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An Ancient Chemosensory Mechanism Brings New Life to Coral Reefs

AILEEN N. C. MORSE'' , KENJI IWAO[2], MASASUKE BABA[S], KAZUYUKI SHIMOIKE[2], TAKESHI HAYASHIBARA[2], AND MAKOTO OMORI[2.4]

[']Marine Biotechnology Center, Marine Science Institute, University of California, Santa Barbara, California 93106; [2]Akajima Marine Science Laboratory, 179 Aka, Zamami-son, Okinawa 901-33, Japan; 'Marine Ecology Research Institute, 4-7-17 A rahama, Kashiwazaki, Niigata, 945-03, Japan,- and [4]Department of Aquatic Biosciences, Tokyo University of Fisheries, 4-5-7 Konan, Minato-ku, Tokyo 108, Japan

Reprinted from THE-BIOLOGICAL. BULLETIN, Vol. 191, No. 2, October 1996
Printed in U.S.A.

Reference: *Biol. Bull.* ***191:*** 149-154. (October, *1996)*

An Ancient Chemosensory Mechanism Brings New Life to Coral Reefs

AILEEN N. C. MORSE[L]*, KENJI IWAO[2], MASASUKE BABA', KAZUYUKI SHIMOIKE`, TAKESHI HAYASHIBARA', AND MAKOTO OMORI-'

Marine Biotechnology Center, Marine Science Institute, University of California, Santa Barbara, California 93106: [2]Akajima Marine Science Laboratory, 179 Aka, Zamami-son, Okinawa 901-33, Japan; 'Marine Ecology Research Institute, 4-7-17 Arahama, Kashiwazaki, Niigata, 945-03, Japan: and 'Department of Aquatic Biosciences, Tokyo University of Fisheries, 4-5-7 Konan, Minato-ku, Tokyo 108, Japan

The first scleractinians, progenitors of modern corals, began to appear 240 million years ago; by the late Jurassic (150 Ma) most families of modern corals had evolved and begun forming reefs (1, 2). Mechanisms controlling the recruitment of new corals to sustain these structures are, however, poorly understood (3). Corals, like many marine invertebrates, begin life as soft-bodied larvae that are dispersed in the plankton (3, 4). As the first step in developing a calcified coral colon v, the larva must settle out of the plankton onto a suitable substratum and metamorphose to the single calcified polyp stage cemented to the reef (3, 5). Our analyses of the metamorphic requirements of larvae in divergent coral families surprised us by revealing the existence of a common chemosensory mechanism that is required to bring larvae out of the plankton and onto the reef This mechanism appears to be quite old, predating both the phylogenetic divergence of these coral families and the development of different triodes of coral reproduct1Ort.

We analyzed the requirements for metamorphosis of larvae from 10 species of Pacific *Acropora—the* acroporid genus with by far the greatest number of known species (76 in the Indo-Pacific, about one-sixth the estimated number of scleractinian species in that region)—and three species representing three common genera of Pacific Faviidae, the second most speciose scleractinian family (1, 2). Most, but not all, species of *Acropora* and *Pavia* (genera that first appear in the fossil record in the Eocene and Cretaceous, respectively) are widely distributed throughout the Indo-Pacific; *Cyphastrea* and *Goniastrea* (first appearing in the Oligocene and Eocene, respectively), although common, are limited to the Indo-Pacific (1, 2). Larvae of the acroporids and faviids that we tested are generated by cross-fertilization of gametes released into the plankton during mass-spawning events, the dominant form of sexual reproduction in corals (3). We found that larval detection of suitable reef substrata is controlled by chemosensory recognition of a cue associated with encrusting red algae, among the major cementers of the reef. A similar process operates in Caribbean agariciid species that brood their larvae (5-10). These agariciids are in two genera, *Agaricia* and *Leptoseris,* that first appeared in the Miocene and Oligocene, respectively (1, 2). Our findings thus suggest that this chemosensory mechanism is common to at least the Acroporidae, Faviidae, and Agariciidae—three major and divergent coral families.

In the laboratory at Akajima, Japan, larvae of the widely distributed mass-spawning Indo-Pacific corals *Acropora nasuta* and .4. *digitifera* exhibit a strict requirement for a specific environmental cue: surface contact with svmpatric crustose red algae is required for cue detection (Fig. I A, B). The strength of the larval response (% metamorphosis) to all five crustose red algae tested varies directly with larval age (days post-fertilization). But regardless of larval age, the response to the seawater and brown algal controls remains nil (0% metamorphosis). Overall, *A_ digitifera* was significantly more responsive to inductive algae than was *A. nasuta* (two-way ANOVA: coral effect: F = 18.3. df = 1, P = 0.0016). Although there was no significant difference between species in their response to these algae (two-way AN-

Received 28 May *1996;* accepted 7 August 1996.
*To whom correspondence should be addressed.

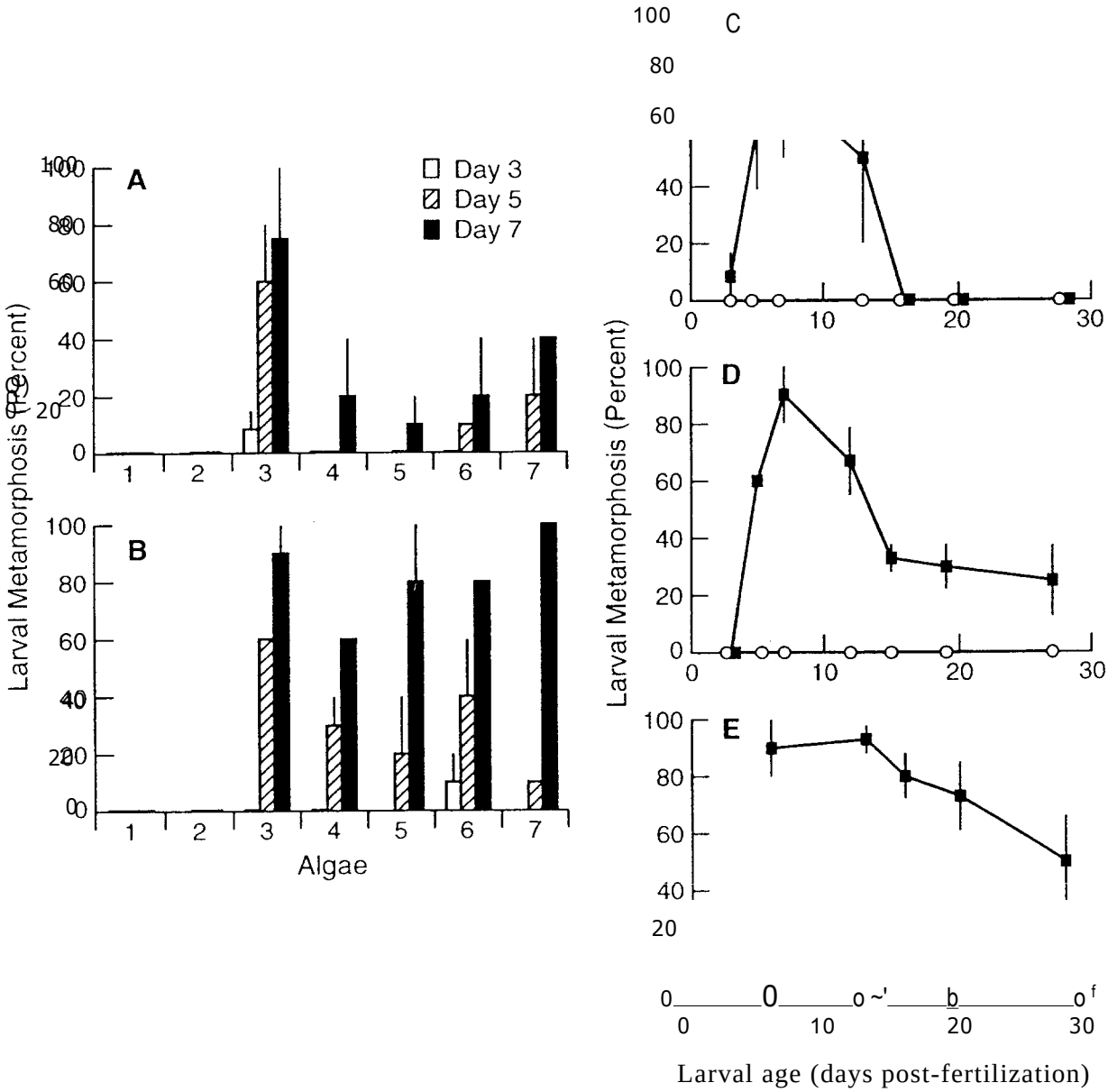

Figure I. Pacific acroporid larvae exhibit a stringent requirement for contact with crustose red algae for metamorphosis; development and decay of metamorphic competence is dependent on larval age. (A) Metamorphosis *of; t* ***cropora nasuta*** larvae (3. 5 and 7 days post-fertilization) in response to various crustose red algae and controls after 48 h incubation in 10 ml filtered seawater (FSW). Algae: I = 0.22-Am FSW alone (control); *2* = ***Lobophora vuriegala*** (brown alga, control); 3 = ***Perssonnelia*** sp.; 4 = ***Hrdro/itfron reinboldii*** (form i); 5 = ***flydrolithon reinboh/ii*** (form *ii); 6 = Ilt*^{s}***drolithon reinboldn*** (form *iii); 7 = He-drolithon reinholdii* (form *iv*). Values are mean % (± I std. error) metamorphosis of five individuals in each of two trials ***(n = 2).*** Percentages were arcsine transformed for analysis. (B) Metamorphic response of ***Acropora digitifera*** larvae (3. 5 and 7 days post-fertilization) to algae and controls. as in (A). (C) Metamorphosis of ***A. uasata*** larvae after a 48-h incubation with ***Peissonnelict*** sp. **(U)** or a parallel exposure to FSW alone (0). Individual points represent ages (days post-fertilization) at challenge: metamorphosis (%) _ mean; error bars = s.e. of ***n = 2*** (days 3–7 or 3 (days > *7*). (D) ***A. digui/f°ra*** larval response as for (C). (E) *A*. ***tennis*** larval response as for (C), ***n*** = 3 all days. Larvae of each species were obtained as follows: The maturity of coral gonads was confirmed (14); colonies were transferred from the reef to laboratory aquaria and kept in darkness until the gamete clusters were ready to be released; the colonies were transferred to individual containers for spawning; gamete clusters from a single colony were collected and dispersed by sequential transfer into FSW; eggs and sperm were separated for immediate cross-fertilization with gametes of other colonies (? 95` fertilization rate); all spawnings (I /species) produced 5-10.000 larvae/batch; each batch was cultured in 3 I FSW (changed daily) at 26°C for ? 30 d; larvae of each species were held in these rearing chambers until randomly selected for assay at the ages indicated. For assays, fragments were

OVA; coral * algae interaction: F = 0.89, df = 4, P --0.503), A. *digitijera* exhibited less variation in response among algae (one-way ANOVA: $F = 0.61$, df = *6, P* = 0.72) than did A. *nasuta* (one-way ANOVA: ***F*** = 2.9, df = *6,* P = 0.095) . Such patterns arc similar to the species-specific differences previously found in agariciid corals (l0).

Larvae maintained in seawater alone (?30 days) continue planktonic swimming and never develop beyond the larval stage illustrated in Fig. 2A (Fig. 1C, D, E). Metamorphosis is initiated on contact with an inductive alga, e.g., *Peyssonnelia sp.* or any of four morphological forms of *Hydrolithon reinboldii;* larvae rapidly stop swimming, their bodies elongate and remain in close contact with the algal surface, and within a few hours, they round up and cement themselves to the algal surface or adjacent substratum. The final stages of metamorphosis are marked by the development of 12 radial skeletal elements, the calcified septa and costae (Fig. 2B). Larvae of the mass-spawning congeners *A. tenuis, A. Florida, A. geinmifera, A. Formosa, A. hyacinthus, A. sp.* 1, *A.* sp.4 and *A. sp.* 5 all exhibit a similar strict requirement for contact with either or both *Peyssonnelia sp. and H. reinboldii* (Fig. 2C; and A. N. C. Morse *et al.,* University of California, Santa Barbara, in prep). Although, in some instances, the brown alga *Lobophora variegata* promoted first stage elongation of the larvae, further development rarely if ever occurred. When larvae from seven acroporid species (50 larvae/species incubated together) were given a choice between crustose red algae and brown algae, all that had metamorphosed after 4-h exposure (70%) were found only on the crustose red algae *(Peyssonnelia sp.* and *H. reinboldii)* (Fig. 2C); no larval metamorphosis was detected on brown algae or on the chamber surfaces; control larvae (same number and species) remained swimming. In a similar experiment, 500 competent larvae from each of five acroporid species (A. *nasuta. A. tenuis, A. Formosa, A. hyacinthus,* and *A. gemmifera,* tested together in a 30-1 flow-through tank) were presented a choice of algae, live corals, inert substrata collected from the reef, "fouled" panels, and a variety of inert materials commonly used as settlement plates; all settlement and metamorphosis occurred only on coralline algae (A. N. C. Morse *et al.,* University of California, Santa Barbara, in prep.).

The stringency of this requirement (no metamorphosis in the absence of an exogenous cue) and the specificity (dependence on crustose red algae) of cue recognition persist for the duration of larval competence for metamorphosis (Fig. IC, D, E). Species-specific differences in the duration of competence are obvious. The magnitude of the larval response for each species is dependent upon larval age (Fig. I). Larvae exhibited little or no response to *Peyssonnelia* sp. at 3 days post-fertilization; responsiveness developed by 5 days, peaked at 7 days, and declined thereafter at rates that are species-specific (Fig. 1C, D, E).

If these results reflect larval potential for dispersal in the plankton, then the differences in the rates of decline of competence among all of the tested acroporid species, with no accompanying loss in stringency or specificity of cue requirement (e.g., Fig. 1), suggest species-specific differences in the windows of opportunity for successful settlement and metamorphosis on the reef. Assuming that rate of decrease of competence with larval age is inversely correlated with the distance of dispersal from parental colonies (all other chemical and hydrodynamic factors being equal), *A. tenuis* appears to have the potential for widest dispersal and significant recruitment for at least 5—30 days post-fertilization. *A. digitijera appears to* have the potential for somewhat wider dispersal than .4. *nasuta,* although the majority of potential recruits from both species will be dispersed over similar distances (5—12 days). Although the bulk of settlement and metamorphosis might occur soon after the larvae reach competence, these differences among species that recognize the same algae may serve to decrease post-settlement competition for space among some of the settlers. Variation among these species in timing of gamete release during mass-spawning events (11-14), in concert with variations in currents and other hydrodynamic factors, may additionally contribute to a reduction in the potential for post-settlement interaction.

Significantly, we believe, larvae of these Pacific acroporids and those in two Caribbean genera, *Agaricia* and *Leptoseris* (Agariciidae), both appear to recognize and require the same class of algal cue for the induction of larval settlement and metamorphosis. This is in spite of their very different modes of sexual reproduction and larval development (3). Acroporids participate in mass-spawning events during which millions of gametes are released into the plankton for cross-fertilization, followed by larval development in the plankton; in contrast, agariciids have evolved the less common mode of

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prepared from algae as previously described (6, 7. 9); live *H. reinholdii* specimens were grouped according to the surface characteristics of different growth forms (by A. N. C. M.): specimens preserved in formalin and seawater were dehydrated, embedded in paraffin, sectioned (8-pm thickness), and identified with a light microscope to species and genus level (by M. *B.)—Lobophora rariegaia* (Lamouroux), *H_rdrefithen reinboldii* (Weber van Bosse et Foslie) Foslie; *Perssormelia* sp. [similar to P. *nhscura* Weber van Bosse and *P. conchicola* Piccone et Grunow (19)].

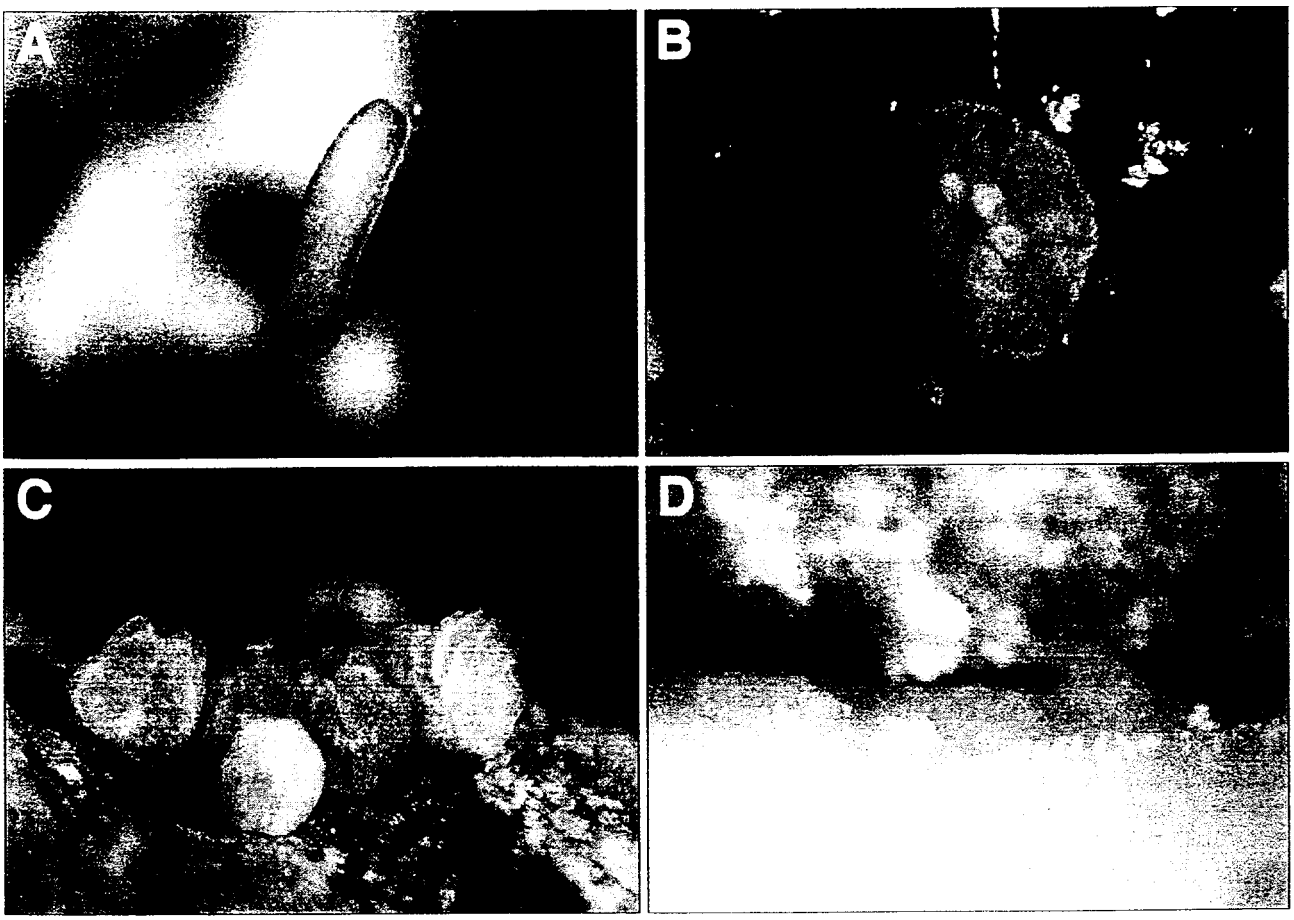

Figure 2. Larval behavior and early metamorphic changes of Pacific acroporid corals in response to a morphogenic cue associated with Pacific crustose red algae. (A) Typical shape of soft-bodied larva ? 3 days post-fertilization:. t. *digiuJera* larva, 8 days post-fertilization, swimming normally in the water column. (B) Final stage of metamorphosis; formation of radial skeletal elements (septa and costae) and elevation of central area around mouth: A. *nasula* larva, 8 days post-fertilization. incubated with *Peyssonielia* sp. *(C)* Early-stage metamorphosis (4 h) of a mixture of larvae of *A. nasuta, A. diga{ 1eia, .-1 tennis. A_ Formosa. A. gemnu%era. a. Jlorida.* A. sp. 5 on whole specimens of *H. rernboldii* and *Peyssonnelia sp.* (D) Metamorphosis of A. *Jlorida* larvae in response to inductive molecules purified from *H. reinboldii* and coupled to resin beads. In (A) and (B) the assays were as described in Fig. I. In (C) 20 competent larvae of each of seven species were incubated together in 200 ml FSW with or without small intact specimens of *Petssonnelia* sp., *Hrdrolithon rervtholdii.* and *Loboplrora varfegaza* In (D) the resin with adsorbed inducer was the same preparation as that assayed in Table l; larvae were batchmates of those in (C).

sexual reproduction in which cross-fertilization occurs internally, and subsequent larval development and brooding occur within the maternal polyps.

The possibility of similar cue recognition in members of these two families was first suggested by the fact that the algal species *(Hrdrolithon reinboldii* and *Pevssonnelia)* that are shown here to induce metamorphosis of Pacific acroporid larvae have congeners in the Caribbean that induce metamorphosis of agariciid larvae (5-10). This suggestion is confirmed by the demonstration (Table I) that the Pacific alga, *Hrdrolithon reinboldii,* contains an extractable polymeric morphogen that is apparently in the same class of molecules as one previously identified in its Caribbean congener, *H . boergesenii.*

Fragments of both the Caribbean and Pacific algal congeners *(Hrdrolithon* and *Pevssonnelia)* induced levels of metamorphosis in *Agaricia htunilis* larvae that are not significantly different (Table I; one-way ANOVA: F = 1. 59, df = 4, P = 0.198). Moreover, when the same procedures developed for biochemical purification, characterization, and coupling (7, 9, 15) of the polymeric inducer of agariciid larvae from *II. boergesenii* to a hydrophobic resin were applied to *H. reinboldii.* the purified molecule adsorbed to resin was recognized by .-1_ *hunulis* larvae (Table 1). Larval settlement and metamorphosis of at least seven species in two genera of Caribbean agriciids is strictly dependent on chemosensory recognition of a unique class of sulfated glycosaminogly-

Table *I*

Metamorphic response of larvae of the Caribbean coral. Agaricia humilis, *to inducers from Caribbean and Pacific algal congeners*

Inducer	*n*	Metamorphosis at 48 h (mean % ± std. error)
Caribbean		
None	10' + 30'	0 ± 0
H_tdroidhon boergesenii fragments	25' + 30[2]	62± 9.1
Peyssonuelia sp. fragments	30'	73± 16.1
Control resin	10*	0 ± 0
Hvdrolithon hoergesenii inducer on resin	10*	90 ± 6.2
Pacific		
None	10' + 30'	0± 0
Hvdrolithon reinboldii (form *iii)* fragments	30'	53 ± 8.4
Hvdrolitlton reinboldii (form iv) fragments	20' + 30[2]	56 ± 7.8
*Pe_vssonellia sp_* fragments	30'	87 ± 6.7
Control resin	10'	0 ± 0
Hvdrolithon reinboldii inducer on resin	10'	30 ± 6.2

Competent A. *humilis* larvae were incubated in 10 ml FSW with or without additions as shown: none = FSW alone; fragments = algae prepared as previously described (6. 7, 9); control resin = hydrophobic interaction chromatography (HIC) resin (9, 15) with no adsorbed chemical inducer; inducer on resin = HIC resin with adsorbed inducer purified from the indicated alga (9, 15). *n* = the total number of larvae tested in each condition in replicate tests (5 larvae/test) performed either in May 1995 ('), May 1996 ([2]), or earlier (*, data from 9). Metamorphosis means development to the single-polyp stage (refs. 5, 15: and Fig. 2B). Percentages were arcsine transformed for statistical analyses. Brooded A *humilis* larvae were obtained by spontaneous release from parental colonies in the laboratory rearing facility at UCSB, under conditions previously described (6, 7. 9); *H. hoergesenii* and *Pe_tssone/ia* sp. were collected from Bonaire, Netherlands Antilles; *H. reinboldii* (forms *iii* & iv) and *Pet'ssonnelia* sp. came from Akajima. Japan. Fragments of all algae were prepared, shipped (—20°C). stored (—80°C); the inducers were purified from fragments and adsorbed to HIC resin by procedures developed with *H hoergesenii (7, 9,* 15). *Resin assays:* 20 mg resin with or without adsorbed inducer from *H boerge.senii* or from *H. reinboldii* (form iv).

can (7, 9) that is associated with the cell walls of a number of Caribbean crustose red algae (5, 7-9, 15). Enzymatic and biochemical analyses demonstrated that this inductive polymer has a molecular weight of 5-10 Kd and does not induce metamorphosis in coral larvae that are not induced by the intact parental algae (7). Both the biochemical characterization of the inducer isolated from an inductive Pacific alga and its recognition by A. *humilis* larvae indicate that this morphogen belongs to the same class of algal cell-wall polysaccharide as the compound obtained from Caribbean red algae. As we show here, acroporid larvae assayed at Akajima metamorphosed in response to both *H. reinboldii* fragments and intact algae (Figs. I, 2B, C). as well as to this same batch of resin-adsorbed morphogen purified from *H. reinboldii* (Fig. 2D) when incubated with resin lacking the adsorbed molecule, larvae of the Pacific corals remained arrested with no metamorphosis. Settlement and metamorphosis in the tested *Acropora* species are thus apparently induced by chemosensory recognition of the same class of algal sulfated glycosaminoglycan.

The acroporids and agariciids are members of the recently defined Glade of complex scleractinians (16). In experiments otherwise identical to those above, larvae of the mass-spawning faviid corals from Akajima—Favia *Javus, Goniastrea retiformis,* and *Cyphastrea* sp.—members of a taxonomically distinct Glade of robust corals (2, 16, 17), also exhibited a strict requirement for the same class of algal morphogen recognized by the complex coral larvae. Thus, the inducer molecule purified from the two Pacific algae, *Hydrolithon reinboldii* and *Peyssonnelia* sp. (each adsorbed to separate batches of hydrophobic resin) induced metamorphosis of *Cyphastrea* sp. larvae. There was no spontaneous metamorphosis in the presence of resin with no adsorbed cue. Fragments of the intact alga *H. reinboldii* induced metamorphosis of *Cvphastraea* sp., whereas seawater alone, dead coral branches, and the brown alga *L. variegata* produced no metamorphic response. Similarly, *Favia favus* and *Goniastrea retiformis* metamorphosed in response to fragments of intact *Pe ssonnelia* sp., but were unresponsive to *L. variegata* and seawater alone. Relatively few of these faviid larvae were available, which limited the testing of the other algae and purified inducers adsorbed to resin with each coral species. The results, however, demonstrate the stringency and specificity of the requirement of these robust corals for the same class of algal inducer (A. N. C. Morse *et al.,* University of California, Santa Barbara, in prep.).

The algal-cue-dependent settlement and metamorphosis of agariciids described here has been shown to operate effectively in the ocean as well as in the laboratory (9) , and to contribute to substratum specificity of agariciid recruitment in the natural environment (6). We further suggest that this mechanism may enhance the probability of successful reproduction of coral species that depend on cross-fertilization. In mass-spawning corals the success of cross-fertilization of gametes in the plankton depends on a rapid encounter with gametes from another colony of the same species, and thus on the propinquity of reproductive colonies of the same species. Similarly, species with internal cross-fertilization depend on the transfer of sperm from one colony to another. Field manipulation of colony distances in *Agaricia humilis* reveals that colonies must be <_ 2 m from their nearest neighbor for successful production of larvae (P. T. Raimondi and A. N. C. Morse, University of California, Santa Barbara, in prep.).

The evidence presented here indicates that representa-

tive species of three very large families of corals, the Acroporidae, Faviidae, and Agariciidae, have evolved similar morphogenic requirements and chemosensory signal recognition systems for larval recruitment from the plankton to the reef. This mechanism is independent of their geographic histories and of their modes of sexual reproduction. Our findings indicate that species in these three families evolved chemosensory receptors that recognize the same class of required chemical morphogen. Unless this mechanism arose independently multiple times, the results suggest an adaptation of a common ancestor. Our own findings, coupled with recent revisions of the evolutionary histories of scleractinian corals based on both molecular phylogenetic analyses (of both nuclear and mitochondrial genes) and morphometric and palaeontological studies (2, 16, 17, 18), suggest that this common mechanism is relatively old. It appears to predate not only the phylogenetic and geographic divergence of the corals we studied, but also the emergence, at 240 Ma, of the mineralized coral skeleton (16, 18).

Acknowledgments

We thank M. flatta and T. Sugiyama for assistance with gamete fertilization, and M. H. Can, L. A. Espada and A. Stewart-Oaten for assistance with statistical analyses. We thank A. Alldredge, J. Connell, E. Delong, S. Gaines, A. Kuris, and D. Morse for helpful suggestions for the manuscript. The project was made possible by the interest and generous support of S. Hosaka, and by grants to A. M. from NSF, Division of Ocean Sciences, the NOAA National Undersea Research Program, and the Jean and Katsuma Dan Fellowship from the Marine Biological Laboratory, Woods Hole, Massachusetts.

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