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Identification of Scleractinian Coral Recruits from Indo-Pacific Reefs

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Russ C. Babcock, Andrew H. Baird, Srisakul Piromvaragorn, Damian P. Thomson and Bette L. Willis (2003) Identification of scleractinian coral recruits from Indo-Pacific reefs. *Zoological Studies* **42**(1): 211-226. Study of the early life history of scleractinian corals has been hampered by the inability to identify recently settled juveniles. To increase taxonomic resolution of coral recruits, we compared the morphology of the skeleton of juveniles raised from known parents for 29 species in 21 genera and 12 families. Juveniles from only 3 families could be reliably distinguished throughout their 1st year of life: the Acroporidae, which have a porous coenosteum, prominent septa, and no columella; the Pocilloporidae, which have a solid coenosteum, prominent septa and a prominent columella; and the Poritidae, which have septa with prominent teeth. Juveniles in the remaining families examined could not be consistently distinguished. In these taxa, the skeleton began as an epitheca with little internal structure, growth was slow, and the pattern of septal development was similar. Within the 3 distinctive families, a number of other taxa could be recognized when juveniles were young. Genera of the Pocilloporidae could be distinguished by size differences in the diameter of the primary corallite. *Isopora*, *Acropora*, and *Montipora* juveniles could be distinguished by differences in the size of the corallum at settlement. Juveniles of the broadcast spawning *Porites* appear to be distinguished from those of brooding *Porites* by the pattern of septal development and by the small size at settlement. The number of taxa that could be distinguished was highest when juveniles were between 4 and 8 wk old. After this time, variation in the growth rates of individuals and thickening of the skeleton obscured differences between the taxa.
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Measuring recruitment patterns of marine organisms is of fundamental importance for understanding the mechanisms that regulate their populations and mediate species coexistence (Underwood and Fairweather 1989). In addition to understanding population dynamics, knowledge of recruitment patterns is a prerequisite for the effective management of marine ecosystems, enabling informed responses to disturbances, such as crown-of-thorns starfish outbreaks, storms and bleaching events (Hughes et al. 1999). The importance of monitoring processes such as recruitment, rather than just changes in adult abundance, in order to understand how reef ecosystems function, is becoming increasingly clear (Karlson 1999). Furthermore, early life history stages are often more susceptible than adults to environmental perturbations such as eutrophication and sedimentation (Ward and Harrison 1996, Gilmour 1999). Consequently, measuring changes in patterns of settlement and recruitment may provide an early warning of potential damage to reefs or impacts on their resilience after disturbance.

Despite the increasing awareness of the importance of understanding settlement patterns, estimating the input of new recruits into coral populations is problematic for a number of reasons.

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Corals are small at settlement and growth is slow (Babcock 1985). Consequently, a year or more may pass before a recruit is visible on the reef substratum (Wallace and Bull 1982). During this period, mortality is high and variable (Rylaarsdam 1983, Sato 1985, Babcock and Mundy 1996). Consequently, it is impossible to determine the extent to which patterns measured when a recruit becomes visible have been altered by post-settlement processes. For example, aggregated recruitment may reflect either gregarious settlement, which involves larval choice, or differential patterns of mortality acting on an essentially random pattern of settlement (Keough and Downes 1982).

Artificial substrata that can be removed for microscopic examination are used to measure coral settlement patterns and minimize the ambiguity that can arise due to the substantial time interval between settlement and visible recruitment in corals (e.g., Birkeland 1977, Wallace and Bull 1982). Coral larvae secrete a skeleton within hours of settlement, leaving a record of settlement even after the polyp dies, unless the skeleton is removed, overgrown, or eroded (Richmond 1985). If the length of time that substrata are in the water is short (i.e., 1 to 2 mo), counts of juvenile skeletons can provide a reasonable estimate of the supply of new recruits (Wallace 1985, Hughes et al. 2000). This technique has been used to examine a number of aspects of coral ecology, for example, spatial and temporal variations in recruitment (Birkeland et al. 1981, Wallace 1985, Baird and Hughes 1997, Mundy 2000, Hughes et al. 2002), cross-shelf differences in the relative abundance of recruits on the Great Barrier Reef (Fisk and Harriott 1990, Sammarco 1991), the effect of competition on coral recruitment (Maida et al. 1995, Baird and Hughes 2000), patterns of dispersal in coral (Sammarco and Andrews 1988, Tioho et al. 2001), and stock recruitment relationships in corals (Hughes et al. 2000). However, the limited level of taxonomic resolution that can be applied to new coral recruits has restricted the range of questions that can be addressed. In particular, studies of the population dynamics of corals that include an estimate of settlement are rare (Hughes 1984).

Identifying coral recruits, particularly in regions such as the central Indo-Pacific, which have a diverse scleractinian fauna, has proven to be difficult because juvenile corals have few useful taxonomic characters. Identification of coral recruits is not as problematic in the Caribbean, where coral assemblages are less diverse and juveniles can more readily be classified to genus or species (e.g., Sammarco 1980, Rogers et al. 1984). In an attempt to increase the level of taxonomic resolution for early recruits, Babcock (1992) raised juveniles from 11 of the 15 scleractinian families common on the Great Barrier Reef (GBR). He concluded that only 3 of these families had distinct taxonomic characters that were sufficient to enable consistent identification: the Acroporidae, Pocilloporidae, and Poritidae. Generally, this is the resolution used in recruitment studies on the GBR, with the remaining juveniles recorded as "others" (e.g., Wallace 1985, Harriott and Fisk 1988, Baird and Hughes 2000). While some authors have distinguished up to 18 different taxa (e.g., Sammarco 1991), no justification for this level of taxonomic resolution has been presented.

Here we raised the juveniles of 29 common coral species, representing 21 genera from 12 families on the GBR, to identify taxonomic characters that would allow skeletons of recruits to be distinguished. We concentrated on the first 6 mo of life, because most studies of coral recruitment have attempted to use recruits of this age to estimate larval supply into populations or habitats. Furthermore, we concentrated on the micro-architecture of the corallum, i.e., those features readily apparent under a stereo-dissection microscope (Wells 1956). While greater taxonomic resolution may be achieved by examining the ultrastructure of the corallum, i.e., the crystalline structure of the skeleton (Wells 1956), taxonomic features identified at this level would not be of practical use when counting the large number of recruits encountered on most settlement tiles.

MATERIALS AND METHODS

The larvae of broadcast spawning coral species were raised using the method described in Babcock and Heyward (1986) or according to the following modifications. Six to 10 colonies of each species were collected from reefs surrounding Orpheus Island (18°46'S, 146°15'E) or Magnetic Island (19°9'S, 146°50'E) in the Townsville Section of the GBR. Colonies were placed in holding tanks, with 1 species per tank. Following spawning, the egg-sperm bundles of hermaphroditic species were collected and broken apart with gentle agitation. The gametes were then placed in plastic buckets with an additional amount of seawater to produce an approximate sperm concentration of 10^5/ml to optimize fertilization success (Oliver and Babcock 1992, Willis et al. 1997).

When the eggs began to cleave (between 2-4 h), approximately 5000 embryos were collected and gently rinsed in sand-filtered sea water (FSW) to remove excess sperm. The embryos were then placed in 15-L fiberglass tanks in sand-FSW. The water was changed after 6 h, 18 h, and then daily until the majority of the larvae were motile. Once motile, the larvae were allowed to settle on conditioned terracotta tiles. Juveniles attached to tiles were maintained on racks in constant flow-through aquaria or in the field. The gametes of gonochoric species were left in the tanks after removal of adults following spawning. The next morning, embryos were collected and placed in culture tanks and maintained as described above. Brooded larvae were collected by holding adults in flow-through aquaria with containers lined with a plankton mesh positioned below the outflow to collect the planulae. Larvae were collected in the morning and allowed to settle on conditioned terracotta tiles. Tiles were then maintained in flow-through aquaria, or in the field on racks fixed to the reef at depths of between 3 and 5 m. A sample of between 9 and 39 eggs or larvae per species was collected following release, and the maximum diameter was measured to the nearest unit with a graticule eyepiece under a stereo-dissection microscope.

Samples of tiles were removed at various times (Table 1) and examined under a stereo-dissection microscope. Live specimens were circled with a pencil. To reveal the skeleton, recruits were bleached in a 10% NaOH solution, then rinsed in fresh water, and dried. Specimens were then examined under a stereo-dissection microscope at 40X, and the maximum diameters of both the corallum and the primary corallite were measured to the nearest unit with a graticule eyepiece. Representative specimens were photographed under a stereo-dissection microscope. Specimens examined by electron microscope were removed from the tiles, mounted, and vacuum-coated with

Table 1. Approximate numbers of specimens examined at each age

Family	Species	Age								
		1 to 3 d	7 to 10 d	2 wk	1 mo	2 mo	3 mo	4 mo	6 mo	10 mo
Acroporidae	*Acropora cytherea*	18	12							
	Acropora millepora	7	6		16		10	9	3	
	Acropora pulchra	14	5							
	Acropora valida	12	15							
	Acropora tenuis				65				10	
	Acropora palifera	8	8		22					
	Montipora digitata	4	9			8			14	
Agaricidae	*Pachyseris speciosa*	8				3				
Caryophylliidae	*Physogyra lichtensteini*				7		23			
Dendrophylliidae	*Turbinaria mesenterina*	5	15		9	18				2
	Tubastrea diaphana									3
Faviidae	*Goniastrea aspera*	23		60			4	2	3	1
	Goniastrea retiformis	2	22				5			
	Leptoria phrygia	36	14						2	
	Platygyra daedalea	26	30			8	5	3		
	Platygyra sinensis	6	3		12		5	5	7	5
Fungiidae	*Fungia horrida*	30	5	19	13		14	4	19	
Oculinidae	*Galaxea fascicularis*							34		
Merulinidae	*Hydnophora exesa*	5					3			
	Merulina ampliata	17		8	9					
Mussidae	*Lobophyllia hemprichii*								2	
Pectiniidae	*Oxypora lacera*									13
	Echinophyllia aspera								2	
Pocilloporidae	*Pocillopora damicornis*	52			30	23				
	Seriatopora hystrix	102			11	45				
	Stylophora pistillata	66			18	28				
Poritidae	*Porites australiensis*	34		11	6		14	32		
	Porites cylindrica	13					10			1
	Goniopora lobata							4	1	2

gold. Photomicrographs were taken with a Phillips XL-20 scanning electron microscope.

RESULTS

Family Acroporidae

Differences in size at settlement could be used to distinguish among juveniles of the 2 subgenera of *Acropora* and the genus *Montipora*. Mean basal plate diameters of the 4 species of *Acropora* (*Acropora*) were very similar, and the largest juvenile was 1375 μ (Table 2). Juveniles of the isoporan, *A. palifera*, were nearly twice this size, and ranged from 2000 to 2700 μ at settlement (Table 2). While the size of the corallum in *Isopora* was significantly larger at settlement, the size of the calyx was similar in species of the 2 subgenera. The greater size of the isoporan corallа reflected their greater coenosteal development at settlement. In contrast, *Montipora digitata* juveniles were 1/2 the diameter of the largest *Acropora* at settlement (Table 2). The largest *Montipora* juvenile was 750 μ, which is considerably smaller than 850 μ, the smallest diameter recorded in the subgenus *Acropora* (Table 2). Although there was no overlap in the size range of juveniles at settlement (*Montipora* < 850 μ; 850 μ < *Acropora* < 1375 μ; *Isopora* > 1375 μ), differences in the rates of growth of the coralla are likely to eliminate the utility of this feature for distinguishing between older juveniles after between 1 and 2 mo (Table 3). Furthermore, differences in the timing of settlement among juveniles on tiles will further complicate the ability to distinguish these taxa on the basis of size.

Subgenus *Acropora*

The pattern of skeleton formation was similar among all *Acropora* species examined. The skeleton began as a basal plate with 12 basal ridges in a single cycle (Fig. 1a). Lateral processes were evident on the inner end of basal ridges (Fig. 1a, b). These processes developed into rods (or synapticulae) which grew perpendicular to the basal ridges and fused with adjacent synapticulae to form the corallite wall (Fig. 1b, c). The corallum appeared to grow by extension of the basal plate. After approximately 1 wk, all the features that distinguish the family Acroporidae were evident in juveniles of the 5 species of *Acropora* (*Acropora*) examined: prominent laminar septa in 2 cycles, a

Table 2. Diameter of the corallum at settlement (this feature was not measured in all species)

Family	Species	Corallum diameter (μ)				
		mean	SE	min.	max.	*n*
Acroporidae	*Acropora cytherea*	1108	29.6	850	1375	18
	Acropora millepora	1144	20.7	1075	1230	7
	Acropora pulchra	1097	12.9	1025	1150	14
	Acropora valida	1186	27.8	1000	1375	12
	Acropora palifera	2323	61.6	2000	2700	8
	Montipora digitata	609	8.1	525	750	8
Agaricidae	*Pachyseris speciosa*	650	14.4	625	675	8
Dendrophylliidae	*Turbinaria mesenterina*	900	35.4	800	1000	5
Faviidae	*Goniastrea aspera*	565	8.6	500	650	23
	Goniastrea retiformis	595	10.6	500	700	2
	Leptoria phrygia	778	13.1	525	950	36
	Platygyra daedalea	607	7.9	525	700	26
	Platygyra sinensis	784	43.5	610	930	9
Fungiidae	*Fungia horrida*	528	22.7	350	750	30
Merulinidae	*Hydnophora exesa*	585	23.2	500	625	5
	Merulina ampliata	572	14.2	400	650	17
Pocilloporidae	*Pocillopora damicornis*	1755	42.2	1375	2275	30
	Seriatopora hystrix	1255	13.8	1300	1375	35
	Stylophora pistillata	1025	50.0	975	1075	28
Poritidae	*Porites australiensis*	576	11.3	400	675	34
	Porites cylindrica	562	17.6	500	600	13

porous coenosteum, and the absence of a columella (e.g., Fig. 1d). Secondary corallites developed between 1 (Fig. 1e) and 5 mo (Fig. 1f). At 5 mo, juvenile *A. millepora* were small and mound-like and had yet to develop adult colony morphology (Fig. 1f). The mean diameters of the coralla at settlement ranged from 1097 ± 12.9 μ (*A. pulchra*) to 1186 ± 27.8 μ (*A. valida*) (Table 2).

Subgenus *Isopora*

The rate of skeleton formation in *Acropora* (*Isopora*) *palifera* was much faster than in juveniles of the subgenus *Acropora* (*Acropora*). Skeletal elements, such as the coenosteum and corallite wall, were deposited rapidly and in synchrony, so that primary corallites of *A. palifera* had many of the features recognized in the adult skeleton after 1 d (Fig. 2a). In addition, the coralla had a more extensive coenosteum than those in the subgenus *Acropora* of a similar age (Fig. 2b). Secondary corallites appeared within 3 wk (Fig. 2c). The mean diameter of newly settled coralla was 2323 ± 61.6 μ, and values ranged from 2000 to 2700 μ (Table 2).

Genus *Montipora*

The pattern of skeletal development in early juveniles of *Montipora digitata* differed from that of

Table 3. Number of scleractinian taxa distinguishable as a function of age since settlement

Genera	1 wk	2 wk	1 mo	2 mo	4 mo	6 mo
Acroporidae				Acroporidae	Acroporidae	Acroporidae
Acropora	*Acropora*	*Acropora*	*Acropora*			
Isopora	*Isopora*	*Isopora*	*Isopora*			
Montipora	*Montipora*	*Montipora*	*Montipora*			
Agaricidae						
Pachyseris						
Caryophylliidae						
Physogyra						
Dendrophylliidae						
Turbinaria						
Tubastrea						*Tubastrea*
Faviidae						
Goniastrea						
Leptoria						
Platygyra						
Fungiidae						
Fungia						
Merulinidae						
Hydnophora						
Merulina						
Oculinidae					Oculinidae	Oculinidae
Galaxea						
Pectiniidae						
Echinophyllia						
Oxypora						
Pocilloporidae						Pocilloporidae
Pocillopora	*Pocillopora*	*Pocillopora*	*Pocillopora*	*Pocillopora*	*Pocillopora*	
Seriatopora	*Seriatopora*	*Seriatopora*	*Seriatopora*	*Seriatopora*	*Seriatopora*	
Stylophora	*Stylophora*	*Stylophora*	*Stylophora*	*Stylophora*	*Stylophora*	
Poritidae					Poritidae	Poritidae
Porites						
Goniopora						
brooders	brooders	brooders	brooders	brooders		
spawners		spawners	spawners	spawners		
Others	others	others	others	others	others	others
Number of taxa	8	9	9	7	7	6

juveniles in the subgenera *Acropora* and *Isopora*. The skeleton began as a basal plate, as in *Acropora* spp., however the basal ridges were less regular and smaller than in the genus *Acropora* (Fig. 3a). In some specimens, an epitheca (defined by Barnes (1972) as "an extension of the edges of the basal plates secreted by a newly settled coral planulae") was evident (Fig. 3b), similar to that of many other scleractinian families (see below), but which was not prominent in other acroporids at this stage. The septa were rod-like spines which projected into the calyx from the epitheca (Fig. 3b). There were usually 6, but septal insertion appeared less regular than that in *Acropora* (Fig. 3c). Growth of the coralla proceeded with an extension of the skeleton beyond the epitheca where a 2nd wall sometimes formed (Fig. 3c). At 3 to 5 mo, the skeletal morphology of juvenile *M. digitata* (Fig. 3d) was generally similar to that of *Acropora* (Fig. 1f) and *Isopora* (Fig. 2c). The mean diameter of the corallum of newly settled *M. digitata* was 609 ± 8.1 μ, and values ranged from 525 to 750 μ (Table 2).

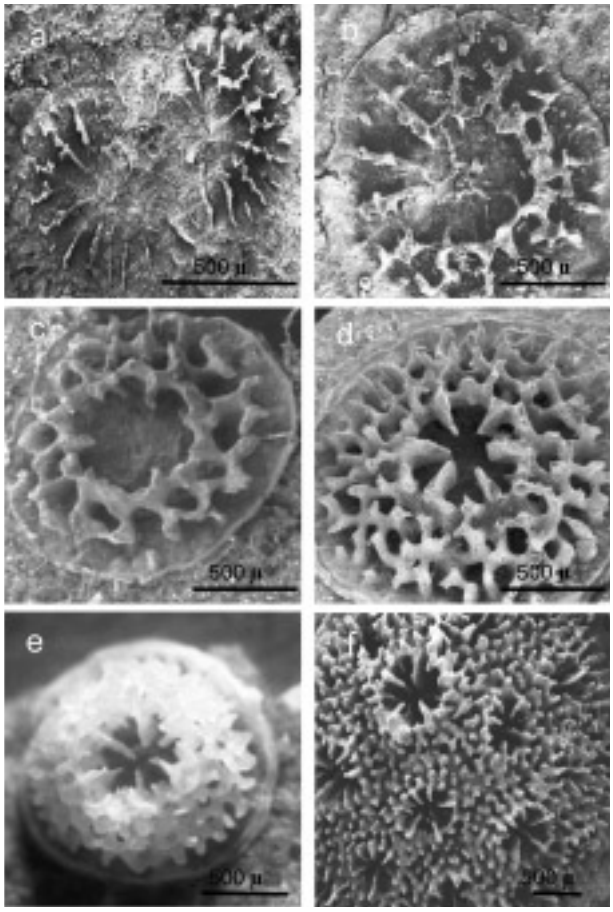

Fig. 1. (a) *Acropora millepora* 1 d; (b) *A. millepora* 2 d; (c) *A. cytherea* 3 d; (d) *A. cytherea* 7 d; (e) *A. tenuis* 1 mo; (f) *A. millepora* 5 mo.

Family Agariciidae

The initial stage in the juvenile skeleton of *Pachyseris speciosa* consisted of an epitheca which appeared within 3 d (Fig. 4a). Further skeletal development was slow. The epitheca grew vertically forming a cup after 6 wk, and 6 primary septa were apparent (Fig. 4b). The septa originated from the rim of the epitheca. The mean size of juveniles at settlement was 650 ± 14.4 μ, and values ranged from 625 to 675 μ (Table 2).

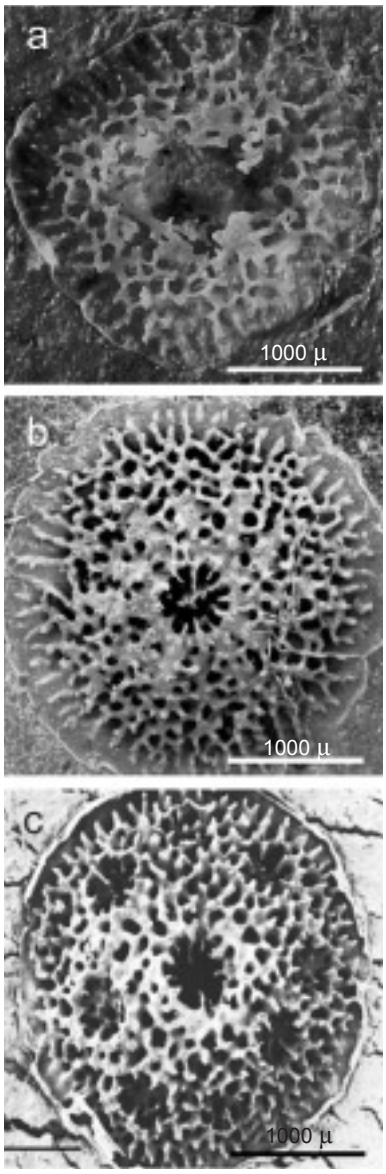

Fig. 2. *Acropora palifera*: (a) 1 d; (b) 3 d; (c) 3 wk.

Family Caryophylliidae

The earliest specimens of *Physogyra lichtensteini* were examined 6 wk after settlement. At this stage, coralla consisted of a simple cup-shaped epitheca, with septa projecting inwards from the epitheca (Fig. 5a). At 5 mo, a 2nd cycle of septa was evident, as was a columella in the shape of a rod (Fig. 5b) or a 3-lobed spine. The coralla now extended beyond the epitheca and onto the adjacent substratum, and in more advanced coralla, costae were evident as extensions of the primary septa (Fig. 5b). The average size of juvenile *Physogyra* at 6 wk was 756 ± 41 μ (*n* = 4).

Family Dendrophylliidae

In *Turbinaria mesenterina*, a basal plate and 3 or 4 rudimentary basal ridges were evident at 7 d (Fig. 6a). At 1 mo, the skeleton consisted of a theca and 6 primary septa. Septa appeared to grow as vertical extensions of the basal ridges (Fig. 6a, b). A second septal cycle, originating from the corallite wall, was also evident, and some septa extended beyond the wall to form rudimentary costae (Fig. 6b). The primary septa had begun to coalesce forming a contorted mass in the center of the corallite (Fig. 6b). At 10 mo, a laminar columella had formed in the center of the corallite, and septa had thickened and developed small granular projections, although the skeleton had yet to extend beyond the corallite wall (Fig. 6c). The mean size of juveniles at settlement was 900 ± 35.4 μ, and values ranged from 800 to 1000 μ (Table 2).

The ahermatypic dendrophyllid *Tubastrea diaphana* was quite distinct from *Turbinaria* in its comparative lack of a columella, even 10 mo after settlement (Fig. 6d). Skeletal surfaces were smooth, almost porcelain-like in appearance, and the septa were lobate (Fig. 6d). Both these features contrast with the spiky appearance and granular features of *Turbinaria*.

Family Faviidae

Skeletal development in all faviids was very slow. The skeleton began as a thin basal plate laid down shortly after settlement (e.g., *Platygyra sinensis*, Fig. 7a; *Leptoria phrygia*, Fig. 8a). At 1 wk, an epitheca had formed in *Goniastrea, Leptoria*, and *Platygyra* (Figs. 7b, 8b, 9a, b) and an epitheca was observed in all faviid species examined. Septa were not evident in any faviid before 2-3 mo. The site of origin of the septa varied. In *P. daedalea*, septa originated from the wall of the epitheca (Fig. 7c); in *L. phrygia*, septa appeared to originate from the basal plate (Fig. 8b); while in *G. retiformis*, septa originated from the rim of the epitheca (Fig. 9b).

Growth of the corallum proceeded as an

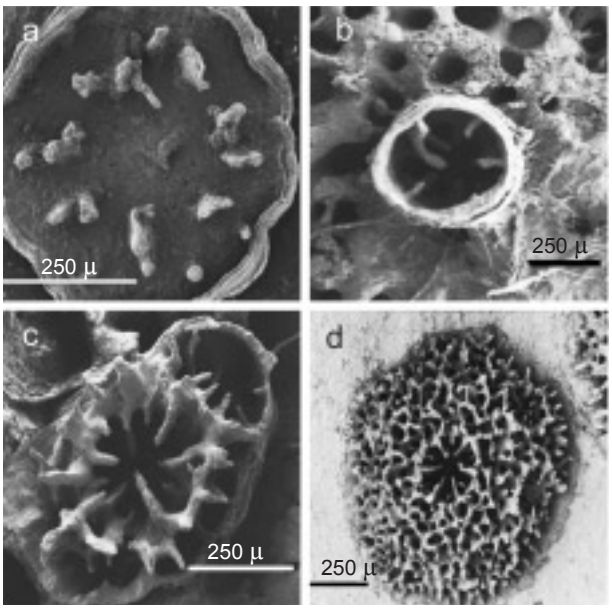

Fig. 3. *Montipora digitata*: (a) 1 d; (b) 5 mo; (c) 5 mo; (d) 5 mo.

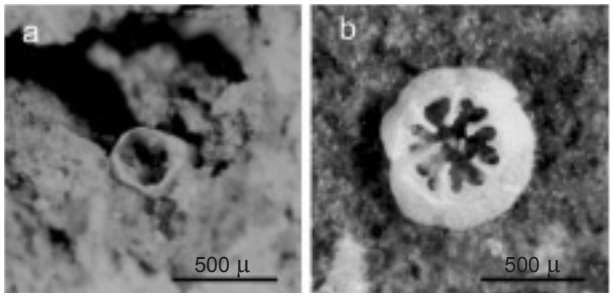

Fig. 4. *Pachyseris speciosa*: (a) 10 d; (b) 6 wk.

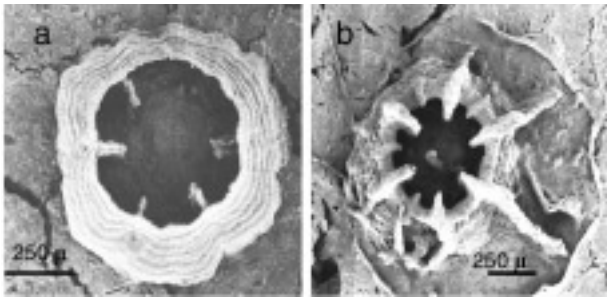

Fig. 5. *Physogyra lichtensteini*: (a) 5 wk; (b) 5 mo.

extension of the basal disc across the surrounding substratum (Fig. 7d). A 2nd less-prominent wall was often evident at the new margin of the basal plate (Fig. 7d, e). At this stage, costae were evident as extensions of the primary septa, beyond the epitheca (Fig. 7d, e). A 2nd septal cycle was observed forming at the perimeter of the basal plate in *P. daedalea* (Fig. 7e). The mean sizes at settlement were similar in *G. aspera*, *G. retiformis*, and *P. daedalea* at 565 ± 8.65, 595 ± 10.6, and 607 ± 7.9 μ, respectively, and values ranged from 500 to 700 μ (Table 2). In contrast, *P. sinensis* and *L. phrygia* juveniles were generally larger, with mean sizes at settlement of 778 ± 13.1 and 784 ± 43.5 μ, respectively (Table 2). Nonetheless, there was considerable overlap in the size range of juveniles at settlement, and therefore size was of little use for distinguishing among early juveniles of these faviid taxa (Table 2).

Family Fungiidae

In *Fungia horrida*, an epitheca had formed by 3 d (Fig. 10a). After 2 wk, rudimentary septa were evident on the rim of the epitheca, and 3 processes had formed in the center of the corallite (Fig. 10b). At 3 wk, these processes had coalesced to form a columella, and 6 septa, which originated from the rim of the primary epitheca, were evident (Fig. 10c). At 3 mo, the coralla had grown by extension of the basal plate beyond the primary epitheca; septa had thickened and extended to the outer limit of the basal plate (Fig. 10d). The columella remained prominent in 3-mo-old juveniles (Fig. 10d). At 4 mo, a 2nd wall had formed beyond the epitheca, presumably as a result of fusion of the synapticulae between the outer edges of the primary and secondary septa (Fig. 10e). The primary septa extended into the center of the corallite and obscured the columella (Fig. 10e). Nonetheless, the epitheca often remained visible at this stage. A 3rd septal cycle had formed at the rim of the new corallite wall. At 4 mo, the septa had prominent teeth and sloped towards the center of the corallite (Fig. 10f). The epitheca was now obscured in many specimens (Fig. 10f). Both the stage of development and size varied considerably among individuals of the same age (Fig. 10f). The mean size of *F. horrida* juveniles at settlement was 528 ± 22.7 μ, and values ranged from 350 to 750 μ (Table 2).

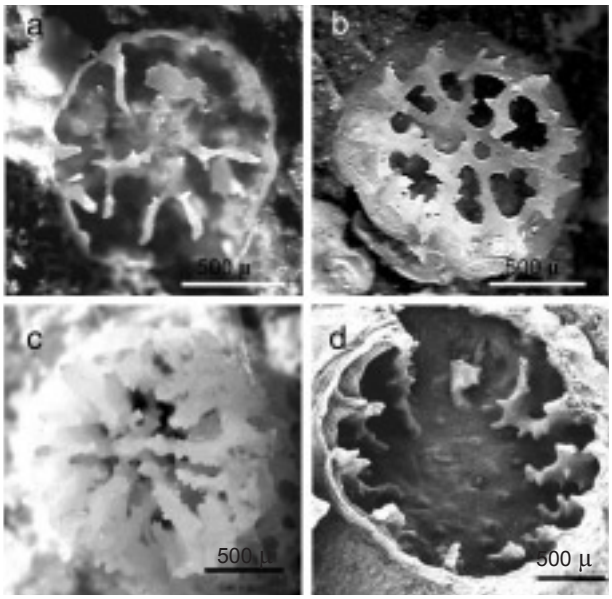

Fig. 6. (a) *Turbinaria mesenterina* 7 d; (b) *T. mesenterina* 2 mo; (c) *T. mesenterina* 10 mo; (d) *Tubastrea diaphana* 10 mo.

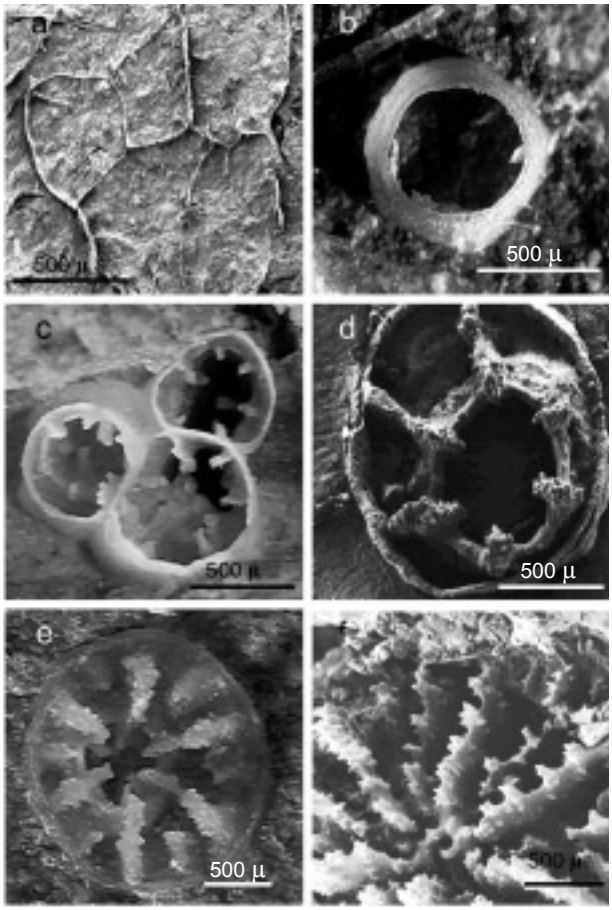

Fig. 7. (a) *Platygyra sinensis* 1 d; (b) *P. daedalea* 10 d; (c) *P. daedalea* 3 mo; (d) *P. sinensis* 4 mo; (e) *P. daedalea* 4 mo; (f) *P. sinensis* 8 mo.

Family Merulinidae

In *Hydnophora exesa* and *Merulina ampliata*, the skeleton began as a thin basal plate (Fig. 11a, c). An epitheca was the 1st element of the skeleton to become apparent (Fig. 11a, c). Further development in 1-mo-old merulinids was restricted to the formation of rudimentary septa, which grew from the basal plate (Fig. 11b, d). The mean size of *H. exesa* juveniles at settlement was 585 ± 23.2 μ, and values ranged from 500 to 625 μ. Juveniles of *M. ampliata* were similar in size, with a mean size at settlement of 572 ± 14.2 μ, and values ranged from 400 to 650 μ (Table 2).

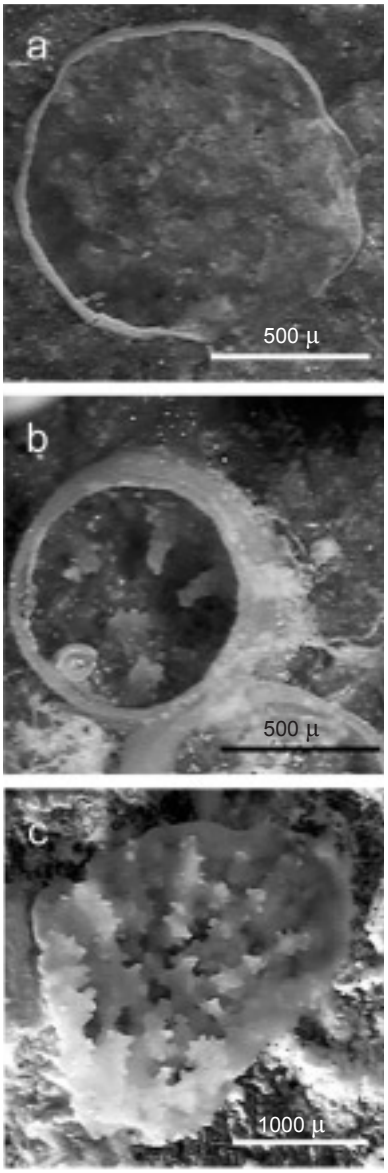

Fig. 8. *Leptoria phyrgia*: (a) 3 d; (b) 1 mo; (c) 6 mo.

Family Mussidae

Six months after settlement, juvenile *Lobophyllia corymbosa* had 2 or more septal cycles as well as a rudimentary columella (Fig. 12a). The septa were exert with numerous irregular spines. Skeletal development occurred entirely within the wall, which formed a low perimeter around the corallum (Fig. 12a, b). Although *Lobophyllia* appeared to be similar to *Platygyra sinensis* at a similar stage of development, the morphology of the septal spines differed. Septal spines in *Lobophyllia* were more robust, nodular, and club-like (Fig. 12b) compared to those of *Platygyra*, which were blade like and projected above the septa, giving them a "saw-tooth" appearance (Fig. 7f).

Family Oculinidae

The earliest stage of development observed in *Galaxea fascicularis* was after 3 mo, by which time a primary epitheca, complete with septa, was present in all specimens. In poorly developed examples, only the 1st cycle of 6 septa was present (Fig. 13a). Other specimens possessed 2 septal cycles (Fig. 13b). The septa were blade-like and the presence of a single cycle in some specimens indicated that septal cycles were inserted sequentially. Both cycles of septa were exert by 3 mo, extending well above the primary epithecal rim in more-developed specimens (Fig. 13a). At 5 mo, septal cycles were well differentiated, with the characteristic highly exert primary septal cycle of *Galaxea* becoming apparent. Primary septa had a crenellated (wavy) appearance caused by the alternate development of septal spines (Fig. 13b).

Family Pectiniidae

Juveniles of *Echinophyllia aspera* and *Oxypora lacera* were not examined until 5 mo after

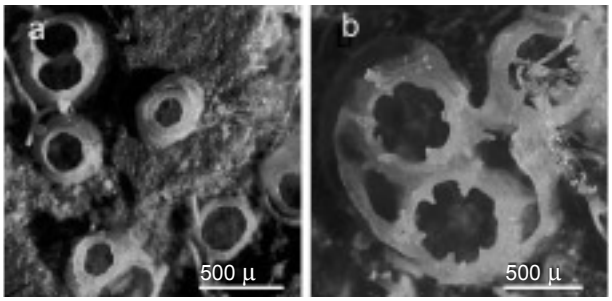

Fig. 9. (a) *Goniastrea aspera* 2 wk; (b) *G. retiformis* 3 mo.

settlement, at which time there were clear indications that the earliest stages of development in these species was an epitheca similar to that in all other taxa, except brooders, acroporids, and dendrophylliids (Fig. 14a, c). Septa either projected from the rim of the epitheca (Fig. 14b, c), or appeared as blade-like structures within the epitheca continuous with elements of the developing columella (Fig. 14d). More-developed specimens had a similar morphology to *Goniastrea* and *Platygyra*, in which a 2nd cycle of septa was inserted at the periphery of the corallum and extended, as the juvenile polyp grew beyond the primary epitheca, to establish a new boundary for the corallum (Fig. 14d). Septal spines more closely resembled those of the *Platygyra* than *Lobophyllia*.

Family Pocilloporidae

The pattern of skeleton formation, including the origin and structure of the septa, columella, and corallite wall, was similar in *Pocillopora damicornis*, *Seriatopora hystrix*, and *Stylophora pistillata*. The 1st signs of skeletal development was the basal plate and 3 clearly differentiated cycles of basal ridges (Fig. 15a). The corallite wall formed through the growth and fusion of lateral outgrowths (synapticulae) of the basal ridges (Fig. 15b). The 3 cycles of basal ridges, and the extension of the 1st cycle into the center of the basal plate, allow these early stages of pocilloporid to be distinguished from young acroporid juveniles (compare Fig. 1a, b to Fig. 15a-c). After 1 wk, all of the features that distinguish the family Pocilloporidae were evident: a solid coenosteum, prominent septa, and a prominent columella.

Despite the similarity in the pattern of development, significant differences in the morphology of the juvenile corallum allow these species to be distinguished. The internal diameter of the primary corallite differed significantly among species (Fig.

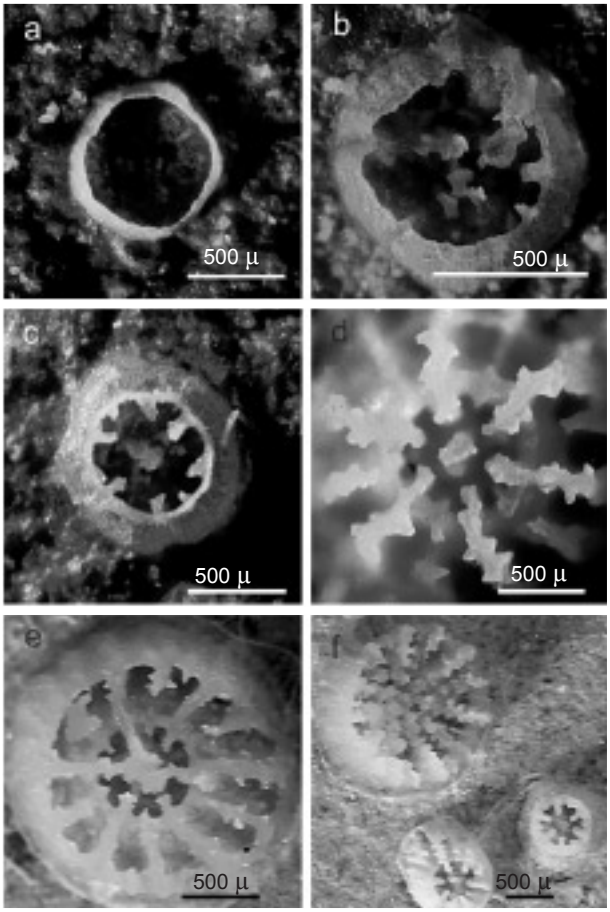

Fig. 10. *Fungia horrida*: (a) 3 d; (b) 2 wk; (c) 3 wk; (d) 3 mo; (e) 4 mo; (f) 5 mo.

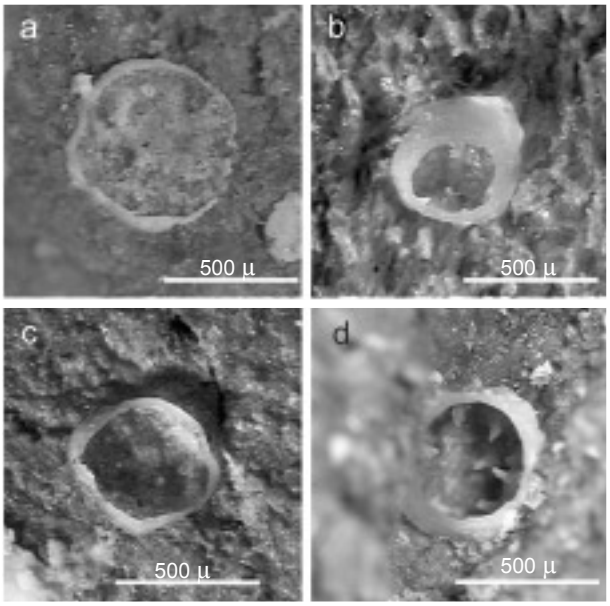

Fig. 11. (a) *Hydnophora excesa* 3 d; (b) *H. excesa* 3 mo; (c) *Merulina ampliata* 2 wk; (d) *M. ampliata* 1 mo.

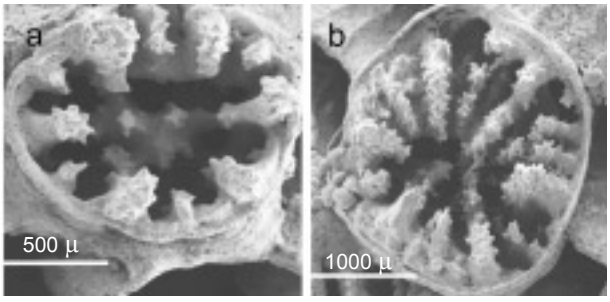

Fig. 12. *Lobophyllia corymbosa*: (a) 3 mo; (b) 6 mo.

15d-f). If the species boundaries are defined as *Seriatopora hystrix* ≤ 450 μ; 450 μ < *Stylophora pistillata* < 550 μ; and *Pocillopora damicornis* ≥ 550 μ, only 3% of the 272 pocilloporid juveniles examined would have been incorrectly identified (see also Baird and Babcock 2000).

Family Poritidae

The pattern and rate of skeletal development were very similar in *Porites australiensis* and *P. cylindrica*. The juvenile skeleton began as a basal plate with an epitheca present by 3 d (Fig. 16a). At 2 wk, six primary septa had formed within the epitheca, originating from the basal plate (Fig. 16b). At 1 mo, the 6 primary septa had thickened, and each had a single prominent vertical tooth (Fig. 16c). At 3 mo, the corallite had grown by an extension of the basal plate beyond the epitheca (Fig. 16d). The primary septa had also grown beyond the epitheca and extended to the perimeter of the new boundary of the basal plate (Fig. 16d). A 2nd cycle of septa that originated at the perimeter of the basal plate was also apparent (Fig. 16d). At 3 mo, the secondary septa had fused with the primary septa to form 4 pairs of laterals and a triplet leaving the directive independent (Fig. 16e). The epitheca was still visible within the juvenile corallite at this time (Fig. 16e). At 5 mo, two corallites were present in some juveniles, and the epitheca was no longer visible. At 8 mo, the juvenile corallum had 10 to 12 corallites. The mean size of *P. australiensis* at settlement was 576 ± 11.3 μ, and values ranged from 400 to 675 μ, which was very similar to *P. cylindrica* with a mean size at settlement of 562 ± 17.62 μ, with values ranging from 500 to 650 μ (Table 2).

The majority of poritid recruits recovered from settlement tiles placed on the Great Barrier Reef for 8 wk (e.g., Hughes et al. 2002) resembled the

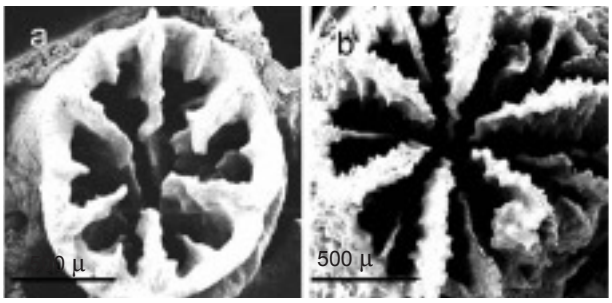

Fig. 13. *Galaxea fascicularis*: (a) 3 mo; (b) 5 mo.

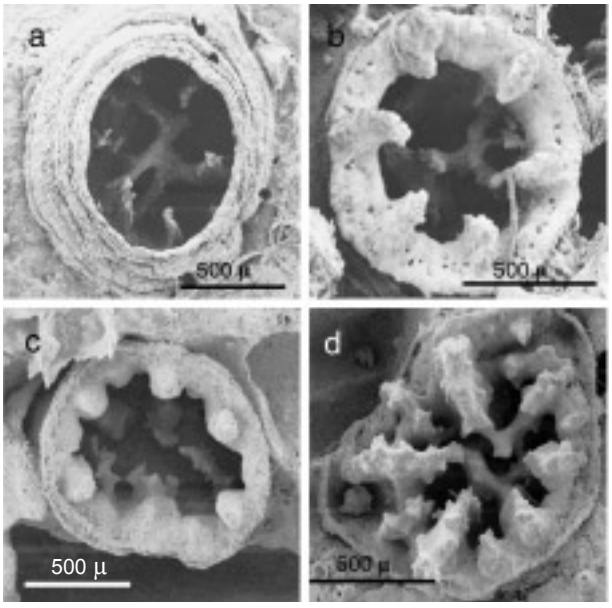

Fig. 14. *Echinophyllia aspera*: (a) *E. aspera* 6 mo; (b) *E. aspera* 6 mo; (c) *Oxypora lacera* 5 mo; (c) *O. lacera* 5 mo.

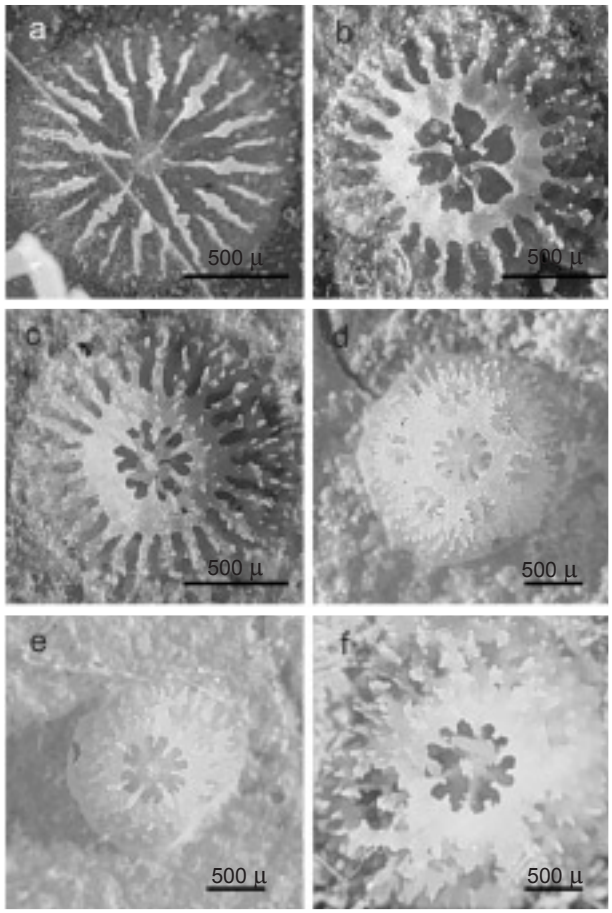

Fig. 15. (a) *Seriatopora hystrix* 12 h; (b) *S. hystrix* 1 d; (c) *S. hystrix* 4 d; (d) *S. hystrix* 2 mo; (e) *Stylophora pistillata* 2 mo; (f) *Pocillopora damicornis* 2 mo.

juveniles of *P. australiensis* and *P. cylindrica* (Fig. 16c) included in our study. However, a 2nd type of poritid recruit was also recovered from these tiles. These recruits were considerably larger, and a typical adult corallite structure (Fig. 16f) was evident. In contrast, the adult pattern of septal arrangement was never present in *P. australiensis* or *P. cylindrica* juveniles of less than 3 mo old.

The pattern of skeletal development in *Goniopora lobata* initially greatly differed from that seen in the genus *Porites*. Skeletal development began with an epitheca (Fig. 17a) from which 6 rudimentary laminar septa projected towards the center of the calyx (Fig. 17b). A rudimentary 2nd cycle of septa, as well as the beginnings of a columella, was also evident (Fig. 17b). The skeletal structures subsequently thickened, and spines developed on the septa and columella, resulting in a structure more closely resembling that seen in adult poritids (Fig. 17c, d).

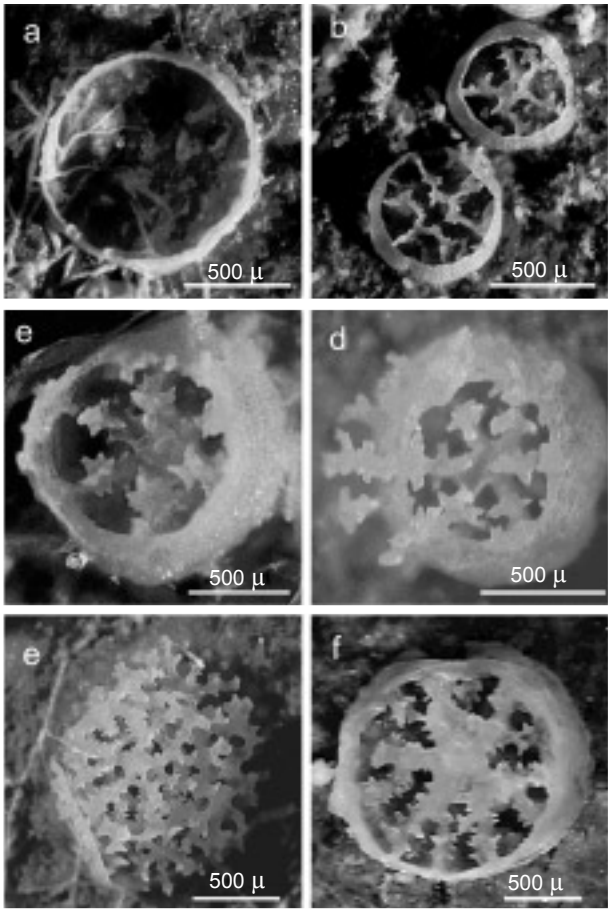

Fig. 16. *Porites australiensis*: (a) 3 d; (b) 2 wk (c) 3 wk (d) 3 mo (e) 5 mo (f) *Porites* sp. 2 mo.

DISCUSSION

Few scleractinian taxa have juvenile skeletal characters that are consistent enough to allow them to be distinguished from other taxa. Juveniles from only 3 families could be reliably distinguished throughout their 1st year of life: the Acroporidae, the Pocilloporidae, and the Poritidae. Juveniles in the remaining families examined could not be consistently distinguished. Within the 3 distinctive families, a number of other taxa could be recognized when juveniles were young.

Juveniles of the family Acroporidae have a porous coenosteum and prominent septa in 2 cycles, and lack a columella. Juvenile skeletons of the 4 species examined within the subgenus *Acropora* were indistinguishable from each other and are very similar to that of the *A. millepora* juveniles pictured in Wallace (1999, Fig. 8). The similarity between the juveniles of different species of *Acropora* persists for up to a year (Wallace 1999). It takes at least 2 yr for *Acropora* colonies to develop sufficient features, such as color and radial corallite structure, to enable species to be identified by an observer familiar with the appearance of adults in the field (Wallace et al. 1986).

The early development of the skeleton in juvenile *Montipora digitata* differed from that of other acroporids. Young recruits had a basal plate, but the basal ridges were less regular and relatively smaller than those of *Acropora*. An epitheca developed from the basal plate in some

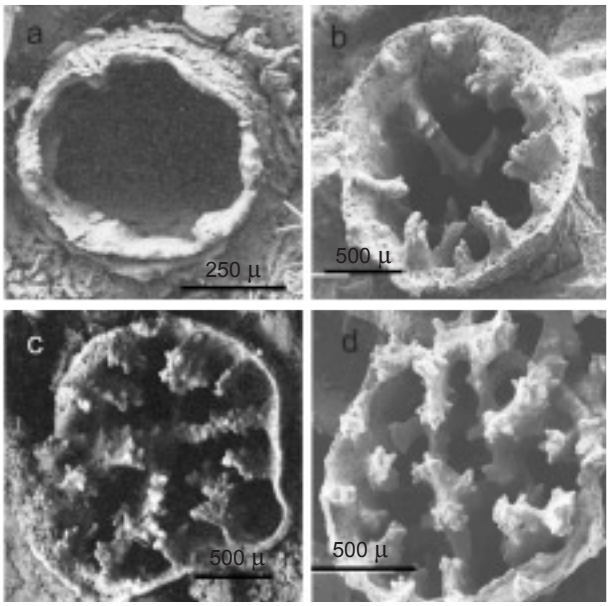

Fig. 17. *Goniopora lobata*: (a) 4 mo; (b) 4 mo; (c) 6 mo; (d) 6 mo.

Montipora specimens, a similar pattern of development to *M. verrucosa* juveniles from Hawaii (Fitzhardinge 1988). The presence of an epitheca may be a general feature of the genus; however, its degree of development was variable and 5-mo-old *M. digitata* juveniles were indistinguishable from other acroporids. Consequently, the presence of an epitheca may only be useful for identification of young *Montipora* recruits. Similarly, while recruits of brooders in the subgenus *Isopora* could be distinguished from other young acroporids by an extensive coenosteum, this difference disappears in older juveniles. For example, it was not possible to distinguish a 5-mo-old *Acropora millepora*, *A. tenuis*, or *M. digitata* juvenile from a 1-mo-old isoporan recruit.

The genera of Acroporidae examined in this study could be distinguished by the size of the juveniles at settlement. The utility of size as a tool for distinguishing wild acroporid recruits depends on how similar the size of juveniles is within each genera. Comparable data on the size of juveniles at settlement is lacking, except for *M. verrucosa*, which has a similar size at settlement to *M. digitata* (Fitzhardinge 1988). However, the high correlation between egg size and size of juveniles at settlement (Fig. 18, r^2 = 0.97) enables the size of the egg to serve as a proxy for the size of juveniles at settlement. Egg size was similar between species within the respective genera and subgenera, *Montipora*, *Acropora*, and *Isopora*. In addition, the reported size range for eggs of other acroporid species (Harrison and Wallace 1990) is within the range of sizes presented here (Table 4). The exception may be some high-latitude *Montipora* which release eggs of 500 μ in diameter (A. Heyward, pers. comm.). However, size differences at settlement are likely to be quickly obscured by the typically highly variable growth rates of individuals. The morphology of juveniles of the genera

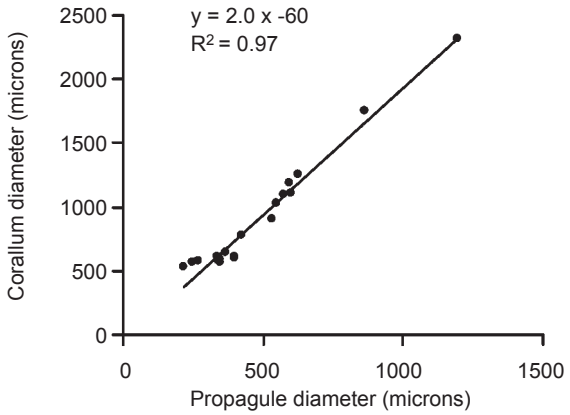

Fig. 18. Diameter of newly settled juvenile corals as a function of propagule diameter. All juveniles were measured less than 2 wk after settlement. Propagules include both eggs and larvae. *n* = 17 species.

Table 4. Diameter of propagules at release

Family	Species	Egg diameter (μ)				
		mean	SE	min.	max.	*n*
Acroporidae	*Acropora cytherea*	600	9.0	525	675	18
	Acropora palifera	1195	11.7	1125	1250	10
	Acropora pulchra	575	9.5	500	650	18
	Acropora valida	596	11.2	550	675	17
	Montipora digitata	337	6.6	175	400	39
Agaricidae	*Pachyseris speciosa*	368	3.6	325	400	30
Dendrophylliidae	*Turbinaria mesenterina*	531	13.7	400	650	20
Faviidae	*Goniastrea aspera*	349	6.1	300	400	29
	Goniastrea retiformis	371	3.6	325	425	38
	Leptoria phrygia	450	6.1	325	500	19
	Platygyra daedalea	396	3.6	350	450	38
Fungiidae	*Fungia horrida*	215	10.0	150	250	10
Merulinidae	*Hydnophora exesa*	348	6.6	275	425	29
	Merulina ampliata	339	6.3	300	425	7
Pocilloporidae	*Pocillopora damicornis*	864	15.1	800	950	9
	Seriatopora hystrix	625	7.9	550	700	25
	Stylophora pistillata	549	7.1	475	625	26
Poritidae	*Porites australiensis*	245	6.8	150	325	20
	Porites cylindrica	250	8.3	200	300	17

Astreopora and *Anacropora* awaits description, and it is not known whether their sizes or other characteristics overlap with those of other acroporid genera.

Juveniles of the family Pocilloporidae could be distinguished from all other families examined in this study by a prominent columella, prominent septa in 2 cycles, and a solid coenosteum. Furthermore, the genera *Pocillopora*, *Seriatopora*, and *Stylophora* could be distinguished by differences in the internal diameter of the primary corallite (Baird and Babcock 2000). However, it remains necessary to establish whether or not the diameter of the primary corallite is a conservative character at the generic or the species level by comparison with other species of the genera *Seriatopora*, *Stylophora*, and *Pocillopora*. These patterns in juvenile size at settlement may be further complicated by the presence of multiple modes of reproduction in some pocilloporid corals (e.g. *P. damicornis*, Ward 1992).

Juveniles of *Porites australiensis* and *P. cylindrica* could not be separated on the basis of skeletal features. This is not surprising given the degree of variability seen between corallites within a single adult coralla in many poritid species. The typical poritid pattern of 4 laterals, a triplet, and a dorsal directive was apparent in these species after 4 mo. However, finer features of the microarchitecture of the poritid corallite which are used to identify adults, such as the pali, were not clearly differentiated. Two distinct types of poritid juveniles were found on tiles placed in the field. We hypothesize that these types correspond to juveniles of brooding and broadcast-spawning poritid species. This hypothesis is supported by the few studies in which juveniles of *Porites* have been reared from known parents. Juveniles of the brooding species *P. stephensoni* (*P. haddoni*) (Stephenson 1931) are initially much larger (typically over 1 mm) than those of the broadcast spawners, *P. australiensis* and *P. cylindrica*. In *P. stephensoni* juveniles, the adult pattern of microarchitecture was evident in 3-wk-old specimens (Stephenson 1931). Furthermore, in the brooders *P. porites* and *P. mayeri*, all primary skeletal elements develop simultaneously (i.e., the intermediate stages of development seen in *P. australiensis* and *P. cylindrica* were not evident), and there was no epitheca (Goreau and Hayes 1977, Jell 1980). An epitheca was, however, evident in juveniles of the broadcast spawning *P. compressa* from Hawaii (Fitzhardinge 1988). Similarly, an epitheca was not evident in brooded agariciid juveniles, e.g., *Agaricia humilis* (Morse and Morse 1991), but was present in juveniles of broadcast-spawned agariciids, e.g., *Pachyseris speciosa* (Fig. 5a). However, the presence of an epitheca in early juveniles would appear to be related to the size of the propagules rather than to phylogeny or reproductive modes. In all species with eggs smaller than 500 μ, an epitheca was the 1st skeletal structure to appear following the basal plate. In contrast, in juveniles of broadcast-spawning taxa with large eggs, such as *Acropora*, the 1st skeletal structures to appear after the basal disc were the basal ridges. The presence of an epitheca may, therefore, enable recruits of brooding species to be distinguished from the recruits of spawning species in genera with mixed modes of development, such as the *Pocillopora*, if the eggs are smaller than brooded larvae at the time of release. However, an epitheca can also develop in *Acropora* juveniles from shaded habitats, and an epithecal rim is often present in *Acropora* juveniles in close association with other sessile invertebrates (A. Baird, pers. obs.). This suggests the possibility of an ecological function of this character. Whether the epithecal cup has an ecological function or is a consequence of skeletal ontogeny in some way related to relative larval size, it is a morphological character of direct taxonomic utility. Environmental and biotic factors are also likely to influence the development of the epitheca, and further studies of factors that mediate the formation of this structure are required.

Development of the skeleton in juvenile *Goniopora lobata* differed in several respects from that of the genus *Porites*, principally in the prominent development of the epitheca, the origin of the septa as spines developing from the epitheca, and the lack of skeletal development in the center of the corallite. These differences may be useful in distinguishing between these 2 genera; however, development in *Goniopora* beyond the toothed epithecal cup stage converged with that observed in *Porites*.

Within the family Dendrophylliidae, the genera *Turbinaria* and *Tubastrea* were clearly distinct, and although *Tubastrea* specimens were rather older than those from *Turbinaria*, the nature of their spination and the surface characteristics make it possible to differentiate them. In fact, no other coralla we examined appeared to have a skeletal surface of the same porcelain-like nature as that found in *Tubastrea*.

Fungia horrida and *Physogyra lichtensteini* had a distinct columella within the epitheca. In

Fungia, the columella was initially comprised of multiple spines, while in *Physogyra* there was a single 3-lobed columella. However, these specimens are very similar to some *Platygyra sinensis* which occasionally developed a columella. Juveniles of the families Agaricidae, Faviidae, Pectiniidae, and Merulinidae were all characterized by very slow rates of development, and in these families, the epitheca was the main element of the skeleton to develop in the first 2 mo. In contrast, in the Acroporidae, Pocilloporidae, and Poritidae, other elements of the skeleton, such as the septa, were well developed within 1 mo of settlement. The structures of the corallite and septa were remarkably similar in the Faviidae, Merulinidae, Mussidae, and Pectiniidae (suborder Faviina), and also in the families Agaricidae, Oculinidae, and Caryophylliidae. Given our present state of knowledge it is not possible to confidently differentiate among juveniles from these families. It is likely to take at least a year before the adult structure of the primary corallite has developed in these families, and species will not be distinguishable for between 2 and 3 yr. While it is not likely to be a useful ecological tool in the near future, details of the micro-architecture are likely to provide additional means of resolving the identity of juvenile corals (e.g., Stolarski 1995).

Greater taxonomic resolution is available when juveniles are young, with the maximum number of taxa distinguishable occurring between 2 to 4 wk after settlement (Table 3). For example, at this stage it was possible to distinguish between the juveniles of the different genera of the Acroporidae and Pocilloporidae (Table 3). We also hypothesize that it is possible to distinguish brooded and spawned poritid juveniles for about 4 mo. Therefore, if greater taxonomic resolution is desired, a short period of emmersion is recommended. Furthermore, the shorter the time between deployment and examination of artificial substrata, the more accurate the estimate of supply, because the loss of recruits through overgrowth by fouling organisms will be minimized. In addition, a shorter interval between deployment and examination will reduce the bias towards species with extended breeding seasons, such as brooding pocilloporids, whose larvae will settle over an extended period (Baird and Hughes 2000, Hughes et al. 2002).

Finally, a word of caution. This study examined juveniles originating from a limited number of parents, from a single location, and usually only 1 cohort was examined for each species. Consequently, it remains necessary to determine whether the findings will apply throughout the geographic range of these species, whether morphology varies between years, and the influence of genetic identity on morphology (although this seems unlikely given the lack of differentiation observed here among families). Furthermore, the morphology of many coral species varies under different environmental conditions, and juveniles raised in aquaria or on tiles may differ from field recruits or juveniles settled on fouled or natural substrata. Future studies are required to address these issues and establish the generality of our results.

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