REPORT

M.J.A. Vermeij

Early life-history dynamics of Caribbean coral species on artificial substratum: the importance of competition, growth and variation in life-history strategy

Abstract The development of a coral community was monitored for 6 years (1998–2004) on 46 m^2 of artificial settlement substrate in Curaçao, Netherlands Antilles. Growth and survival of recruits ($n = 1385$) belonging to 16 different species were quantified in relation to characteristics of the benthic community developing around them. The early life history dynamics (i.e. growth rate, growth strategy and survival) of corals differed among species although these differences were small for species occupying similar habitats (i.e. underside versus topside of substratum). In contrast to recruit survival, juvenile growth rates were highly variable and unrelated to benthic community structure, at least at the scale of this study. Competing benthic organisms affected coral recruitment success through space preemption (mainly by macroalgae) or recruit overgrowth (mainly by sponges). The results highlight the small spatial scale (mm–cm) at which the processes responsible for recruitment success or failure occur and emphasize the need to include such small-scale observations in studies of coral early life-phase dynamics.

Keywords Recruitment · Life history strategy · Growth · Survival · Competition · Artificial substratum

Introduction

The recovery and maintenance of coral communities depend on the arrival of coral planulae followed by settlement and growth of surviving individuals. Planulae

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can enhance their future survival through adaptive pre-settlement behavior (e.g. Mundy and Babcock 1998, 2000; Vermeij and Bak 2002), but post-settlement survival, depending on a large suite of biotic and abiotic factors, is an additional structuring process. Post-settlement survival is likely to alter initial settlement patterns (often studied as visible settlement on tiles) thereby determining the fraction of settled corals that becomes part of the adult community (Caley et al. 1996).

Post-settlement processes of growth and survival will be controlled by species-specific characteristics, interactions with other reef organisms and environmental factors. Early growth rates differ from species to species and vary little in response to environmental conditions (Van Moorsel 1985, 1988; Fitzhardinge 1988; Babcock and Mundy 1996; Edmunds et al. 2004). In contrast, post-settlement survival depends on a wide variety of environmental factors: e.g. the presence of other benthic organisms (Birkeland et al. 1981; Maida et al. 1995; Hughes and Connell 1999; Raimondi and Morse 2000; Carlon 2001), sedimentation (Gilmour 1999), hurricanes (Rogers et al. 1991) and activities by fish, urchins (Sammarco 1980; Sammarco and Carleton 1981) and man (Tomascik 1991). The aforementioned factors often act synergistically, which hinders straightforward interpretation of spatial differences in recruitment (e.g. Edmunds 2000; Ruiz-Zárate and Arias-González 2004; but see Hughes et al. 2000). Therefore, detailed studies are needed that address the mechanisms driving post-settlement processes at a spatial scale at which the earliest coral life-stages experience them, i.e. mm–cm. Small scale approaches have proven useful for studying pre-settlement processes (Mundy and Babcock 1998; Raimondi and Morse 2000); however, they are rarely used to study post-settlement processes (but see Vermeij 2005a).

This lack of information on small-scale ecological mechanisms makes interpretations of recruitment data difficult (Caley et al. 1996; Connell et al. 1997). Although sponges and algae co-occur with coral juveniles, their effect on coral survival and growth remains

largely understudied (but see Connell 1973; Hughes and Jackson 1985; Connell et al. 1997) and coral settlement rates per se are obviously reduced when coral settlers face well developed benthic communities (Jackson and Buss 1975; Sebens 1982). To address the effect of benthic organisms on the fate of coral recruits, long-term monitoring is required. Edmunds et al. (2004) showed that only long-term surveys on the fate of coral settlers (i.e. survival and growth) can determine the importance and nature of post-settlement processes in the structuring of juvenile coral communities. Here, I want to combine a small spatial scale with a long-term temporal scale in studying early life-history dynamics of Caribbean coral species and will ask the following questions: (1) Are early growth and survival rates species-specific? (2) If so, are species-specific rates dependent on characteristics of the benthic habitat that immediately surrounds a coral recruit? (3) Which of these benthic habitat characteristics contribute to recruit mortality? (4) How do interactions between coral recruits and other benthic organisms change over time in a developing benthic reef community?

To address these questions, I report on a 6 year-study on the natural dynamics of the earliest life-stages of Caribbean coral species recruiting on large (46 m^2) artificial substrata.

## Materials and methods

Settlement racks

In 1998, two large frames, carrying settlement panels (or racks), were placed at Buoy Two, leeward coast of Curaçao (12°05′N, 69°00′W), Netherlands Antilles (for site information see Van Moorsel 1985; Fig. 1). The frames were deployed on the upper (12 m) and lower (30 m)

reef slope. Hard coral cover was relatively high at both depths (20–30%; Bak and Nieuwland 1995). For descriptions of this reef and its zonation, see Bak (1977), Van den Hoek et al. (1978) and Van Duyl (1985). On each frame there were four formica settlement panels (each 1.2×0.6 m), two mounted vertically and two horizontally (Fig. 1). The whole surface area of each side of the panels was covered by cells (1.1L×1.1W×0.9H cm), the walls of which were made from an egg crate material, whilst the bottom of each cell was the formica of the panel. All panels were positioned 0.8 m above the surrounding reef substratum. Each panel had a total available surface area of 5.78 m^2 resulting in a total area of 23.12 m^2 per frame. During this study, only the formica surfaces (top and undersides) of the horizontal panels were monitored. Microhabitats such as the three-dimensional structure of the egg-crate, or the different type of substrate (Formica or egg-crate) were not included because these were impossible to distinguish due to the colonization and growth of crustose coralline algae and other calcifying organisms (Van Moorsel 1989; Vermeij personal observation). Recruitment on the vertical panels also proved too low for these panels to be included in the analyses. For further technical details on the settlement racks, see Van Moorsel (1988). Van Moorsel (1983, 1985, 1988) showed that data on coral growth and survival on these settlement panels did not differ from those observed on the reef.

Coral recruit surveys

Over a period of 5 years (1999–2004), all scleractinian recruits (i.e. visible coral settlers) were scored each November. The smallest recruits observable consisted of one polyp measuring approximately 1 mm^2. The size (in mm^2), position on the panel (x, y; in mm) and side on

Fig. 1 Photograph of settlement rack at 12 m with a schematic representation of its design. Egg crate cells cover both sides of panels but are too small to be easily discerned in the photograph
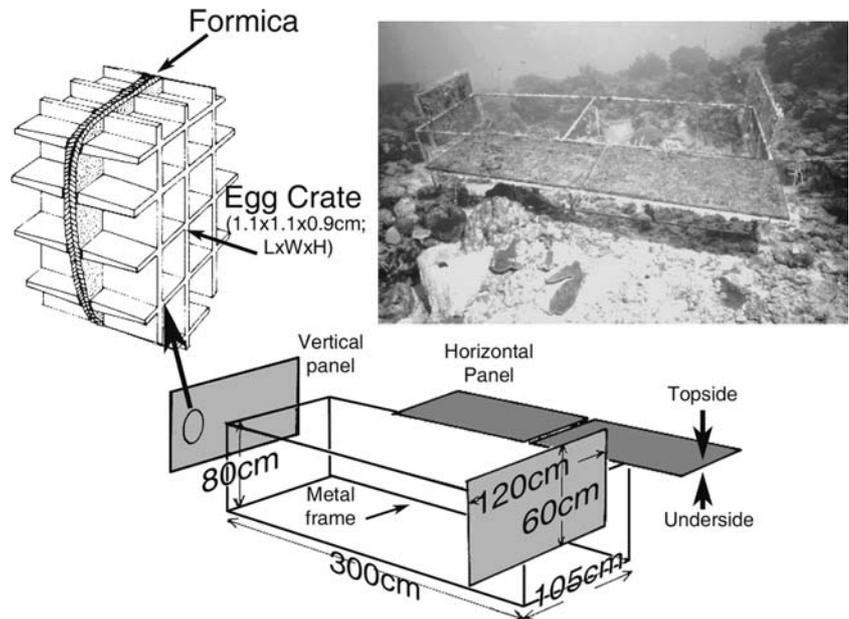
the panel (topside or underside) of each recruit was noted. The majority of recruits (~90%) possessed a simple two-dimensional morphology, so planar surface areas were measured. The surface of species whose colonies developed three-dimensionally (e.g. *Eusmilia fastigiata* and *Tubastrea coccinea*) was also measured as planar surface. Each recruit was notionally subdivided into simple geometric shapes (e.g. squares, parallelograms and ovals), these surfaces were then measured separately (in 0.1 mm) using calipers and summed to represent actual colony surface area. These measurements of surface area (in mm^2) deviated at most 4% from the actual surface of the recruit (Vermeij unpublished data). Polyp size was measured as the maximum corallite diameter and the area between corallites (coenosteum) was not considered in these measurements.

The fate of each recruit was monitored during annual surveys each November. If a recruit had died, its skeleton was located and the organism that had overgrown it identified and tentatively attributed with its death. The cause of death was noted as "unknown," when the skeleton could not be found.. A detailed map was drawn of the positions of each fragment, if a recruit showed fission,. Fragments were subsequently followed individually during subsequent surveys.

Taxonomic classification of colonies smaller than 0.5 cm^2 was sometimes difficult in the genera *Agaricia* and *Porites*. *Agaricia humilis* and *A. agaricites*, and *Porites astreoides* and *P. porites* were therefore pooled by genus and referred to as "taxa" rather than "species".

Community development

In addition to the recruit surveys in November, each panel was photographed at a resolution in such a way that benthic composition could be determined at a 1 cm^2 scale. Dominant benthic components [Abiotic Substratum, Ascidians, Coral, Crustose Coralline Algae (CCA), Dead Coral with Algae, Macroalgae, *Millepora*, Sponges and Zoanthids] on all panels were quantified using the program CPCe v2.8 (National Coral Reef Institute/Nova Southeastern University Oceanographic Center, 2001–2004). Each panel was overlain with 600 random points and underlying benthos was assigned to one of the nine categories mentioned above. In 2002–2004, the preference of corals to recruit on topside and undersides of the horizontal panels was investigated by relating the number of newly arrived recruits in randomly placed 20×20 cm subplots (*n* = 30) in year 1 (2002–2003) with the number of recruits arriving in year 2 (2003–2004) to the same plots.

Statistical analysis

Correlation analyses were used to determine the degree to which (1) the increase in benthic components and time were related, (2) recruitment density corresponded to the amount of open space (defined as the panel surface not occupied by sponges and macroalgae), (3) increased abundance of a benthic component corresponded to its increased contribution to recruit mortality, (4) increased polyp size corresponded to lower mortality rates and/or growth rates, (5) corals found to recruit in similar locations on the panels from year to year. Multidimensional scaling (MDS) was used to describe temporal changes in the benthic community that developed on the two sides of the settlement panels at two depths. Differences in growth rates between species, depth and year were investigated using ANOVA. Regression analyses were used to determine if colony size can successfully predict (1) growth rates, (2) colony size and (3) survival probabilities for the following year.

Results

Community development and overall recruitment

The benthic community that developed on either side of the panels (topside and underside) was similar at both depths (Fig. 2). The relative abundance of all benthic components on both sides was similar for both depths (Spearman rank correlations > 0.72; $p < 0.05$). On the undersides, open space decreased linearly with time (*r*: 0.88; $p < 0.05$), due to increasing cover of sponges, CCA and ascidians (*r*: 0.97–0.41; $p < 0.05$). On the topsides, open space decreased linearly as well (*r*: 0.94; $p < 0.05$). Here, CCA, macroalgae and sponge cover increased with time (*r*: 0.98–0.64; $p < 0.05$). Community development proceeded gradually on both sides of the panels and was highly predictable. At all times, macro-algae (mainly *Lobophora* spp. and *Dictyota* spp.) dominated the topsides of the panels whereas CCA and sponges dominated the undersides.

Siderastrea siderea (*n* = 10) and *Diploria strigosa* (*n* = 2) were the only species recruiting to the vertical panels. Because they represented less than 0.01% of the total number of recruits (Table 1), vertical panels were not considered in further analyses.

In each year after 2000, the number of recruits found on the underside of the panels was on average 17.7 times higher than the number found on their topside (Table 1). On both sides, total yearly recruitment increased from 1999 to 2002 and then decreased slightly towards the end of the study (Table 1). This pattern could not be attributed to yearly variations in the contribution of different species to the overall number of new recruits: 10 of the 16 coral taxa that settled on the racks followed a similar temporal pattern (Table 1). After 2002, the observed probability for a recruit to die during the following year increased. Increased mortality lowered the number of corals present on the panels despite ongoing recruitment (Fig. 3). Only *A. solitaria*, *Rhizosmilia maculata* and *T. coccinea* increased in number over the entire study period. Brooding species dominated the recruit population, only five of the 15
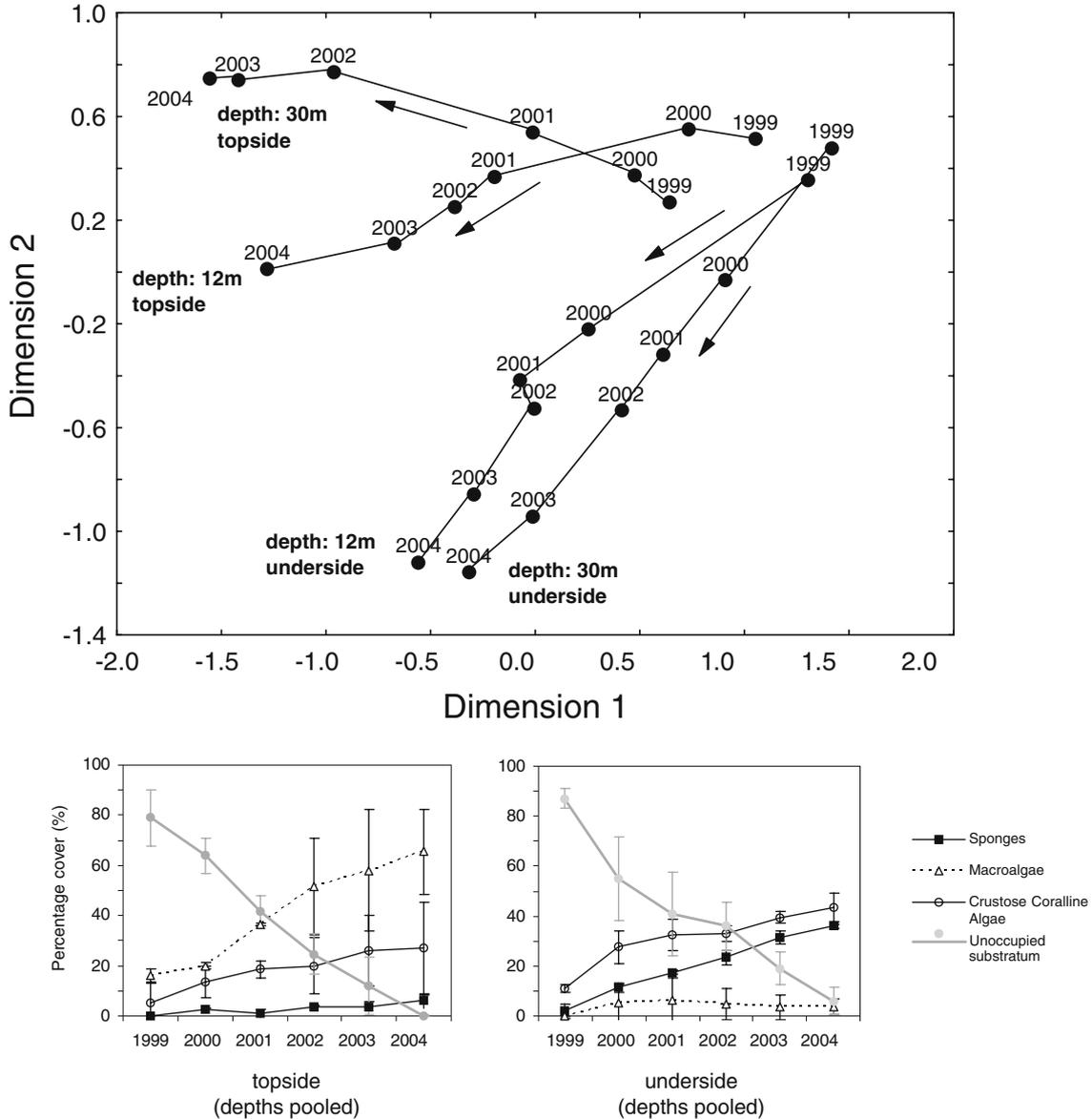
Fig. 2 Multi-dimensional scaling (*MDS*) of the changes in benthic composition of the panels used in this study. Temporal patterns are given for each depth/side combination and averaged over both panels for each year

taxa with known reproductive modes were spawners (Table 1). The brooding species *A. solitaria*, *Madracis pharensis*, *R. maculata* and *T. coccinea* represented the majority of the observed recruits (91.4%; $n = 1385$). The large number of recruits of these species, together with *Agaricia* spp. ($n = 51$) and *Porites* spp. ($n = 24$), allowed for further investigations of their early life-history dynamics.

Recruitment and mortality

All recruits ($n = 1385$) were initially found attached to the panel material, and/or dead or living crustose coralline algae, and to dead parts of other encrusters (e.g. foraminifera, bryozoans and bivalves). It was,

however, impossible to identify the settlement surface of each recruit as, even at small sizes ($< 0.5 \text{ cm}^2$), they often occurred on multiple substrate types and their point of initial attachment was hard to determine. Preference of recruits for either the topside or underside of the settlement panels was species or taxon-specific (Table 1). The azooxanthellate corals *A. solitaria*, *R. maculata* and *T. coccinea* showed strict preference to recruit on the underside of the panels, as did the zooxanthellate species *M. pharensis*. With these four species excluded, 99.5% of the remaining recruits were found on the topside of the panels.

For both topside and undersides of the panels, there was no significant relationship between the number of new recruits and area of substratum available for recruitment, defined as surface area not

Table 1 Sexual recruitment of scleractinian species expressed as the total number of new individuals observed in November of each year at two depths (12 and 30 m)

Preferred habitat				Year											
Species	Reproductive mode	Panel side	By % of recruits	Depth: 12 m						Depth: 30 m					
				1999	2000	2001	2002	2003	2004	1999	2000	2001	2002	2003	2004
Agaricia spp.	Brooder	Top	98.1	0	0	0	26	21	3	0	0	0	1	0	0
A. lamarcki	Brooder	Under	100.0	0	0	0	3	2	0	0	0	0	0	0	0
A. solitaria	Brooder	Under	100.0	0	4	0	26	158	163	0	2	0	35	70	74
D. labyrinthiformes	Spawner	Top	100.0	0	0	0	2	0	2	0	0	0	0	0	0
D. strigosa	Spawner	Top	100.0	0	0	0	2	0	0	0	0	0	0	0	0
E. fastigiata	Brooder	Top	100.0	0	1	0	3	1	0	0	0	0	3	0	0
M. annularis s.l.	Spawner	Top	100.0	0	0	0	0	0	1	0	0	0	0	0	0
M. cavernosa	Spawner	Top	100.0	0	0	0	1	0	0	0	0	0	1	0	0
M. decactis	Brooder	Top	100.0	0	0	0	1	0	0	0	0	0	0	0	0
M. pharensis	Brooder	Under	99.1	0	23	78	155	62	28	0	6	37	30	15	11
M. meandrites	Spawner	Top	100.0	0	0	0	2	2	2	0	0	0	0	0	4
S. roseus	Brooder	Top	100.0	0	0	0	0	2	0	0	0	0	0	0	0
Porites sp.	Brooder	Top	95.9	0	0	0	16	5	3	0	0	0	0	0	0
R. maculata	Brooder	Under	100.0	0	5	3	9	11	3	0	80	1	41	4	4
S. siderea	Spawner	Top	100.0	0	0	0	4	3	1	0	0	0	2	0	0
T. coccinea	Brooder	Under	100.0	0	0	2	31	16	45	0	1	0	14	11	14
Unknown spp.	?	Under		0	0	0	16	10	1	0	0	0	7	5	0
Total		Top + bottom		0	33	83	278	279	251	0	89	38	127	100	107
Totals including *A. solitaria* and *R. maculata*		Top		0	1	0	57	32	12	0	0	0	7	0	4
		Bottom		0	32	83	221	247	239	0	89	38	120	100	103
Totals without *A. solitaria* and *R. maculata*		Top		0	1	0	57	32	12	0	0	0	7	0	4
		Bottom		0	23	80	186	78	73	0	7	37	44	26	25

The total available surface at each depth is 23.12 m^2. The preferred panel side of each species indicates the side preferred by the majority of recruits (percentage indicated in the successive column). Recruitment rates for all species combined are given for each year/depth/panel side combination with and without the solitary corals *R. maculata* and *A. solitaria*

occupied by macroalgae or sponges ($r < 0.71$; $p > 0.08$), suggesting that space per se was not limiting recruitment on the panels. Recruits that arrived in different years (period 2002–2004) preferred similar areas on the panel for settlement. Recruit density within randomly placed 20×20 cm quadrats was correlated between years (r: 0.63; $p < 0.001$, $n = 30$) indicating that corals recruited consistently more (or less) in certain areas of the settlement rack. Spawning species never recruited on the underside of the panels (i.e. in cryptic habitats).

During the periods 2002–2003 and 2003–2004, benthic community composition and apparent causes of death of coral recruits were monitored simultaneously. Few of the corals that had settled in exposed (i.e. topside) habitats died (2.4% per year) and therefore, mortality rates were determined only in cryptic (i.e. underside) habitats (Table 2). Overall, 46.6% of the individuals in cryptic habitats died annually. At 12 m, recruit mortality through apparent overgrowth by nearby benthic organisms (mainly sponges, crustose coralline algae and bivalves) was highly correlated with the abundance of such space competitors (Table 2). At 30 m such a relationship was not observed, possibly due to the smaller sample sizes and lower diversity in benthic taxa. Despite the fact that CCA's were abundant at 12 and 30 m, they

appeared to contribute disproportionably little to coral mortality at both depths compared to other benthic groups (e.g. sponges and bivalves). When CCA's were removed from the 30 m-analyses, the relationship between the abundance of a benthic group and its apparent contribution to recruit mortality became highly significant (2002–2003: r: 0.96; $p < 0.01$; 2003–2004: r: 0.99; $p < 0.01$).

Due to the large number of recruits of brooding species (*A. solitaria*, *M. pharensis*, *R. maculata* and *T. coccinea*) on the 12 m-panels, survival rates could be investigated as a function of size for the period 2003–2004 (Fig. 4). Survival rates increased towards higher size-classes for all species except for *R. maculata*, as none of this species' 13 recruits died; consequently, its survival probabilities were one for all size-classes. At the taxon level, larger average polyp diameter corresponded to lower overall mortality rates (r: 0.81; $p < 0.05$, $n = 5$; taxa included in analysis: *R. maculata*, *A. solitaria*, *M. pharensis*, *T. coccinea* and *Agaricia* spp.). Only *Porites* spp. did not fit this pattern and showed higher survival rates than expected from polyp diameter. In addition, polyp diameter and growth rate were not related at the species level (r: 0.60; $p = 0.10$, $n = 6$; taxa included in analysis: *R. maculata*, *A. solitaria*, *M. pharensis*, *T. coccinea*, *Agaricia* spp. and *Porites* spp.).

Table 2 Overview of benthic groups responsible for mortality of recruits on the underside of panels (contribution in percentages to the total recruit mortality per year) at two depths (12 and 30 m) for two successive years (2002–2003 and 2003–2004)

|	Depth: 15 m				Depth: 30 m			
	Period				Period			
	2002–2003	Abundance[a]	2003–2004	Abundance[a]	2002–2003	Abundance[a]	2003–2004	Abundance[a]
Mortality caused by								
Bivalves[b]	6	**4**	3	**3**	18	**8**	10	**8**
CCA[c]	18	**38**	21	**42**	18	**41**	20	**48**
Macroalgae	3	**7**	5	**6**	2	**< 1**	3	**2**
Millepora	5	**2**	7	**3**	0	**< 1**	0	**< 1**
Sponges	34	**30**	37	**39**	34	**33**	43	**35**
Tubastrea sp.	0	**< 1**	1	**< 1**	0	**< 1**	0	**< 1**
Tunicates	6	**6**	6	**8**	0	**1**	0	**2**
Unknown	22	**< 1**	19	**2**	26	**< 1**	24	**1**
Worms	3	**< 1**	0	**< 1**	2	**< 1**	0	**< 1**
Bryozoans	1	**< 1**	1	**< 1**	0	**< 1**	0	**< 1**
Blue-green algae	1	**< 1**	0	**< 1**	0	**< 1**	0	**< 1**
N	279		134		192		56	
Correlation	$r^2 = 0.85$; $p < 0.01$, $n = 9$		$r^2 = 0.92$; $p < 0.01$, $n = 9$		$r^2 = 0.73$; $p = 0.1$; $n = 6$		$r^2 = 0.77$; $p = 0.13$, $n = 5$	

The abundance of each benthic group is also listed in percentages (in *bold*), together with the correlation statistics describing the relationship between their abundance and their contribution to recruit mortality
[a]This column does not add up to 100% as certain habitat types do not contribute to mortality (i.e. open space)
[b]Percentage cover determined independently from other substrate types
[c]Crustose coralline algae

Fig. 3 Changes in processes shaping the coral community are given in a top, and b underside of the panels (depths pooled). *Bars* represent: recruitment (solitary corals *R. maculata* and *A. solitaria* are omitted), corals present (total number of colonies present that recruited in previous years) and the overall probability of mortality in next the next year (*right axis*)
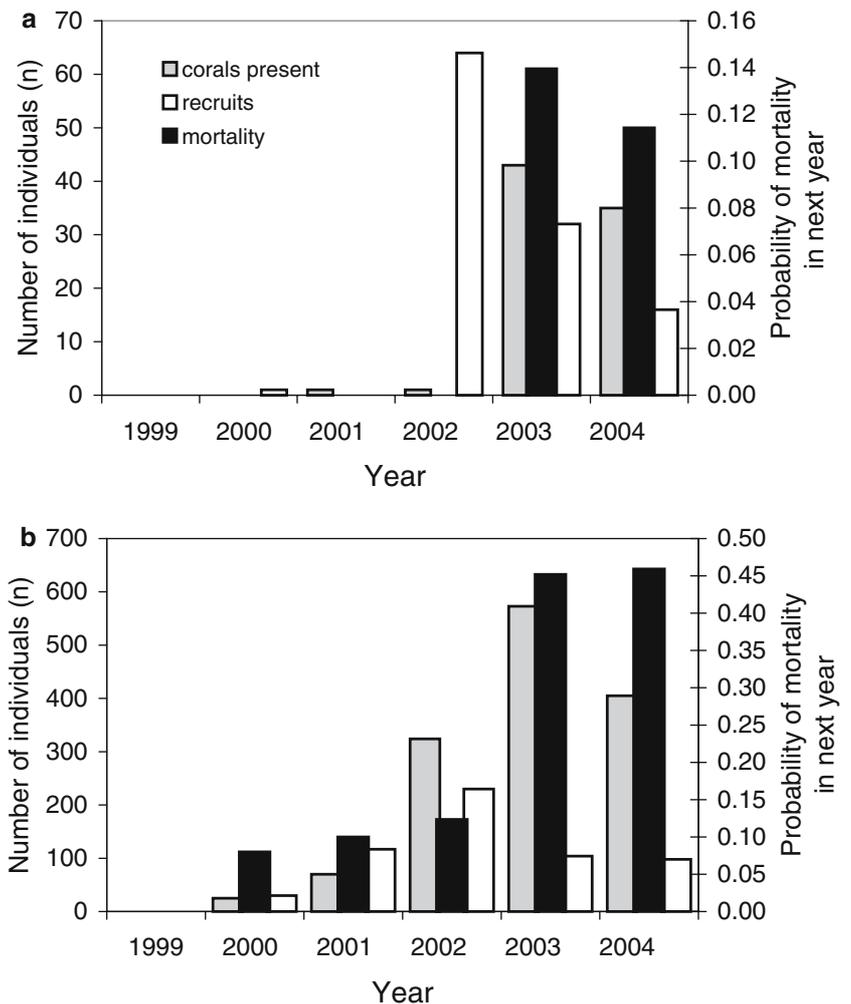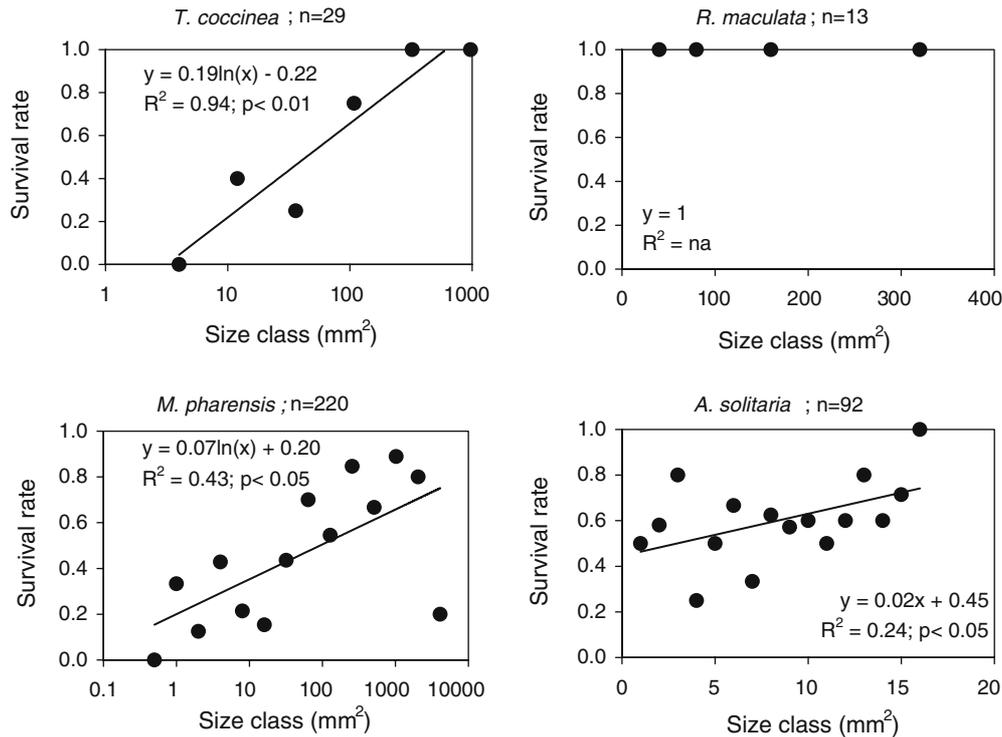
Fig. 4 Survival rate (proportion of recruits that survived from November 2003 to November 2004) for four coral species as a function of colony size class. *n* indicates the total number of colonies, whereas the range of size-classes was arbitrarily chosen to include approximately equal numbers of individuals in each size-class. Each data point indicates the survival rate (defined as the proportion of recruits surviving to the following year) for individuals in that size class

Growth rates of species

In the period 2002–2004, sufficient numbers of recruits were present to allow interspecific growth rate comparisons. Average growth rates differed among species (ANOVA, $F_{5,139} = 3.74$, $p < 0.01$) but not between years (ANOVA, $p > 0.27$) or between depths (ANOVA, $p > 0.42$). The strict taxon specific preference for either side of the panels did not allow for intraspecific comparisons of growth rates between topsides and undersides of the panels. Among the hermatypic taxa, *Meandrina meandrites*, *Agaricia* spp. and *Porites* spp. had highest average growth rates (Table 3) although higher growth rates did not correspond to higher survival rates in inter-specific and intra-specific comparisons of these species ($r < 0.69$; $p > 0.20$). Negative growth rates (indicative of colony shrinkage) were uncommon in these species, and recruits gradually increased in size without signs of partial mortality or fragmentation. The growth process of *M. pharensis*, *T. coccinea*, *A. solitaria* and *R. maculata* showed more variation. These species displayed bidirectional growth, i.e. growth rates were positive and negative (Fig. 5). Colony size in one year related linearly to colony size in the following year for all species, probably due to temporal autocorrelation caused by revisiting the same colonies. For all species, colony size was a poor predictor of an individual's future growth rate ($r^2 < 0.20$; $p > 0.08$) and the success of using colony size as a predictor of colony growth rates was variable between successive years (Table 3). An individual that grew fast in the year 1, did not necessarily do so in the following year. Therefore, growth rates of individual colonies could not be used to predict their growth rates in the following year (species included in analysis: *M. pharensis*, *T. coccinea*, *A. solitaria* and *R. maculata*). Coral community development was, therefore, extremely difficult to predict even for a simple coral community as the one studied here on an artificial substratum in Curaçao.

The complex dynamics during the earliest life-stages was best illustrated by *M. pharensis*. At small size, this species displayed all aspects of clonal growth, i.e. bidirectional growth, partial mortality, fission and fusion (Fig. 6). For example, fission occurred in colonies as small as 49 mm² and in 2004, 47.1% of the *M. pharensis* colonies were produced asexually (80.1% in 2003). This indicated that small colony size did not necessarily represent recent recruitment or young age. The average yearly survival rate of asexually produced individuals is 0.52 ($n = 250$; Fig. 7), which was similar to that of non-fragmented colonies (0.56; $n = 200$). Fragments were never observed fusing if they did not originate from the same genet (i.e. a colony that (1) originated from one settled planulae and (2) had fragmented earlier).

Table 3 Growth rates for scleractinian species that settled on the artificial substratum (depths pooled) from 2002–2004

Year: 2002 Species	Growth rate (mm^2 year^{-1}) Average	SD	N		Size 2003 %	p	Growth rate 2002–2003 %	p	Growth function
Agaricia spp.	195.0	280.0	13	Variation explained by size in 2002	57.1	< 0.001	31.6	< 0.01	$S_{t2} = 2.52 S_{t1} - 51.4$
Porites spp.	87.2	98.7	13		15.5	ns	3.9	ns	–
M. pharensis	16.3	234.6	147		6.2	< 0.01	36.5	< 0.01	–
T. coccinea	302.6	263.3	29		60.5	< 0.001	1.7	ns	$S_{t2} = 1.19 S_{t1} + 274.9$
A. solitaria	2.0	4.6	21		34.2	< 0.01	7.2	ns	–
R. maculata	−6.6	13.9	10		75.2	< 0.01	1.0	ns	$S_{t2} = 0.58 S_{t1} + 31.06$
M. meandrites	1056.3	982.7	3						
E. fastigiata	351.6	195.9	4						

Year: 2003 Species	Growth rate (mm^2 year^{-1}) Average	SD	N		Size 2004 %	p	Growth rate 2003–2004 %	p	Growth function
Agaricia spp.	85.2	102.5	18	Variation explained by size in 2003	68.1	< 0.001	0.7	ns	$S_{t2} = 1.06 S_{t1} + 73.63$
Porites spp.	68.4	84.2	19		76.1	< 0.001	16.2	ns	$S_{t2} = 1.38 S_{t1} + 3.43$
M. pharensis	6.2	16.4	54		25.5	< 0.001	2.6	ns	–
T. coccinea	−31.7	219.6	11		94.9	< 0.001	67.7	< 0.01	$S_{t2} = 0.75 S_{t1} + 110.29$
A. solitaria	3.4	4.2	34		38.6	< 0.001	44.9	< 0.01	–
R. maculata	−1.3	22.1	12		42.5	< 0.05	28.2	ns	–
M. meandrites	891.6	605.3	6						
E. fastigiata	1930.0	1575.3	2						
Diploria spp.	230.2	175.4	4						

The percentage variation in colony size and growth that can be explained from the size of the same colony in the preceding year is shown for the periods 2002–2003 and 2003–2004. When colony size (S_{t1}) explained more than 50% of colony size variation in the successive year (S_{t2}) a simple growth function was calculated that defines the relationship between S_{t1} and S_{t2}

Discussion

This study showed that species or taxon-specific characteristics of recruits and the composition of the competing benthic community are important in determining coral community composition and structure. Some recruiting scleractinian species showed strict preference for either exposed surfaces that became dominated by macroalgae or for cryptic communities that became dominated by sponges and CCA (Table 1). The overall similarity in growth strategy of species occupying the same habitat (topsides versus undersides) further suggests that species have adapted similarly to either habitat. Species in exposed habitats on the settlement racks (*Agaricia* spp., *Porites* spp., *Diploria* spp., *M. meandrites* and *E. fastigiata*), all grew as gradually expanding circles and showed high growth rates relative to species that preferred cryptic habitats (Tables 1, 3). The cryptic species (*M. pharensis*, *A. solitaria*, *R. maculata* and *T. coccinea*) faced sponges and bivalves as major competitors and showed more dynamic growth strategies: *T. coccinea* was able to escape unfavorable conditions through formation of runners (Vermeij 2005b), *M. pharensis* increased the number of new individuals through fragmentation (up to 80%) and was capable of extremely fast unidirectional growth (11.6 mm per month; Van Moorsel 1988). *R. maculata*, *T. coccinea* and *A. solitaria* increased local abundance by: (1) reaching maturity at small size allowing early onset of

planula production and (2) short larval dispersal distances (Vaughan 1919; Van Moorsel 1989; Fenner and Banks 2004). Larger size increased survival rates in all these species as well as in other corals (Hughes and Connell 1987; Meesters et al. 1996; Bruno 1998); however, 6–76% of the variation in survival rates remained unexplained (Fig. 4). Multiplicity in numbers rather than in size then becomes an additional strategy to ensure local species persistence in environments characterized by high mortality risks.

Because the substratum surface, especially in cryptic habitats, became gradually occupied by benthic groups that grew faster than corals (e.g. sponges and bivalves), the initial advantage of corals as successful space colonizers through adaptive larval behavior (e.g. Morse et al. 1988; Mundy and Babcock 1998; Raimondi and Morse 2000; Morgan 2001) could disappear. As succession progresses, the capability of corals to settle in optimal microhabitats, could be outweighed by their inferior competitive abilities combined with slow growth relative to other benthic groups. Since competitive impacts on coral survival varies greatly among different species of sponges (Aerts and Van Soest 1997) or macroalgae (McCook et al. 2001), quantifying species abundances in addition to overall "cover" will help to more precisely predict future patterns of recruit abundance. Despite the often suggested negative effect of macroalgae on coral survival (Miller and Hay 1998; McCook 1999), overall survival rates of individuals on exposed surfaces characterized by high macroalgal cover were 19.4 times

higher than for recruits in cryptic communities. In contrast, overall density was 15.6 times lower than in cryptic habitats. As species showed strict preference for either habitat, it was difficult to determine whether the observed differences in overall mortality and density resulted from environmental or species-specific factors. The similarity in strategies of species occupying either habitat on the settlement racks was, however, striking: in exposed habitats species grew fast, reached maturity at larger size and occured in low densities compared to species in cryptic habitats.
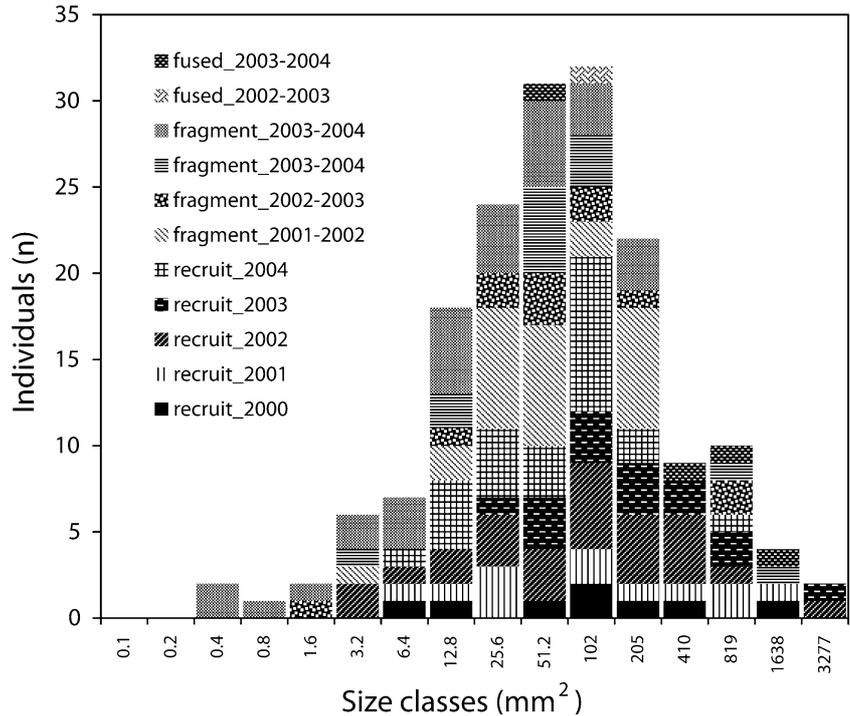
The lower densities of recruits in macroalgal dominated habitats support earlier suggestions that macroalgae negatively affect recruitment, either through preemption of settlement surfaces, by increasing post-settlement mortality risks or by inhibition of settlement through allelopathic interactions (Miller and Hay 1996; Birkeland 1977; Edmunds and Carpenter 2001; Nugues et al. 2004).

Although cover by other benthic invertebrates was a good indicator of survival potential of coral recruits (Table 2), growth rates were highly variable between
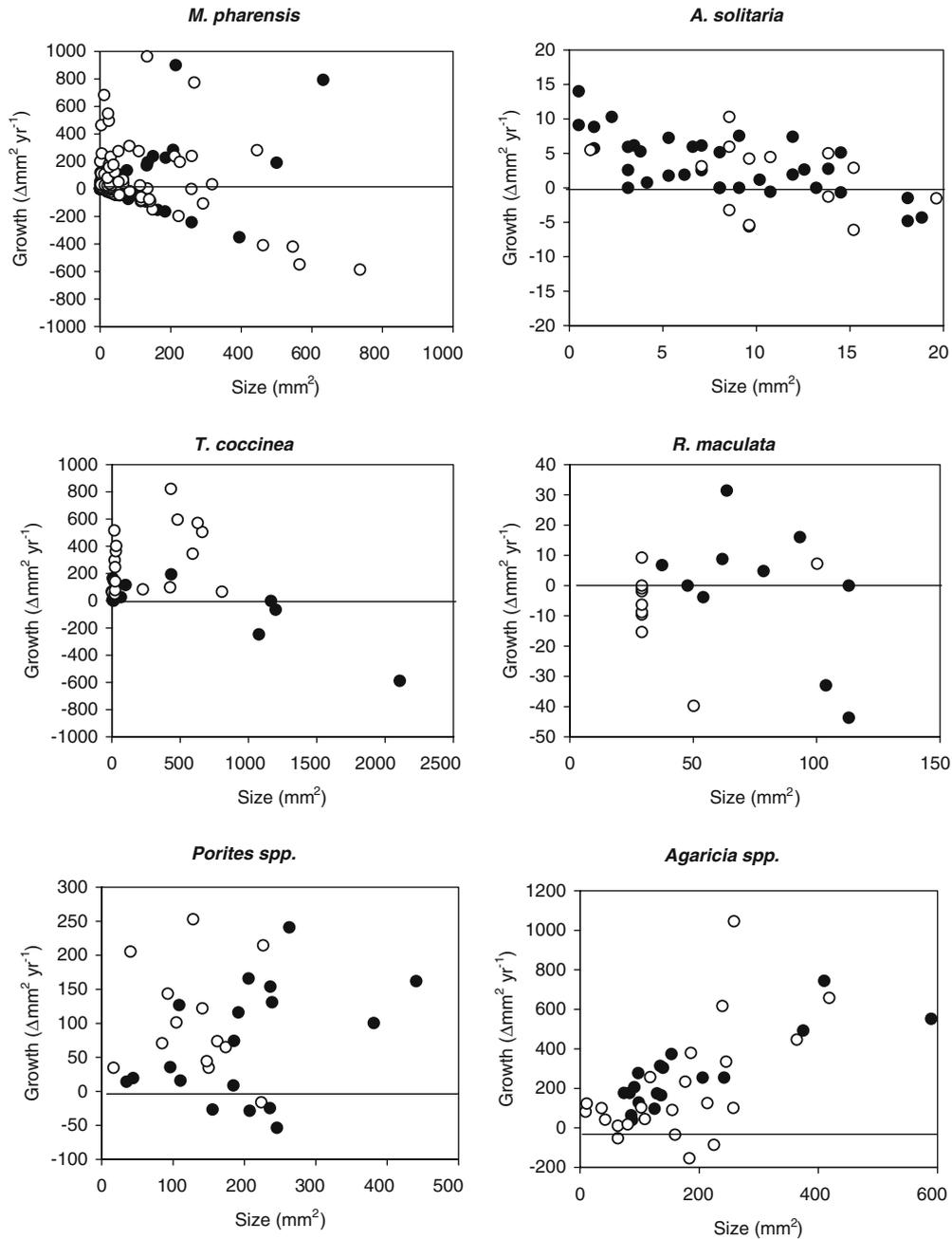
Fig. 5 Interannual variation in growth rates as a function of colony size for six coral species for two periods. *Each circle* represents a colony. *White circles* 2002–2003, *black circles* 2003–2004

Fig. 6 Origin of individual *M. pharensis* colonies present on the panel undersides in 2004 at a depth of 12 m. *Legend* indicates process that initially formed the colony followed by the time or period that the process (recruitment, fragmentation (i.e. fission) or fusion) took place. Colonies are distributed over logarithmic size classes

Fig. 7 Fate of colonies that arose through fragmentation as a function of size. Colonies either fused with the colony that generated them, died or survived

and within species (Table 3, Fig. 5). The growth rates presented here are difficult to compare to other studies because there are surprisingly few studies describing growth rates for Caribbean coral recruits (e.g. Van Moorsel 1988; Edmunds 2000; Edmunds et al. 2004). These studies often report maximum or linear extension rates or do not distinguish among species. Linear extension rates cannot be straightforwardly translated to changes in total colony surface as corals often grow allometrically (Bak 1976; Van Moorsel 1985). As colony growth rates are highly variable and not species specific

or size specific, they could not be used to predict future population structure on the artificial settlement racks (Table 3). It is therefore important not only to define the mechanisms that affect growth and mortality of coral recruits (i.e. presence of benthic competitors), but also to study them at the right spatial and temporal scales. This is especially relevant for processes whose outcome can vary continuously (e.g. growth) compared to processes with limited outcomes (e.g. survival).

Van Moorsel (1989) deployed identical artificial substrata at the same location between 1979 and 1981. Although rigorous comparison was impossible due to lack of replication within one year, and the unavailability of recruitment data from 1982 to 1998, the differences in coral community development from 1979 to 1981 and the period studied here (1998–2004) were enormous. The upper sides of his panels were completely dominated by crustose coralline algae and macroalgae were not observed on the topsides of his settlement racks throughout the entire study period (1979–1981). This contrasted with the findings presented here, where macroalgae dominated the topside of the settlement racks at both depths. After two years, Van Moorsel observed 859 *Agaricia* spp. recruits and 122 *Porites* spp. recruits (Van Moorsel 1989), whereas I found none until the third year. Species that recruited to the panels in 1979–1981 but not in 1999–2004 are the spawning species *Acropora* spp. (39 colonies in two years), *Colpophyllia natans* (15) and *Manicina areolata* (5). Overall recruit density was 5.16 times less on the topsides of the panels in 1998–2004 compared to the 1979–1981 survey, whereas recruit density was only 1.14 times less on the undersides. Coral communities developing on the settlement panels in the present study were less di-
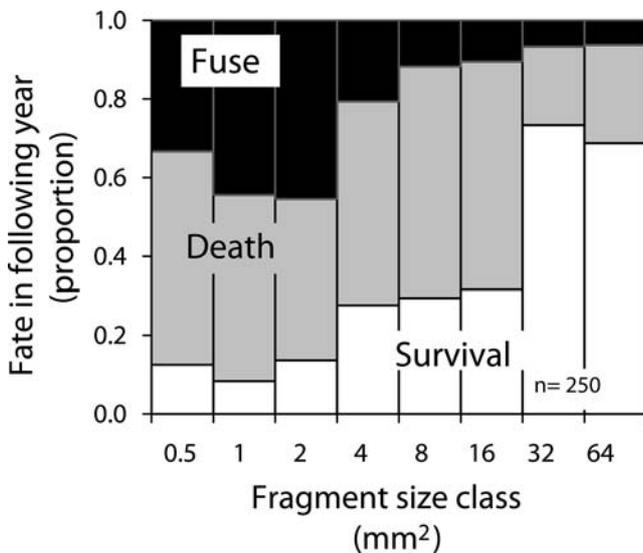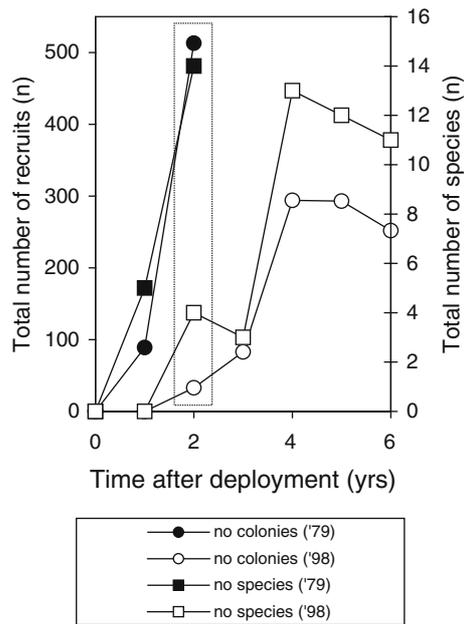
Fig. 8 Coral community development on identical artificial substrata (46 m²) from 1979–1981 (*black symbols*) and from 1998–2004 (*white symbols*). *Circles* (*left axis*) indicate the total number of recruits present on the panels for each following year; *squares* indicate the total number of species present (*right axis*). The *outline* indicates the difference in coral community structure for the first two years of monitoring in this study (1999–2000) and that of Van Moorsel (1979–1981; data from: Van Moorsel 1989). After two years, Van Moorsel stopped his study, which makes further comparisons impossible

verse, consisted of fewer individuals and the onset of recruitment started two years later compared to the 1979 study (Fig. 8). This is especially true for the upper sides of the panels. Three explanations exist: (1) the size of the larval pool has decreased either through reduced adult fecundity (Hughes et al. 2000) or a decreasing adult population, (2) there has been pre-emption of settlement surface or successive smothering of recruits by higher abundances of macroalgae on the upper sides of the panels (Bak and Engel 1979; Connell et al. 1997) and (3) there has been a lowered production of settlement cues due reduced cover by crustose coralline algae (Morse et al. 1988). The observed decrease in recruits exceeds yearly natural fluctuations in larval supply, as such fluctuations would not be expected to exceed one order of magnitude over decadal time-scales despite a decreasing adult population (Connell et al. 1997; Hughes and Tanner 2000). Space pre-emption by other benthic organisms (especially macroalgae, that were not observed by Van Moorsel) is a likely candidate to explain the observed decrease in recruitment on the upper sides of the panels between the surveys of Van Moorsel and the one presented here. The high survival rates of recruits that were successful in settling in macroalgae dominated habitats further suggest that the negative effect of macroalgae on coral population development mainly occurred during the settlement step confirming

earlier suggestions in this direction (Birkeland 1977; Miller and Hay 1996; Connell et al. 1997; Edmunds and Carpenter 2001; Nugues et al. 2004). Reduced adult abundance resulting in fewer planulae could also cause a reduction in recruitment rates. The Caribbean wide die-off of shallow water *Acropora* spp. in the 1980 s corresponded with a complete disappearance of these species in the 1998–2004 surveys, whereas 39 recruits were observed before the die-off in 1979–1981. However, adult cover between depths from 10 to 30 m had only been reduced by 5% on average between 1981 and 2001 (Bak and Nieuwland 1995), making reduced adult cover a less likely candidate to explain the observed reduction in recruitment rates.

In the present study, the early life history dynamics of corals were characterized by processes that were highly variable (e.g. juvenile growth rates), and processes that were predictable because of their relation to environmental parameters (e.g. juvenile survival rates). Although recruitment itself was highly variable (e.g. due to variation in larval supply, planktonic survival and adult fecundity) subsequent population development was dependent on a variety of factors that need to be taken into account in order to make useful interpretations of recruitment data. Benthic organisms affected recruitment success through space preemption (algae and sponges) and overgrowth (mainly sponges) indicating the importance of competition and succession as structuring factors in benthic community formation. The scale at which these processes took place was smaller (mm–cm) than that normally addressed in coral community studies (m). In order to fully understand the mechanisms underlying observable patterns on reefs, processes that generate them and interspecific differences should be studied at these small scales. Only then can the processes responsible for recruitment success or failure be resolved and the role of recruitment and early-life phases in population survival assessed.

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