Environmental Control of Holocene Changes to the World's Most Northern Hermatypic Coral Outcrop[1]

J. E. N. VERON[2]

ABSTRACT: Tateyama, near Tokyo (35° N lat.), is the site of the world's most northern occurrence of living hermatypic corals and is also the site (in the Numa beds) of a substantial outcrop of Holocene fossil corals with a radiocarbon date of 5000–6000 yr B.P. This extraordinary co-occurrence provides the opportunity for a detailed reconstruction of environmental change during the Holocene, especially change in sea-surface temperature. The present study, combined with a series of previous studies, reveals 72 coral species in the Numa beds, of which 53 have been identified with reasonable certainty; and 34 species of extant corals at Tateyama, of which 25 have been located and identified. These data are compared with recently completed studies of the distribution of extant corals of Japan, and sea-surface temperatures of the principal regions of extant corals. Nearly one-half of all species from the Numa beds have remained extant at Tateyama until recent times, 85% are extant as far north as Kushimoto on the Kii Peninsula (33.5° N lat.), and all except two have been recorded extant somewhere in mainland Japan. There has been a major change in species dominance at Tateyama. The identified species from the Numa beds and those of the Izu Peninsula and Tateyama show a high degree of dissimilarity compared with other coral communities of mainland Japan. The closest extant fauna to the corals from the Numa beds appears to be that of Kushimoto. Based on six ways of measuring the temperature regimes of coral communities of modern mainland Japan, over the past 40 yr, this geographic comparison corresponds to a mean sea-surface temperature increase of 1.7°C. Although there are several assumptions in arriving at this number, the increase is clearly less than 2.1°C, which is the temperature difference corresponding to the substantially richer coral communities of Tanegashima at the southern tip of mainland Japan. This study shows that an increase in sea-surface temperature of <2°C, such as is widely predicted in response to the "greenhouse effect," should result in a greatly increased diversity of corals in high-latitude locations. It also shows that this temperature increase is sufficient to create a "high latitude subtropical" community in a region that appears almost devoid of corals in a fossil sequence.

THE NUMA (OR NOMA) BEDS of Tateyama (near Tokyo, Japan) (Figure 1) have long attracted the attention of Japanese geologists and geographers with a view to determining climatic changes and crustal movements that have taken place during the Holocene. This paper has the same intention, by combining a revised and updated account of the fossils of the Numa beds with data from two recently completed studies: a monograph of the hermatypic corals of Japan (Veron 1992) and a study of the correlation between sea-surface temperature and the distribution of hermatypic corals in Japan (Veron and Minchin, in press).

In a global context, there is a general lack of information about faunistic changes that take place over periods of thousands of years, compared to those that take place over ecological time scales of a few decades and those
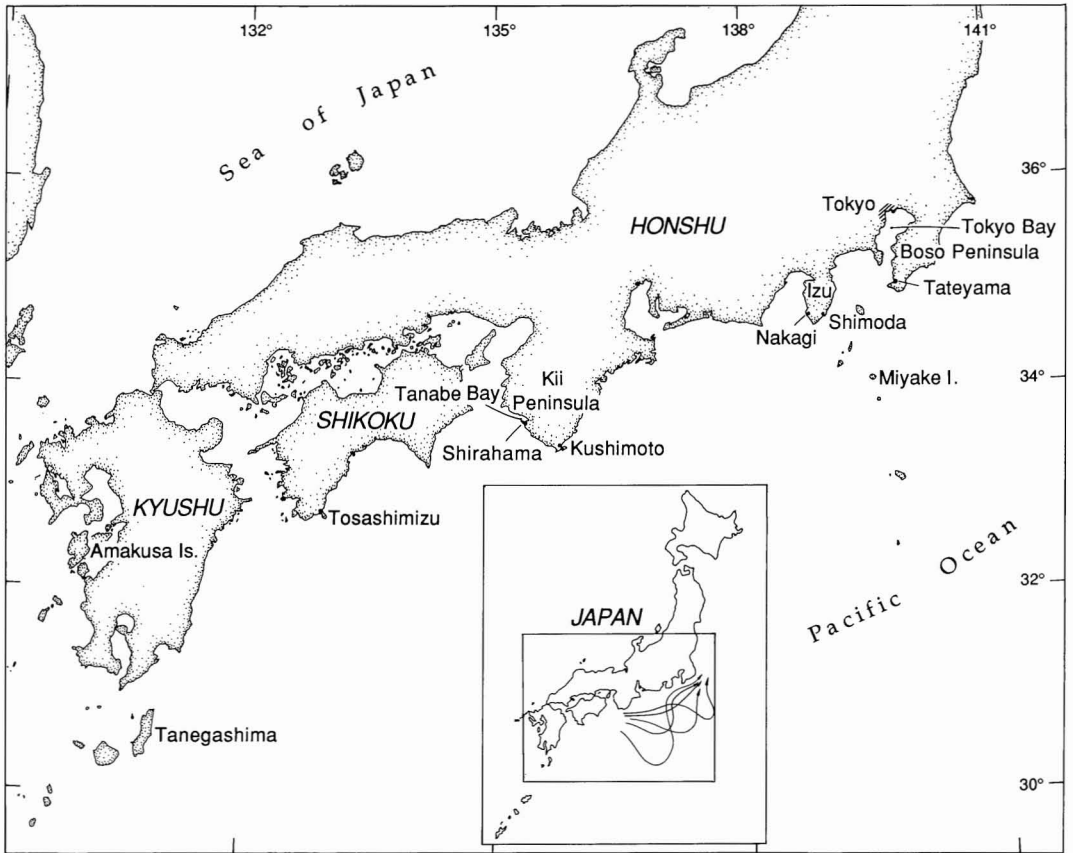

FIGURE 1. Regional place names cited in the text. Principal variations in the path of the Kuroshio Current are indicated in the key diagram.

that take place over palaeontological time scales of hundreds of thousands of years. Studies of coral fauna are no exception, and those that have been undertaken have mostly been on Caribbean corals. Within the Indo-Pacific, few reefs are raised above sea level, or are otherwise protected from wave action, to retain a fossil sequence sufficiently well preserved to allow short-term change in faunistic composition to be reliably determined.

The Numa bed fossils are important as indicators of temperature change because (a) they occur at the northernmost limit of distribution of extant hermatypic corals in Japan and (b) the diversity decrease along southeast Honshu is temperature-correlated. The Boso Peninsula is the last place of mainland Japan

under the influence of the warm Kuroshio Current, the western boundary current that is responsible for the distribution of tropical organisms to high latitudes, even to the southern shores of Honshu (Figure 1). At Tateyama, the eastern-flowing Kuroshio meets the cold southern-flowing Oyashio Current of eastern Honshu and thereafter leaves the continental shelf as the Kuroshio Extension, the Pacific counterpart of the Gulf Stream. These are major currents that are likely to have been in place since the Mesozoic (Haq and Eysinga 1987) and certainly would have been flowing throughout most of the late Cenozoic. The fossil outcrop is geographically positioned exactly at the extremes of temperature tolerance of extant corals: there are no known
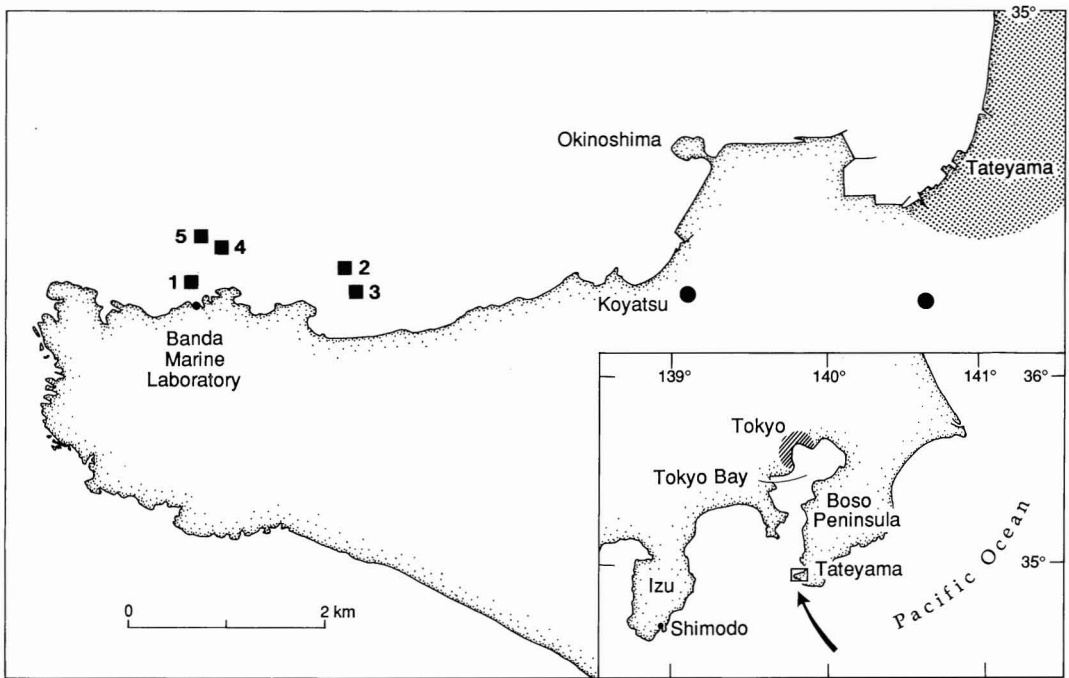
FIGURE 2. Study sites at Tateyama. Squares and circles respectively indicate sites of extant and fossil corals studied. Sites where extant corals were studied are as follows: (1) opposite Banda Marine Laboratory (9 m depth); (2) Hasama (14–18 m depth); (3) Hasama (12–15 m depth); (4) Hasama (14–18 m depth); (5) near Banda Marine Laboratory (16–22 m depth).

hermatypic corals farther north, and to the southwest diversity gradually increases as temperature increases.

Study Sites of Fossil and Extant Corals

FOSSIL CORALS OF TATEYAMA. Tateyama is the southern tip of the Boso Peninsula, which projects about 80 km into the Pacific Ocean and forms the eastern margin of Tokyo Bay (Figure 1). The region is tectonically unstable because it lies in close proximity to the triple junction between the Philippine, Pacific, and Urasian lithospheric plates. In historical times, it has been the site of several large earthquakes, two of which (in 1703 and 1923) were of magnitude 8 on the present-day Richter scale and caused considerable crustal deformation and destructive tsunamis (Matsuda et al. 1978). Both earthquakes resulted in an uplift of several meters, the former up to 6 m, and a coastal retreat of up to

800 m (Imamura 1925), producing a terrace 3–6 m high.

The area under study (Figure 2) lies in the west-coast valley area, south of Tateyama Bay, where Neogene sediments are covered by a thin (0 to 40 m) veneer of unconsolidated Holocene sediments forming four marine terraces. The surface of the highest terrace (Numa 1) is 20–25 m above sea level. ^{14}C datings of the shells and wood incorporated into the sediment indicate emergence about 5000–6000 yr B.P. (Hoshino 1967, Konishi 1967). Frydl (1982) gave a summary of the geological history of the whole Boso Peninsula.

Fossil corals have been found in at least 12 sites in the Tateyama region, but most of these have been destroyed by land development. However, two of the richest sites were visited during the present study, that with the highest diversity being ca. 500 m east of the village of Koyatsu where corals imbedded in sediment

are exposed in a small gully and irrigation drain. The second site is ca. 1 km south of the southern foreshore of Numa where corals have mostly been exposed by the construction of a pond. A group of colonies, mostly unrecognizable *Cyphastrea* spp. up to 70 cm diam., presumably unearthed during the construction of the pond, are enclosed in a municipal monument.

Records from past and present studies are summarized in the Appendix. An important historical aspect of these past studies is that they are all based on the taxonomy of Yabe and his colleagues, a taxonomy that does not reflect the intraspecific variation found in most hermatypic corals. As a result, reliable species identifications are mostly restricted to families or genera in which species are few in number or are relatively distinct. Thus, major genera that display extensive intraspecific variation (notably *Montipora*, *Acropora*, *Porites*, and *Turbinaria*) are largely identified according to the British Museum catalogues of Bernard and Brook. In contrast, other genera that were more fully studied (e.g., *Caulastrea* and *Lithophyllon*) have been given a complex of species and subspecies names that do not reflect true intraspecific variation and that belie the fact that similar variation occurs in most other hermatypic genera.

Comparing records of different studies, it is clear that there has been a substantial change in dominance at Tateyama, in terms of both numbers of colonies of major genera and numbers of species in major genera. Yabe and Sugiyama (1935a) found *Caulastrea tumida* (= *C. yokoyamai*), *Favia speciosa*, *Echinophyllia aspera* (= *Echinophyllia* sp.), and *Lithophyllon undulatum* (= *Podabacia lobata*) to be dominant species. They also recorded *Cyphastrea chalcidicum*, *Leptastrea purpurea*, and *Turbinaria frondens* (= *T. contorta* and *T. frondens*) as abundant. Frydl (1982) recorded *Echinophyllia aspera*, *Favia speciosa*, and *Favites flexuosa* (= *F. favosa*) as dominant at one site, and predominantly plating corals, *Echinophyllia aspera*, *Physophyllia aylenai*, *Pectinia lactuca*, and *Lobophyllia robusta* as dominant in another. The present study indicates that the Numa beds are characterized by the paucity of *Acropora* and

the prevalence of faviids (notably *Caulastrea tumida* and *Favia speciosa*), pectiinids (*Echinophyllia aspera* and *Oxypora lacera*), and *Stylocoeniella guentheri*. There is too much agreement between these studies for the relative abundance estimates of *Caulastrea tumida*, *Favia speciosa*, and *Echinophyllia aspera* (at both the same and different collecting stations) to be the result of chance or a sampling bias.

EXTANT CORALS OF TATEYAMA AND OTHER PRINCIPAL MAINLAND OUTCROPS. There is very little environmental diversity at Tateyama. The foreshore consists of small beaches interspersed between low rocky promontories. All intertidal and subtidal areas are likewise either sand or flat rock, mostly protected from strong wave action but with relatively turbid water. The proportion of rock substrate gradually decreases offshore. It is dominated by kelp (*Ecklonia* and *Sargassum*) at depths of ca. 10 m or less, and the coral fauna is restricted to occasional colonies of *Favia speciosa*, *Psammocora profundacella*, *Oulastrea crispata*, and *Alveopora japonica*. At greater depth, the benthos gradually becomes more diverse until, at 15 m or more, it is dominated by a wide diversity of mostly temperate fauna of sponges and coelenterates. The above-mentioned species remain the most common corals along with *Cyphastrea serailia*, *Echinophyllia aspera*, *Hydnophora exesa*, *Porites heronensis*, and *Psammocora superficialis*. Other species are recorded from one (in the case of *Blastomussa wellsi*) or a few colonies only. The highest diversity observed (collecting station 5) was at 16–18 m depth where the substratum was deformed, giving vertical and undercut surfaces. The water is much less turbid in this region than at shallower depths. There is usually a sharp temperature stratification in the water column (Y. Koike, pers. comm.).

All colonies except *Psammocora profundacella* are deeply colored relative to their tropical counterparts and none shows any observable appearance of environmental stress. Colonies of all species except *Alveopora japonica* have flattened to encrusting growth forms. *Blastomussa wellsi* is completely plo-

coid, in contrast to the phaceloid colonies of reefal environments, and even *Hydnophora exesa* is completely explanate, without any tendency to form vertical upgrowths or laminae. *Hydnophora* and *Euphyllia* have tentacles fully extended during the day. The largest colonies, 1–2 m diam., are formed by *Favia speciosa, Cyphastrea serailia, Echinopora aspera, Hydnophora exesa,* and *Psammocora superficialis.*

Previous studies of Tateyama corals were made by Yabe and Sugiyama (1935*a*), who recorded seven species; Hamada (1963*a,b*), who recorded an additional 10 species; and Eguchi and Mori (1973), who made a composite list of all records, with six to eight additions. The original specimens on which these identifications were based were not reexamined during the present study. Where the identity is doubtful, the most likely species is indicated with a "?" in Table 1. These species [listed by Hamada as *Acropora* cf. *studeri* Brook, *Favites favosa* (Ellis & Solander), *Goniastrea pectinata* (Ehrenberg), *Goniopora* sp., *Hydnophora* sp., *Montastrea curta* (Dana), *Montipora hispida* (Dana), *Platygyra phrygia* (Ellis & Solander), *Porites* sp., *Stylophora* sp., *Turbinaria brueggemanni* Bernard, and *Turbinaria contorta* Bernard, to which Eguchi and Mori (1973) added *Acanthastrea echinata* (Dana)] have been included in numerical analyses in this study, but not in those of Veron (1992), where only extant verified records were used.

Assuming that these "most likely" identifications are correct, the total number of extant species collected from Tateyama over the last 60 yr is ca. 32. Many of these are probably not now extant, due to land reclamation.

In contrast to Tateyama, the environmental diversity of the Izu Peninsula, on either side of the entrance to Nakagi Port, is very great, reflecting the irregular mountainous terrain both above and below water. Corals, intermixed with algae, are predominant in the most exposed areas and most occur to depths of at least 30 m. The highest diversity of all occurs at a partly protected station at the northern tip of Hirido Island, which forms the eastern edge of Nakagi Port, at the southern tip of the peninsula. As at Tateyama, most corals are flattened or encrusting (the *Acropora* being notable exceptions) and most are deeply colored.

Further details of the corals of these and the other regions listed in Table 1 are given in Veron (1992). The most important aspect is that all these regions have extensive shallow-water communities, overwhelmingly dominated by *Acropora.*

Temperature Regimes of Extant Corals

Veron and Minchin (in press) have shown that the distribution of extant corals north to Tateyama is highly correlated with latitudinal decrease in sea-surface temperature. This correlation is complicated along the southern coastline of Honshu by the Kuroshio Current forming several paths, including a straight path virtually parallel to the coast and several meandering paths (Figure 1). These paths are unusual in that they last for several years, reflecting the Kuroshio's inlet velocity and eddy viscosity.

The large meander path of the Kuroshio is the more prevalent, having been present over 35 yr between 1895 and 1984 (Kawabe 1985); it has a relatively low volume transport and a greatly increased transport time east of the Kii Peninsula. However, all paths (and most recorded variations of them) provide transport to Tateyama from Tanegashima, southern Kyushu, southern Shikoku, and Kushimoto.

Japanese sea-surface data used in this study are from three main sources: (1) Macro-scale monthly records of the Japan Oceanographic Data Centre (JODC) since 1945 for areas of one Marsden square (each square being 1° latitude × 1° longitude). These are pre-remote sensing, surface-temperature records and are of great value because of the ecologically meaningful time period over which they are spread, the (usually) large numbers of measurements included, and the compatibility of the data throughout the geographic range studied. (2) Meso-scale data records from marine stations, where available in the vicinity of coral localities studied. Although these data are more directly relevant to the present localities, they are not as useful for inter-

regional comparisons as macro-scale records because methods of measurements vary, they cover only restricted periods of time, and they are not available for some localities. (3) Micro-scale records of lethal low-temperature limits of specific species.

RESULTS

Table 1 shows that there has been a decrease in the number of species at Tateyama from at least 70 to fewer than 34 over the last 5,000–6,000 yr. Nearly one-half (26) of all identified Numa bed species were extant at Tateyama earlier this century, 85% are now extant as far north as the Kii Peninsula, and all except two (*Leptoria phrygia* and *Porites rus*) are extant somewhere in mainland Japan. (Those two are extant in the Ryukyu Islands.)

There are no extensive extant communities known to me that exactly parallel the Numa bed species composition, but it is clear, from both the paucity of *Acropora* and the prevalence of the dominant species recorded, that the Numa bed corals grew in a shallow, protected, and probably turbid embayment.

When the species complement of extant corals and the Numa bed fossils are combined in the same analysis (Figures 3 and 4), there are essentially four groupings: western and central extant corals form one group, the two highest-latitude localities (Izu and Tateyama) form second and third groups, and the Numa bed fossils form a fourth. Therefore, the identified Numa bed corals and the extant corals of Tateyama and Izu are more dissimilar from each other than are any of the remaining extant coral communities of mainland Japan; the disimilarity in the case of the Numa bed fauna is clearly influenced by the large number (at least 15) of unidentified species.

The closest extant fauna to the Numa bed corals appears to be that of Kushimoto: the total number of species is comparable (at least 70 recorded in the Numa beds, 95 now present at Kushimoto); there is an 85% overlap in all species recorded; all dominant species except *T. mesenterina* are in common. Extant temperature differences between these localities

are indicated in Table 2: the closest approximation to a single number is 1.7°C, that being the mean difference of the six temperature indicators (the columns) listed. Although there are many assumptions in arriving at this number, even Tanegashima, with a total species complement of 151, which includes all but two of the Numa bed species, is only 2.1°C warmer.

DISCUSSION

Speculations and limitations of previous authors about the reasons for the diversity decrease at Tateyama are in part due to incomplete data, especially about the extant fauna. Nevertheless, there has been general agreement that the decrease in diversity results primarily from a decrease in sea temperature, a conclusion strongly supported by the present study. Although Tateyama might well have undergone a reduction in environmental diversity since the deposition of the Numa beds (and indeed the extant fauna exists only in a narrow range of biotopes), the same cannot be said of Izu, which has almost all types of nonreefal biotopes available for colonization, including a wide range of combinations of depth, exposure to wave action, exposure to currents, substrate type, and abundance of other macrobenthos including algae.

There is good reason to believe that the distribution limits of many species, especially those in high latitudes, change over very short time periods. *Blastomussa wellsi, Euphyllia ancora,* and *Pavona venosa* are rare at Tateyama; *Acanthastrea lordhowensis, Hydnophora bonsai, Mycedium elephantotus,* and *Oxypora lacera* are rare at Izu. These species, and others like them, at these and other mainland regions, are likely to be itinerant species existing under temporary environmental regimes or by chance recruitment. This has been the case with the *Cycloseris* of Miyake Island recorded by Tribble and Randall (1986), which have since died out in likely response to an El Niño Southern Oscillation event (R. Moyer, pers. comm.). The same observation has been made in other countries: *Blastomussa*

TABLE 1

DISTRIBUTION OF EXTANT HERMATYPIC CORALS IN PRINCIPAL REGIONS OF MAINLAND JAPAN AND THE NUMA BEDS OF TATEYAMA

SPECIES	TANEGASHIMA	TOSASHIMIZU	AMAKUSA IS.	KUSHIMOTO	SHIRAHAMA	IZU	TATEYAMA	NUMA BEDS
Acanthastrea amakusensis	×	×	×	×	×	×	—	—
Acanthastrea bowerbanki	—	×	×	—	—	—	—	—
Acanthastrea echinata	×	×	×	×	×	—	?^{2}	×^{2}
Acanthastrea hemprichii	×	×	×	×	×	—	—	×$^{1-4}$
Acanthastrea hillae	×	—	×	×	×	—	—	—
Acanthastrea ishigakiensis	×	—	—	—	—	—	—	—
Acanthastrea lordhowensis	×	×	×	×	—	×	—	×^{1}
Acanthastrea rotundoflora	×	—	—	—	—	—	—	—
Acropora anthocercis	×	—	—	—	—	—	—	—
Acropora aspera	—	×	×	×	×	—	—	—
Acropora copiosa	×	—	—	—	—	—	—	—
Acropora cuneata	×	—	—	—	—	—	—	—
Acropora dendrum	—	×	×	×	×	—	—	—
Acropora digitifera	×	—	×	—	—	—	—	—
Acropora divaricata	×	×	×	—	—	—	—	—
Acropora florida	×	×	×	×	×	—	—	—
Acropora glauca	×	×	×	×	—	—	—	—
Acropora hyacinthus	×	×	×	×	×	—	—	—
Acropora insignis	—	—	×	—	—	—	—	—
Acropora latistella	×	—	×	—	—	—	—	—
Acropora listeri	×	—	—	—	—	—	—	—
Acropora loripes	×	×	×	—	—	—	—	—
Acropora mirabilis	×	—	—	—	—	—	—	—
Acropora pruinosa	—	×	×	—	—	×	—	—
Acropora samoensis	×	—	—	—	—	—	—	—
Acropora solitaryensis	×	×	×	×	×	×	?^{3,4}	—
Acropora stoddarti	×	—	—	—	—	—	—	—
Acropora striata	×	—	—	—	—	—	—	—
Acropora subulata	×	×	—	—	—	—	—	—
Acropora tanegashimensis	×	—	—	—	—	—	—	—
Acropora tumida	—	×	—	×	×	—	—	?^{1}
Acropora valida	×	×	×	×	×	—	—	—
Acropora verweyi	×	—	—	—	—	—	—	—
Acropora willisae	—	×	—	—	—	—	—	—
Acropora sp.	×	—	—	—	—	—	—	—
Alveopora excelsa	×	—	—	×	×	—	—	—
Alveopora japonica	×	×	×	×	×	×	×$^{1-3}$	×$^{1-3}$
Alveopora spongiosa	—	—	×	—	×	—	—	—
Astreopora explanata	×	—	—	—	—	—	—	—
Astreopora gracilis	—	×	—	×	—	—	—	—
Astreopora incrustans	×	×	—	×	×	—	—	—
Astreopora macrostoma	×	—	—	—	—	—	—	—
Astreopora myriophthalma	×	×	×	—	—	—	—	—
Barabattoia amicorum	×	×	×	×	×	—	—	×^{1}
Blastomussa wellsi	×	×	×	×	—	—	×^{1}	—
Catalaphyllia jardinei	—	—	—	×	×	—	—	—
Caulastrea tumida	×	×	×	×	×	—	×^{2}	×$^{1-4}$
Coscinaraea columna	×	×	×	×	×	×	—	×$^{?2}$
Coscinaraea crassa	×	—	—	—	×	—	—	—
Coscinaraea hahazimaensis	×	×	—	×	—	×	—	—

TABLE 1 (continued)

SPECIES	TANEGASHIMA	TOSASHIMIZU	AMAKUSA IS.	KUSHIMOTO	SHIRAHAMA	IZU	TATEYAMA	NUMA BEDS
Coscinaraea monile	×	×	—	—	—	—	—	—
Coscinaraea wellsi	—	—	—	—	—	—	—	—
Cycloseris cyclolites	—	×	×	×	×	×	×[2-4]	×[2,3]
Cycloseris patelliformis	×	—	—	—	×	—	—	×[2,3]
Cycloseris vaughani	—	—	×	—	—	—	—	—
Cycloseris sp.	×	—	—	—	—	—	—	—
Cynarina lacrymalis	×	×	×	×	×	—	—	×[1]
Cyphastrea chalcidium	×	×	×	×	×	×	×[2]	×[2,3]
Cyphastrea japonica	×	×	×	×	×	×	—	×[2,3]
Cyphastrea microphthalma	×	×	×	×	—	—	×[2]	×[2,3]
Cyphastrea serailia	×	×	×	×	×	×	×[1,2]	×[1-4]
Echinophyllia aspera	×	×	×	×	×	×	×[1,2]	×[1-3]
Echinophyllia echinata	—	×	×	—	—	—	—	×[1]
Echinophyllia nishihirai	—	×	—	—	—	—	—	—
Echinophyllia patula	×	—	—	—	—	—	—	—
Echinopora lamellosa	×	×	—	—	—	—	—	—
Euphyllia ancora	×	×	×	×	×	—	×[1]	×[2,3]
Euphyllia paraglabrescens	×	—	—	—	—	—	—	—
Favia danae	×	×	—	—	—	—	—	—
Favia favus	×	×	×	×	×	—	—	?[1]
Favia helianthoides	—	×	×	×	—	—	—	—
Favia laxa	×	×	×	×	—	—	—	×[1]
Favia lizardensis	×	×	×	×	—	×	—	—
Favia maxima	×	×	—	—	×	—	—	—
Favia pallida	×	×	×	×	—	—	—	—
Favia rotumana	×	—	—	—	—	—	—	—
Favia rotundata	×	—	—	×	—	—	—	—
Favia speciosa	×	×	×	×	×	×	×[1,2]	×[1-4]
Favia veroni	×	×	×	×	×	—	—	—
Favites abdita	×	×	×	×	×	×	—	×[1-4]
Favites chinensis	×	×	×	—	—	—	—	—
Favites complanata	×	×	×	×	×	×	—	—
Favites flexuosa	×	×	×	×	×	×	?[2,4]	×[2,3]
Favites pentagona	×	×	×	×	×	×	—	—
Favites russelli	×	×	×	×	×	—	—	—
Fungia fungites	—	×	—	—	—	—	—	—
Fungia scutaria	×	—	—	—	—	—	—	—
Galaxea astreata	—	×	—	—	—	—	—	—
Galaxea fascicularis	×	×	—	—	—	—	—	—
Gardineroseris planulata	×	—	—	—	—	—	—	—
Goniastrea aspera	×	×	—	×	—	×	—	—
Goniastrea australensis	×	×	×	×	×	×	—	—
Goniastrea deformis	×	×	×	×	×	×	×[1,?2-4]	—
Goniastrea edwardsi	—	×	—	—	—	—	—	—
Goniastrea favulus	×	×	×	×	×	×	—	—
Goniastrea pectinata	×	×	—	—	—	—	—	—
Goniastrea retiformis	×	×	×	×	—	—	—	×[1,?2]
Goniopora cellulosa	×	×	—	—	—	—	—	—
Goniopora columna	—	—	—	—	—	×	×[1]	—
Goniopora djiboutensis	×	—	—	—	—	—	—	—
Goniopora lobata	×	×	×	×	×	—	?[3]	×[1,3]
Goniopora pendulus	×	—	×	×	—	—	—	—

TABLE 1 (continued)

SPECIES	TANEGASHIMA	TOSASHIMIZU	AMAKUSA IS.	KUSHIMOTO	SHIRAHAMA	IZU	TATEYAMA	NUMA BEDS
Goniopora polyformis	—	—	×	—	—	—	—	×[1]
Goniopora somaliensis	×	—	—	—	—	—	—	—
Goniopora stokesi	×	×	×	—	—	—	—	—
Goniopora stutchburyi	—	×	—	×	×	—	—	—
Goniopora sp.	—	—	—	—	×	—	—	—
Hydnophora bonsai	—	×	×	×	×	×	?[2-4]	—
Hydnophora exesa	×	×	×	×	×	×	×[1-3]	×[1-4]
Leptastrea bewickensis	×	—	—	—	—	—	—	—
Leptastrea pruinosa	—	×	—	—	—	×	—	—
Leptastrea purpurea	×	×	×	×	×	×	×[1-4]	×[1-4]
Leptoria phrygia	—	—	—	—	—	—	?[2,3]	×[2,3]
Leptoseris hawaiiensis	×	—	—	—	—	—	—	—
Leptoseris mycetoseroides	×	×	×	×	×	×	×[1,2]	×[?2,3]
Leptoseris scabra	—	—	—	—	—	—	—	—
Leptoseris solida	×	—	—	—	—	—	—	—
Leptoseris yabei	×	—	—	—	—	—	—	—
Lithophyllon undulatum	×	×	×	×	×	—	×[2]	×[1-4]
Lobophyllia corymbosa	×	—	—	—	—	—	—	—
Lobophyllia hataii	×	—	×	×	—	—	—	×[2]
Lobophyllia hemprichii	×	—	×	×	×	—	—	×[2,3]
Lobophyllia robusta	×	—	×	×	—	—	—	×[2-4]
Madracis asanoi	—	—	—	×	—	—	—	—
Merulina ampliata	×	—	—	—	—	—	—	—
Merulina scabricula	×	—	—	—	—	—	—	—
Montastrea curta	×	×	×	×	×	—	—	—
Montastrea magnistellata	×	×	—	—	—	—	—	—
Montastrea multipunctata	×	—	—	—	—	—	—	—
Montastrea valenciennesi	×	×	×	×	—	—	—	—
Montipora aequituberculata	×	—	—	—	—	—	—	—
Montipora danae	×	×	—	×	—	—	—	—
Montipora efflorescens	—	—	—	—	—	×	—	—
Montipora effusa	—	×	×	×	—	—	—	—
Montipora friabilis	×	—	—	—	—	—	—	—
Montipora hispida	×	×	×	×	×	—	?[2,3]	—
Montipora hoffmeisteri	×	—	—	—	—	—	—	—
Montipora incrassata	×	—	—	—	—	—	—	—
Montipora informis	×	×	×	×	×	—	—	—
Montipora millepora	—	×	×	×	×	—	—	—
Montipora mollis	×	×	×	×	×	—	—	—
Montipora monasteriata	×	—	—	—	—	—	—	—
Montipora spongodes	×	—	×	×	×	—	—	—
Montipora spumosa	×	—	—	×	—	—	—	—
Montipora stellata	—	—	—	—	—	—	—	—
Montipora turgescens	×	×	×	×	×	×	—	—
Montipora undata	×	×	—	—	—	—	—	—
Mycedium elephantotus	×	×	×	×	×	×	—	—
Oulastrea crispata	×	×	×	×	×	×	×[1-3]	×[1-3]
Oulophyllia crispa	×	×	×	×	×	—	—	—
Oxypora lacera	×	×	×	×	×	×	—	×[1,3]
Pachyseris speciosa	×	×	—	—	—	—	—	—
Pavona cactus	×	—	—	—	—	—	—	—
Pavona decussata	×	×	×	×	—	—	—	×[1-3]

TABLE 1 (continued)

SPECIES	TANEGASHIMA	TOSASHIMIZU	AMAKUSA IS.	KUSHIMOTO	SHIRAHAMA	IZU	TATEYAMA	NUMA BEDS
Pavona explanula	×	×	×	—	—	×	—	—
Pavona frondifera	×	—	—	—	—	—	—	×[2,3]
Pavona maldivensis	×	—	—	—	—	—	—	—
Pavona minuta	×	—	×	—	—	—	—	—
Pavona varians	×	—	—	—	—	—	×[1]	×[1]
Pectinia lactuca	—	×	×	×	×	—	—	×[1-3]
Pectinia paeonia	—	—	×	×	×	—	—	—
Physophyllia ayleni	—	×	×	×	×	—	—	×[1-3]
Platygyra contorta	×	×	×	×	×	×	—	?[1,3]
Platygyra daedalea	×	×	×	×	×	×	—	—
Platygyra pini	—	×	×	—	—	—	—	×[1,3]
Platygyra sinensis	×	—	—	×	—	—	—	—
Platygyra verweyi	×	—	—	—	—	—	—	—
Plesiastrea versipora	×	×	×	×	×	×	×[1,2,4]	×[1-3]
Pocillopora eydouxi	—	×	—	—	—	—	—	—
Pocillopora damicornis	×	×	×	×	×	—	—	×[2-4]
Pocillopora verrucosa	×	—	—	—	—	—	—	—
Porites cylindrica	—	×	—	—	—	—	—	—
Porites heronensis	×	×	×	×	×	×	×[1]	×[2,3]
Porites lichen	×	—	—	—	—	—	—	—
Porites lobata	—	×	—	—	—	—	—	—
Porites lutea	—	×	—	—	—	—	—	—
Porites okinawensis	—	—	—	—	—	×	—	—
Porites rus	—	—	—	—	—	—	—	×[2-4]
Psammocora contigua	×	—	—	—	—	—	—	—
Psammocora nierstraszi	×	—	—	—	—	—	—	—
Psammocora profundacella	×	×	×	×	×	×	×[1,?2]	×[2-4]
Psammocora superficialis	×	×	×	×	×	×	×[1]	×[2-4]
Stylocoeniella armata	—	×	—	×	×	×	—	—
Stylocoeniella guentheri	×	×	×	×	×	—	—	×[1-4]
Stylophora pistillata	×	×	×	—	—	—	?[2-4]	×[2-4]
Symphyllia agaricia	×	×	—	—	—	—	—	—
Symphyllia radians	×	×	—	—	—	—	—	—
Symphyllia recta	—	×	—	—	—	—	—	—
Symphyllia valenciennesii	—	×	×	×	×	—	—	—
Trachyphyllia geoffroyi	×	×	×	×	×	—	—	—
Turbinaria frondens	×	×	×	—	×	—	?[4]	×[?2,?3]
Turbinaria irregularis	×	×	×	×	×	—	—	—
Turbinaria mesenterina	×	×	—	—	—	—	—	×[1,3]
Turbinaria peltata	×	×	×	×	—	—	—	×[1-4]
Turbinaria reniformis	×	×	—	—	—	—	?[3,4]	?[1-3]
Turbinaria stellata	×	×	—	×	×	—	—	—
Total Species	151	120	99	95	77	42	32	55

NOTE: Distribution records for regions other than Tateyama are from Veron (1992) and include previous publications.

[1] This study (Tateyama only).
[2] Record from Eguchi and Mori (1973).
[3] Record from Hamada (1963*a,b*).
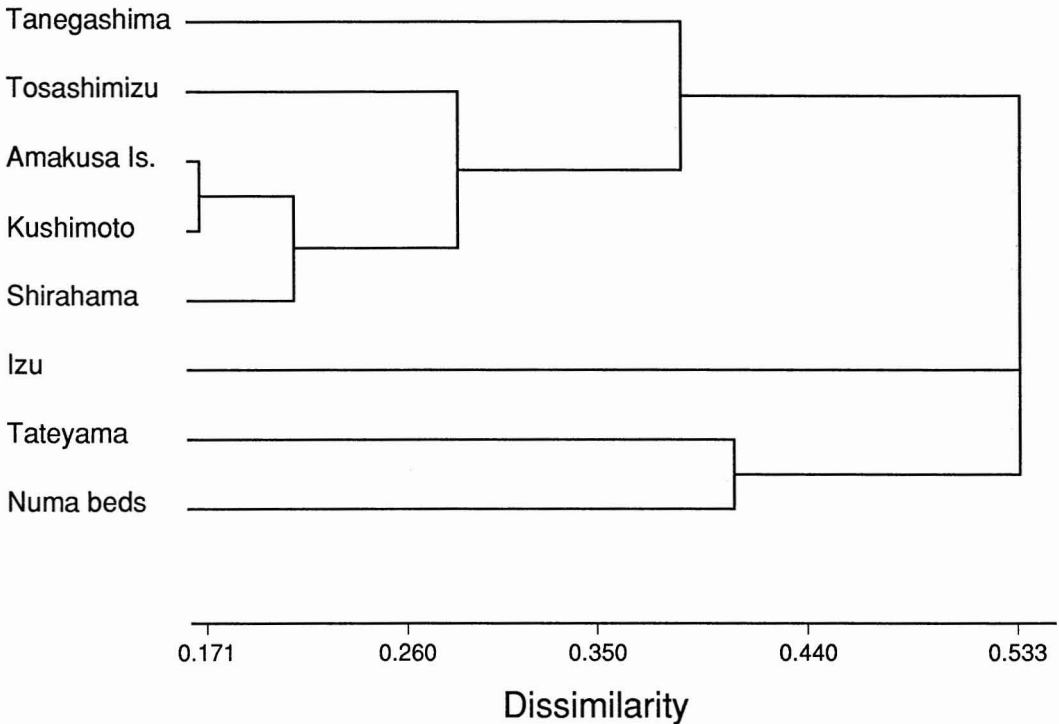[4] Record from Yabe and Sugiyama (1931 and/or 1935*b*).

FIGURE 3. Agglomerative hierarchical classification of the Numa bed corals and principal coral regions of mainland Japan. Data used are the records in this publication (summarized in Table 1). The classification, ordination, and group diagnostic proceedures are components of the PATN package of Belbin (1987), using the Bray-Curtis dissimilarity coefficient and flexible unweighted pair mean averages.

wellsi, for example, has been recorded at the southernmost reefs (Houtman Abrolhos Islands) of Western Australia, but nowhere else along the western coastline, and has also been recorded from Newcastle on the far southeastern Australian coast (Pickett 1981), but no other coastal region south of the Great Barrier Reef (Veron 1986).

Despite increasing interest in global warming due to the "greenhouse effect," a clear understanding of Holocene sea temperature changes, either from primary data or derived regional syntheses (Bradley 1985 and others), is far from complete. The microfauna of the Numa beds was investigated by Asano (1936), who found no species characteristic of tropical coral reefs and concluded that the climate at the time of deposition was not markedly different from the present one. Frydl's (1982) work on Numa bed ostracods allows a

detailed reconstruction of relative sea level changes over the past 10,000 yr, but environmental changes recorded reflect lateral shifts in ostracod biofacies that are not necessarily correlated with temperature changes.

On a regional scale, the few Quaternary paleoclimatic studies that are available from Japan and eastern Asia are primarily from pollen and, to a lesser extent, radiolarian sequences to 30,000 yr B.P. (Sarro et al. 1984, Heusser and Morley 1985a,b); there are few correlations between continental and marine sequences. Heusser and Morley's (1985a) correlation between pollen sequences and sea-surface temperature from a deep-sea core some 700 km east of Hokkaido is an exception: maximum concentrations of pollen from warm temperate oak forests occur between 11,000 and 4000 yr B.P., and warmest Holocene sea-surface temperatures are re-
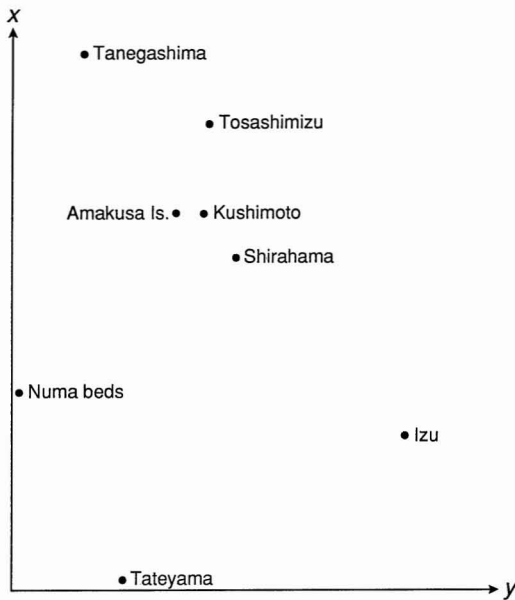
FIGURE 4. Multidimensional scaling of the Numa bed corals and principal coral regions of mainland Japan. Data used are the records in this publication (summarized in Table 1). The ordination group diagnostic procedures are components of the PATN package of Belbin (1987), using the Bray-Curtis dissimilarity coefficient. Third and fourth dimensions and associated stress values were both generated and showed no additional information.

corded from 4000 to 6000 yr B.P. Heusser and Morley (1985a) concluded that their marine and terrestrial records of this time reflect a dynamic interaction between northeastern

Asian atmospheric and ocean systems overprinting global climatic signals.

On a global scale, the Climate Mapping and Prediction (CLIMAP Project Members 1976) and Cooperative Holocene Mapping Project (COHMAP Project Members 1988) reconstructions to the Last Glacial Maximum (18,000 yr B.P.) are central to comparative marine and terrestrial reconstructions. The Cooperative Holocene Mapping Project (COHMAP Project Members 1988), primarily using pollen, lake level, and marine plankton records, has shown that at 6000 yr B.P. changes in solar radiation arising from changes in the orientation of the earth's axis produced summer temperatures for the northern hemisphere 2–4°C higher than at present and that increased solar radiation in summer 12,000–6000 yr B.P.) enhanced the thermal contrast between land and sea. Even at 18,000 yr B.P., Moore et al. (1980), in a review of proxy data from all major microfossil groups of the Pacific Basin, concluded that sea-surface temperatures within the centers of subtropical gyres were generally as warm as, or warmer than, modern sea-surface temperatures.

Most of what is specifically known of Holocene sea temperatures comes from correlations between marine microfauna, notably foraminifera, oxygen isotope studies and the composition of shallow-water fossil communities, notably hermatypic corals and mangroves. Correlations between these various data sources, including coral communities

TABLE 2

SEA-SURFACE TEMPERATURES AT THE LOCALITIES OF EXTANT CORALS

LOCALITY	AVERAGE OF MEANS OF COLDEST MONTHS	AVERAGE OF MINIMA OF COLDEST MONTHS	MINIMUM MONTHLY RECORD	ABSOLUTE MINIMUM RECORDED	AVERAGE OF MEANS OF WARMEST MONTHS	AVERAGE OF MAXIMA OF WARMEST MONTHS
Tanegashima	19.3	15.5	14.1	(14.1)	28.0	29.3
Tosashimizu	17.8	15.5	13.2	(13.2)	27.7	29.2
Amakusa Is.	14.4	13.2	10.2	(10.2)	26.9	28.6
Kushimoto	17.8	15.3	13.8	13.2	27.8	29.7
Shirahama	14.3	13.1	12.6	10.4	27.3	27.8
Izu	16.4	13.4	12.8	10.1	26.1	28.6
Tateyama	16.1	14.1	11.9	10.6	25.9	29.0

NOTE: Data are from Veron and Minchin (in press); primary sources are indicated in the text.

and isotopes in coral skeletons, may be conflicting (e.g., Erez 1978, Swart and Coleman 1980, Adams et al. 1990). Cyclical variations in global climate over periods of 50–300 yr do, however, seem to be a ubiquitous phenomenon during the Holocene (Stocker and Mysak 1989).

The essential contribution of the present study to the understanding of Holocene paleoclimates is that (1) diverse coral communities, but not coral reefs, that might be described as "high latitude subtropical," can exist where sea-surface minima regularly drop below 15°C; (2) that diversity becomes very restricted when temperature regularly drops below 13°C; (3) that a rise of ca. 2°C in marginal locations can double species diversity and create a major increase in overall abundance; and (4) that relatively minor or localized temperature increase in a very short period of geological time can give rise to a fossil fauna that is very different from its extant equivalent.

These conclusions indicate that greenhouse warming of only 2°C should result in a greatly increased diversity of corals in high-latitude locations. They also contain a warning that paleoclimates should only be inferred from fossil assemblages with a great deal of caution because moderately diverse communities can occur at lower temperatures than generally recognized and can result from what may be a minor short-term regional surface-temperature fluctuation.

APPENDIX

Synopsis of Fossil Corals Recorded at Tateyama

The number of identified and unidentified species listed by previous authors differs substantially from that accepted by the present author. This is largely due to taxonomic differences and problems, most of which have been resolved by detailed taxonomic work on extant species (Veron 1992). As noted above, Yabe and Sugiyama (1931 and 1935b) listed 51 and 46 species (respectively), of which

35–38 are likely to be real. Hamada (1963a,b) listed 74 hermatypic species (one ahermatype), of which 50–53 are likely to be real. Nine new identified records have been made during the present study, bringing the total list of identified species accepted by me to 54. When unidentified but very likely valid species are added to this list (specimens identified to genus only, but representing species other than those listed), the estimated total number of hermatypic species for the Numa beds is 70.

The history of research on the Numa beds, together with the geological history and geography of the region, has been well documented by Frydl (1982). Yokoyama, in ?1904, in manuscript, originally recorded 11 genera of hermatypic Scleractinia, a list largely unrecognizable because it includes a high proportion of Caribbean genera. In 1911, Yokoyama recorded a second list of nine (mostly Indo-Pacific) genera, commenting that these "are not now living north of the Ryukyus or Bonin Islands." In 1926 Hamada made a preliminary examination of the beds, an important study that was to become the start of coral research at Tohoku University, Sendai, later to receive widespread international recognition through the work of Yabe and his colleagues. In his account, Hamada (1931) expanded the Numa beds fauna to ca. 25 species belonging to 18 genera. Yabe and Sugiyama (1931, 1935a,b) increased this to 35–38 true species (51 species according to their 1931 listing, which includes five species of *Antillia*, three *Hydnophora*, and three *Podabacia*, and 46 species according to their 1935b listing, which includes some corrections), the identities of which are largely verifiable today by comparison with their studies of extant corals.

Yabe and Sugiyama (1935a) gave the first detailed observations of Pliocene to Recent climatic changes in Japan and Taiwan based principally on the raised Ryukyu (Riukiu) limestones, of which Nakamori (1986) gave a comprehensive recent account, and the Numa beds. Yabe and Sugiyama noted that the alluvial plain at Numa is ca. 20 m higher than present sea level and consists of a more or less extended bed, 2–3 m thick, beneath the present alluvial silt. Many corals originally

retained upright positions on Neogene sediments of the Miura Group and formed what Yabe and Sugiyama believed was an "incipient coral reef grown in rather calm water immediately after the land submerged" and that "subsequent copious settling of mud at the heads of the submerged valleys, and probably also the slight simultaneous lowering of the temperature of the sea water, soon prevented further growth of the coral reefs, and the mud penetrated and filled up the interspaces between the coral stocks" (p. 197). Yokoyama (1911) incorrectly attributed the deposits to a warm period of the Pleistocene, Yabe and Sugiyama (1935a) correctly attributed them to the early Holocene "nearly equivalent to the Neolithic beaches of England."

In a post-war revival of interest in the Numa bed fauna, Hamada (1963a,b) re-examined Yabe and Sugiyama's specimens and made substantial additional collections. Hamada recorded 50–53 species (75 according to his list, which includes one ahermatype, three species of *Caulastrea*, seven *Lobophyllia*, three *Pectinia*, and four *Podabacia*). By comparison with the extant corals of Tanabe Bay (Kii Peninsula), he concluded that "the bed had been formed not at the tidal line as has long been thought, but on a fairly deep and calm sea bottom (5–29 m) without distinct coral reefs." Hamada's results are well illustrated by a publication of the Geological Education Research Group in Chiba Prefecture (Hamada 1963a), which, together with reexamination of some specimens, has allowed me to reidentify most species. Some of these specimens have been retained by the Natural History Museum and Institute, Chiba (NHM&I,C), but many have been lost. Eguchi and Mori (1973) presented a composite list of Hamada and Yabe's identifications with some taxonomic corrections and two additions, *Lobophyllia hataii* and *Acanthastrea echinata*, from the first site I studied. They concluded that some 100 species of coral occur there and that they grew in calm inland bay facies. Most recently, Frydl (1982) gave accounts of both Numa bed and extant corals. Eguchi and Mori's account is based on a combination of original observation and Hamada's observations and taxonomy; no

new discoveries are listed. Frydl's account is based on his own shallow-water observations of a relatively few species northwest of the island of Okinoshima where colonies were >1 m diam. and had partly dead growth surfaces. These have now been destroyed by recent land reclamation. Eguchi and Mori (1973) combined Hamada and Yabe's identifications of extant corals for the Tateyama region and made some additions, some of which (notably *Diaseris distorta* Michelin) require confirmation, others of which (notably *Caulastrea tumida* and *Lithophyllon undulatum*) are the only records of extant occurrences of dominant Numa bed species. These may also have been recently destroyed.

The following account is a summary of records of the present and past studies.

Family ASTROCOENIIDAE Koby, 1890

Genus *Stylocoeniella* Yabe & Sugiyama, 1935

Stylocoeniella guentheri Bassett-Smith, 1890. Second in abundance only to *Caulastrea tumida*. Colonies are large and have a compact nodular growth form similar to that of extant colonies elsewhere on mainland coastlines (but not Ryukyu Islands reefs).

Previous records: *S. hanzawai* (Yabe & Sugiyama): Hamada (1963a,b); *Stylocoenia elegans* Yabe & Sugiyama: Yabe and Sugiyama (1932); *Stylocoeniella armata* (Ehrenberg): Eguchi and Mori (1973).

Family POCILLOPORIDAE Gray, 1842

Genus *Pocillopora* Lamarck, 1816

Pocillopora damicornis (Linnaeus, 1758)

Previous records: *P. damicornis* (Linnaeus): Eguchi and Mori (1973); *P.* cf. *caespitosa* (Dana): Hamada (1963a,b), Yabe and Sugiyama (1931).

Genus *Stylophora* Schweigger, 1891

Stylophora pistillata (Esper, 1797)

Previous records: *S. pistillata* (Esper): Eguchi and Mori (1973); *S.* cf. *pistillata* (Esper): Yabe & Sugiyama (1931); *S.* cf. *danae* (Edwards & Haime): Hamada (1963a,b).

Family ACROPORIDAE Verrill, 1902

Genus *Montipora* de Blainville, 1830
Three species [*M. verrilli* Vaughan, cf. *M. ramosa* Bernard, and *M. hispida* (Dana)] were recorded by Hamada (1963*a,b*). Yabe and Sugiyama (1931) also recorded *M.* cf. *ramosa* (Bernard). These have been lost. A specimen identified as *M. hispida* in Hamada (1963*b*) is a platelike *Acropora*. Eguchi and Mori (1973) added *M. informis* Bernard.

Genus *Acropora* Oken, 1815
Only two species of *Acropora* have been recorded during the present study, only one of which can be identified with any degree of certainty. The unidentified species is the *Acropora* sp. of Hamada (1963*a,b*).

Yabe and Sugiyama (1931) recorded *A.* cf. *angulata* (Quelch). Eguchi and Mori (1973) listed three species: *A* cf. *studeri*, *A.* cf. *angulata*?, and *Acropora* sp.

?*Acropora tumida* Verrill, 1866. This is not the same species as the *A. tumida* of Yabe and Sugiyama.

Family PORITIDAE Gray, 1842

Genus *Porites* Link, 1807
Yabe and Sugiyama (1931) and Eguchi and Mori (1973) recorded *P.* cf. *bernardi* Vaughan. This has not been reexamined during this study and is not recognizable from the illustrations. Eguchi and Mori (1973) recorded an additional unidentified species.

Porites heronensis Veron, 1985
Previous records: *P.* cf. *discoides* Studer: Hamada (1963*a,b*), Eguchi and Mori (1973).

Porites rus (Forskål, 1775)
Previous records: *P.* cf. *hawaiiensis* Vaughan: Yabe and Sugiyama (1931), Hamada (1963*a*,b), Eguchi and Mori (1973).

Genus *Goniopora* de Blainville, 1830
Three species are recorded, one of which is not sufficiently well preserved for identification. Hamada (1963*a,b*) recorded two species. Yabe and Sugiyama (1931) recorded *G.* cf. *djiboutiensis* Vaughan; this has not been re-

examined. Eguchi and Mori (1973) listed "*G. bernardi* aff. Faustino."

Goniopora lobata Edwards & Haime, 1860. I recorded it from two well-preserved specimens.
Previous record: ?*Goniopora* sp. A: Hamada (1963*a*; illustrated, p. 51, fig. A).

Goniopora polyformis Zou, 1980. I recorded it from five specimens, two of which are doubtful.

Genus *Alveopora* de Blainville, 1830
Eguchi and Mori (1973) recorded *Alveopora* sp., which may be a reference to *A. verrilliana* Vaughan, after Hamada.

Alveopora japonica Eguchi, 1968. Common; I recorded it from many well-preserved specimens.
Previous records: *A.* cf. *verrilliana* Vaughan: Eguchi and Mori (1973), Hamada (1963*a,b*).

Family SIDERASTREIDAE Vaughan & Wells, 1943

Genus *Psammocora* Dana, 1846
Yabe and Sugiyama (1931), Hamada (1963*a,b*), and Eguchi and Mori (1973) recorded *Psammocora japonica* Yabe & Sugiyama, 1931. This species has not been recorded elsewhere, and its taxonomic status is unknown. A forth unidentified *Psammocora* was recorded by Eguchi and Mori (1973).

Psammocora superficialis Gardiner, 1898
Previous records: *P. superficialis* Gardiner: Yabe and Sugiyama (1931), Hamada (1963*a,b*), Eguchi and Mori (1973).

Psammocora profundacella Gardiner, 1898
Previous records: *P. profundacella* Gardiner: Yabe and Sugiyama (1931), Hamada (1963*a,b*), Eguchi and Mori (1973).

Genus *Coscinaraea* Edwards & Haime, 1848
Hamada (1963*a,b*) and Eguchi and Mori (1973) recorded one *Coscinaraea* species; this specimen has not been reexamined.

Coscinaraea columna (Dana)

Previous record: *C. columna* (Dana): Eguchi and Mori (1973).

Family AGARICIIDAE Gray, 1847

Genus *Pavona* Lamarck, 1801

Yabe and Sugiyama (1931) and Hamada (1963*a,b*) recorded two species, *P. danae* Edwards & Haime, 1860 and *Pavona* sp., neither of which have been reexamined during the present study; they are not recognizable from illustrations in Hamada (1963*a*).

Pavona decussata (Dana, 1846). Recorded from three small specimens, only one of which is well preserved.

Previous records: *Pavona cactus*: Hamada (1963*a,b*), Eguchi and Mori (1973).

Pavona frondifera Lamarck, 1816

Previous records: *P. frondifera* Lamarck: Hamada (1963*a,b*), Eguchi and Mori (1973).

Pavona varians Verrill, 1864. I recorded it from several specimens.

Genus *Leptoseris* Edwards & Haime, 1849

Leptoseris mycetoseroides Wells, 1954

Previous records: *L. minikoiensis* Gardiner: Hamada (1963*a*) (from a reexamination of the specimen illustrated, p. 101). Eguchi and Mori (1973) also recorded *L. minikoiensis*.

Family FUNGIIDAE Dana, 1846

Genus *Cycloseris* Edwards & Haime, 1849

Yabe and Sugiyama (1931) recorded *Fungia fragilis* Vaughan and *F. sinensis* Edwards & Haime, which are likely to be two *Cycloseris* species.

Cycloseris cyclolites (Lamarck, 1801)

Previous records: ?*Fungia cyclolites* Lamarck: Eguchi and Mori (1973), Hamada (1963*a,b*); ?*Fungia cyclolites* (*Diaseris* form): Eguchi and Mori (1973), Hamada (1963*a b*).

Cycloseris patelliformis (Boschma, 1923)

Previous records: ?*Fungia* cf. *patellata* (Ellis & Solander): Hamada (1963*a,b*); ?*C. patella* (Ellis & Solander): Eguchi and Mori (1973).

Genus *Diaseris* Edwards & Haime, 1849

Eguchi and Mori (1973) recorded *Cycloseris* (*Diaseris*) *fragilis* Alcock, a very doubtful identification, as no *Diaseris* has been correctly recorded elsewhere from mainland Japan.

Genus *Lithophyllon* Rehberg, 1892

Lithophyllon undulatum Rehberg, 1892. Very common, recorded from many well-preserved specimens. Records follow a very confused treatment of *L. undulatum* by Yabe. Specimen 6292701 from NHM&I,C is an unusual growth form of what is probably this species.

Previous records: *Podabacia elegans* (van der Horst, 1921): Yabe and Sugiyama (1931), Hamada (1963*a,b*); *P. lobata* (van der Horst): Yabe and Sugiyama (1931); *P. nomaensis* (Yabe & Sugiyama): Yabe and Sugiyama (1931); *P. elegans lobata*: Hamada (1963*a,b*); *P. elegans lobata* forma *nomaensis*: Hamada (1963*a,b*); *P. elegans lobata* forma *vanderhorsti* Yabe & Sugiyama: Hamada (1963*a,b*); *L. elegans*: Eguchi and Mori (1973); *L. nomaensis*: Eguchi and Mori (1973); *L. vanderhorsti*: Eguchi and Mori (1973); *L. lobata*: Eguchi and Mori (1973).

Family PECTINIIDAE Vaughan & Wells, 1943

Genus *Echinophyllia* Klunzinger, 1897

Yabe and Sugiyama (1931) listed two unidentified *Echinophyllia*; Eguchi and Mori (1973) listed three species, *E. aspera*, *E. tosaensis* (Yabe & Eguchi) (a subspecies of *aspera* according to Yabe and Eguchi, 1935 and Yabe et al. 1936), and *Echinophyllia* sp.

Echinophyllia aspera (Ellis & Solander, 1786). One of the most common species I collected.

Previous records: *E. aspera* (Ellis & Solander): Hamada (1963*a*; extensively illustrated), Eguchi and Mori (1973).

Echinophyllia echinata (Saville-Kent, 1871). Recorded from three well-preserved specimens.

Genus *Oxypora* Saville-Kent, 1871

Oxypora lacera (Verrill, 1864). One of the most common species I collected.

Previous record: *Oxypora lacera* (Verrill): Hamada (1963*a*).

Genus *Pectinia* Oken, 1815

Recorded by Yabe and Sugiyama (1931) as *Tridacophyllia*. Hamada (1963*a,b*) and Eguchi and Mori (1973) also recorded a *Pectinia* sp.; these specimens have not been reexamined.

Pectinia lactuca (Pallas, 1766). Recorded from several specimens.

Previous records: *P. lactuca* (Pallas): Hamada (1963*a,b*), Eguchi and Mori (1973); *P. lactuca japonica* (Yabe & Eguchi): Hamada (1963*a,b*), Eguchi and Mori (1973).

Genus *Physophyllia* Duncan, 1884

Physophyllia ayleni Wells, 1934. Very common.

Previous records: *P. ayleni* Wells: Hamada (1963*a*: 93), Eguchi and Mori (1973).

Family MUSSIDAE Ortmann, 1890

Genus *Cynarina* Brüggemann, 1877

Cynarina lacrymalis (Edwards & Haime, 1848). Recorded from three well-preserved specimens.

Genus *Acanthastrea* Edwards & Haime, 1848

Acanthastrea echinata (Dana, 1846)

Previous records: *A. echinata* (Dana): Eguchi and Mori (1973); *Moseleya* sp.: Eguchi and Mori (1973).

Acanthastrea hemprichii (Ehrenberg, 1934). Recorded from several specimens.

Previous records: *A. hemprichii* (Ehrenberg): Yabe and Sugiyama (1931), Hamada (1963*a,b*), Eguchi and Mori (1973).

Acanthastrea lordhowensis Veron & Pichon, 1982. Recorded from a single well-preserved specimen.

Genus *Lobophyllia* de Blainville, 1830

Recorded from a single specimen not sufficiently well preserved for identification. This is likely to be the same species as *Antillia constricta* and an unidentified *Antillia* of Yabe and Sugiyama (1931) and *L. nomaensis* Yabe & Sugiyama and *L. constricta* (Brüggemann) of Hamada (1963*a,b*). Eguchi and Mori (1973) recorded five species; four are identified as indicated below.

Lobophyllia hemprichii (Ehrenberg, 1834)

Previous records: *L. hemprichii* (Ehrenberg): Hamada (1963*a,b*), Eguchi and Mori (1973); *L. costata*: Hamada (1963*a,b*), Eguchi and Mori (1973).

Lobophyllia robusta Yabe & Sugiyama, 1936

Previous records: *L. robusta* Yabe & Sugiyama: Hamada (1963*a,b*), Eguchi and Mori (1973); *Antillia japonica* Yabe & Sugiyama: Yabe and Sugiyama (1931); *L. japonica*: Hamada (1963*a,b*).

Lobophyllia hataii Yabe, Sugiyama & Eguchi (1936)

Previous record: *L. hataii* Yabe, Sugiyama & Eguchi: Eguchi and Mori (1973).

Genus *Symphyllia* Edwards & Haime, 1848

Eguchi and Mori (1973) recorded *Symphyllia radians*; this record has not been verified.

Previous record: ?*Protolobophyllia* (Yabe & Sugiyama, 1935): Eguchi and Mori (1973).

Family MERULINIDAE Verrill, 1866

Genus *Hydnophora* Fischer de Waldheim, 1807

Hydnophora exesa (Pallas, 1766). Common, with well-preserved specimens.

Previous records: *H. exesa* (Pallas, 1766): Yabe and Sugiyama (1931), Eguchi and Mori (1973); *H. grandis* Gardiner: Hamada (1963*a,b*), Eguchi and Mori (1973).

Family FAVIIDAE Gregory, 1900

Genus *Caulastrea* Dana, 1846

Caulastrea tumida Matthai, 1928. Very common, amounting to ca. 20% of all skeletal debris, and forms large colonies or monospecific stands. This is a major departure from any known extant coral community: this species is often common in mainland regions, but has never been observed to be a dominant. Yabe and Sugiyama (1931) gave an extensive account of the variations of Japanese *Caulastrea tumida* subfossils, describing three new species, *yokoyamai*, *multiseptata*, and *gigantea*.

Previous records: *C. aiharai* Yabe & Sugiyama: Yabe and Sugiyama (1931); *C. yokoyamai* Yabe & Sugiyama: Yabe and Sugiyama (1931); *C. yokoyamai* var. *gracilis* Yabe & Sugiyama: Yabe and Sugiyama (1931); *C.* cf. *multiseptata* Yabe & Sugiyama: Hamada (1963*a,b*), Eguchi and Mori (1973); *C. tumida* Matthai: Hamada (1963*a,b*), Eguchi and Mori (1973); *C. tumida gracilis* (Yabe & Sugiyama): Hamada (1963*a,b*), Eguchi and Mori (1973); *C. gigantea* Yabe & Sugiyama: Yabe and Sugiyama (1931).

Genus *Favia* Oken, 1815

The most diverse genus of the Numa beds, six species having been recorded. Of these, only three are identifiable. Yabe and Sugiyama (1931) recorded five species, *F. magnistellata*, *F.* cf. *amplior*, *F.* cf. *matthai*, *F. pallida*, *and F. speciosa*, of which only the latter can be associated with the present nomenclature. Hamada (1963*a,b*) recorded four species: cf. *ehrenbergi*, cf. *pallida*, *speciosa*, and *magnistellata*. Eguchi and Mori (1973) recorded all but the last of these.

Favia laxa (Klunzinger, 1879). Recorded from a single well-preserved specimen.

Favia speciosa (Dana). Recorded from many specimens.

Previous records: *F. speciosa* (Dana): Yabe and Sugiyama (1931), Hamada (1963*a,b*), Eguchi and Mori (1973).

Favia favus (Forskål, 1775). Recorded with doubt from a single specimen.

Genus *Barabattoia* Yabe & Sugiyama, 1941

Barabattoia amicorum (Edwards & Haime, 1850). Recorded from a single specimen.

Genus *Favites* Link, 1807

Hamada (1963*a,b*) recorded five, and Eguchi and Mori (1973) recorded six species under the names *abdita*, *favosa*, cf. *flexuosa*, cf. *halicora*, *virens*, and *Favites* sp.

Favites abdita (Ellis & Solander, 1786). Recorded with doubt from a single specimen.

Previous records: *F. abdita* (Ellis & Solander): Hamada (1963*a,b*), Eguchi and Mori (1973); *F.* cf. *abdita*: Yabe and Sugiyama (1931); ?*F.* cf. *halicora* (Ehrenberg): Hamada (1963*a,b*).

Favites flexuosa (Dana, 1846)

Previous records: *F.* cf. *flexuosa*: Eguchi and Mori (1973); ?*Favites favosa* (Ellis & Solander): Hamada (1963*a,b*); ?*F. virens* (Dana): Eguchi and Mori (1973).

Genus *Goniastrea* Edwards & Haime, 1848

Goniastrea retiformis (Lamarck, 1816). Forms large, well-preserved colonies.

Previous record: ?*G. pectinata* (Ehrenberg, 1834): Eguchi and Mori (1973).

Genus *Platygyra* Ehrenberg, 1834

Yabe and Sugiyama (1931) listed two unidentified species. Hamada (1963*a,b*) recorded a *Platygyra* sp., but this has not been reexamined and cannot be recognized from the illustrations of Hamada (1963*a*). Eguchi and Mori (1973) listed three species, two identified as *P. gigantea* and *P. rustica*.

Platygyra pini Chevalier, 1975. I recorded this from a single well-preserved specimen.

Previous records: *Favia* cf. *ehrenbergi* (Klunzinger): Hamada (1963*a,b*). Specimen 6210614 of *Platygyra rustica* from Hamada (1963*b*) may also be this species.

Platygyra contorta Veron, 1990. Recorded with doubt from a single specimen.

Previous records: *P. rustica* (Dana): Hamada (1963*a,b*).

Genus *Leptoria* Edwards & Haime, 1848

Leptoria phrygia (Ellis & Solander, 1786)

Previous records: *Platygyra phrygia* (Ellis & Solander): Hamada (1963*a,b*), Eguchi and Mori (1973).

Genus *Oulastrea* Edwards & Haime, 1848

Oulastrea crispata (Lamarck, 1816). Common. The black skeletal pigment found in extant coralla is retained in most, but not all, of the fossil coralla.

Previous records: *O. crispata* (Lamarck): Hamada (1963*a,b*), Eguchi and Mori (1973).

Genus *Plesiastrea* Edwards & Haime, 1848

Plesiastrea versipora (Lamarck, 1816). Recorded from a single well-preserved specimen.

Previous records: *P. curta* (Dana): Eguchi and Mori (1973); *Montastrea curta* (Dana): Hamada (1963*a,b*; as illustrated by Hamada [1963*a*: 113]), Eguchi and Mori (1973).

Genus *Leptastrea* Edwards & Haime, 1848

Leptastrea purpurea (Dana, 1846). Recorded from several specimens.

Previous records: *L. purpurea* (Dana): Yabe and Sugiyama (1931), Hamada (1963*a,b*), Eguchi and Mori (1973); *Acanthastrea hemprichii* (Ehrenberg): Hamada (1963*a*; specimen reexamined by me).

Genus *Cyphastrea* Edwards & Haime, 1848
Specimens I collected appear to be of more than one species although only one can be clearly identified. Additional records are all from Hamada (1963*a,b*).

Cyphastrea serailia (Forskål, 1775). Common.

Previous records: *C. serailia* (Forskål): Yabe and Sugiyama (1931), Hamada (1963*a*), Eguchi and Mori (1973); ?*Montastrea curta* (Dana, 1846): Hamada (1963*a*: 61 and 63).

Cyphastrea chalcidicum (Forskål, 1775)

Previous records: *C. chalcidicum* (Forskål): Hamada (1963*a,b*), Eguchi and Mori (1973).

Cyphastrea japonica Yabe & Sugiyama, 1932

Previous records: *C. chalcidicum tanabensis* Yabe & Sugiyama: Hamada (1963*a,b*), Eguchi and Mori (1973).

Cyphastrea microphthalma (Lamarck, 1816)

Previous records: *C. microphthalma* (Lamarck): Hamada (1963*a,b*), Eguchi and Mori (1973).

Family CARYOPHYLLIIDAE Gray, 1847

Genus *Euphyllia* Dana, 1846

Euphyllia ancora Veron & Pichon, 1980

Previous records: *E. fimbriata* (Spengler): Hamada (1963*a,b*), Eguchi and Mori (1973). (This is an assumed identification on biogeographic grounds, because this species cannot be distinguished from *E. divisa* without soft parts.)

Family DENDROPHYLLIIDAE Gray, 1847

Genus *Turbinaria* Oken, 1815
Yabe and Sugiyama (1931) recorded *Turbinaria auricularis* Bernard.

Turbinaria peltata (Esper, 1794). Uncommon, recorded from a single specimen.

Previous records: *T. peltata* (Esper): Yabe and Sugiyama (1931), Hamada (1963*a,b*), Eguchi and Mori (1973).

?*Turbinaria frondens* (Dana, 1846)

Previous records: ?*T. contorta* Bernard: Hamada (1963*a,b*), Eguchi and Mori (1973) as *Turbinaria mesenterina* (Lamarck, 1816). I recorded it from a single well-preserved specimen.

Turbinaria reniformis Bernard, 1896. Recorded with doubt from a single specimen.

Previous records: ?*T. brueggemanni* Bernard: Hamada (1963*a,b*), Eguchi and Mori (1973).

LITERATURE CITED

ADAMS, C. G., D. E. LEE, and B. R. ROSEN. 1990. Conflicting isotopic and biotopic evidence for tropical sea-surface temperatures during the Tertiary. Palaeogeogr. Palaeoclimatol. Palaeoecol. 77: 289–313.

ASANO, K. 1936. Foraminifera of the Numa coral bed. J. Geol. Soc. Jpn. 43(519): 921 (in Japanese).

BELBIN, L. 1987. PATN Pattern analysis package reference manual. CSIRO Division of Wildlife and Rangelands Research, Canberra.

BRADLEY, R. S. 1985. Quaternary paleoclimatology. Allen and Unwin.

CLIMAP PROJECT MEMBERS. 1976. Science (Wash., D.C.) 191: 1131–1136.

COHMAP PROJECT MEMBERS. 1988. Science (Wash, D.C.) 241: 1043–1052.

EGUCHI, M., and R. MORI. 1973. A study of fossils from Tateyama city and its environs and recent coral fauna of Chiba Prefecture, Central Japan. Bull. Tokyo Coll. Domest. Sci. 13: 41–57 (in Japanese).

EREZ, J. 1978. Vital effect on stable-isotope composition seen in foraminifera and coral skeletons. Nature (Lond.) 273: 199–202.

FRYDL, P. 1982. Holocene ostracods in the southern Boso Peninsula. In T. Hanai, ed. Studies on Japanese Ostracoda. Univ. Mus., Univ. Tokyo Bull. 20.

HAMADA, T. 1931. On the so-called coral bed of Norma, Province of Awa. Pages 119–133 in H. Yabe and T. Sugiyama. A study of recent and semi-fossil corals of Japan. Sci. Rep. Tohoku Imp. Univ., ser. 2 (Geol.) 14.

———. 1963a. In [Scleractinia] Geological figures of Chiba-ken. Geological Education Research Group in Chiba Prefecture 4: 94–119 (in Japanese).

———. 1963b. Some problems on the Numa Coral Bed in Chiba Prefecture. Geol. Soc. Jpn. (Spec. Bull.): 94–119 (in Japanese with English abstract).

HAQ, B. U., and F. W. B. VAN EYSINGA. 1987. Geological time table. Elsevier, New York.

HEUSSER, L. E., and J. J. MORLEY. 1985a. Correlative 90 kyr northeast Asia–northwest Pacific climate records. Letters. Nature (Lond.) 313: 470–472.

———. 1985b. Pollen and radiolarian records from deep-sea core RC14-103: Climatic reconstructions of northeast Japan and northwest Pacific for the last 90,000 years. Quat. Res. (Tokyo) 24(1): 60–72.

HOSHINO, M. 1967. Radiocarbon age of Numa coral bed. Earth Sci. (Chikyu Kagaku) 21(6): 38–39 (in Japanese).

IMAMURA, A. 1925. Change of the coastline in Boso Peninsula. Rep. Imp. Earthquake Invest. Comm. 100(2): 91–93 (in Japanese).

KAWABE, M. 1985. El Nino effects in the Kuroshio and western north Pacific. Pages 31–43 in W. S. Wooster and D. L. Fluhardy, eds. El Nino North: Nino effects in the eastern subarctic Pacific Ocean. Washington.

KONISHI, K. 1967. Rate of vertical displacement and dating of reefy limestones in the marginal facies of the Pacific Ocean. Quat. Res. (Tokyo) 6(4): 207–223 (in Japanese).

MATSUDA, T., Y. OTA, M. ANDO, and N. YONEKURA. 1978. Fault mechanism and recurrence time of major earthquakes in the southern Kanto district, Japan, as deduced from coastal terrace data. Geol. Soc. Am. Bull. 89(11): 1610–1613.

MOORE, T. C., L. H. BRUCKLE, K. GEITZENAUER, B. LUZ, A. MOLINA-CRUZ, J. H. ROBERTSON, H. SACHS, C. SANCETTA, J. THIEDE, P. THOMPSON, and C. WENKAM.

1980. The reconstruction of sea temperatures in the Pacific Ocean of 18,000 B.P. Mar. Micropaleontol. 5:215–247.

NAKAMORI, T. 1986. Community structures of Recent and Pleistocene hermatypic corals in the Ryukyu Islands, Japan. Sci. Rep. Tohoku Univ., ser. 2 (Geol.) 56(2): 71–133.

PICKETT, J. 1981. Late Pleistocene coral fauna from Evans Head, N.S.W. Alcheringa 5: 71–83.

SARRO, T., L. E. HEUSSER, and J. J. MORLEY. 1984. Marine and continental environments of Japan: 60,000 years of record from the Sea of Japan and Honshu. Geol. Soc. Am. Abstr. 16:62.

STOCKER, T. F., and L. A. MYSAK. 1989. Climatic fluctuations on the century time-scale: A review of high-resolution proxy-data. Climate Res. Group McGill Univ. Rep. 89-13.

SWART, P. K., and M. L. COLEMAN. 1980. Isotopic data for scleractinian corals explain their palaeotemperature uncertainties. Nature (Lond.) 283:557–559.

TRIBBLE, G. W., and R. H. RANDALL. 1986. A description of the high-latitude shallow water coral communities of Miyake-jima, Japan. Coral Reefs 4:151–159.

VERON, J. E. N. 1986. Corals of Australia and the Indo-Pacific. Angus and Robertson, Sydney, London.

———. 1992. Hermatypic corals of Japan. AIMS Monogr. Ser. 9: 1–234.

VERON, J. E. N., and P. R. MINCHIN. (in press). Correlations between sea surface temperature and the distribution of hermatypic corals in Japan. Cont. Shelf Res.

YABE, H., and T. SUGIYAMA. 1931. A study of recent and semi-fossil corals of Japan. Sci. Rep. Tohoku Imp. Univ., ser. 2 (Geol.) 14:119–133.

———. 1932. Reef corals found in Japanese seas. Sci. Rep. Tohoku Imp. Univ., ser. 2 (Geol.) 15(2):143–168.

———. 1935a. Revised lists of the reef corals from the Japanese seas and of the fossil reef corals of the raised reefs and the Ryukyu Limestone of Japan. J. Geol. Soc. Jpn. 42(502): 279–403.

———. 1935b. Geological and geographical distribution of reef-corals in Japan. J. Paleontol. 9(3): 183–217.

YOKOYAMA, M. 1911. Climatic changes in Japan since the Pliocene Epoch. J. Coll. Sci. Imp. Univ. Tokyo 32(5): 1–16.

YOON, J., and I. YASUDA. 1987. Dynamics of the Kuroshio large meander: Two-layer model. J. Phys. Oceanogr. 17(1): 66–81.