A New Mothed of Classifying the Growth Form of Corals and its Application to a Field Survey of Coral-Associated Animals in Kabira Cove, Ishigaki Island*

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Abstract: In order to classify the growth form of corals, the following "growth form index" was defined to denote coral shape objectively: Growth Form Index=Coral Surface Area/ (Coral Wet Weight)$^{2/3}$. On the basis of this index, growth forms of corals were classified into four major forms: massive, irregular shaped, branching, and highly branching. Coral-associated animals were classified into four groups according to their mode of living: free-living epi-, sessile epi-, boring crypto-, and secondary crypto-bionts. For the quantitative study of the distribution of coral-associated animals in each growth form of coral and in each habitat of the study area, living coral heads were collected using SCUBA from 10 stations representing various habitats in Kabira Cove, Ishigaki Island, Yaéyama Group, Okinawa Prefecture. By comparing the proportions of four life forms of animals associated with each of the four different growth forms of corals at each station, some consistent patterns were found: massive corals were dominated by both boring and secondary cryptobionts, while branching and highly branching corals were dominated by free-living and sessile epibionts. In addition, the absolute numbers as well as the proportions of the four life forms of animals associated with a given growth form of coral changed from the outer-reef outside the bay to the bay head. From these various distribution patterns, it became clear that the growth forms of corals have a strong influence on the micro ecological distribution of coral-associated animals at each station, while the physical environment regulates the distribution of these animals in a given locality on the macroscopic scale.

1. Introduction

In the tropical coastal water ecosystem, hermatypic corals not only make up the framework of the reef, but these corals, living and dead, also provide an important substratum for other organisms to live on. A variety of animals living on or in the coral have been defined as the coral-associated animals. They constitute an important part of the reef dwelling fauna. In spite of the abundance of such animals, knowledge of their ecology still remains poor (PATTON, 1976). To date studies have been concentrated only on autecological descriptions and focused mainly on rock or coral destroying organisms such as sponges (GOREAU and HARTMAN, 1963), bivalves (HIGHSMITH, 1980; SCOTT, 1980), polychaetes (HUTCHINGS and

WEATE, 1977) and sipunculoids (WILLIAMS and MARGOLIS, 1974).

Although MORTON and CHALLIS (1969) drew attention to coral heads as microhabitats for animal communities, they reported only qualitative observations of such communities. MCCLOSKEY (1970) and AUSTIN et al. (1980) studied all the animals inhabiting the coral heads quantitatively. However, MCCLOSKEY (1970)'s sampling stations were situated in two geographically separated areas, and the scarcity of stations within these areas does not seem to adequately represent each area. In the case of AUSTIN et al. (1980), stations were concentrated in a smaller area than those of MCCLOSKEY (1970), but only four stations were sampled, and these do not seem to be sufficient to cover all the major habitats of the studied area. Moreover, these works dealt with the animal communities associated with only one particular species of coral, and thus on this point, they are not

considered to be very different from other au-
tecological studies. In contrast, in the present
study, we took a synecological approach. Various
coral species were classified categorically into
four morphological forms, and on the basis of
such classification, we attempted to clarify the
relationships between these coral forms and the
associated animal communities within a small
inlet of an island in the southernmost part of
the Japanese islands, as a case study of the
synecology of coral-associated communities in a
"physiographic unit" of the regional ecosystem
of tropical coastal waters (HORIKOSHI, 1979;
HORIKOSHI, MS).

There are some serious difficulties in the
ecological investigation of coral-associated ani-
mals. One of the problems is that the habitat
on or in which the animals are living is a hard
substratum, and for the quantitative sampling
of this kind of substratum no adequate gear
has hitherto been devised. Another difficulty,
which is more important, is caused by the
various three dimensional morphological forms
of corals which offer different micro-environ-
ments for the animals. For example, BRANDER
et al. (1971) found that the compositions of
coral-associated animals were different in different
coral genera, such as Acropora, Pocillopora
and Leptoseris, HUTCHINGS and WEATE (1977)
pointed to the importance of the shape of dead
coral as a micro-environment for polychaete
assemblages, and MACGEACHY (1977) also
emphasized the importance of the growth form
of coral in the regulation of the distribution of
sponges. Classification of the growth form of
corals has previously been attempted by some
authors (ROSEN, 1971; MORTON, 1974). How-
ever, their schemes of classification were not
satisfactory because they compared the growth
form of corals only on an intrageneric basis,
and then only subjectively. To overcome this
problem, classification in the present study was
based upon an objective numerical index. On
the basis of this index, it became possible to
classify the growth form of corals into four
major forms.

Field studies were carried out in Kabira Cove,
which is a small inlet on Ishigaki Island, in the
Yaéyama Group, located at the southernmost
part of the Japanese islands near Taiwan. This
inlet is an ideal place to carry out a field survey

of the ecology of coral-associated animals, not
only because the coral reef in this region is one
of the most luxuriant in Japanese waters, but
also because a special project involving an in-
tensive interdisciplinary survey of the tropical
coastal water ecosystem has been carried out
in this cove (HORIKOSHI, 1979; MS), and various
and extensive information on the ecological
distribution of numerous kinds of organisms as
well as data on various physico-chemical en-
vironmental factors have already been obtained
from this study area.

As mentioned above, previous studies that
compared coral-associated animal communities
between different sampling sites were not ex-
tensive and the locations of the established
stations do not seem to be very representative
of the habitat or habitats within the area studied
(BRANDER et al., 1971; MCCLOSKEY, 1970).
In the present locality, Kabira Cove, however,
several habitats with broadly different environ-
mental characteristics were clearly recognized
from the results of the studies carried out by
the other members of the special project men-
tioned above.   Therefore, it was possible to
choose the positions of the stations so as to
represent these habitats adequately, and it was
thus possible to make a comprehensive study
on the distribution of coral-associated animals
throughout the Kabira area.

2.   Study area
2.1.   General description of Kabira Cove
Kabira Cove is a small bay situated near the
northwestern corner of Ishigaki Island. The
cove opens northwards towards the open sea,
but the bay mouth is blocked by several islets,
Koshima, Majajima and some others (Fig. 1).
The main part of the cove landward of these
islets is 1.5 km in length and 0.5-1.0 km wide.
A fringing reef ca. 500-m wide is developed out-
side the bay.   On the west side of the bay
mouth, a narrow channel connects the inner
bay with the open sea.   Within the inner bay,
there is a wide expanse of tidal flat, while the
main basin of the inner bay is rather narrowly
restricted.   The gentle inclination of the tidal
flat continues into the subtidal zone to a depth
of about 2 m, at which depth the bottom in-
clination suddenly becomes precipitous and the
topography is shoulder-like.

The main course of the channel extends out into the outer fringing reef, while in its innermost part, where it connects to the main basin, there is a terminal, vestibule-like broadening which leads to the main basin and which has environmental characteristics intermediate between those of the channel and those of the main basin. The main basin is divided into two parts, the outer and inner halves, by a topographical constriction in the middle of the bay. From these topographic characteristics, three major habitats, outer reef, channel, and inner bay were recognized, and in addition, the latter two major habitats were subdivided into outer and inner halves.

The outer margin of the outer reef has no sediment cover and is made of reef rock. In the outer part of the channel, the bottom sediment is coral gravel with "algal-foram skeletal sand" (nomenclature of the bottom sediments after KONISHI, MS: in HORIKOSHI, 1979, Fig. 4. 34) and some exposures of reef rock can also be seen, while in the inner part of the channel, the sediment consists mainly of sandy materials (algal-foram skeletal sand). Within the inner bay, a clear distinction in the distribution of some sediment types is seen between the east and west sides. On the west side, the distribution of "algal-foram skeletal sand", which is brought into the bay from the outer reef area where it is produced, is restricted to the confines of the channel area, and "terrigenous-" and "mollusc-coral skeletal sands" are widely distributed along the west side as well as in the bay head. In contrast, the "algal-foram skeletal sand" is distributed along the entire length of the east-coast shore. This clear distinction between the east and west sides suggests that the small channel on the east side of Koshima conveys both sediment and seawater of the outer reef into the bay through this channel towards the bay head much further along the east side than on the west side.

The tidal range is quite large, with a maximum spring tidal range of around 200 cm. As a result, during spring tides currents of more than 2 knots occur in the western main channel, though they drop to less than 0.2 knots within the main basin. The distance of tidal excursion is 1.5-2.0 km which corresponds to the distance from the outer end of the channel on the periphery of the outer reef to the outermost part of the main basin of the inner bay (MAZDA, MS). It is thus natural to find that the channel is more strongly affected by the waters of the open sea than the main basin, both physico-chemically and biologically.

Unlike the subaereal climate of the Yaéyama region which is recognized to be subtropical, the submarine climate outside the bay is tropical since it is influenced by the warm Kuroshio current. The water temperature in the outer reef is 22-23°C even in midwinter and never falls below 20°C, however it drops to 17-18°C and even to 16°C at the bay head during winter (MURAKOSHI et al., 1978; KITANO, MS: in HORIKOSHI, 1979, Fig. 4. 30). In addition, very low temperatures as low as 13°C have at times been observed on the tidal flat in severe cold weather (NISHIHIRA, MS). Therefore, the present locality is somewhat different climatically from any other localities in equatorial regions.

2.2. *Sampling sites and coral associations*

Ten sampling stations were established from the outer margin of the outer reef (fringing reef) to the bay head so as to represent each part of the five habitats described above (Fig. 1).

Stns. CA-1 and 2 are situated at the margin of the outer reef, facing to the open sea. Stn. CA-1 is located at the tip of a spur in the outermost part of the spur-groove system at a depth of 12 m, while Stn. CA-2 is located at the head of a groove in the inner margin of this system, at a depth of 5 m. In these stations, stout, branching corals especially some *Acropora* species like *A. pectinata* (BROOK) and *A. humilis* (DANA) grow luxuriantly on reef rocks.

Three stations (Stns. CA-3~5) were established in the channel. Among them, Stns. CA-3 (5 m) and 4 (3 m) are located along the outermost part of the main channel. The coral fauna here is dominated by staghorn corals of *Acropora hebes* type, and *Porites australiensis* VAUGHAN is also characteristic of this locality. At these stations, corals grow not only on reef rocks but also on sandy sediment and can be called "loose-lying corals" (MORTON and CHALLIS, 1969). Some branching species of *Montipora* are also found at Stn. CA-4. In the inner part of the channel (Stn. CA-5 (4 m)), the coral stand is slightly different. *Acropora hebes* type is still
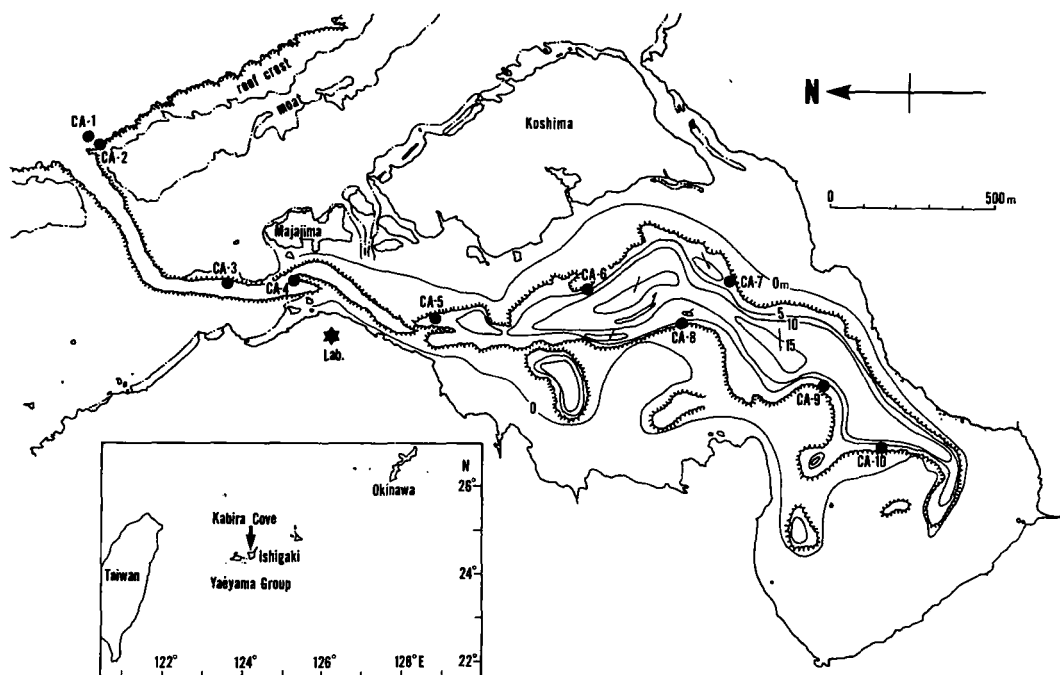
Fig. 1. Submarine topography of Kabira Cove with the location of stations. Contour interval is 5 m.

the most dominant coral, but *Pavona decussata* DANA and some branching *Montipora* are found alongside with the dominant staghorn corals.

Most of the corals found in the inner bay are of "loose-lying" type growing on sandy sediments, and the coral rocks found here, if any, are only coalescens of dead coral heads, 2~3 m in size, and never form extensive rock as in the outer reef. As indicated earlier the outer and inner halves of the main body of the inner bay differ somewhat in both biota and environmental conditions. Moreover, in the outer half of the main basin (Stns. CA-6~8), species composition of the coral stand differs between the east and west sides. On the east side (Stns. CA-6 and 7), *Acropora* species such as *A. hyacinthus* (DANA) and *A. delicatula* (BROOK), but not *A. hebes* type, dominate in association with *Pavona decussata* and branching *Montipora*. A belt of *A. striata* VERRILL is found in deeper waters at Stn. CA-7 (4 m), although this species is not common at Stn. CA-6 (3 m). On the west side (Stn. CA-8 (3 m)), however, *Porites lobata* DANA and *P. lutea* MILNE-EDWARDS et HAIME are dominant together with *Fungia paumotensis* STUTCHBURY rather than *Acropora* species.

In the inner half on the main basin, *Porites*

lobata, P. lutea together with *Cyphastrea serailia* (FORSKÅL) are dominant both at Stn. CA-9 (2 m) and Stn. CA-10 (3 m). *Cyphastrea chalcidicum* (FORSKÅL) was found only at the latter station in the present sampling series.

3. Materials and methods
3.1. Sampling and sample treatment

Ninety living coral head samples were collected during August 18-27, 1977 at 10 stations from the outer reef to the bay head (Stns. CA-1~ 10). Fifty-nine additional samples were also collected during April 3-13, 1978, in the same locality. All coral heads were collected by SCUBA diving. After wrapping a large polyethylene bag around a coral head, only the living part of the head was pried up from the substratum with a hammer and chisel. Then the bag was closed with a piece of thin wire, hauled up on board a boat, and kept in the bag separately in a water-filled plastic container.

In the laboratory, each coral head sample was divided into two unequal parts: the larger part for the collection of coral-associated animals and the smaller part for the determination of the "growth from index" discussed later. After weighing to the nearest gram on a platform

scale, the larger part was broken carefully with a hammer into small fragments less than 0.5 cm in size. During this process, all readily visible animals were removed and their mode of living was recorded. These coral chips were then washed with seawater from a tap through a sieve of 1.0 mm mesh, fixed and preserved with 10% neutralized formalin. The samples were sorted under a stereoscopic binocular microscope and all coral-associated animals were classified, counted, and weighed (wet formalin weight).

Only a particular size class of animals was considered here, the so-called "smaller macrobenthos" which is larger than 1 mm and lighter than 1 g (HORIKOSHI, 1970, 1977; HORIKOSHI et al., 1977), in order to avoid bias in the gravimetrical composition due to the occasional occurrence of single large specimens.

The remaining smaller part of each coral head was used to measure the surface area of the coral as described in the next section. After measurement of the surface area, the corals were bleached with sodium hypochloride for identification of the coral species.

3.2. Classification of growth form of corals based upon "Growth Form Index"

As mentioned earlier the growth form of corals is known to be one of the most important factors which regulates the distribution of coral-associated animals. But hitherto proposed classifications of the growth form of corals dealt with only intrageneric comparisons. To classify the growth form of corals in more general morphological terms as well as intergenerically, it is desirable to devise a proper index which indicates the degree of branching of the coral objectively.

The degree of complexity of coral growth form can be expressed as a relation between the surface area of the coral and its volume. Although ideally the volume should be measured precisely, this is not so easy to do in practice. On the other hand, a comparatively high level of precision can be obtained in the measurement of wet weight, rather easily. Therefore, in the present study, wet weight of coral was measured as well as volume of all the coral heads (90 in total). These two parameters, wet weight and volume, were found to be so closely correlated that the correlation coefficient between them was highly significant ($r = 0.96$, $p < 0.001$). From this, wet weight was considered to be a practically acceptable parameter equivalent to volume, and thus we can obtain a formula denoting the degree of branching, "growth form index", as follows:

$$\text{Growth Form Index} = \frac{\text{Coral Surface Area}}{(\text{Coral Wet Weight})^{2/3}}$$

The "growth form index" has two characteristics: (1) If the growth forms of two different corals are geometrically similar, the indices are independent of the mass (weight) of these corals and have similar values. (2) For two corals of the same mass, the index of a coral bearing slimmer branches has a higher value.

This can be shown schematically as follows: if we compare a cube of side 1 cm with a cube of side 2 cm, their growth form indices are identical having the same value of 6, when the densities of both are the same, e.g. 1 g cm^{-3}. On the other hand, if we compare the cube of side 1 cm with two equal halves of the same cube, the growth form index of the latter has a larger value of 8 (Fig. 2). Because of these two characteristics, one can easily see that indices of massive corals will be smaller than those of branching corals, and also that indices of corals with thicker branches are smaller than those with thinner branches.
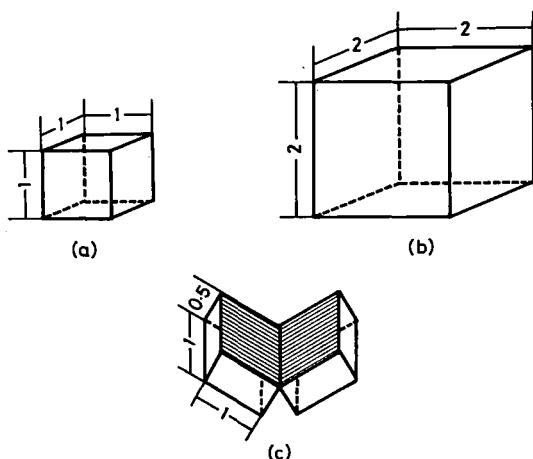

Fig. 2. Schematic figure illustrating the nature of the "growth form index". The indices of (a) and (b) are independent of their masses and both have a value of 6, while the index of (c) has a value of 8 in spite of having the same mass as (a).

As a simple and practical method for the measurement of the surface area of the coral, aluminium foil was used instead of latex for covering the surface. After weighing wet weight of the coral head to the nearest gram on a platform scale and measuring its displacement volume with a volumetric cylinder, all surfaces of the coral head which had been in contact with seawater during life were covered carefully with a monolayer of aluminium foil. The weight of the aluminium foil was weighed to the nearest tenth of milligram on a direct reading balance (Shimazu: Model NL-TPA). The surface area of the coral was calculated by dividing the total weight of aluminium foil by that of unit area $(4.461 \pm 0.007\,\mathrm{mg\,cm^{-2}})$. For finely branching corals, an even smaller subsample was used to economize on time of foil covering.

The growth form indices of two sets of living coral heads, i.e. 90 and 59 specimens collected in summer, 1977 and in early spring, 1978 respectively, were arranged in the form of cumulative frequency curves (Fig. 3). Although these two sets of corals were collected randomly and separately, their curves are divisible into four groups with the same range of growth form index by step-like breaks that occur in both curves at common values.

The groups are named Forms I to IV in order of increasing magnitude of growth form index. The range of indices for Forms I to IV are <7.4, $7.5 \sim 10.4$, $10.5 \sim 20.0$, and >20.1 respectively. Form I includes the so-called massive forms such as most of the faviids and massive *Porites*, Form II includes shapes with thick branches or thick brackets (irregular shaped) such as *Acropora humilis*, *Porites andrewsi* VAUGHAN, and *Pavona decussata*, Form III includes ordinary branching types such as *Acropora rosaria* (DANA) and *Montipora digitata* (DANA), and Form IV includes highly branching and/or slender types such as *Acropora echinata* (DANA), *Pocillopora damicornis cespitosa* (DANA) and *Seriatopora caliendrum* EHRENBERG (Table 1). This classification corresponds well with the subjective classifications by previous authors mentioned above, and it is quite possible to classify any corals categorically into these four "major forms" objectively, on the basis of the newly devised growth form index proposed here.
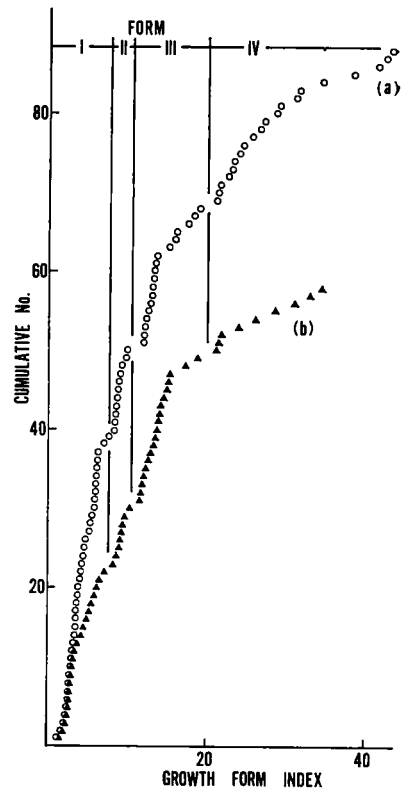

Fig. 3. Cumulative frequency curves of the growth form indices of two sets of corals, i.e. 90 specimens collected in summer, 1977 (a), and 56 specimens collected in early spring, 1978 (b). Note the presence of three step-like breaks in both curves at common values of growth form index. These breaks allow recognition of four major morphological types (Forms I~IV) of coral.

3.3. Classification of coral-associated animals according to their life form

To investigate the ecology of the coral-associated animals, it is important to classify the animals into life form groups (PREOBRAZHENSKY, 1977). The classification of marine organisms according to life form was first proposed by PETERSEN (1913: p. 11; 1914) who distinguished "epifauna" from "infauna". GISLEN (1930: pp. 75-84; 1931) added one more type calling it "hypobiose", in addition to "epibiose" and "endobiose". Both schemes are based only on the different situations occupied by organisms. Utinomi (1950) proposed to subdivide these three groups into nine subgroups according to the tolerance of exposure of intertidal animals. MORTON and CHALLIS (1969) proposed six life

Table 1. List of coral genera belonging to the four major growth form types classified according to their growth form index.

Form	Range	Genera	No. of spp.	No. of samples
I (massive)	<7.4	*Goniastrea*	5	7
		Porites (massive)	4	13
		Cyphastrea	4	8
		Platygyra	3	4
		Montipora (massive)	3	4
		Favia	2	4
		Favites	2	4
		Millepora	2	2
		Galaxea	1	3
		Mycedium	1	2
		Pavona (massive)	1	1
		Hydnophora (massive)	1	1
		Euphyllia	1	1
		Astreopora	1	1
		Echinopora	1	1
		Symphyllia	1	1
II (irregular shaped)	7.5–10.4	*Acropora*	4	4
		Porites (thickly branching)	2	6
		Montipora (thickly branching)	2	3
		Pavona (thick plate)	1	5
		Pachyseris	1	1
III (branching)	10.5–20.0	*Acropora*	9	16
		Montipora (slenderly branching)	8	19
		Porites (irregularly branching)	4	7
		Pavona (thin plate)	2	2
		Pocillopora	1	4
IV (highly branching)	20.1<	*Acropora*	12	16
		Montipora (slenderly branching)	2	6
		Pocillopora	1	2
		Seriatopora	1	1

forms, "peri-", "para-", "epi-", "hypo-" "endo-", and "crypto-bions", for the coral-associated animals. However, their definition of these terms seems to be in some cases too narrow while in other cases too broad. Their term "epibion" was narrowed from the original sense of PETERSEN (1913, 1914) and GISLEN (1930, 1931), by restricting the terms to only immobile organisms "attached or growing on surfaces recently dead", while within "crypto-bion" they had only suggested the presence of two types, pioneer and secondary species, without incorporating them into their scheme of classification. But the presence or absence of active boring ability is of great importance to the ecology of coral-associated animals.

Therefore, in the present paper, the following terminology is proposed: free-living epi-, sessile epi-, boring crypto-, and secondary cryptobionts. The free-living epibiont refers to those animals which exist on the surface of the substratum and which are actively mobile.   The main members of this life from are crustaceans, especially anomuran crabs like *Porcellana* sp. and brachyuran crabs such as *Tetralia glaberrima* (HERBST), and several species of *Trapezia* and *Cymo*.   In addition, some gastropods, chitons, ophiuroids, echinoids, and turbellarians also belong to the free-living epibionts.

The animals which live on the surface of the coral but are not actively mobile and/or attach permanently or semipermanently are termed sessile epibionts. Bivalves are the main members of this life form. Among these bivalves, *Electroma ovata* (QUOY et GAIMARD), *E. japonica* (DUNKER), *Chlamys (Coralichlamys) madre-*

porarum (SOWERBY) tend to be attached to branching corals.

The cryptobionts are those animals which live within the coral skeleton and cannot be collected unless the coral skeleton is broken down into fragments. Among cryptobionts, the boring cryptobionts have the ability to bore the coral skeleton actively. A date mussel, *Lithophaga laevigata* (QUOY et GAIMARD) [for type specimen, taxonomy and ecology of this species confer KLEEMANN, 1980], is the dominant member of this life form in Kabira Cove. A boring bivalve, *Gastrochaena* [syn. *Rocellaria*] *cuneiformis* (SPENGLER), eunicid polychaetes, acrothoracican cirripeds, sipunculoids such as *Cloeosiphon aspergillum* (QUATREFAGES) and several *Aspidosiphon* species also belong to this group.

The secondary cryptobionts are those animals which, like boring cryptobionts, live within the coral skeleton but do not have any ability to bore actively. This category includes two groups. One group of species are mobile and utilize natural interstice and/or biogenic crevices or holes in the coral skeleton. The other species are immobile and are covered and buried passively in the coral skeleton by coral growth. The representative species of the former group are polychaetes, snapping shrimps (*Alpheus* spp.) and small gastropods, while barnacles such as *Savignium elongatum* HIRO and some polychaete species such as *Spirobranchus giganteus* (PALLAS) belong to the latter group.

4. Results

4.1. Composition of coral-associated fauna

When individual coral heads were examined (Fig. 4), it can be seen that particular life forms of coral-associated animals are associated with particular types of coral growth form and the proportion of the four life forms in terms of biomass showed some consistent patterns throughout almost all the stations (Fig. 4 (a)). Generally speaking, the heads of massive corals (Form I) were dominated by cryptobionts, especially borers, while branching (Form III) and highly branching (Form IV) corals were dominated by free-living epibionts. Such a distinct pattern in micro-distribution of coral-associated animals was recognized at every station, except in the outer part of the channel (Stns. CA-3 and 4) where sessile epibionts predominated even on

the massive corals. The characteristics of the animal community associated with the irregular shaped corals (Form II) were not clear. In this type of coral, both epi- and cryptobionts were found in nearly equal proportions in a single head at some stations. On the other hand, at some other stations, a single coral head was dominated by either one of these two life forms and such coral heads coexisted at one and the same station.

The composition of the numerical population (Fig. 4 (b)) showed similar basic patterns of micro-distribution of coral-associated animals as those of biomass. However, secondary cryptobionts constitute a higher proportion of the population than in the case of biomass, not only in the massive corals but also in the other types of corals at all stations. This is because the greater part of the members of this life form consists of the polychaetes. The average size of this group of animals is small, and hence much lighter in weight, in comparison to the size and weight of animals of other life forms.

From these results, it is clear that the morphological type or the growth form of corals is an important factor in determining the micro-distribution of coral-associated animals at each station. Therefore, it does not seem unreasonable to compare coral-associated faunules inhabiting a single type of coral amongst the different habitats of Kabira Cove, even if they do not necessarily belong to the same coral species.

The compositions of coral-associated animals were examined for each form of coral (i.e. grouping data for coral heads of the same form) (Fig. 5). It was found that, for biomass, a certain life form predominated on each form of coral either within a given major habitat or habitat (Fig 5 (a)). In the case of massive corals (Form I), boring and/or secondary type cryptobionts predominated everywhere except in the outer part of the channel (Stns. 3 and 4). Among these cryptobionts, the boring type dominated only in the inner half of the main basin. On irregular shaped corals (Form II) either cryptobionts or epibionts tend to become dominant in different major habitats. Cryptobionts tend to predominate in the main basin of the inner bay, while epibionts tend to dominate in the other major habitats. In the case

(a)

(b)

⊠ Boring Cryptobiont ▨ Secondary Cryptobiont ▦ Sessile Epibiont ☐ Free-living Epibiont
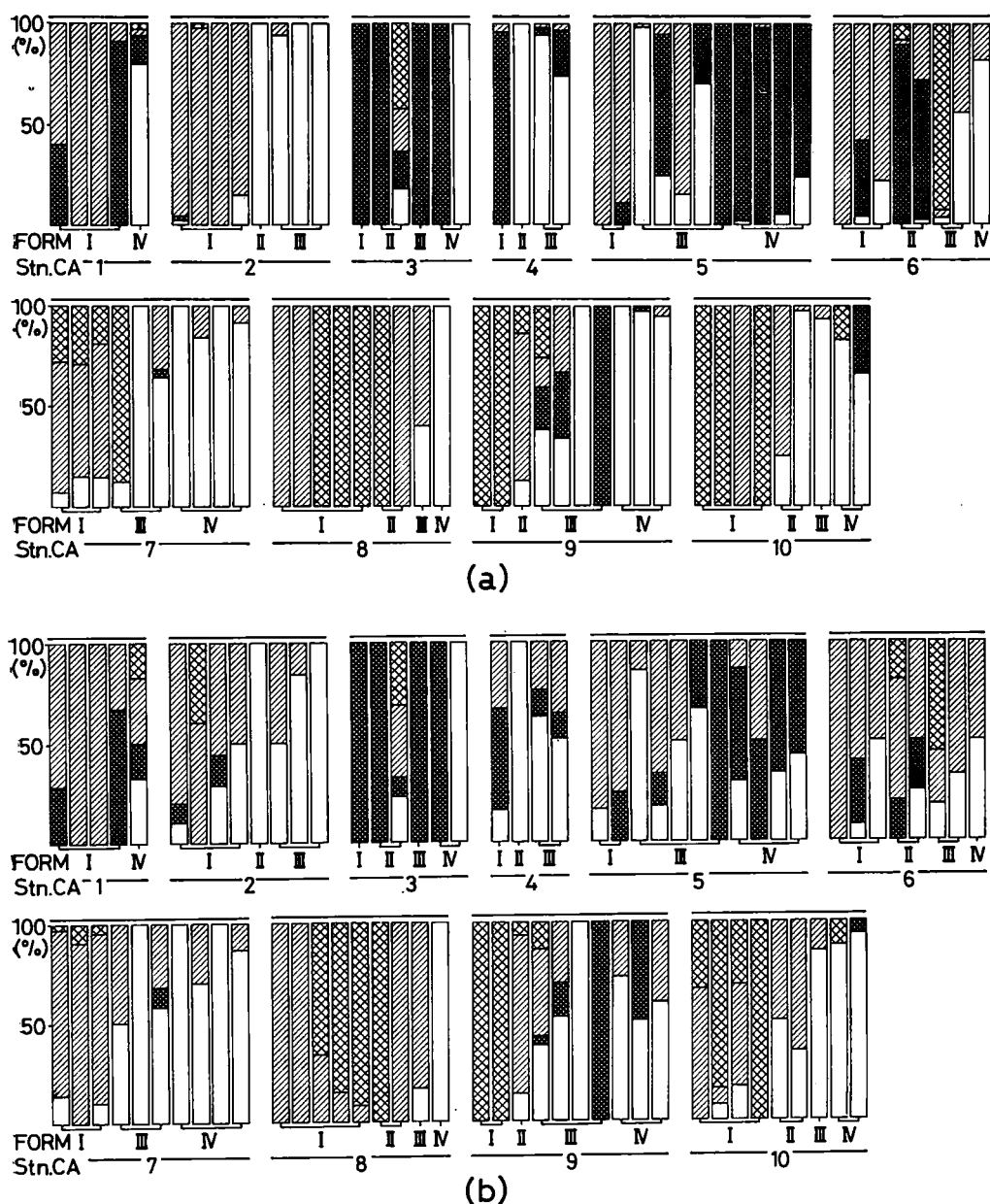
Fig. 4. The compositions (%) of biomass (a) and of numerical population (b) of coral-associated
    animals in *individual* coral heads for the four different forms of coral (Form I: massive;
    II: irregular shaped; III: branching; IV: highly branching) at each station.

of branching (Form III) and highly branching
(Form IV) corals, epibionts were dominant
throughout the Kabira area. However, a slight
difference was found between these two growth
forms in that both sessile and free-living epi-
bionts were conspicuous throughout the Kabira

area on Form III corals, while on Form IV
corals, the sessile type predominated only in
the channel and in the other habitats the free-
living type predominated.

Among the stations in the outer half of the
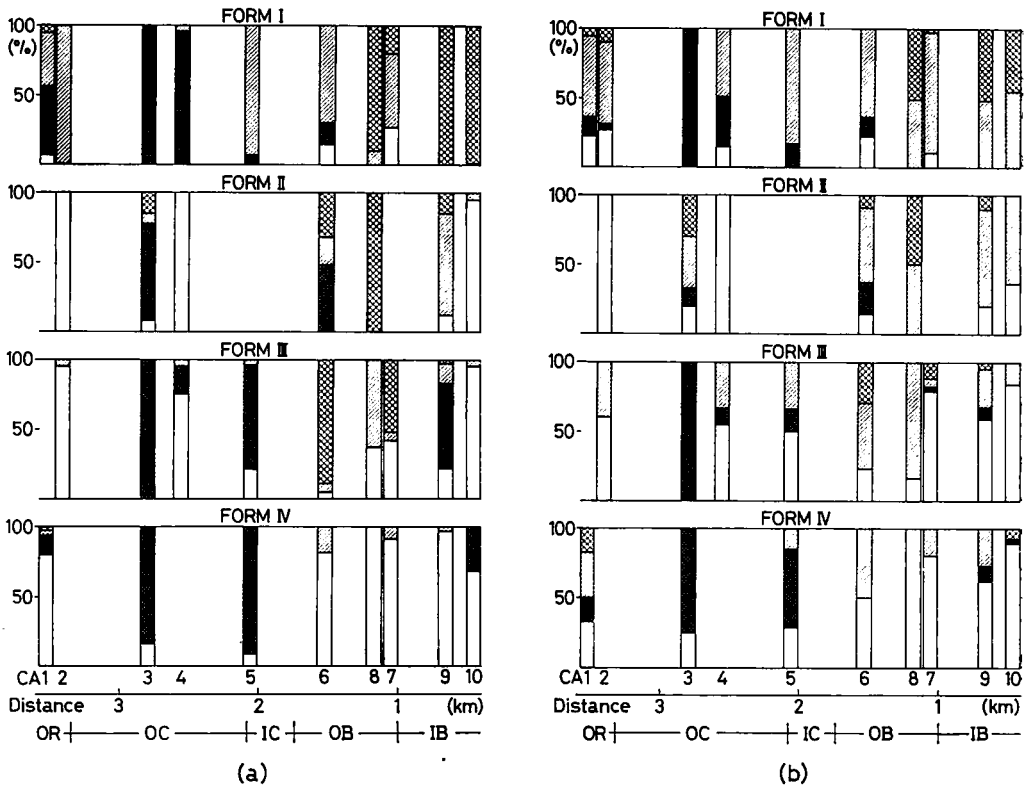main basin (Stns. CA-6~8), Stn. CA-8 had a

Fig. 5. The compositions of coral-associated animal communities in terms of percentage of the mean biomass (a) and of mean numerical population (b) within the four different forms of coral (i.e. *grouping data* for individual coral heads of same form) (Form I: massive; II: irregular shaped; III: branching; IV: highly branching) at each station. The ranges of the five major habitats are indicated; OR: outer reef; OC: outer half of the channel; IC: inner half of the channel; OB: outer half of the main basin; IB: inner half of the main basin.

peculiar composition of coral-associated fauna. Although this station was situated slightly nearer to the bay mouth than Stn. CA-7, the composition was unlike those at the other stations in this habitat, but was rather similar to those in the inner half of the main basin (Stns. CA-9 and 10). In the case of massive (Form I) corals, for example, the boring type of cryptobiont, which was conspicuous in the inner half of the main basin, was dominant at Stn. CA-8 rather than secondary cryptobionts, and secondary cryptobionts and free-living epibionts coexisted in branching (Form III) corals.

In the composition of numerical population, the basic distribution patterns of the four life forms of coral-associated animals (Fig. 5 (b)) were, generally speaking, similar to those of biomass. However, the secondary type of cryptobionts are more conspicuous than in the case

of biomass which is due to the reason given previously, namely the smaller average body size of polychaetes results in an increase in the population number of animal of this life form.

4.2. *Distribution of biomass and numerical population*

The total biomass (wet weight per kg coral) of all animals associated with a single form of coral varies between different habitats (Fig. 6(a)). In the case of massive coral (Form I), a large peak in total biomass was found in the inner half of the main basin, while such a prominent peak of biomass could not be seen in either irregular shaped (Form II) or ordinary branching (Form III) corals. There were two distinct peaks in the case of highly branching (Form IV) corals: a large one within the channel and a smaller one in the inner half of the main basin.

The greater part of the total biomass was shared by molluscs and crustaceans throughout the Kabira area. Among molluscs, boring crypto-bionts predominated in the massive corals, while sessile epibionts dominated in the highly branching corals. The former type consisted exclusively
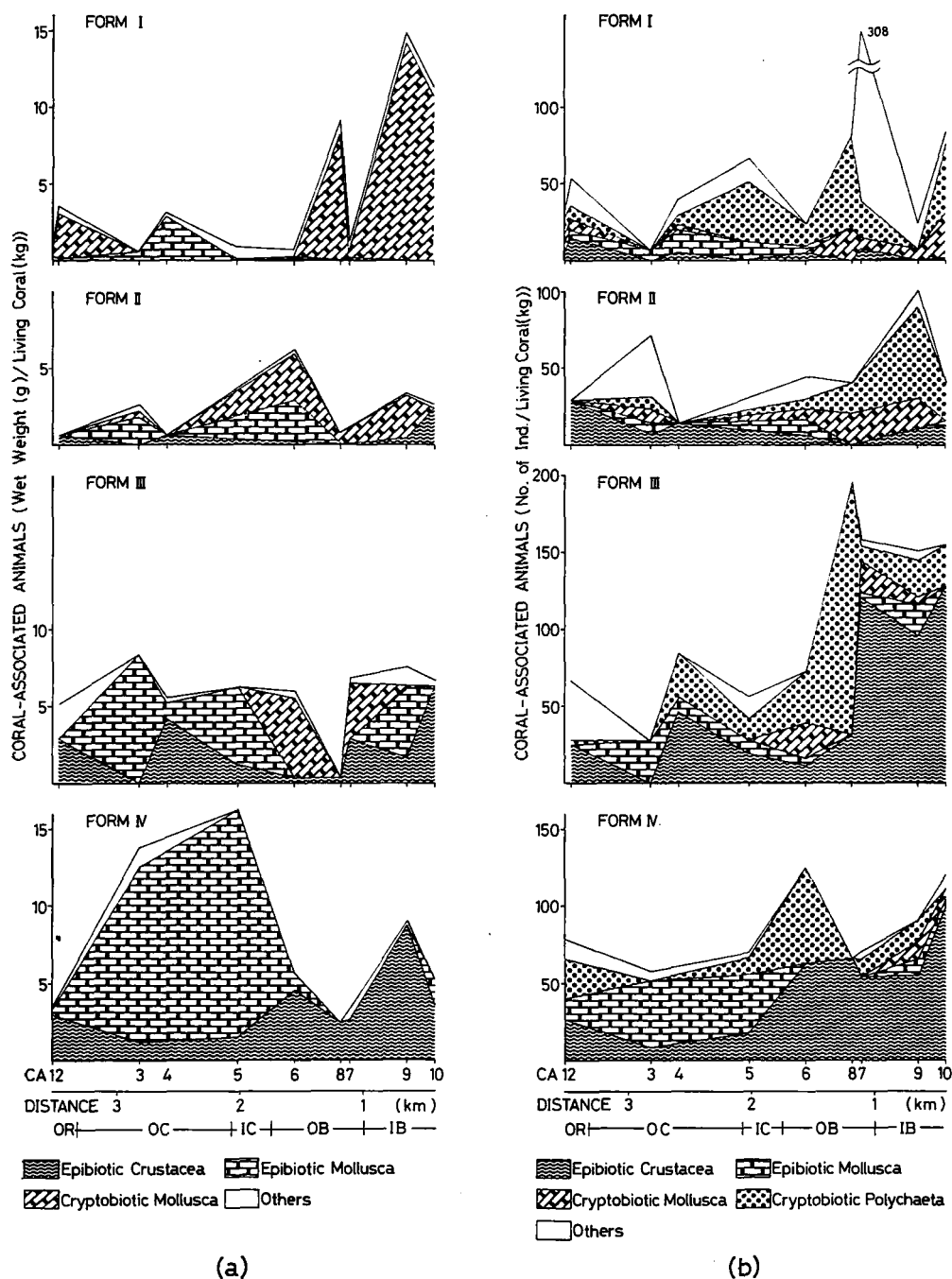

Fig. 6. The mean biomass (a) and mean numerical population (b) of several groups of coral-associated animals within the four different forms of coral (i.e. *grouping data* for individual coral heads of same form) (Form I: massive; II: irregular shaped; III: branching; IV: highly branching) at each station.

of *Lithophaga laevigata*, while commonest species of the latter type were *Electroma ovata*, *E. japonica* and *Chlamys* (*Coralichlamys*) *madreporarum*. Among crustaceans, only free-living epibionts were conspicuous particularly on the highly branching corals. One of the two representative members of these crustaceans, a brachyuran crab, *Tetralia glaberrima*, was widely spread both within and outside the bay, while the other, an anomuran crab, *Porcellana* sp., was distributed almost exclusively within the bay.

Although the general trends of distribution of the numerical population on the large scale were essentially similar to those of biomass, the numerical population of molluscs was less conspicuous while that of crustaceans was more noticeable than in the case of biomass (Fig. 6(b)). This is related to the difference in average body size of these two animal groups. Polychaetes, which were not noticeable in the case of biomass, were present in large numbers at many stations in every form of coral.

5. Discussion

Despite the importance of classification of morphological types of corals in the study of coral-associated animals, previously suggested classifications (MORTON, 1974; ROSEN, 1971) have been, as indicated before, unsatisfactory because they are rather subjective and are only applicable at the intrageneric level. In the present study, it was clearly demonstrated that, using a newly devised "growth form index", objective classification of many corals belonging to many different genera (i.e., intergeneric classification) was accomplished. All the corals collected from the present locality were classified very clearly into four major morphological types. In addition to this, several pertinent categories of mode of life of coral-associated animals were recognized. Recognition of life form is a prerequisit for the synecological investigation of these animals to avoid difficulties caused by the bewildering richness of coral reef fauna (THORSON, 1957: pp. 463–466; HESSE *et al.*, 1951: pp. 328–330). In the classification of coral-associated animals proposed by MORTON and CHALLIS (1969), only a mere suggestion of the distinction between pioneer and secondary species within the "cryptobion" of their definition can

be found. But the different ecological characteristics of these two types were clearly demonstrated in the present study in that the boring type of cryptobiont was conspicuous only within the coral heads of massive form (Form I) within the inner bay (Stns. CA-7~10), while cryptobionts of secondary type were found indiscriminately on all forms of corals throughout the Kabira area.

The degree of association between coral-associated animals and corals differ even within the same life form. Among secondary cryptobionts, for example, the degree of association ranges from a permanent one, such as between *Millepora* and barnacles, to an opportunistic one, such as between any species of coral and polychaetes. Nevertheless, a consistent pattern of association between the growth form of the coral and the life form of coral-associated animals was suggested from the result of the present synecological study, and it is clearly demonstrated that the growth form of the coral is very effective in controlling the micro-distribution of coral-associated animals.

The importance of the physical environment, such as water movement and/or light, in the regulation of the distribution of tropical shallow water fauna was previously reported for some animals, e.g. ophiuroids (KISSLING and TAILOR, 1977) and sponges (VACELET and VASSEUR, 1977). In the case of coral-associated animal communities, the present finding that the dominant life form changed from habitat to habitat in the community associated with a single morphological type of coral suggests the importance and even priority of the physical environment over the coral growth form in controlling the distribution of these animals. The peculiar case of Stn. CA-8, in the outer half of the main basin of the inner bay, clearly illustrates the importance of the physical environment. Although Stn. CA-8 is nearly the same distance or even slightly nearer to the bay mouth than CA-7, the composition of coral-associated animals at the former station is quite unlike that of the latter (Stn. CA-7) which lies in the outer half of the main basin but is rather similar to those in the inner half of the same major habitat (Stns. CA-9 and 10). In particular in the case of massive corals (Form I), a species of boring cryptobiotic mollusc, *Lithophaga laevigata*,

which predominates in the inner part of the main basin, is also exclusively dominant at this particular station in the outer part of the main basin. As mentioned in the section on the general description of the Kabira area, there is a clear difference in the physical environment between east and west sides within this habitat, which is demonstrated especially by the distribution of sediment type. Along the east side (Stn. CA-7), a belt of algal-foram skeletal sand is found, which is considered to be transported from the outer fringing reef through the minor channel situated on the east side of Koshima, while terrigenous- and mollusc-coral skeletal sands, which are typical in the inner half of the inner bay, are the characteristic sediment types on the west side (Stn.CA-8). This distribution pattern of sediment is closely related to that of coral-associated animals and this relationship suggests the importance of the physical environment in regulating the distribution of these animals.

A more obvious example was found in the outer half of the channel, especially at Stn. CA-3, where only sessile epibionts were dominant or at least conspicuous on every form of coral, even on massive coral head. A tidal current always flows through this habitat, and the velocity of the current at times becomes very high, up to 2 knots at spring tide, this unusually vigorous water movement is thought to be responsible for this rather exceptional coral-associated community. Such water movement might prevent larvae and juveniles of cryptobionts from settling and/or boring into the coral skeleton, and the current may also prevent free-living epibionts from settling and living on the coral surface. Although the settling mechanism of sessile epibiotic molluscs still needs to be studied, we suspect that once they are attached by their byssus, they should be able to remain stable in the presence of high velocity currents.

In addition to the growth form of corals, there seems to be some other important micro-environmental factors for coral-associated animals, e.g. hardness of coral skeleton, shape and size of the single coral polyp, living or dead state of the coral head etc. These matters and several other ecological problems such as the effects of season and the ecological difference

amongst coral-associated animal species belonging to the same life form will be described and discussed in more detail in a subsequent paper.

6. Acknowledgement

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珊瑚成長形の新たな分類法とその石垣島川平湾における珊瑚付随性動物の調査への適用

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要旨: 珊瑚成長形の数量的な類型化のために，珊瑚表面積/(珊瑚湿重量)$^{2/3}$によって示される値を"成長形指数"と定義し，これによって成長形を分類した．この指数により珊瑚の成長形は塊状型，不規則型，枝状型，細枝型の4型に分類された．珊瑚付随性動物はその生活様式から，自由表在性，固着表在性，穿孔内在性，二次内在性の4種に分類した．沖縄県八重山諸島石垣島の川平湾において，湾内外の5つの生息場所を代表する10地点から潜水により生珊瑚を採集し，珊瑚付随性動物の珊瑚成長形別の分布および地域別の分布を群集生態学的観点に立って定量的に研究した．4種の珊瑚付随性動物と4型の珊瑚成長形との間には一定の関係が見られ，塊状型では内在性種が，一方枝状型および細枝型では表在性種が優先していた．同一成長型に付随する動物の絶対数および組成に関しては湾外から湾奥へ向って変化が見られた．以上の分布様式から，珊瑚の成長形が各地点における珊瑚付随性動物の微細分布に強い影響を及ぼす一方，本地域における珊瑚付随性動物の巨視的分布は物理的環境により規制されることが明らかになった．

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