LONG-TERM DYNAMICS OF CORAL POPULATIONS: CONTRASTING REPRODUCTIVE MODES

T.P. HUGHES

Dept of Biological Sciences, University of California,
Santa Barbara, CA, USA 93106

ABSTRACT

Population dynamics of 4 species of Caribbean
corals (*Agaricia agaricites*, *A. lamarcki*,
Leptoseris cucullata, and *Montastrea annularis*)
were measured annually in Jamaica over a 10 year
period. Like many corals, these species can
reproduce sexually (by the production of larval
recruits), or asexually (by fission). Here I
examine for the first time the relative contribu-
tion of these two processes in maintaining the
size of local coral populations.

Survivorship from 1977-1987 of colonies originally
present ranged inter-specifically from 7-61%. The
longer lived species, *M. annularis* and
A. lamarcki, had only 7 larval recruits, while the
shorter-lived species, *A. agaricites* and
L. cucullata, had 167.' More colonies were
generated locally by asexual fission than by
larval recruitment into the permanent plots, for 3
of the 4 species. The per species ratio of
recruits to fissions ranged more than 20-fold,
from less than 1:10 to greater than 2:1. By 1987,
all colonies could be identified as (1) survivors
of those already present 10 years earlier, (2)
daughter colonies formed by fission of old
survivors, or (3) larval recruits of known age.
The relative number of each of these three
categories varied widely from species to species,
indicating substantial differences in colonizing
ability, and in genet longevity and turnover.

INTRODUCTION

The population dynamics of clonal organisms are
strongly influenced by modular processes (polyp
mortality, colony fission and fusion), as well as
the more familiar demographic events of genet
birth and death (e.g. Harper 1977, Hughes 1984,
Lasker 1984, Heyward & Collins 1985). Clonal
animals, such as most corals, bryozoans and
asidians, grow by repeated budding of modules
(e.g. polyps). Many clonal species undergo
asexual reproduction, when single modules or
clumps of modules (i.e. daughter colonies) bud or
break off (e.g. Hughes & Jackson 1980, 1985,
Hunter & Kehoe 1985, Jackson & Hughes 1985,
Richmond 1987). The sum of all modules, whether
physically connected or not, comprises each genet,
or genetically distinctive individual. Because of
asexual reproduction, the number of colonies in a
coral population often greatly exceeds the number
of genets (e.g. Gilmore & Hall 1976, Hughes &
Jackson 1980, 1985, Bothwell 1981, Highsmith 1982,
Jokiel et al. 1983). Mortality rates of asexually
produced daughter colonies may differ from that of
coral recruits (Hughes 1985). Thus, the genetic
diversity and turnover of a population is strongly
influenced by the relative rates of sexual and
asexual reproduction.

I present here preliminary results from a long-
term demographic study, which illustrate a large
inter-specific range in amounts of different modes
of coral reproduction. Four common Caribbean
species were chosen for study, *Agaricia
agaricites*, *A. lamarcki*, *Leptoseris cucullata*, and
Montastrea annularis. In deep water, these
species form foliaceous, plate-like corals which
are particularly amenable to photographic
censusing. The ecological and genetic differences
between larval recruits and daughter colonies
result in substantial discrepancies in colonizing
ability, age structure, longevity and genetic
diversity of these coral populations.

METHODS

Rates of larval recruitment and colony fission
were recorded by photographic monitoring of 12 1m2
quadrats tied permanently at a depth of 35m onto
Pinnacle 1 reef, near the Discovery Bay Marine
Laboratory in Jamaica. Each quadrat was divided
into 1/4m2 sections by monofilament line, and
these were photographed annually using a Nikonos
11, 111, 1V or V camera equipped with a 28mm lens
and strobe, from a vertical distance of 1-1.5m.

Each 1/4m2 photograph (colour transparency) was
projected, and all colonies of the four selected
species were identified, traced, numbered,
digitized, and followed through time (a total of
3,591 records). New larval recruits and daughter
colonies were assigned a number when they first
appeared. Daughter colonies in these species are
not dispersed, except by directional growth.
Thus, the close proximity of daughter colonies (at
least in the first year after fission took place),
their common skeletal connections and their
identical colour makes them easily distinguishable
from larval recruits. Quantitative descriptions
of the site and further methodological details are
given in Hughes & Jackson (1985).

RESULTS

Sexual and Asexual Reproduction

A total of 428 colonies were generated by recruit-
ment and fission from 1977 to 1987, an amount
equivalent to 111% of the original number present
at the first census. On an annual basis, the mean
rate of local production of colonies by both means
combined was 3.5/m2/year. Of these, 41% were
larval recruits, 59% were generated asexually by
fission.

Rates of recruitment varied greatly between the
four species (Table 1). *Agaricia agaricites* and
L. cucullata accounted for 63 and 33% of recruits,
respectively, while *A. lamarcki* and *M. annularis*
together comprised only 4%. By 1987, only 24% of
the recruits detected each year remained alive,
leaving 31 live recruits for *A. agaricites* and 11
for *L. cucullata*. Net recruitment for
M. annularis and *A. lamarcki* was zero over the 10
year period (Table 1).

Table 1. Number and survivorship of recruits.

Species	No. Recruits 1977-1987	% Alive in 1987
A. agaricites	110	28
L. cucullata	57	19
A. lamarcki	6	0
M. annularis	1	0
Total	174	24

Rates of fission also varied from species to species (Table 2). *Montastrea annularis*, the worst recruiter, had the highest per capita rate of fission (mean annual rate of 0.09), and accounted for 36% of all daughter colonies formed from 1977-1987. In contrast, the most copious recruiter, *A. agaricites*, had the lowest mean annual per capita fission rate of 0.03, amounting to 17% of daughter colonies formed by the 4 species. *Leptoseris cucullata* and *A. lamarcki* both had an annual rate of fission of 0.07, and they formed 38% and 9% of daughter colonies, respectively. By 1978, 43% of the daughter colonies formed each year remained alive. Survivorship of daughter colonies varied significantly between species (Table 2, P<0.005). Seventy-seven percent of surviving daughter colonies belonged to the two species that were poor recruiters, *M. annularis* and *A. lamarcki*.

Table 2. Number and survivorship of daughter colonies.

Species	No. Daughter Colonies 1977-1987	% Alive in 1987
A. agaricites	42	29
L. cucullata	96	14
A. lamarcki	24	67
M. annularis	92	74
Total	254	43

With the exception of the most copious recruiter, *A. agaricites*, more colonies were generated locally by fission than by recruitment in each species. The ratio of local recruits to fission per species for all years combined ranged more than 20-fold, from less than 1:10 for *M. annularis* to more than 2:1 for *A. agaricites* (*A. agaricites* > *L. cucullata* > *A. lamarcki* >> *M. annularis*). Moreover, over the entire 10 year period, the only successful input into local populations of *M. annularis* and *A. lamarcki* was by asexual fission, since the few larval recruits that were observed each year had all died by 1987 (Table 1).

Population structure and turnover

Over the entire 10 year period, survivorship of colonies initially present varied inter-specifically from 7-61%, with a mean for all species combined of 28% (Table 3). The net production of colonies by sexual and asexual means combined was not enough to compensate for mortality of colonies originally present in 1977, and the number of colonies declined from 386 initially to 257 by 1987 (Table 3). Only one species, *M. annularis*, showed a local increase in number of colonies, and that occurred exclusively through asexual fragmentation.

By 1987, all corals could be identified as (1) colonies at least 10 years old that were initially present in 1977, (2) daughter-colonies derived asexually from these old survivors, or (3) younger colonies that recruited to the permanent plots during the study period. The relative number of these three kinds of colonies varied enormously between the four coral species (P<0.001, Table 3; Figure 1).

Populations of *A. agaricites* and *L. cucullata* had the highest rate of mortality (Table 3), and in 1987 contained a large proportion of young recruits, i.e. colonies not yet present at the initial census in 1977 (amounting to 41% and 36% of the final colony counts, respectively; Figure 1). Turnover of colonies of these two species was rapid, and they both declined in number by more than 50% during the study period (Table 3). In contrast, the entire population of *A. lamarcki* and *M. annularis* in 1987 consisted of genets older than 10 years. Survivorship of these latter species was very high (44% and 61%, respectively; Table 3), and numbers of colonies were more stable, despite the complete lack of successful recruitment for at least the last decade.

The proportion of colonies alive in 1987 that were generated asexually by fission during the study (the middle bar in Figure 1) varied widely from species to species. In *A. agaricites*, a low per capita rate of fission, high mortality and a high rate of recruitment resulted in relatively few daughter colonies, only 16% of the total count in 1987. In contrast, in *L. cucullata*, *A. lamarcki* and *M. annularis*, 40% or more of colonies alive in 1987 were derived asexually during the study. Because of unrecorded fissions which undoubtedly occurred before 1977, this indicates the very minimum amount by which counts of colonies exceed the number of genets in these populations.

DISCUSSION

The generation of larval recruits and daughter colonies constitute two demographically signifi-
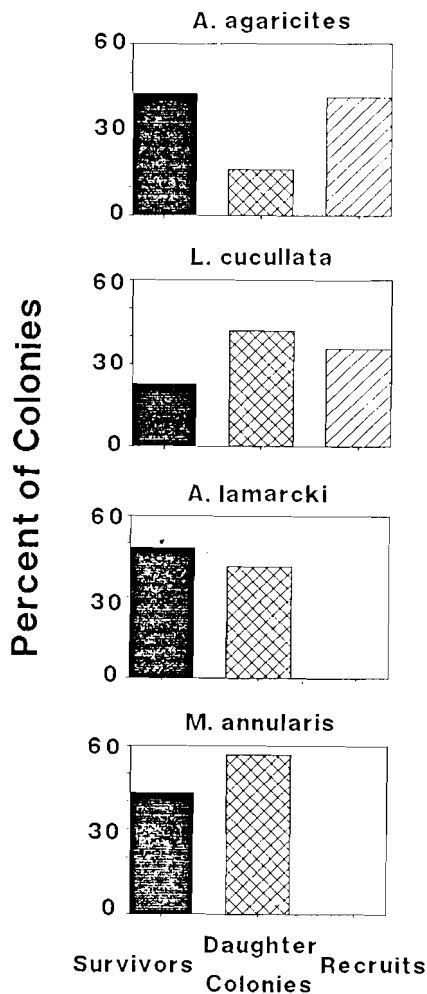
Table 3. Population structure and turnover.

Species	Initial No. in 1977	Survivors in 1987	Net reproduction Fissions	Net reproduction Recruits	Total in 1987
A. agaricites	168	32	12	31	75
L. cucullata	98	7	13	11	31
A. lamarcki	34	15	16	0	31
M. annularis	86	52	68	0	120
Total	386	106	109	42	257

A. agaricites

L. cucullata

A. lamarcki

M. annularis

Survivors   Daughter Colonies   Recruits

Figure 1. Percent of colonies at the 1987 census that were (1) survivors of those already present in 1977, (2) daughter colonies formed by fission of old survivors, or (3) recruits detected in 1978 or later. Sample sizes are given in Table 3.

cant reproductive processes in these foliaceous coral species, both leading to substantial increases in numbers of colonies. However, recruitment and fission differ profoundly in a number of important ecological and evolutionary characteristics, as outlined briefly below.

Daughter colonies formed by fission of a single genet are mitotically homogeneous, i.e. they share the same genotype because of their common ancestry through asexual budding. In contrast, sexually produced larvae are genetically unique, because of meiosis. Therefore, it seems likely that the genetic diversity of sexually reproducing populations like *A. agaricites* should be greater

than that of asexually replicating populations with limited amounts of gene flow. Note however, that not all planktonically dispersed coral propagules are produced sexually (Sammarco 1982, Stoddart 1983). Furthermore, by analogy with clonal plants (e.g. Whitham and Slobodchikoff 1981), it is at least feasible that daughter colonies of long-lived species like *Montastrea annularis* could also diverge in genetic composition by the accumulation of somatic mutations.

Apart from genetic differences, different types of coral propagules vary greatly in their dispersal capabilities. Daughter colonies of the four species studied here have only a limited ability to move apart, by directional growth. In other sessile corals, particularly loosely branching acroporids, colony fragmentation and tumbling during storms can also result in considerable local dispersal (e.g. Gilmore and Hall 1976, Highsmith 1982). However, it appears that movement from reef to reef is usually effected only by dispersal of planktonic propagules (e.g. Jackson 1986, Sammarco 1988), or occasionally by passive rafting of mature colonies (Jokiel 1984). As a result, recolonization by sessile corals following local extinction can only begin through settlement from the plankton (or by rafting), since colonies formed by fission and fragmentation cannot move far from their source.

Daughter colonies and larval recruits are also demographically distinctive, particularly since the former vary in size, while the latter are initially much smaller. As a result, it is generally assumed that daughter colonies have a high rate of survival and that fission and fragmentation are always adaptive, although there is little data to support this latter hypothesis. Recent studies have shown that mortality of unattached coral fragments is even higher than rates reported here for attached daughter-colonies (Highsmith et al. 1980, Knowlton et al. 1980, Bak & Criens 1981, Hughes 1985, Connell & Hughes, in prep.). In the present study, mortality of larval recruits was almost twice as high as daughter colonies, for all four species combined (Table 1,2). However, examination of each species separately indicates that recruits survive as well or better than daughter colonies despite the differences in size, at least in the two species, *A. agaricites* and *L. cucullata*, which had sufficient numbers of each to allow comparison. Daughter colonies and larval recruits also have different fecundity schedules. Because larval recruits are initially small, there is a considerable time-lag before which they can grow sufficiently large to reproduce sexually (e.g. Connell 1973, Rinkevich and Loya 1979, Kojis & Quinn 1981, Babcock 1984) or asexually (Hughes and Jackson 1985). In contrast, large daughter colonies may be capable of immediate reproduction.

In this study, *A. agaricites* and *L. cucullata* accounted for the majority of recruits (96% of the total observed from 1977-1987, Table 1), confirming similar findings from short-term studies throughout the Caribbean (Dustan 1977, Bak and Engel 1977, Rylaarsdam 1979, Rogers et al. 1984, Morse et al. 1988). Consequently, these species are among the first to invade experimental panels or clearings (Rogers et al. 1984, Hughes

1985), and their populations contain a relatively
high proportion of young colonies (Figure 1). In
contrast, *M. annularis* and *A. lamarcki* are slow to
invade newly disturbed areas (Hughes 1985), but
once genets become established they persist and
proliferate locally by asexual fission (Figure 1).
Colonies of the faster growing species,
A. agaricites and *L. cucullata* (see Hughes &
Jackson 1985), can potentially "move" up to a
meter apart in a decade, although few genets live
as long as 10 years (Table 3; Figure 1).
Montastrea annularis and *A. lamarcki* grow more
slowly but they also live much longer (Table 3),
producing clones of daughter colonies up to 5m
across (Hughes & Jackson 1985). The relative
number of colonies generated locally by
recruitment and asexual reproduction in these
populations ranged inter-specifically more than
20-fold (Table 1, 2). It seems likely that future
studies will show similar demographic variation in
other habitats and populations.

REFERENCES

Bak, R.P.M., & Criens, S.R. 1981. Survival after
fragmentation of colonies of *Madracis
mirabilis*, *Acropora palmata* and *A.
cervicornis* (Scleractinia) and the
subsequent impact of a coral disease. In:
Proc. 4th Int. Coral Reef Symp., Manila
1981. Vol. 2, pp. 221-227.

Bak, R.P.M., & Engel, M.S. 1979. Distribution,
abundance and survival of juvenile
hermatypic corals (Scleractinia). and the
importance of life history strategies in the
parent coral community. Mar. Biol. 54:341-
352.

Connell, J.H. 1973. Population ecology of reef
building corals. In: Biology and geology of
coral reefs, Jones, O.A., & Endean, R.
(eds.), Academic Press, New York, Vol.2, pp.
205-245.

Dustan, P. 1975. Vitality of reef coral
populations off Key Largo, Florida:
recruitment and mortality. In:
Environmental geology, Springer-Verlag, New
York, pp. 51-58.

Highsmith, R. 1982. Reproduction by fragmentation
in corals. Mar. Ecol. Prog. Ser. 7: 207-226.

Highsmith, R.C., Riggs, A.C., and D'Antonio, C.M.
1980. Survival of hurricane generated coral
fragments and a disturbance model of reef
calcification/growth rates. Oecologia
46:322-329.

Heyward, A.J., & Collins, J.D. 1985.
Fragmentation in *Montipora ramosa*: the genet
and ramet concept applied to a reef coral.
Coral Reefs 4: 35-40.

Hughes, T.P. 1984. Population dynamics based on
size rather than age: A general model with a
reef coral example. Am. Nat. 123:778-795.

Hughes, T.P. 1985. Life histories and population
dynamics of early successional corals. Proc.
5th Int. Coral Reef Congress, Tahiti. Vol.4,
pp.101-106.

Hughes, T.P., & Jackson, J.B.C. 1980. Do corals
lie about their age? Some demographic
consequences of partial mortality, fission
and fusion. Science. 209:713-715.

Hughes, T.P., & Jackson, J.B.C. 1985. Population
dynamics and life histories of foliaceous
coral. Ecol. Monogr. 55:141-166.

Hunter, C.L., & Kehoe, C.C. 1985. Patchwork
patchreefs: the clonal diversity of the
coral *Porites compressa* in Kaneohe Bay,
Hawaii. In: Population Biology of coral
reefs, Jokiel, P.L., & Richmond, R.H.,
(eds.). Hawaii Inst. Mar. Biol., Tech. Rep.
No. 37.

Jackson, J.B.C. 1986. Dispersal and distribution
of clonal and aclonal benthic invertebrates.
Bull. Mar. Sci. 39:588-606.

Jackson, J.B.C., & Hughes, T.P. 1985. Adaptive
strategies of coral reef invertebrates. Am.
Sci. 73:265-274.

Jokiel, P.W. 1984. Long distance dispersal of
reef corals by rafting. Coral Reefs 3:113-
116.

Jokiel, P.L., Hildeman, W.H., & Bigger, C.H. 1983.
Clonal population structure of two sympatric
species of the reef coral *Montipora*. Bull.
Mar. Sci. 33:181-187.

Knowlton, N., Lang, J.C., M.C. Rooney, & P.
Clifford. 1981. Evidence for delayed
mortality in hurricane-damaged Jamaican
staghorn corals. Nature 294:251-252.

Kojis, B.L., & Quinn, N.J. 1981. Aspects of
sexual reproduction and larval development
in the shallow water hermatypic coral
Goniastrea australensis (Edwards & Haime,
1857). Bull. Mar. Sci. 31:558-573.

Lasker, H.R. 1984. Asexual reproduction,
fragmentation, and skeletal morphology of a
plexaurid gorgonian. Mar. Ecol. Prog. Ser.
19: 261-268.

Morse, D., Hooker, N., Morse, A.N.C., & Jensen,
R.A. 1988. Control of larval metamorphosis
and recruitment in sympatric agariciid
corals. J. Exp. Mar. Biol. Ecol. (In
Press).

Rinkevich, B., & Loya, Y. 1979. The reproduction
of the Red Sea coral *Stylophora pistillata*.
II. Synchronization in breeding and
seasonality of planulae shedding. Mar.
Ecol. Prog. Ser. 1:145-152.

Richmond, R.H. 1987. Energetic relationships and
biogeographical differences among fecundity,
growth and reproduction in the reef coral
Pocillopora damicornis. Bull. Mar. Sci.
41:594-604.

Rogers, C.S., Fitz, H.C., Gilnack, M., Beets, J.,
& Hardin, J. 1984. Scleractinian coral
recruitment patterns at Salt River submarine

Canyon, St. Croix, U.S. Virgin Islands. Coral Reefs 3:69-76.

Rylaarsdam, K.W. 1983. Life histories and abundance patterns of colonial corals on Jamaican reefs. Mar. Ecol. Prog. Ser. 13:249-260.

Sammarco, P.W. 1982. Polyp bail-out: an escape response to environmental stress and a new means of reproduction in corals. Mar. Ecol. Prog. Ser. 10:57-65.

Sammarco, P.W., and Andrews, J.C. 1988. Localized dispersal and recruitment in Great Barrier Reef corals: The Helix experiment. Science. 239:1422-1424.

Stoddart, J.A. 1983. Asexual reproduction of planulae in the coral *Pocillopora damicornis*. Mar. Biol. 76:279-284.

Whitham, T.G., & Slobodchikoff, C.N. 1981. Evolution by individuals, plant-herbivore interactions, and mosaics of genetic variability: the adaptive significance of somatic mutations in plants. Oecologia 49:287-292.