

Morphology offers no clues to asexual vs. sexual origin of small *Acropora cervicornis* (Scleractinia: Acroporidae) colonies

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Abstract: Sexual recruitment of the staghorn coral, *Acropora cervicornis*, is accepted to be very rare. Instead, these branching corals proliferate through fragmentation leading to dense mono-specific and possibly mono-clonal stands. For acroporid corals, which have suffered drastic population declines, dominance of asexual reproduction results in low levels of genotypic diversity and limited ability to re-colonize extirpated areas. Small colonies with a single encrusting, symmetrical base, and few incipient branches are frequently presumed to be the result of a settled planula (i.e. sexual reproduction). Here, we show that colonies fitting this description (i.e., presumed sexual recruits) can result from asexual fragmentation. *Acropora cervicornis* colonies (~20 cm diameter) were tagged and observed over eighteen months. In several cases, colony offshoots fused with the adjacent substrate forming secondary disc-like attachment points. Following natural fragmentation, these discs of tissue became separated from the original colony, and were observed to heal and give rise to smaller colonies with striking similarity to the expected morphology of a sexual recruit. Thus, presuming a colony is a sexual recruit based on appearance is unreliable and may lead to inflated expectations of genetic diversity among populations. The accurate assessment of recruitment and genetic diversity is crucial to predicting the recovery potential of these imperiled and ecologically irreplaceable reef corals. Rev. Biol. Trop. 54 (Suppl. 3): 145-151. Epub 2007 Jan. 15.

Key words: recruitment, fragmentation, staghorn coral, clonal, colony, *Acropora cervicornis*.

Acropora cervicornis (Caribbean staghorn coral; Lamark 1816) proliferates largely through fragmentation leading to dense monospecific (e.g. Gilmore and Hall 1976, Tunnicliffe 1981) and likely mono-clonal stands. Once a colony is broken, reattachment of the loose fragment generally occurs when a growing (apical) tip encounters the surrounding substrate (Gilmore and Hall 1976, pers. obs.) but may also occur along the branch when the polyps/corallites fuse with the substrate (Gilmore and Hall 1976, Tunnicliffe 1981). *Acropora cervicornis* can rapidly dominate local environments through this form of asexual reproduction. Alternatively, sexual

recruitment is needed to colonize distant areas and introduce genetic diversity.

Acropora cervicornis reproduces sexually by releasing egg-sperm bundles in a mass spawning event (Vargas-Angel and Thomas 2002) that presumably occurs annually. With one exception (van Moorsel 1989), recruitment studies in the Caribbean employing artificial substrates have found settled acroporid planulae (from here referred to as 'sexual recruits') to be rare (Sammarco 1980, Rylaarsdam 1983, Ruiz-Zárte and Arias-González 2005, Quinn and Kojis 2005). Rylaarsdam (1983) describes a new recruit as 'a small patch on the substratum with projecting corallites, one of which

gives rise to a single branch' based on the one sexual recruit that appeared on marked substrates in that study. This description (eg. Fig. 1a) certainly fits our expectation of how a settled planula might grow into a small colony; however, direct observations of development from settled planula to a branching colony are lacking.

Several field studies report finding juvenile *A. cervicornis* that are presumed, based on their size, morphology or placement, to have originated from settled planulae (Gilmore and Hall 1976, Tunnicliffe 1981, Rylaarsdam 1983, Knowlton *et al.* 1990). Given that re-attached fragments are generally easily recognized (Fig. 1b) it seems reasonable to conclude that small sexual recruits should be discernable based on these criteria. Colonies situated on vertical or sloped surfaces could particularly be reasoned to be sexual recruits since loose fragments are unlikely to be retained in such locations, gravitating instead to flat surfaces. Here, we document a scenario whereby fragmentation can result in a small colony morphologically consistent with a sexual recruit.

MATERIALS AND METHODS

A monitoring study of *A. cervicornis* was initiated in summer 2002 at three sites in the Florida Keys (USA) including Anniversary Reef (25°23.293'N, 80°09.869'W, ANR), Elkhorn Reef (25°21.714'N, 80°09.937'W, ELR) and White Bank Dry Rocks (25°02.595'N, 80°22.156'W, WBDR). The ANR site is shallow (3 m) back reef/hard bottom habitat, while the ELR site is a slightly deeper (4-5 m) weakly zoned fore reef habitat. WBDR is a well-defined patch reef with a flat topside at 2-3 m depth. Both ANR and ELR differed notably from WBDR in that their foundations were unconsolidated reef rubble over sand with scattered *Thalassia testudinum*, while the topside of WBDR was generally consolidated limestone with relatively little loose rubble or sand.

The *Acropora cervicornis* population at all three sites consisted of isolated (non-thicket) colonies scattered among gorgonians, sponges and small head corals. Individual colonies were haphazardly chosen, measured (gross colony dimensions of length, width, height),



Fig. 1. Is it possible to distinguish *Acropora cervicornis* sexual and asexual recruits based on morphology of small colonies? a) Morphology of this small *A. cervicornis* colony is consistent with published descriptions of sexual recruits (scale to the left in cm). b) Fragment of *Acropora cervicornis* that has reattached to the substrate at several attachment points (scale bar is 3 cm).

Fig. 1. ¿Es posible distinguir entre reclutas sexuales y asexuales de *Acropora cervicornis* basándose en la morfología de las colonias pequeñas? a) La morfología de esta colonia pequeña de *A. cervicornis* es coherente con descripciones publicadas de reclutas sexuales (escala a la izquierda en cm). b) Fragmento de *A. cervicornis* que se ha acoplado al sustrato en varios puntos (escala 3 cm).

photographed, and a numbered tag was nailed to the adjacent substrate to allow re-identification of the same colony over time (Table 1). Colonies were surveyed approximately every four months between June 2002 and November 2003 (see Williams and Miller 2006) for detailed explanation of methods and overall report of monitoring results). During these periodic surveys, each colony was located, measured, and photographed from several angles.

Time series' of monitoring photographs for individual colonies were examined to specifically investigate the frequency of fragmentation events leading to small, encrusting remnants of *A. cervicornis* tissue. We quantified 'secondary attachment points', colony disruption, and resulting 'orphan colonies'. 'Secondary attachment points' (SAP) were classified as encrusting skeletal growths occurring where a live branch (usually the tip) grew into contact with the surrounding substrate, but not including the primary basal attachment. 'Colony disruption' was defined as a subset of the observed fragmentation events whereby a substantial break (e.g. to the basal attachment of the colony) resulted in the colony being dislodged.

'Orphan' colonies were identified as living encrusting patches of tissue that, although formerly observed as SAP of a parent colony, were subsequently observed disconnected from the parent colony following a colony disruption event. This analysis documents orphan colony formation and growth into a 'pseudo-sexual recruit', and characterizes the frequency of such events within the monitored populations.

RESULTS AND DISCUSSION

We documented the formation of several orphans (Table 1, Fig. 2) over the 18 month monitoring period. For each observed orphan colony, a SAP was observed on the parent colony at one survey, and at the following survey the parent colony was either entirely gone or dislodged and resting nearby. The remnant SAP remained attached to the substrate resulting in an orphan colony. Orphan colonies ranged in size from 2 - 5 cm diameter when they were first observed. The orphans later produced branches and grew in a symmetrical manner that resembled a 'sexual recruit', with no

TABLE 1
Parameters for A. cervicornis colonies at three reefs between June 2002 and Oct 2003

CUADRO 1
Parámetros de A. cervicornis en tres arrecifes entre junio 2002 y octubre 2003

Site	# colonies	Diameter (cm) (median, IQR)	# colonies w/ SAP	total # of SAP	# disrupted colonies	# orphans
ELR	18	15, 11-19	5	7	3	3
ANR	28	17, 16-22	18	33	8	4
WBDR	19	19, 15-28	4	12	2	0

Colony diameter (cm) (median and inter-quartile range (IQR)), number of colonies with, and total number of secondary attachment points (SAP), colony disruption (fragmentation) and orphans (small, encrusting colony remnants) (see text for full explanation) observed among tagged *A. cervicornis* colonies at Elkhorn Reef (ELR), Anniversary Reef (ANR) and White Bank Dry Rocks (WBDR).

Diámetro de las colonias (cm) (intervalo medio e inter-cuartil IQR), número de puntos de unión secundaria (SAP), drupción de las colonias (fragmentación) y huérfanos (pequeños remanentes incrustantes de colonias) (ver texto para explicación completa), observados entre las colonias de *A. cervicornis* etiquetados en el arrecife Elkhorn (ELR), el arrecife Anniversary (ANR) y el White Bank Dry Rocks (WBDR).

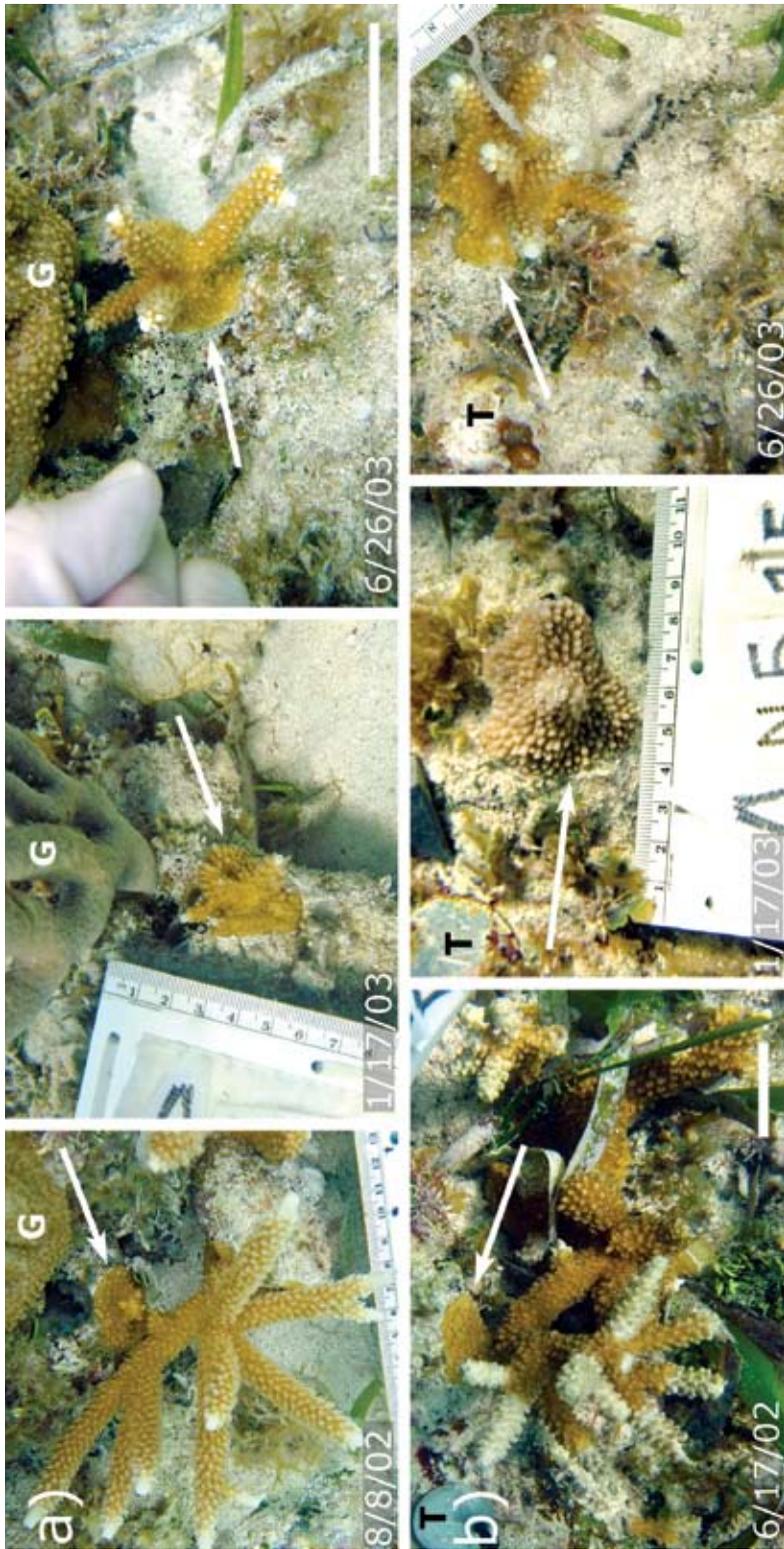


Fig. 2. Time series of two *Acropora cervicornis* colonies showing formation of 'orphan colonies' detached from the parent colony which is still present; in the 2nd frame only the SAP remains with small protobranches (orphan), resembling a sexual recruit which grew larger by the following survey (3rd frame). Note the gorgonian (G) at the top of the frame for spatial reference. b) In the 1st frame the parent colony has formed a SAP (arrow); in the 2nd frame the parent has become dislodged and a small scar is all that remains from the break with the parent colony; by the 3rd frame there is no trace of fragmentation. Note the location of the aluminum tag (T) for spatial reference in each frame.

Fig. 2. Series de tiempo de dos colonias de *A. cervicornis* que muestran la formación de colonias huérfanas (regla en cm, barra de escala = 3 cm). a) En el 1^{er} cuadro se observa un pequeño punto secundario de unión (SAP; flecha) ya habiéndose desprendido de la colonia madre, que aún está presente; en el 2^{do} cuadro sólo hay remanentes del SAP con pequeñas proto-ramas (huérfano), semejando a un recluta sexual que creció más para el siguiente sondeo (3^{er} cuadro). Notar al gorgonio (G) en la parte superior del cuadro como referencia espacial. b) En el 1^{er} cuadro la colonia madre ha formado un SAP (flecha); en el 2^{do} la colonia madre se desliga y una pequeña cicatriz es todo lo que queda del rompimiento con la colonia madre; para el 3^{er} cuadro ya no hay señales de la fragmentación. Notar la ubicación de la etiqueta de aluminio (T) como referencia espacial en cada cuadro.

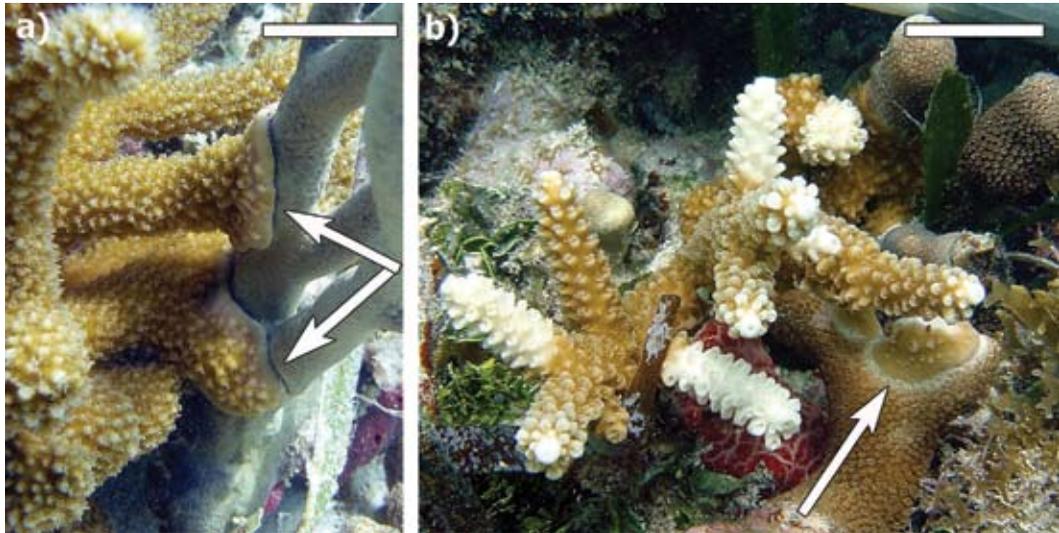


Fig. 3. *Acropora cervicornis* encrusting a) a gorgonian (*Pseudoplexaura* sp.) and b) another scleractinian (*Porites porites*) (scale bars =3 cm). Note the slim gap (arrow) suggesting poor adhesion with the gorgonian while the attachment with *P. porites* yielded a small 'orphan' *A. cervicornis* colony (arrow).

Fig. 3. *Acropora cervicornis* incrustando a) un gorgonio (*Pseudoplexaura* sp.) y b) otro escleractíneo (*Porites porites*) (escala =3 cm). Notar el delgado espacio (flecha) que sugiere pobre adhesión con el gorgonio, mientras que la unión con *P. porites* produjo una pequeña colonia huérfana de *A. cervicornis* (flecha).

apparent signs that it resulted from fragmentation (i.e. a pseudo-sexual recruit). Furthermore, several orphans were formed on a sloping surface, further disguising their asexual origin.

Colonies observed forming SAPs ranged in size from 9 - 31 cm in diameter (median=12 cm), suggesting that SAP formation is more a function of substrate proximity to growing branch tips (Gilmore and Hall 1976) rather than a function of colony size. In addition to reef substrate, SAPs formed with surrounding organisms including gorgonians, sponges and other species of hard corals including *Porites porites* (Pallas, 1766; Fig. 3) and *Siderastrea siderea* (Ellis and Solander, 1786). SAPs that were formed on hard corals resulted in orphans while those on gorgonians or sponges usually failed to adhere. In cases where the SAP failed to adhere to the substrate, it remained intact with the dislodged parent colony, (Fig. 4) indicating that not all SAPs become orphans. Based on these observations, the scenario for 'orphan' formation involves three elements. First, *A. cervicornis* must form a SAP with the

substrate; then the parent colony must be dislodged, and finally, the SAP must adhere to the substrate through the fragmentation event.

We observed the formation of three orphans from 18 (17%) monitored colonies at ELR, and four from 28 (14%) monitored colonies at ANR (Table 1) over the 18 month study period. SAPs were observed at all three sites (Table 1), and in many cases a single colony formed multiple (up to six) attachments. However, orphans were only found at ELR and ANR. The substrate at these two sites was relatively unconsolidated compared to WBDR. At these two sites colony attachments (including basal attachments) were often on unstable substrate. While we did not observe orphans among our tagged colonies at WBDR, all the necessary elements (SAP and colony disruption) were present, though not in the same colony, suggesting that they could occur there. A major disease outbreak at WBDR resulted in substantial mortality of *A. cervicornis* (Williams and Miller 2005) by April 2003, which likely compromised formation and/or detection of attachment points.

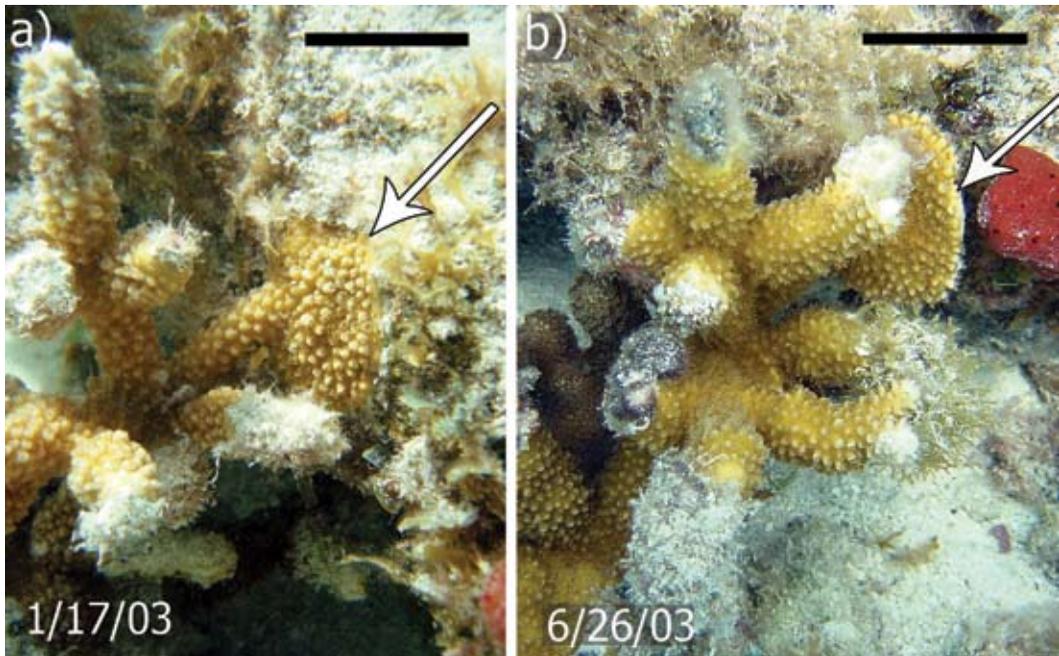


Fig. 4. a) Encrusting Secondary Attachment SAP point) between *Acropora cervicornis* and adjacent substrate (scale bars =3 cm). b) Same colony has dislodged and the encrustation (arrow) has remained with the parent rather than becoming an 'orphan'.

Fig. 4. a) Unión incrustante secundaria (flecha) entre *Acropora cervicornis* y el sustrato adyacente (escala = 3 cm). b) La misma colonia se ha desligado y la incrustación (flecha) se mantiene con la madre en lugar de convertirse en una huérfana.

The orphan colonies we observed were notably consistent in morphology with sexual recruits, however they were indisputably of asexual origin and hence could be termed 'pseudo-sexual recruits'. Since our monitoring program was not originally designed to detect this phenomenon, we cannot provide a robust estimate of orphan frequency among *A. cervicornis* populations. Nonetheless, we provide clear evidence that orphan formation does occur, and present a plausible, natural mechanism for the occurrence of 'pseudo-sexual recruits'.

In May 2006 *Acropora cervicornis* was listed as a 'Threatened Species' under the U.S. Endangered Species Act (Anonymous 2006) due to its Caribbean-wide demise that began in the 1980s (e.g. Bruckner 2003). In highly clonal species such as *A. cervicornis*, individual colonies often do not represent

genetically unique individuals (Baums *et al.* in press) meaning that the 'effective population size' is likely to be substantially smaller than colony counts alone would suggest. Recovery of *A. cervicornis* in the future is likely more dependent on successful sexual recruitment than were historical populations (Bruckner 2003) since widespread mortality has drastically reduced fragment sources in many areas. The morphological similarity between sexual recruits and some asexual recruits can hamper estimates of genotypic diversity, dispersal and thus the evaluation of recovery potential of this imperiled species.

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RESUMEN

Se ha aceptado que el reclutamiento sexual del coral asta de venado, *Acropora cervicornis*, es muy raro. Por el contrario, estos corales ramificados proliferan a través de fragmentación, generando densas bases monoespecíficas e incluso monoclonales. Para corales acropóridos, los cuales han sufrido disminuciones de población drásticas, la dominancia de reproducción asexual resulta en bajos niveles de diversidad genotípica y habilidad limitada para recolonizar áreas de donde han sido erradicados. Frecuentemente se presume que las colonias pequeñas con una sola base incrustante simétrica y unas pocas ramas incipientes, son el resultado del asentamiento de una plánula (reproducción sexual). Aquí, nosotros demostramos que algunas colonias que calzan con esta descripción (supuesta reproducción sexual) pueden resultar de fragmentación asexual. Se etiquetaron y observaron colonias de *Acropora cervicornis* (~20 cm de diámetro) durante 18 meses. En muchos casos, los retoños de la colonia se fusionaron con el sustrato adyacente formando puntos de acoplamiento con forma de disco. Siguiendo con la fragmentación natural, estos discos de tejido se separaron de la colonia original, cicatrizaron y dieron paso a pequeñas colonias con tremenda similitud a la morfología esperada para un recluta sexual. Por lo tanto, asumir que una colonia es un recluta de origen sexual basándose en apariencia es poco fiable y puede generar expectativas infladas de diversidad genética entre poblaciones. La evaluación certera del reclutamiento y la diversidad genética es crucial para predecir la recuperación potencial de estos arrecifes de coral, los cuales están en peligro y son irremplazables.

Palabras clave: reclutamiento, fragmentación, coral asta de venado, clonal, colonia, *Acropora cervicornis*.

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