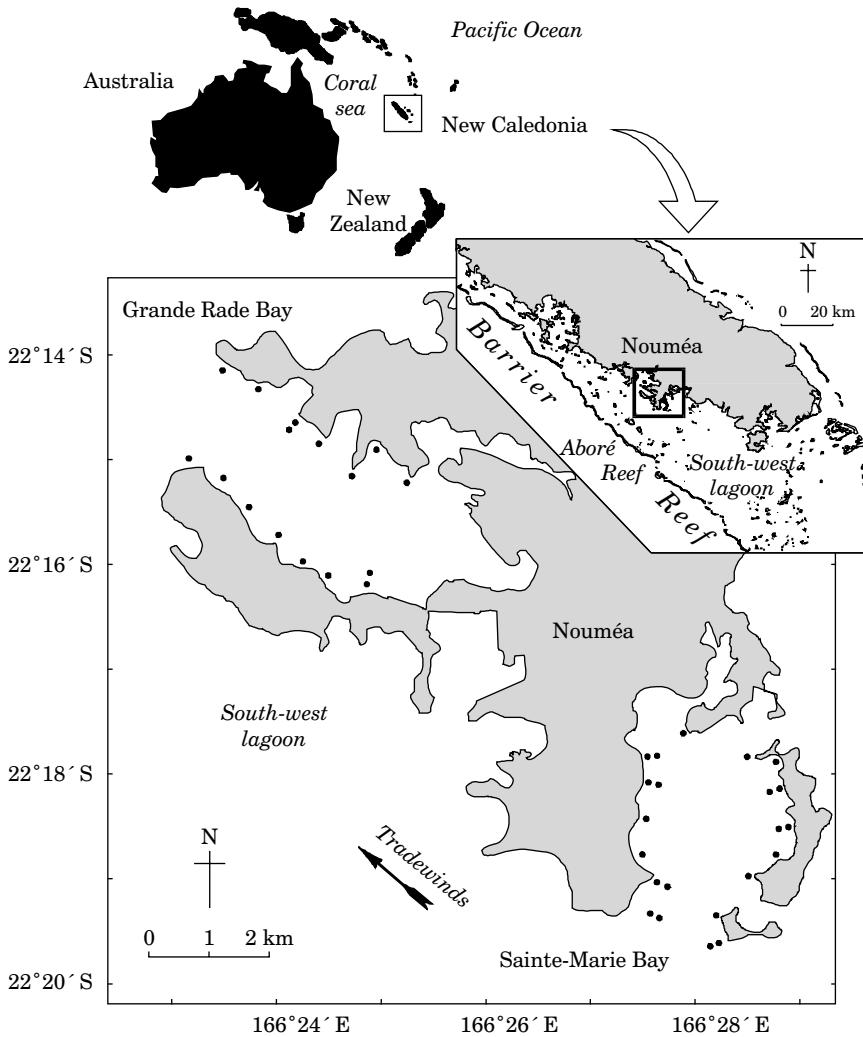


FIG. 1. Study area showing the location of the 38 sampling stations in the two studied bays of Nouméa, in the South-west lagoon of New Caledonia.

The fringing reefs are formed by a succession of three different zones before reaching the bay sandy bottoms. A reef flat (depth range: 0.5–2 m) with a poor coral cover usually precedes the reef crest, characterized by flourishing corals (1–3 m depth range). Then, a slight slope connects the fringing reef to the sandy bottom of the bays (up to 6 m depth in places). The slope has similar coral formations to the reef crest.

FISH SAMPLING

The reef crest and the reef slope were sampled in 1998 with a total of 38 reef sampling stations (22 in Sainte-Marie Bay and 16 in Grande Rade Bay). Butterflyfishes as well as other fish species were surveyed by underwater visual census within a 50 × 5 m belt transect, parallel to the shoreline. Two experienced scuba divers swam each on one side of the transect line, and counted simultaneously all fish species. The strip transect technique is the most frequently used for ecological studies of reef fish assemblages

(Bellwood & Alcalá, 1988). Biases associated with visual estimates (Kulbicki, 1998; Ackerman & Bellwood, 2000), however, restrict the census to diurnal and non-cryptic fish species. To reduce the effect of dominant species, a logarithmic transformation was applied to fish abundances after they were reported for a 250 m² area.

ENVIRONMENTAL CHARACTERISTICS

The reef habitat structure was examined on each sampling station using linear point intercept (LPI) sampling (Ohlhorst *et al.*, 1988). Two 50 m surveyor's tapes were laid 3 m apart from the fish transect line. Along these three parallel transect lines, the various substratum types and structural species (*i.e.* large sessile organisms) were recorded beneath each 1 m mark on the tapes (Table I). Therefore, the per cent coverage of each substratum type and structural species was estimated from 150 point counts. Large echinoderms were also counted, *i.e.* regular echinoids and holothurians, over a 1 m belt along each transect line. Abundance of the long-spined sea urchin *Diadema setosum* was separately recorded from other urchins (mainly *Echinothrix diadema* and *Echinothrix calamaris*), assuming that a high abundance of *D. setosum* impact reef habitat structure by 'bioerosion'. Abundances of large echinoderms were also estimated for a 250 m² area and ln-transformed. Finally, environmental variables were organized into three data sets hereafter referred as mineral substratum, coverage of structural species and abundance of large echinoderms.

DATA ANALYSIS

Spatial variations of chaetodontids and environmental variables were jointly investigated using multivariate analysis. Concordance analysis (Lafosse & Hanafi, 1997) was performed to assess the respective influence of mineral substratum, coverage of structural species and abundance of large echinoderms on chaetodontid assemblages. This multi-table method provides a solution to the problem of matching several independent environmental tables to a faunistic table (Townsend *et al.*, 2003). Concordance analysis is a version of co-inertia analysis (Dolédec & Chessel, 1994; Dray *et al.*, 2003) expanded

TABLE I. Environmental variables and categories used to characterize the habitat structure of each sampling station

| Mineral substratum (%) | Coverage in structural species (%) | Large echinoderms (individuals 250 m ⁻²) |
|-------------------------|---|--|
| Mud | Seagrass bed | <i>Diadema setosum</i> |
| Fine sand | Green algae (Halimedaceae, Caulerpaceae) | Other sea urchins |
| Coarse sand | Brown algae (Sargassaceae) | Holothurians |
| Gravel | Soft corals (Alcyonarians) | |
| Debris (1–5 cm) | Small branching corals | |
| Small block (5–30 cm) | Large branching corals (<i>Acropora</i> spp.) | |
| Large block (30–100 cm) | Massive and encrusting corals | |
| Rock | Fire corals (Milleporidae) | |
| Beach rock | Sponges | |
| Underlying substratum* | Other sessile organisms | |
| | No sessile organisms | |

*Dead coral and hard substratum found beneath covering organisms.

to match several tables (three tables of environmental variables in the present case) with one reference table (abundances of butterflyfish species in the present case). In a manner similar to co-inertia analysis, concordance analysis searches for combinations of variables in each environmental table that are coherent together and that are the most covariant with the chaetodontid abundances table. Consequently concordance analysis optimizes a covariance and, thus, assesses the correlation between each combination of environmental set and the chaetodontid abundance table.

To evaluate the influence of the three sets of environmental variables on chaetodontid abundance, the correlation between each pair of tables was measured using the Rv -coefficient, which is a multidimensional equivalent of the ordinary correlation coefficient between two variables (Robert & Escoufier, 1976). The Rv -coefficient was computed between each set of environmental variables and the chaetodontid assemblages. The statistical significance of each Rv -coefficient was further evaluated by a random permutation test. The resulting distribution of 1000 replicated matches of two tables (after random permutations of array rows) enabled a comparison with the observed Rv -coefficient. For example, if only one of the 1000 permutation values was higher than the observed Rv -coefficient of the two original tables, the relationship between the two tables had an estimated significance of $P = 0.001$.

Finally, Kendall rank correlations were performed between the site scores of each table along the first two concordance axes (*i.e.* scores of sampling stations) and several fish community variables (chaetodontid species richness, total abundance and abundance of trophic groups of chaetodontids, total species richness and total abundance of the whole fish community) in order to quantify fish-habitat associations. Most calculations and graphs were made with ADE-4 (Thioulouse *et al.*, 1997). The package can be obtained freely from pbil.univ-lyon1.fr, in the `/pub/mac/ADE/ADE4` directory. Kendall rank correlations were computed using the R freeware (Ihaka & Gentleman, 1996).

RESULTS

BUTTERFLYFISH ASSEMBLAGES

A total of 17 chaetodontid species were sighted at the 38 sampling stations (Table II). The species *Chaetodon kleinii* Bloch was considered as rare and neglected in the subsequent analyses since only one individual was encountered in the two bays. Eight species occurred in at least 50% of the sampling stations. Among them, the corallivores *Chaetodon speculum* Cuvier, *Chaetodon plebeius* Cuvier, *Chaetodon lunulatus* Quoy & Gaimard and *Chaetodon melannotus* Bloch & Schneider, and the omnivore *Chaetodon auriga* Forsskål were the most abundant species (Fig. 2). The mean abundance of chaetodontids (all species considered) was higher in Sainte-Marie Bay (mean \pm s.e. 39.1 ± 4.4 fishes per 250 m^2 , $n = 22$) than in Grande Rade Bay (28.1 ± 10.4 fishes per 250 m^2 , $n = 16$). This was explained by higher abundances of corallivorous chaetodontids in Sainte-Marie Bay [Fig. 2(a), (b)]. Omnivorous chaetodontids were equally distributed in the two bays [Fig. 2(c)].

ENVIRONMENTAL CHARACTERISTICS

The two bays exhibited slight differences in substratum cover [Fig. 3(a)]. Hard bottoms (rock and 'underlying substratum') covered larger areas in Sainte-Marie Bay than in Grande Rade Bay, where soft bottoms (fine and coarse sand) were prominent. The coverage of structural species was more developed in Sainte-Marie Bay [Fig. 3(b)], especially for small and large branching corals and

TABLE II. Occurrence of each chaetodontid species in the two studied bays, Sainte-Marie (SMB) and Grande Rade (GRB), and their feeding categories

| | | SMB (n = 22) | GRB (n = 16) | Total (n = 38) | Feeding category | References |
|--|----------------|-----------------|-----------------|-------------------|---------------------|------------|
| <i>Chaetodon auriga</i> Forsskål | <i>C. auri</i> | 13 | 11 | 24 | OM | 1, 3, 4 |
| <i>C. bennetti</i> Cuvier | <i>C. benn</i> | 12 | 8 | 20 | OC | 4, 5 |
| <i>C. citrinellus</i> Cuvier | <i>C. citr</i> | 4 | 3 | 7 | OM | 1, 3, 4 |
| <i>C. ephippium</i> Cuvier | <i>C. ephi</i> | 12 | 3 | 15 | OM | 1, 3, 4 |
| <i>C. flavirostris</i> Günther | <i>C. flav</i> | 11 | 10 | 21 | OM | 6 |
| <i>C. kleinii</i> Bloch* | <i>C. klei</i> | 1 | 0 | 1 | | |
| <i>C. lineolatus</i> Cuvier | <i>C. line</i> | 12 | 4 | 16 | OM | 4 |
| <i>C. lunulatus</i> Quoy & Gaimard | <i>C. lunu</i> | 13 | 7 | 20 | OC | 2, 3, 4 |
| <i>C. melannotus</i> Bloch & Schneider | <i>C. mela</i> | 18 | 8 | 26 | FC | 2, 4 |
| <i>C. plebeius</i> Cuvier | <i>C. pleb</i> | 19 | 13 | 32 | OC | 2, 4 |
| <i>C. speculum</i> Cuvier | <i>C. spec</i> | 21 | 8 | 29 | FC | 4, 5 |
| <i>C. trifascialis</i> Quoy & Gaimard | <i>C. trif</i> | 4 | 2 | 6 | OC | 2, 3, 4 |
| <i>C. ulietensis</i> Cuvier | <i>C. ulie</i> | 7 | 3 | 10 | FC | 2, 3, 4 |
| <i>C. vagabundus</i> L. | <i>C. vaga</i> | 13 | 10 | 23 | OM | 1, 3, 4 |
| <i>Heniochus acuminatus</i> L. | <i>H. acum</i> | 1 | 5 | 6 | OM | 6 |
| <i>H. chrysostomus</i> Cuvier | <i>H. chry</i> | 1 | 4 | 5 | FC | 3, 4, 5 |
| <i>H. monoceros</i> Cuvier | <i>H. mono</i> | 2 | 4 | 6 | OM | 5 |

OC, obligate corallivore; FC, facultative corallivore; OM, omnivore.

*Species not used in the multivariate analyses because of insufficient occurrences.

(1) Hiatt & Strasburg, 1960; (2) Reese, 1977; (3) Harmelin-Vivien & Bouchon-Navaro, 1983; (4) Sano *et al.*, 1984b; (5) Sano, 1989; (6) Randall *et al.*, 1997.

brown algae. The long-spined urchin *D. setosum* was clearly more abundant in Grande Rade Bay [Fig. 3(c)] whereas abundance of other urchins and holothurians showed no significant differences.

RELATIONSHIPS BETWEEN BUTTERFLYFISHES AND HABITAT VARIABLES

The first two axes of a concordance analysis accounted for 54.4% of the total variability of chaetodontid abundance and for 93.6, 96.3 and 90.5% of the mineral substratum, the coverage of structural species and the abundance of large echinoderms sets, respectively. *Rv*-coefficients indicated that the three environmental sets had a significant, but unequal influence on the spatial distribution of chaetodontids (Table III), the coverage of structural species having the strongest influence on butterflyfish assemblages.

The first concordance axis revealed a gradient in the abundance of corallivorous chaetodontids [Fig. 4(a)] since most obligate and facultative coral feeders have a high positive score along this axis. Corallivores were especially sensitive to a gradient of increasing coverage of branching corals [Fig. 5(a), (b)]. Chaetodontids did not occur in blocks and coarse sand areas (*i.e.* poor biotic cover). This habitat was instead associated with *D. setosum* [Fig. 5(c)]. The first

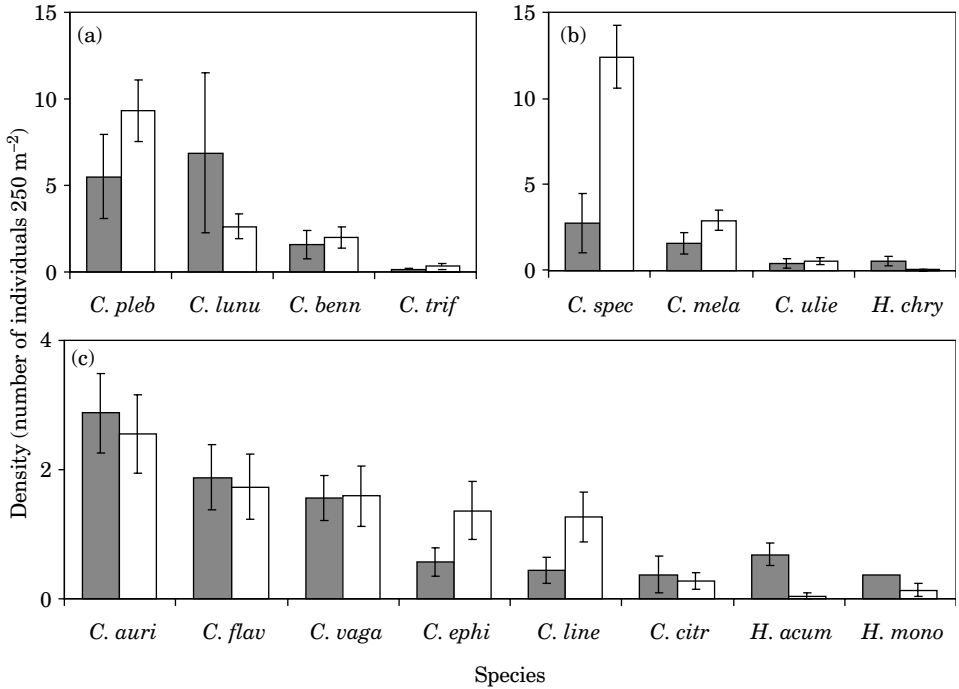


FIG. 2. Mean \pm s.e. densities (a) obligate corallivore, (b) facultative corallivore and (c) omnivore butterflyfish species (see Table II in Grande Rade Bay (■, $n = 16$) and Sainte-Marie Bay (□, $n = 22$).

concordance axis clearly separated the sampling stations of Sainte-Marie and Grande Rade Bays [Fig. 4(b)]. The site scores of the two bays along this axis were significantly different for the three environmental tables ($P < 0.05$, $P < 0.001$, $P < 0.001$, for mineral substratum, structural species cover and abundances of echinoderms, respectively) as well as for chaetodontid abundance table ($P < 0.01$).

The second concordance axis revealed a gradient in abundance of the three omnivorous species *Chaetodon flavirostris* Günther, *Chaetodon vagabundus* L. and *C. auriga* [Fig. 4(a)]. These species dominated rocky habitats with a mixed coverage of structural species (brown algae, massive and encrusting corals, and small branching corals). These habitats occurred mostly at the entrance of the two bays [Fig. 4(c)]. In contrast, *Chaetodon bennetti* Cuvier dominated areas characterized by an extensive coverage of large branching corals. These areas were restricted to the sheltered parts of Sainte-Marie Bay. Sea urchins other than *D. setosum* were frequently associated with this latter habitat [Fig. 5(c)].

CORRELATIONS BETWEEN FISH DESCRIPTORS AND THE ENVIRONMENTAL GRADIENTS

Kendall rank correlations showed that the abundance of chaetodontid coral feeders was highly correlated with the site scores of each along the first con-

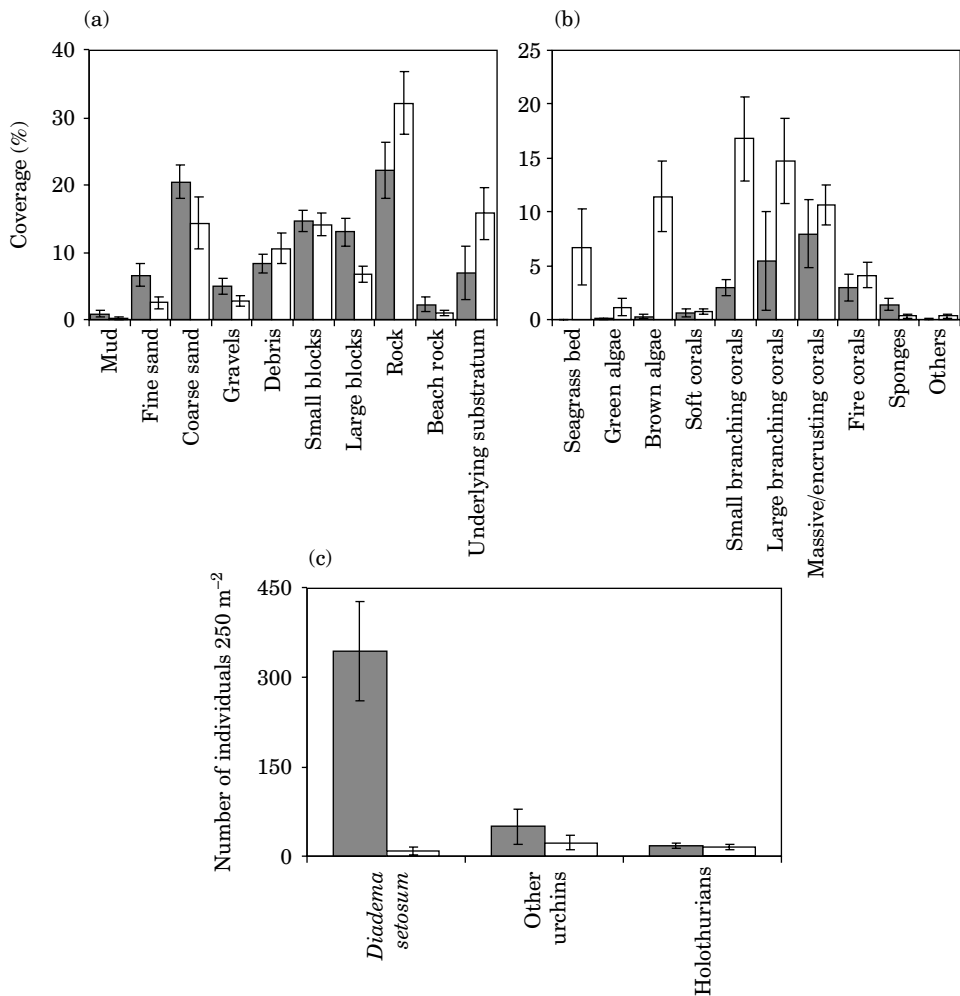


FIG. 3. Mean \pm s.e. percentage cover of (a) mineral substratum and (b) 'structural species' and (c) mean \pm s.e. abundance of large echinoderms in Grande Rade Bay (■, $n = 16$) and Sainte-Marie Bay (□, $n = 22$).

TABLE III. Results of a concordance analysis. R_v , correlation coefficient between the faunistic table and the corresponding environmental set; P , estimated probability equal to the frequency of random values (out of 1000) higher than the observed R_v

| Environmental set | R_v | P |
|--------------------------------|-------|--------|
| Mineral substratum | 0.348 | <0.001 |
| Coverage of structural species | 0.507 | <0.001 |
| Abundance of large echinoderms | 0.248 | <0.005 |

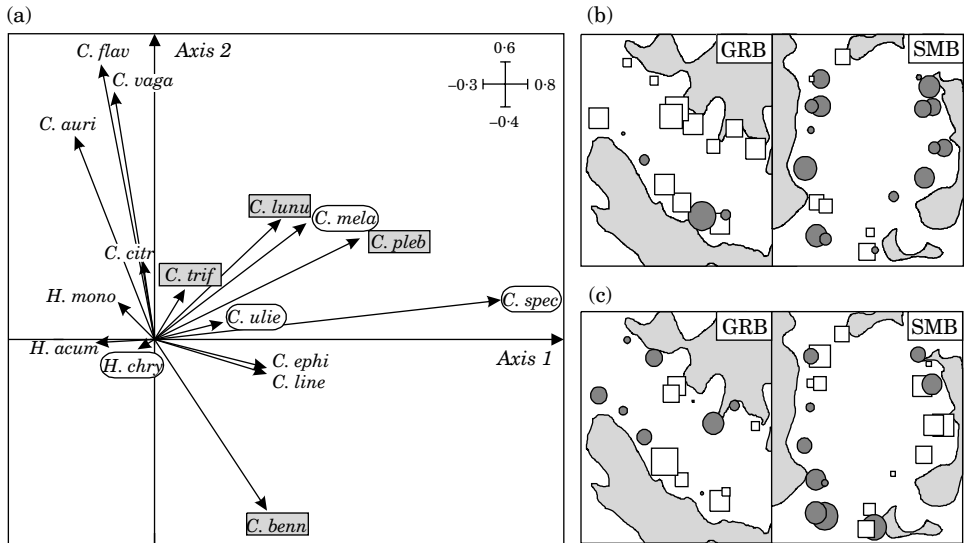


FIG. 4. Results of a concordance analysis showing (a) the ordination of species (see Table II) along the first two axes. Arrow length is proportional to species weights. Obligate corallivores are shaded, facultative corallivores are circled. Corresponding faunistic scores are plotted onto the geographical map for (b) the first and (c) the second concordance axis. The size of closed circles is proportional to positive scores whereas the size of open squares is proportional to negative scores (GRB, Grande Rade Bay; SMB, Sainte-Marie Bay).

cordance axis (Table IV). The correlation was higher for facultative corallivores than for obligate corallivores. In contrast, the abundance of omnivorous chaetodontids exhibited no significant correlation with the first concordance axis, but was correlated with the sites scores of the mineral substratum and structural species along the second axis, while corallivores were not. When all fish species were considered, total abundance was highly correlated with the first concordance axis, but not with the second axis. Butterflyfish species richness and total species richness were weakly correlated with the two axes.

DISCUSSION

BUTTERFLYFISH ASSEMBLAGES AND HABITAT FEATURES ON THE REEFS OF NOUMÉA BAYS

Among the 32 species of butterflyfishes present in New Caledonia (Kulbicki & Rivaton, 1997), 17 species were observed on the fringing reefs of the two bays of Nouméa. By comparison, 21 chaetodontid species were found with a quite similar sample size ($n = 33$) on Aboré Reef (Kulbicki *et al.*, 1996), a marine reserve located on the barrier reef, 20 km away from Nouméa (see Fig. 1). The mean abundance of butterflyfishes was higher in the bays ($\text{mean} \pm \text{s.e. } 34.5 \pm 5.1 \text{ fishes } 250 \text{ m}^{-2}$, $n = 38$) than Aboré Reef ($15.5 \pm 1.3 \text{ fishes } 250 \text{ m}^{-2}$, $n = 33$) (Kulbicki *et al.*, 1996). As a result, species richness and abundance of butterflyfish

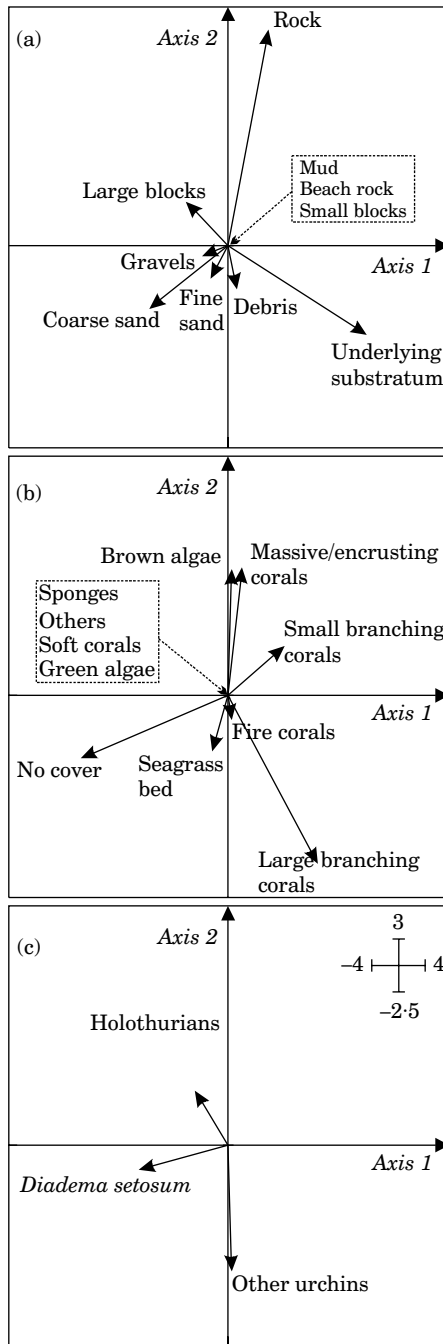


FIG. 5. Results of a concordance analysis showing the ordination along the first two axes of (a) substratum types, (b) structural species and (c) large echinoderms. Arrow length is proportional to species weights.

TABLE IV. Kendall rank correlation (τ) between fish assemblage variables and the site scores of each environmental factor along the two first concordance axes ($H_0: \tau = 0, n = 38$)

| | Mineral substratum | Structural species | Large echinoderms |
|---------------------------|--------------------|--------------------|-------------------|
| Concordance axis 1 | | | |
| Chaetodontids | | | |
| Species richness | 0.204* | 0.210** | 0.046 |
| Total abundance | 0.432*** | 0.469*** | 0.243* |
| OC abundance | 0.408*** | 0.443*** | 0.252* |
| FC abundance | 0.511*** | 0.634*** | 0.367*** |
| OM abundance | -0.040 | -0.007 | -0.028 |
| Whole fish community | | | |
| Species richness | 0.143 | 0.269** | 0.137 |
| Total abundance | 0.530*** | 0.467*** | 0.291** |
| Concordance axis 2 | | | |
| Chaetodontids | | | |
| Species richness | 0.183* | 0.234* | 0.100 |
| Total abundance | 0.137 | 0.220* | 0.043 |
| OC abundance | 0.090 | 0.185 | 0.070 |
| FC abundance | 0.007 | 0.185 | 0.028 |
| OM abundance | 0.278** | 0.313** | 0.045 |
| Whole fish community | | | |
| Species richness | 0.287** | 0.298** | 0.079 |
| Total abundance | 0.011 | 0.068 | 0.037 |

*, $P = 0.05$; **, $P = 0.01$; ***, $P = 0.001$.

OC, obligate corallivore; FC, facultative corallivore; OM, omnivore.

assemblages can be considered high in the Nouméa bays despite the human influence.

The fringing reefs of the two bays exhibited strong differences regarding the biotic cover. Live coral cover was more developed in Sainte-Marie Bay than in Grande Rade Bay. The concordance analysis highlighted two main types of habitat in Sainte-Marie Bay. In areas where wave action and wind exposure were reduced, large branching *Acropora* spp. form dense coral-beds. By contrast, at the entrance of Sainte-Marie Bay, a mixed coverage of massive and incrusting corals, small branching corals and brown algae dominated. Conversely, the fringing reefs of Grande Rade Bay exhibited a poor cover of structural species. The mixed coverage including various growth forms of corals is more reduced. The two bays were expected to suffer anthropogenic disturbances. Sainte-Marie Bay receives domestic sewage mainly discharged in the inner part of the bay, which results in eutrophication mostly confined to the bottom of the bay due to prevailing currents (Labrosse *et al.*, 2000). Disturbances in Grande Rade Bay, which combine industrial pollution (chemical factories for nickel extraction and, oil and gas depots) and sediment deposition due to reduced circulation of water (Douillet *et al.*, 2001) are likely to cause higher degradation on habitat and fish assemblages. In addition, high abundance of

D. setosum was observed, which may result from various human-induced disturbances (Bak, 1990; Hughes, 1994). These long-spined urchins play an important role in the erosion of the reef substratum through their grazing activity and spine abrasion (Sammarco, 1980; Bak, 1994). For example, McClanahan & Mutere (1994) found that a lower coral cover was more frequent on urchin-dominated than fish-dominated reefs. Therefore, the high abundance of *D. setosum* in Grande Rade Bay probably adds to urban activities in damaging coral cover.

INFLUENCE OF LIVE CORAL COVER ON BUTTERFLYFISH ASSEMBLAGES

Although the three selected environmental components of the reef habitat (mineral substratum, coverage of structural species and abundance of large echinoderms) were all relevant for explaining the spatial distribution of chaetodontid species, the coverage of structural species was the major controlling factor, reflecting the role of hard corals in structuring butterflyfish assemblages. The results indicate positive correlations between live coral cover and abundance of corallivorous chaetodontids as well as the overall fish assemblages. The live coral cover is generally positively correlated with the number of species and the abundance of chaetodontids (Reese, 1981; Bell & Galzin, 1984; Bouchon-Navaro *et al.*, 1985; White, 1988; Bouchon-Navaro & Bouchon, 1989; Öhman *et al.*, 1998; Cadoret *et al.*, 1999). Furthermore, the abundance and diversity of fish assemblages is positively correlated with the live coral cover (Carpenter *et al.*, 1981; Bell & Galzin, 1984; Chabanet *et al.*, 1995). It is not clear, however, which aspect of coral cover is important for butterflyfishes (Findley & Findley, 1985). Coral is a food source to corallivorous fishes, and its architecture provides shelters to fishes and many mobile invertebrates (Hixon, 1991; Friedlander & Parrish, 1998), which are in turn food sources for many reef fishes. Sano *et al.* (1984a) have shown that a decrease in structural complexity of branching *Acropora* spp. resulted in a decrease in fish diversity and abundance due to a reduction in shelter availability. Bouchon-Navaro *et al.* (1985) suggested that rather than the total live coral cover, the abundance of large branching corals is of primary importance for determining the development of a richer chaetodontid community.

On the fringing reefs of the Nouméa bays, the gradient of live coral cover can be interpreted as a gradient of topographic complexity afforded by the various growth forms of corals (from massive and encrusting to small then large branching corals). The greater shelter availability offered by branching corals is potentially important to the corallivorous chaetodontids. The stronger correlation obtained between the first axis of a concordance analysis and corallivorous chaetodontids in comparison to the overall fish assemblage suggests that corals also act as a food source for the former species. The combined influence of shelter availability and food source on corallivores does not explain all the spatial variations of these species. When *C. speculum* was very sensitive to the global gradient of coral cover, *C. bennetti* was clearly associated with the large *Acropora* spp. coral-beds, whereas *C. lumulatus*, *C. plebeius* and *C. melannotus* were rather associated with a rich coral cover dominated by small branching

corals. Such differences among corallivore species may be explained by particular feeding preferences. The abundance of omnivorous chaetodontids, such as *C. auriga*, *C. vagabundus* and *C. flavirostris*, was not correlated with the gradient of branching corals. In contrast, their abundance was correlated with the second concordance axis that can be interpreted as a gradient of heterogeneity of the benthic cover, since it opposes homogenous habitats (areas with a very poor biotic cover or dense coral-beds) from more heterogeneous habitats with a mixed biotic cover of various coral growth forms and brown algae. For omnivorous chaetodontids, corals appear to have a structural role in providing a greater variety of microhabitats sharing various resources.

RELATIONSHIPS BETWEEN HABITAT STRUCTURE AND FISH COMMUNITY STRUCTURE

There has been little consistency in the definition and measurement of habitat structure between ecological studies (McCoy & Bell, 1991). In addition, it is often difficult to separate the effects of distinct habitat features on ecological communities and to identify their functional roles (McCoy & Bell, 1991; Beck, 2000). In the present study, concordance analysis allowed two environmental gradients that may be interpreted as two independent components of habitat structure to be identified. When the first concordance axis encompasses a gradient of topographic complexity, the second concordance axis reflects a gradient of heterogeneity in the coverage of benthic life-forms. These two environmental gradients are independent as the two axes are orthogonal to each other. One benefit of such a multitable technique is that numerous variables measured in the field are synthesized into environmental gradients. The chaetodontid composition played a central role in the emergence of such gradients since the spatial distribution of chaetodontids forced the ordination of habitat variables. When the site scores on the two concordance axes are considered as values of two new habitat variables, their association with the entire fish assemblage is instructive. Total fish abundance and diversity were linked to the gradient of topographic complexity, as already observed in numerous descriptive studies (Jones & Syms, 1998). This illustrates the importance of habitat complexity on coral reef fish assemblages, although the underlying processes (*i.e.* mediation of predation and competition) are not well identified (Almany, 2004). The positive correlation between fish diversity and the gradient of habitat heterogeneity is more remarkable. It seems that independently of habitat complexity, the diversity of structural species enhances fish diversity, perhaps in promoting a greater variety of microhabitats and resources for resident fishes. The functional role of habitat heterogeneity on fish assemblages is worthy of more examination.

INDICATOR FUNCTION OF CORALLIVOROUS BUTTERFLYFISHES

Because obligate coral feeders have developed morphological and behavioural adaptations for coral feeding, it was suggested that changes in the distribution of butterflyfish species could provide an 'early warning' on a sub-lethal change

occurring on the reef (Reese, 1977, 1981; Hourigan *et al.*, 1988; Crosby & Reese, 1996). No study, however, has yet demonstrated that stress on hard corals causes immediate effects on butterflyfish distribution (Jameson *et al.*, 1998). To date, the only conclusion is that a decrease in live coral cover can result in a decrease in the abundance and diversity of chaetodontids. If butterflyfishes provide no early warning before a reduction in hard corals occurs, live coral cover may be directly monitored (Williams, 1986; Jameson *et al.*, 1998).

In the present study the abundance of both obligate and facultative corallivorous butterflyfish species was used to detect a disturbance gradient affecting live coral cover and topographic complexity. Nevertheless, such disturbance effects were quite obvious since a direct sampling of live coral cover would have been sufficient to detect changes on the reef habitat structure. The results, however, suggest that corallivorous chaetodontids may be good indicators of the overall fish community, since abundances were correlated. Such patterns should be confirmed by further investigations, since monitoring chaetodontid assemblages has a lower cost than monitoring the whole fish community.

As long as the early-warning function of corallivorous chaetodontids is not clearly established, butterflyfish species should be used cautiously as indicators in monitoring programme. Underwater visual censuses may be biased due to the proportion of hidden individuals over extensive live coral cover (Roberts *et al.*, 1988). Furthermore, butterflyfishes are sometimes subject to human exploitation, as favourite targets for marine aquarium collectors (Erdmann, 1997). Finally, factors other than live coral cover may explain the variations in abundance of butterflyfishes, such as recruitment processes (Bell *et al.*, 1985). This should be considered if large-scale variations in the abundance and composition of butterflyfishes from monitoring surveys are to be explained. As an illustration, the study revealed that abundance and diversity of chaetodontids on Nouméa fringing reefs, probably the most disturbed reef zone in New Caledonia, were far above those found on Aboré Reef, a marine protected area located on the barrier reef.

Field data of the present study were part of a larger research programme intended to analyse the influence of terrigenous and anthropogenic inputs on tropical marine coastal environments (ECOTROPE programme). Many thanks go to R. Fichez and D. Douillet for providing us information on water chemical composition. We also wish to address special thanks to G. Mou-Tham for his assistance in collecting data.

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