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MONSOONAL UPWELLING AND EPISODIC *ACANTHASTER* PREDATION AS PROBABLE CONTROLS OF CORAL REEF DISTRIBUTION AND COMMUNITY STRUCTURE IN OMAN, INDIAN OCEAN

BY

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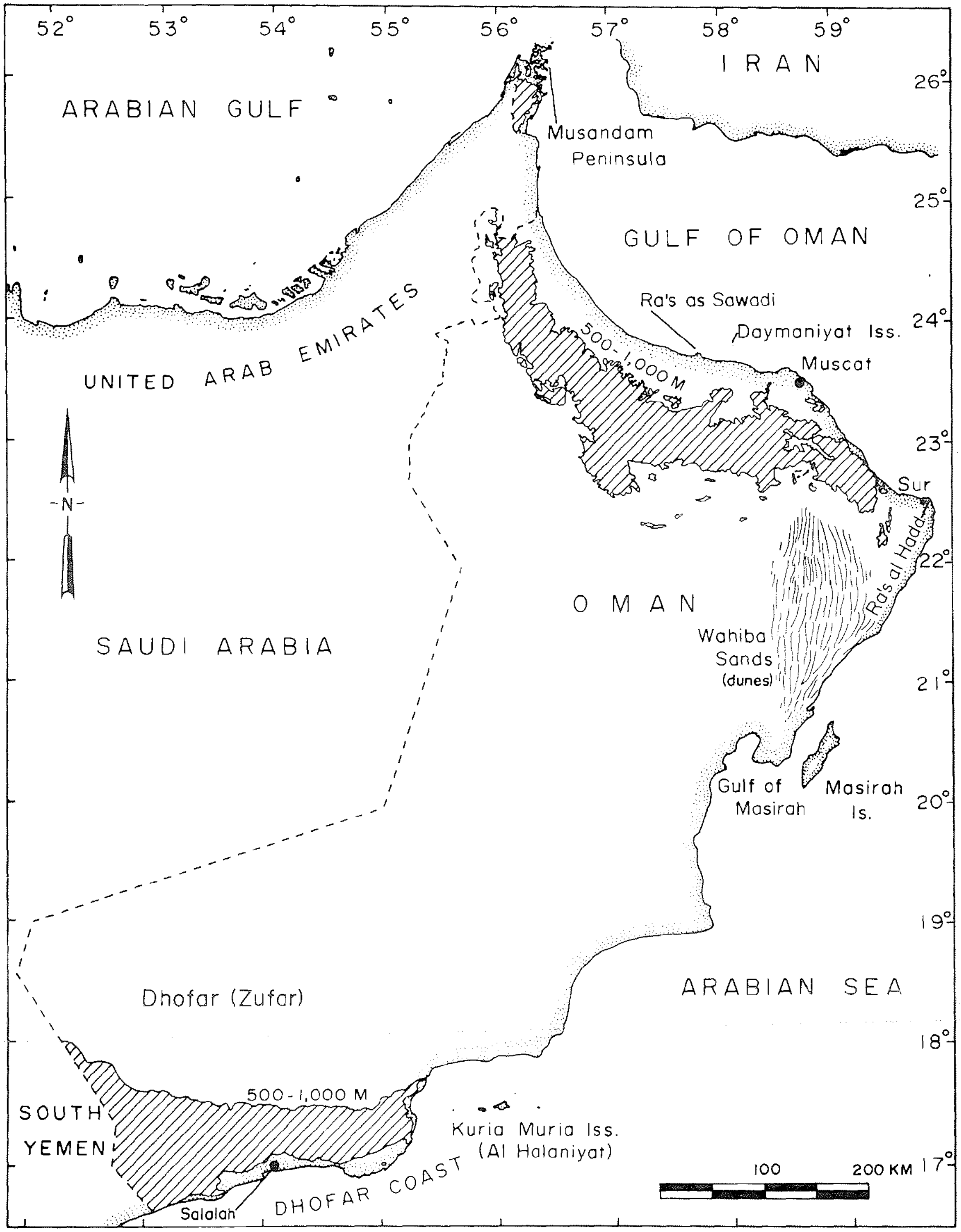

Figure 1. Sultanate of Oman and surrounding waters. After the topographic map of Shell Markets (Middle East) Ltd., 1977, scale 1:1,000,000. Mountains (hatched areas) only shown for Oman.

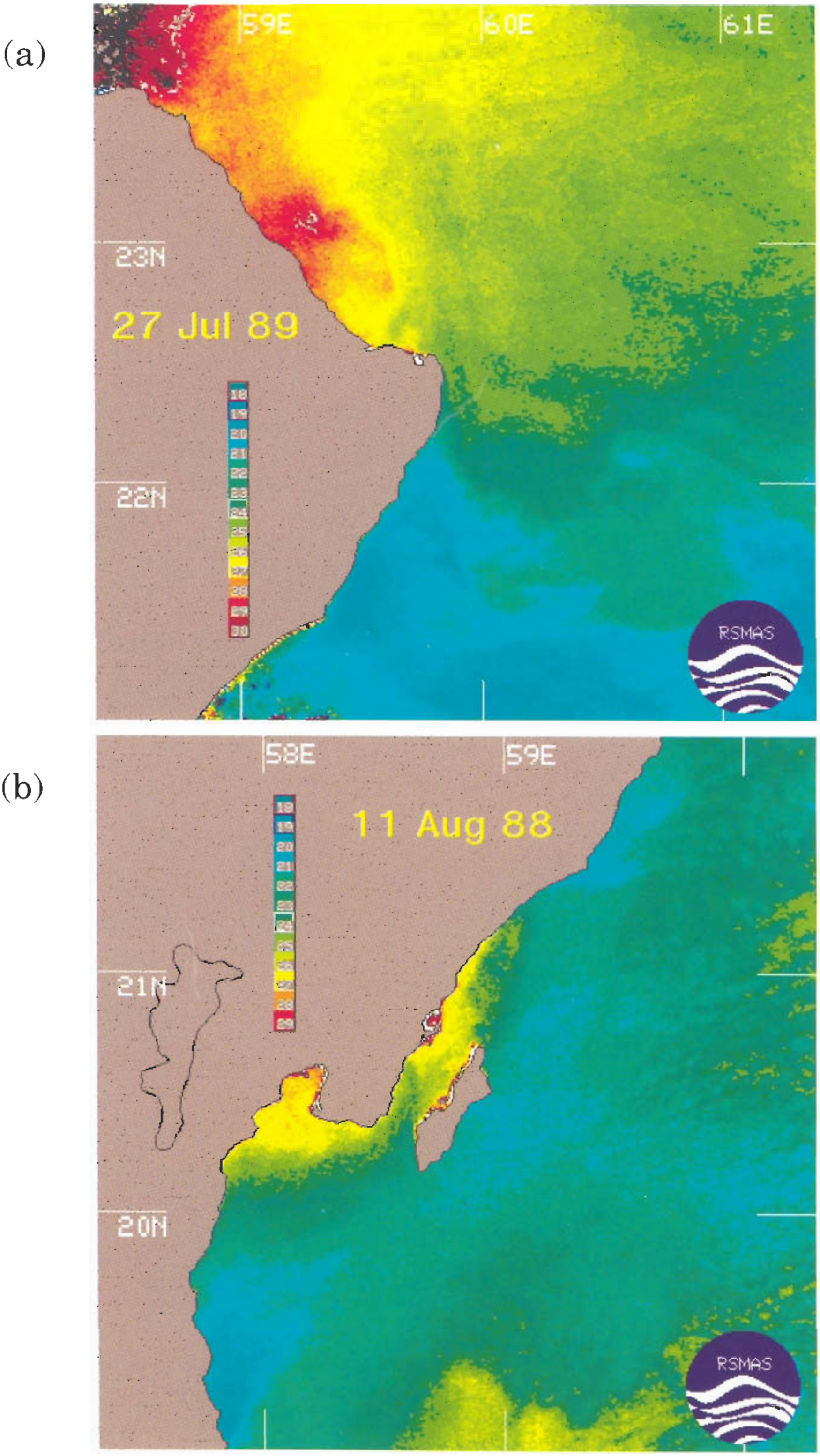

Plate 1. Satellite-derived sea surface temperature (SST) fields off Oman. (a) Easternmost Arabian Peninsula with a marked SST gradient along the Gulf of Oman/Arabian Sea boundary; (b) Masirah Island with high SSTs in Masirah Channel and the northern Gulf of Masirah. An SST scale (°C) is provided with each image. [P.W. Glynn]

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ABSTRACT

Fringing and patch coral reefs are present on the Arabian (Persian) Gulf shores of northern Oman (Musandam) and in the Gulf of Oman, notably off the Daymaniyat Islands and in the Capital (Muscat) area. Coral reefs are generally absent from the Arabian Sea coast of southern Oman, most likely a result of monsoon-induced upwelling. However, fringing reefs are present on the northwest (leeward) side of Masirah Island and on the mainland opposite, both areas that are partly sheltered from open coast upwelling. *Acanthaster planci* was observed in the coral rich Gulf of Oman only, where it caused widespread and selective coral mortality during a population outbreak. Starting in 1978-79, with diminishing effects to 1982, coral reefs with high acroporid coral cover experienced high mortalities with virtually all *Acropora* spp. eliminated on many reefs. Reefs with high pocilloporid coral cover largely escaped predation, probably because *Acanthaster* encountered difficulties in traversing continuous stands of this coral: the coral's nematocysts and the presence of symbiotic crustacean guards deter the starfish. Thus, where environmental conditions are suitable for reef development, sporadic, high level *Acanthaster* predation can modify coral community structure through the differential survival of coral prey and hence lead to the development of *Acanthaster* resistant reef types.

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INTRODUCTION

This paper grew out of surveys conducted in the Sultanate of Oman to assess damage to coral reefs caused by the starfish corallivore *Acanthaster planci* (Linnaeus). The Ministry of Agriculture and Fisheries (MAF) received reports during 1978-1980 indicating that population outbreaks of *A. planci* were causing high mortalities among reef corals in the Daymaniyat Islands and along the coast near Muscat (Gulf of Oman), also known as the Capital area (Figure 1). Since so little was known of the extent of coral community development and the distribution of *A. planci* in Oman at that time, the MAF decided to extend the survey to four other areas in Oman, including (1) the Musandam Peninsula at the southern end of the Arabian (Persian) Gulf, (2) Ra's al Hadd (east of Sur), which borders the Gulf of Oman and Arabian Sea, (3) Masirah Island, and (4) the coastal area of Dhofar (Zufar), the latter two areas in the Arabian Sea.

When the present field studies were conducted in 1982 the only information available on Omani corals was that in Rosen (1971) and Cornelius et al. (1973), both of whom reported on corals in the Musandam Peninsula region. Fifteen reef-coral genera were listed by Rosen (1971), and Cornelius et al. (1973) claimed that 'true reefs', i.e. structures with significant framework development, were absent from this region. Stoddart's (1971a) synoptic map of the distribution of coral reefs in the Indian Ocean shows coral reefs present only in the Capital area and along the Arabian Sea coast of Oman.

Several important studies on the corals and coral reefs of Oman have appeared since the early 1980s. In the UNEP/IUCN (1988) handbook of Coral Reefs of the World (vol. 2), 11 studies were listed that dealt with reef corals from the coastal areas of Oman. These papers were published mainly as technical reports between 1983-1986. The studies of Green and Keech (1986), Glynn (1987), Sheppard (1988), and Sheppard and Salm (1988), generally more accessible than the technical reports, provide information on the general biology, systematics and ecology of Omani corals and coral reefs. More recently, Sheppard et al. (1992) present a general account of coral reef ecology in the Arabian region, and the following article by Salm (1993) in this issue offers new information on various disturbances to coral reefs and the extent of reef development along the Arabian Sea coast of Oman.

Coral communities and coral reefs in the Gulf of Oman and Arabian Sea experience upwelling. Strong upwelling impacts corals and restricts reef development. For example, coral reef development is limited or absent in upwelling areas in the eastern Pacific (Dana, 1975; Glynn and Wellington, 1983), Marquesas Islands (Ladd, 1971; Sournia, 1976), and off equatorial west Africa (Laborel, 1974) and the Venezuelan coast (Antonius, 1980). When sea water temperatures fall below about 18°C for an extended period (2-4 weeks or longer) corals suffer partial or total tissue death (Glynn and Stewart, 1973; Birkeland, 1977; Glynn and D'Croz, 1990) and can be competitively displaced by macroalgae, which usually show accelerated growth as a result of increased nutrients. The elevated nutrient concentrations in upwelled waters around coral reefs (Sournia, 1976), as well as in waters bathing many high latitude reefs (Johannes et al., 1983; Hatcher, 1985, 1991; Coles, 1988), favor the growth of phytoplankton and macroalgae. Although the monsoonal upwelling system of the Arabian Sea coast of Oman has been well known in general terms (Currie et al., 1973; Bruce, 1974), only during the past decade have studies revealed detailed patterns of coastal upwelling (Elliott and Savidge, 1990; Savidge et al., 1990; Brock and McClain, 1992; Brock et al., 1992). This study contrasts thermal environments in the Gulf of Oman and Arabian Sea, derived from long-term ship measurements and recent remote sensing observations, to reveal the influence of upwelling on the spatial distribution of Omani coral reefs.

Several recent studies have demonstrated a strong effect of *Acanthaster* predation on Indo-Pacific coral communities, especially at high corallivore population densities (Potts, 1982; Moran, 1986; Glynn, 1990a). The effects of *Acanthaster* on corals in Oman were unknown before the 1980s. I observed relatively large numbers of *Acanthaster* in the Gulf of Oman in 1982, evidently the remnants of a population outbreak that occurred there between 1978-80. From observations of extensive, recently killed corals and the feeding activities of *Acanthaster*, this predator can exercise a strong influence on coral survivorship in some areas of Oman. Further, prey selectivity data revealed that *Acanthaster* also can have a significant effect in altering the species composition of coral communities (Glynn, 1987). In this paper, I will evaluate the relative importance of upwelling and predation respectively in regulating coral community structure and in controlling the distribution of coral reefs under upwelling and non-upwelling conditions.

METHODS

The coastal surveys in Oman, from the Musandam Peninsula in the north to the Dhofar Province in the south (Figure 1), were conducted from 20 September to 25 October, 1982. Coral habitats were located with the help of personnel from the MAF, by local fishermen and sports divers, from hydrographic charts, by surveying shorelines from elevated sites (hill tops and towers), and by aerial reconnaissance. Work underwater was carried out by surface diving and scuba during daylight hours from small boats that could be maneuvered near shore. The nature and extent of coral cover, and the physical dimensions of coral framework construction were determined at each station. Only crude estimates of reef framework thickness were obtained. On small, thin reefs the thickness of coral buildups was estimated visually and by modest surface excavation. On larger reefs, the depth range of vertical buildups was estimated from the depth differences of the reef crest or reef flat and the reef base, measured with a standard, calibrated depth gauge. Bottom areas were measured with a chain marked at 1 m intervals. Field sketches of some reefs were made, which emphasized coral zonation and vertical relief. Reef dimensions also were estimated from near-vertical aerial photographs taken at 600 m elevation. The sizes of reef features in the aerial photographs were determined from ground-truth measurements and with reference to distance scales on hydrographic charts.

Wainwright's (1965) distinction between coral communities and structural coral reefs was followed in this study. That is, coral formations were recognized as true reefs when it could be determined that corals, calcareous algae and other associated organisms were actively contributing to the accumulation of interlocking framework structures. These structures form significant topographic features, which result from the skeletal accumulation of modern calcifying organisms (Stoddart, 1969). No Pleistocene reef structures were found in this study. The recognition of coral reefs by Sheppard and Salm (1988) was more restrictive than the above, requiring the presence of a "...characteristic reef topography of a horizontal reef flat at low tide and a reef slope.". I prefer Wainwright's (1965) definition because several relatively large coral buildups observed in this study (4-6 m thick, 1-2 ha) lacked obvious reef flats, but otherwise would qualify as true structural reef formations.

Coral species composition and percent live cover were determined from 10 m-long chain transects and from 0.25 m^2 point quadrat counts. Chain transects (with 1.4 cm links) were positioned along isobath contours in all coral zones (Porter, 1972a). Chain transect sampling intervals of 5, 10 and 15 m were used depending on reef widths. Also, 6 to 7 transects (with 710 sampling points each) were sampled on each reef. Additional sampling on reefs was performed with quadrats, each with 16 uniformly spaced sampling points (Glynn, 1987). Usually each reef zone was sampled with 10 haphazardly located quadrats. Species diversity, employing the Shannon-Wiener index (H', see Pielou, 1977), was calculated for each zone. Coral species and colony condition (i.e., live, eaten, recently dead, etc.), and the general substrate type (i.e., algae, sponge, soft coral, bryozoans, sand, rock, etc.) were recorded. Voucher specimens of questionable or unknown species were collected for later identification (see Table 1). John W. Wells identified all specimens except *Acropora* spp. and this collection was donated to the U.S. National Museum, Smithsonian Institution, Washington, D.C. Carden C. Wallace identified *Acropora* species and these were deposited in the collections of the Queensland Museum, North Queensland Branch, Townsville, Australia. A total of 75 sites were surveyed in this study. Their locations, enumerated chronologically, are shown in Figures 2-7. Site 24 (Ra's as Sawadi) was located about 85 km west of Muscat. Surface sea water temperatures were measured with a calibrated mercury thermometer at Arabian Sea sites, and horizontal water visibility and sea state also were noted.

Adult *Acanthaster* were located by swimming over coral substrata and searching under corals and in other cryptic habitats. The search effort was intensified in areas with presumed feeding scars. No other corallivore was found in Oman that produces a feeding scar similar to that of *Acanthaster*. An effort was made to find juvenile *Acanthaster* by searching with scuba in

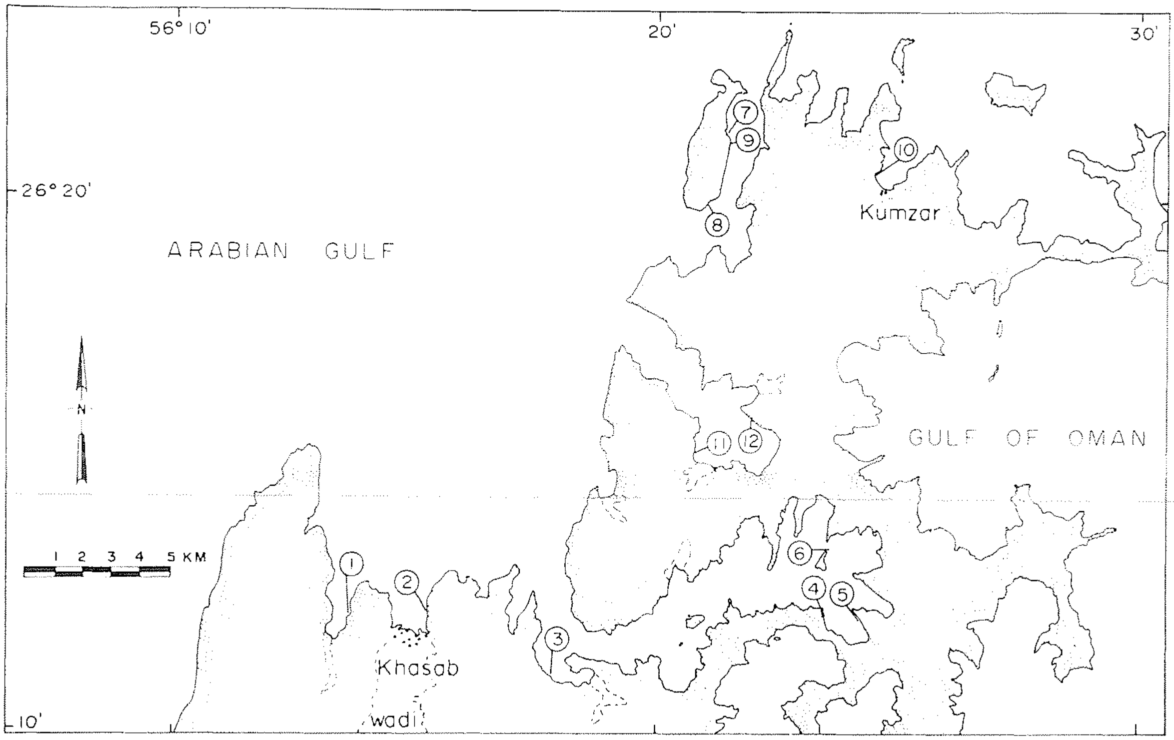

Figure 2. Location of sites surveyed on the Musandam Peninsula, northern Oman. From chart of Oman and United Arab Emirates (Kumzar), scale 1:100,000, series K668, editions 4-GSGS and 2-GSGS. Director of Military Survey, Ministry of Defence, United Kingdom, 1975.

Table 1. Zooxanthellate scleractinians identified from voucher specimens collected at the various localities indicated. M, Musandam; C, Capital area; R, Ra's Abu Da'ud to Ra's al Hadd; MR, Masirah; D, Dhofar.

Family	Species	Locality				
		M	C	R	MR	D
Thamnasteriidae	*Psammocora contigua* (Esper)	+	+			
Pocilloporidae	*Pocillopora damicornis* (Linnaeus)	+	+			
	Stylophora erythraea von Marenzeller					+
	Stylophora pistillata (Esper)	+	+			
	Stylophora pistillata (Esper) *mordax* (*palmata*) form				+	
	Stylophora subseriata (Ehrenberg)	+				+
Acroporidae	*Acropora aspera* (Dana)				+	
	Acropora cytherea (Dana)	+	+			+
	Acropora glauca (Brook)					+
	Acropora cf. glauca (Brook)		+			+
	Acropora haimei (Milne Edwards & Haime)	+				
	Acropora nasuta (Dana)	+	+			
	Acropora pharaonis (Milne Edwards & Haime)	+	+			
	Acropora cf. selago (Studer)	+				
	Acropora valida (Dana)	+				
	Acropora sp.	+	+			
	Astreopora myriophthalma (Lamarck)		+			
	Montipora cristagalli (Ehrenberg)				+	
	Montipora effusa (Dana)		+	+		
	Montipora foliosa (Pallas)				+	
	Montipora gracilis Klunzinger	+	+			+
	Montipora laevis Bernard				+	
	Montipora scutata Bernard	+			+	
	Montipora tuberculosa (Lamarck)		+			
	Montipora venosa (Ehrenberg)				+	
	Montipora cf. M. multiformis Bernard					+
	Montipora cf. M. solanderi Bernard				+	
Agariciidae	*Pavona angularis* Klunzinger			+		
	Pavona cactus (Forskaal)	+				
Siderastreidae	*Anomastrea irregularis* von Marenzeller		+			
	Coscinaraea monile (Forskaal)					+

Table 1 - continued

		M	C	R	MR	D
Siderastreidae	*Siderastrea lilacea* Klunzinger				+	
Poritidae	*Goniopora savignyi* Dana	+	+		+	
	Porites cylindrica Dana				+	
	Porites columnaris Klunzinger	+				
	Porites solida (Forskaal)				+	
	Porites cf. P. cocosensis Wells		+		+	
Faviidae	*Cyphastrea chalcidicum* (Forskaal)		+			
	Cyphastrea microphthalma (Lamarck)	+				
	Cyphastrea serailia (Forskaal)		+		+	+
	Echinopora hirsutissima Milne Edwards & Haime		+			
	Echinopora lamellosa (Esper)	+				
	Favia favus (Forskaal)				+	
	Favia pallida (Dana)					+
	Favites abdita (Ellis & Solander)				+	+
	Favites complanata (Ehrenberg)				+	+
	Favites pentagona (Esper)		+	+	+	+
	Favites cf. F. spinosa (Klunzinger)	+	+			
	Leptastrea transversa Klunzinger	+	+			
	Platygyra rustica (Dana)	+			+	+
	Platygyra sinensis (Milne Edwards & Haime)	+				
	Plesiastrea versipora (Lamarck)		+			
Oculinidae	*Galaxea astreata* (Lamarck)		+			
Merulinidae	*Hydnophora exesa* (Pallas)	+			+	+
	Hydnophora microconos (Lamarck)		+	+		
Mussidae	*Acanthastrea echinata* (Dana)	+	+		+	
	Symphyllia radians Milne Edwards & Haime	+		+		
Pectiniidae	*Echinophyllia aspera* Ellis & Solander		+			
	Oxypora lacera (Verrill)	+	+			
Dendrophylliidae	*Turbinaria crater* (Pallas)		+			+
	Turbinaria peltata (Esper)		+			
	Turbinaria cf. T. calicularis Bernard				+	

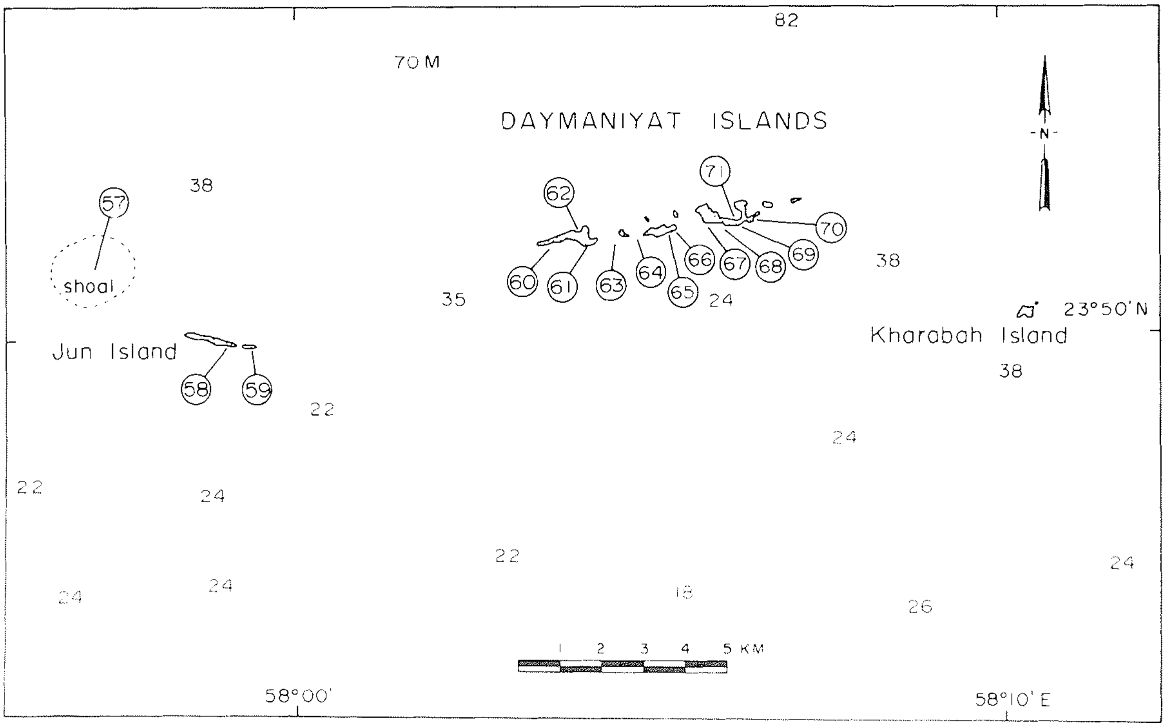

Figure 3. Location of sites surveyed in the Daymaniyat Islands, Gulf of Oman. Map sketched and enlarged from chart published by D Survey, scale 1:100,000, Ministry of Defence, United Kingdom, 1971. Soundings (in m) from marine chart 2851, Masirah to Ruus al Jibal, Admiralty, London, 9 May 1952.

the small cavities of live and dead corals, by searching in coral rubble, and by lifting and examining the undersurfaces of large, live and dead corals. The search effort was recorded in man-hours. Starfish that could be lifted from the substrate were measured in a relaxed state with a cm rule. Both total (arm tip to arm tip) and disc diameters were measured. Coral species prey were noted and 80 point counts of potential prey in the vicinity of feeding *Acanthaster* were recorded as described in Glynn (1987).

Sea surface temperature (SST) data from Nansen casts, spanning the period 1933-1979, were obtained from the National Oceanographic Data Center (NOAA), Washington, D.C. The temperature measurements were generally recorded to the 0.01 place and probably have a minimum precision of ± 0.1°C. Monthly SST plots were constructed by manual contouring.

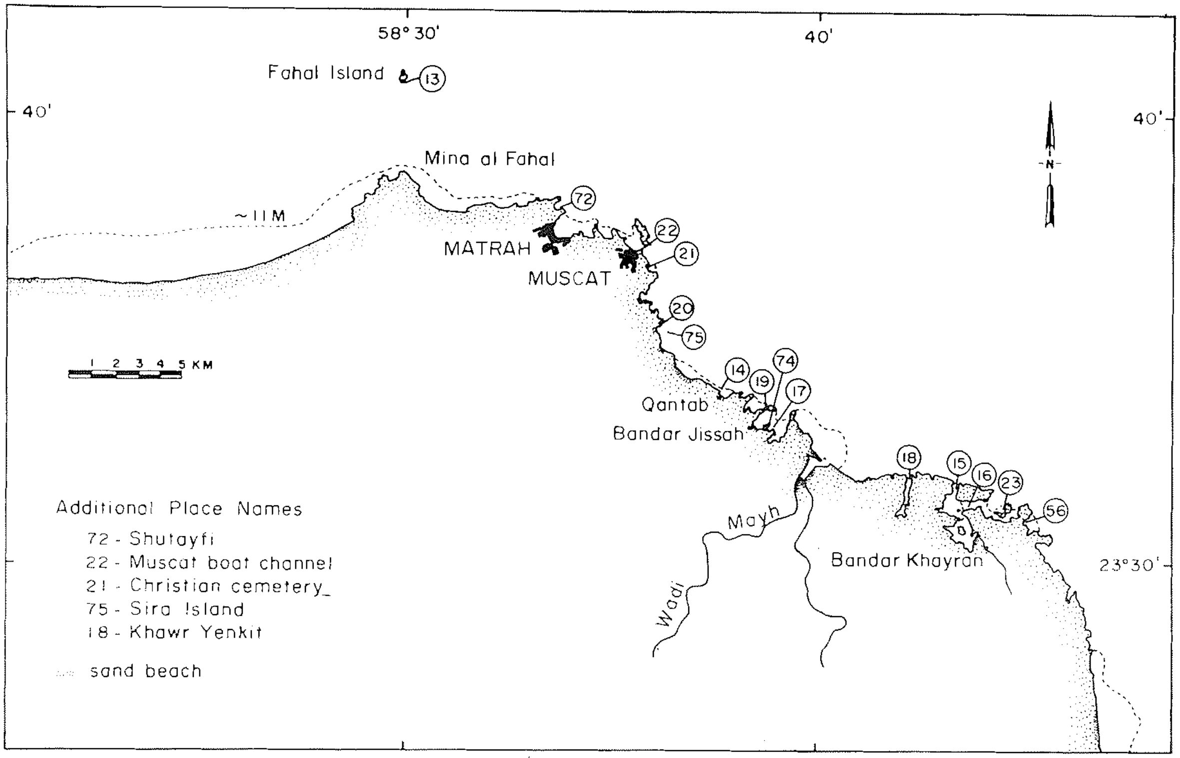

Figure 4. Location of sites surveyed in the Capital (Muscat) area, Gulf of Oman. Dark patches at Matrah and Muscat indicate areas of high population density. After Admiralty Chart 3522, Gulf of Oman, London, 1967.

Satellite infra-red data from 1988 and 1989 were analyzed to reveal near-shore SST patterns and the location of thermal fronts during the summer monsoon season. The time series includes observations from late May to late September, obtained from the Advanced Very High Resolution Radiometer (AVHRR), Local Area Coverage (LAC) data. SST was calculated using a multispectral algorithm described by McClain et al. (1985). These data are archived in the Division of Meteorology and Physical Oceanography, Rosenstiel School of Marine and Atmospheric Science. The NOAA satellite carrying the AVHRR was located in a sun-synchronous polar orbit with ascending passes at approximately 0300 and 1500 (± 50 min.) local sun time. The early morning passes usually provided the clearest images. All SST imagery was mapped to a fixed geographic grid covering the area 55-64°E, 18-26°N with a spatial resolution of approximately 2 km. Detailed analyses were confined to 1° square grids centered over Masirah Island and the Muscat area, and a 6° rectangular grid centered over the Gulf of Oman-Arabian Sea boundary [see Remote sensing data (1988, 1989) below].

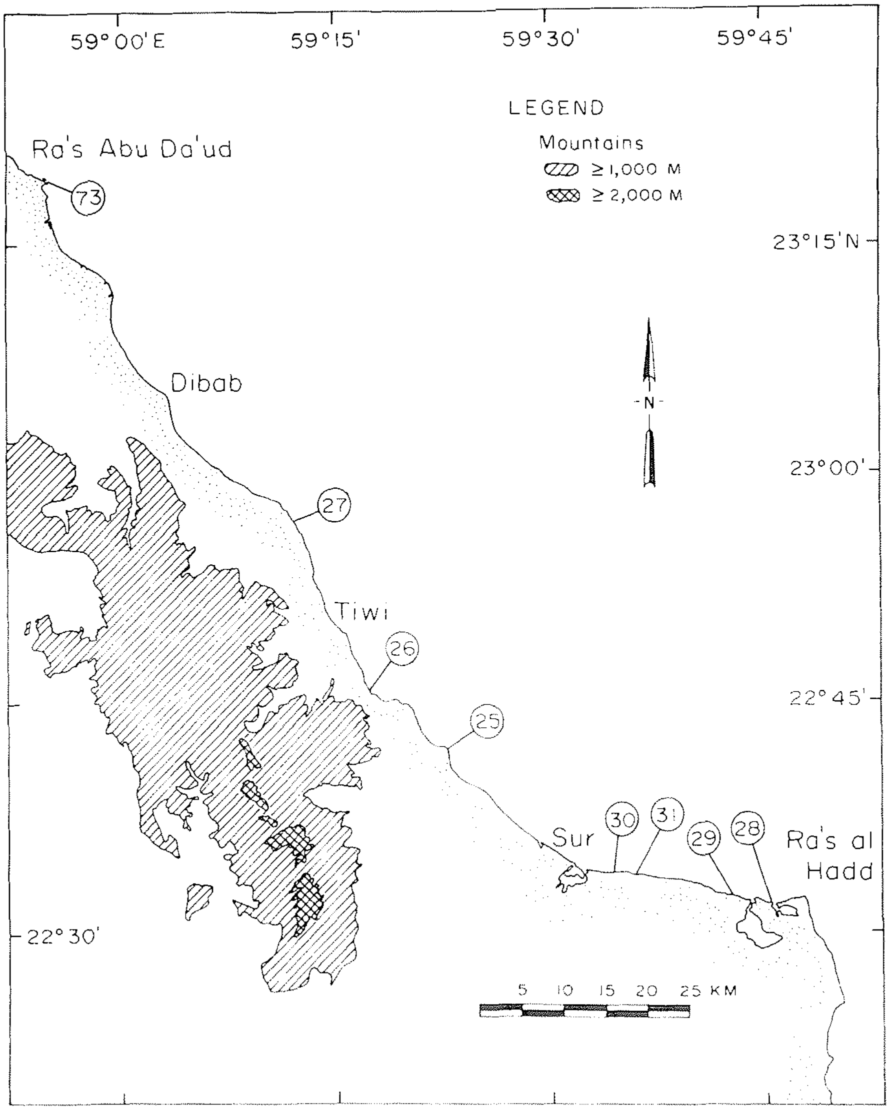

Figure 5. Location of sites surveyed from Ra's Abu Da'ud to Ra's al Hadd, Gulf of Oman. From charts of Muscat and Sur, scale 1:250,000, series 1501, editions 3-GSGS. Director of Military Survey, Ministry of Defence, United Kingdom, 1975.

Excluding periods of high cloud cover, the analysis included 47 days each over Muscat and Masirah in 1988 and 58 and 61 days respectively over Muscat and Masirah in 1989. The total number of images analyzed over the boundary zone was 42 in 1988 and 58 in 1989. Color transparencies were obtained from the SST color images and the positions of thermal fronts and upwelling areas were mapped from these onto acetate film overlays.

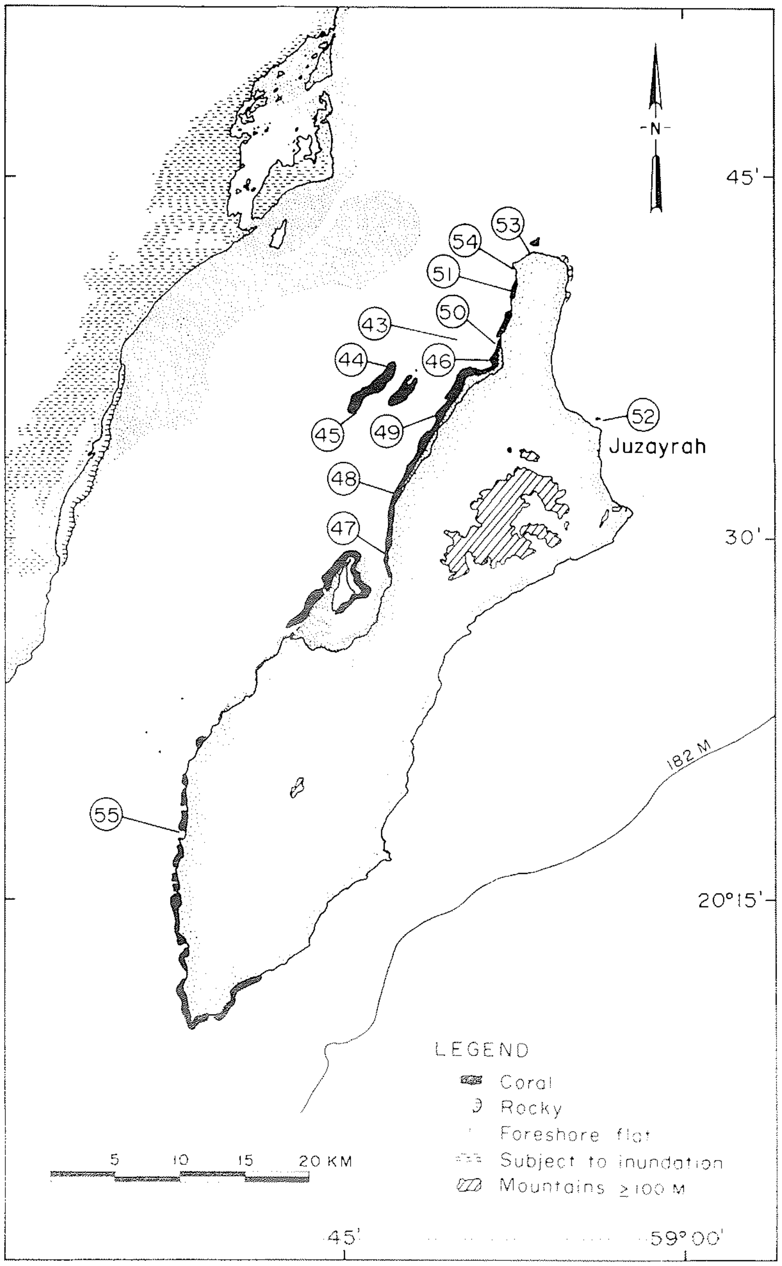

Figure 6. Location of sites surveyed at Masirah Island, Arabian Sea. From chart of Al Masirah, scale 1:250,000, series 1501, edition 2-GSGS. Director of Military Survey, Ministry of Defence, United Kingdom, 1981.

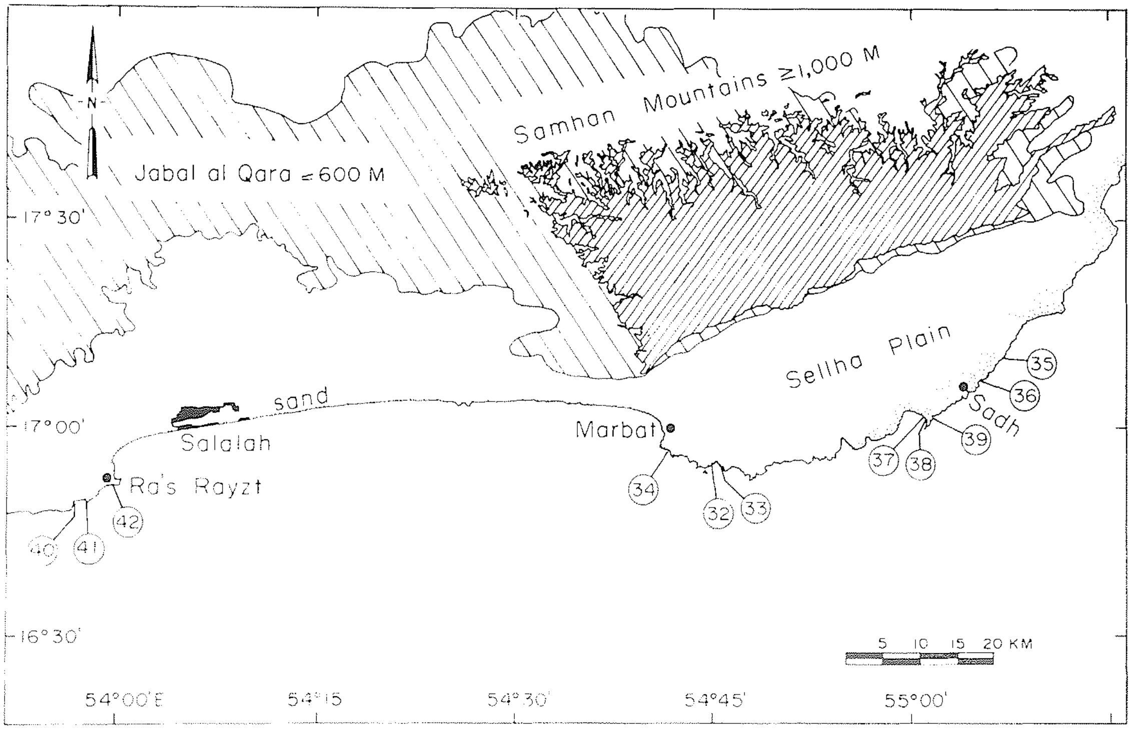

Figure 7. Location of sites surveyed in the Dhofar area, Arabian Sea. Dark patch at Salalah indicates area of high population density. From chart Salala (= Salalah), scale 1:250,000, series 1501, edition 2-GSGS. Director of Military Survey, Ministry of Defence, United Kingdom, 1980. Elevation of al Qara Mountains from Map of Oman, The Sultanate of Oman (2nd ed. revised, 1983), Malt International, P.O. Box 8357, Beirut, Lebanon).

RESULTS

Distribution and Nature of Coral Communities and Coral Reefs

Musandam. Ramose and table *Acropora* species predominated in the areas investigated in the Musandam, although *Pavona, Porites, Goniopora, Montipora,* and *Pocillopora* species also were patchily abundant. The occurrence of coral formations was sporadic, but where present live coral cover tended to be high (often ≥ 60%). Zooxanthellate corals ranged in depth from about the extreme low water tidal datum to 10-12 m. Numerous coral species were present at five sites (1, 3, 6, 10 and 11), but no reef development was evident. Reef frame construction, ranging between 2 and 4 m (maximum) in relief, was observed at sites 2, 4, 5, 7, 8, 9 and 12 (Figure 2). A minimum of 22 reef-building coral species were present at the 12 sites (Table 1).

A small, but well developed fringing reef was present on the east side of the bay at Khasab (site 2). The water was turbid, due to wind-generated waves that suspended fine calcareous sediments, with maximum lateral visibility of 5 m. Massive *Porites* colonies dominated coral cover on the reef flat and from surface views seemed to contribute importantly to reef slope construction as well. The majority of the *Porites* colonies on the reef flat were dead, and these were interspersed with live species of *Platygyra, Favia* and *Favites*. Many of the corals on the reef flat were covered with fine sediment. Species of *Acropora, Goniopora, Platygyra,* and *Stylophora pistillata** were present on the reef slope. A few large (1-2 m diameter) colonies of *Acropora cytherea* were present on the upper reef slope. Corals thinned out at 4 m depth on a gently sloping sand bottom. Maximum relief of this reef was between 3-4 m.

Coral cover was high within the inner reaches of the fjord-like inlets (sites 4-6, 11 and 12) where winds and wave action were reduced and water visibility increased to about 10 m. Fringing reefs were present at sites 4 and 5 with maximum reef frame relief of 2-3 m. The reef flats were only 4-5 m in width and bordered deeply notched (1-2 m), limestone cliffs. The notches were at mid-tidal elevation and presumably formed by lithophagine bioerosion and sand scouring (Cornelius et al., 1973). Corals were distributed sparsely on most reef flats with the following genera observed: *Cyphastrea, Favia, Favites, Goniopora, Pavona, Platygyra,* and *Porites*. The forereefs in this area exhibited 80-100% cover of *Pavona cactus,* and this coral was abundant from the upper reef slope (2 m) to 10-12 m depth. Some branching *Acropora* species also were present on the upper reef slope.

Coral species richness appeared highest at sites 7-9 (Goat Island or Jazirat el Ghanam). Branching and tabular *Acropora* spp. were abundant (Figures 8 and 9). Several *A. cytherea* colonies 1-1.5 m in diameter were observed at site 7. Some massive *Porites* colonies attained 4 m in height. At site 8, monogeneric thickets of branching *Acropora* spp. formed 1-3 m thick coral frameworks (Figure 8). Also at site 8, virtually monospecific stands of *Pocillopora damicornis* formed reef frameworks that were 3-4 m thick (Figure 9). A few scattered colonies of *Porites solida* were present within the pocilloporid patch reefs. The acroporid and pocilloporid reefs, usually centered between 1 and 5 m depth, covered about 0.5 ha each. *Dendrophyllia*

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*The authors of the scientific names of coral species identified in this study are provided in Table 1.

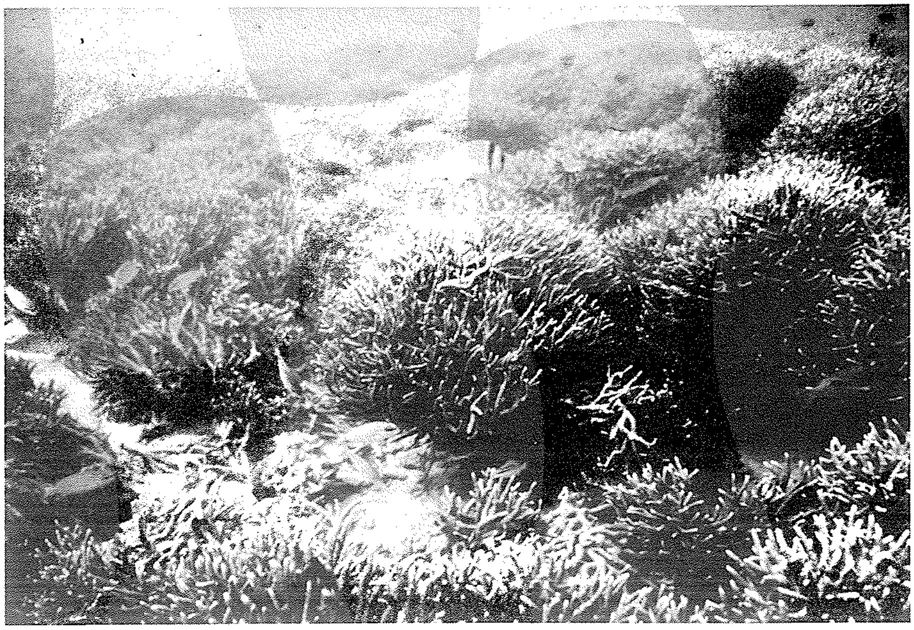

Figure 8. Underwater view of *Acropora* spp. corals, Musandam Peninsula, site 8 (Fig. 2), 4 m depth (21 September 1982).

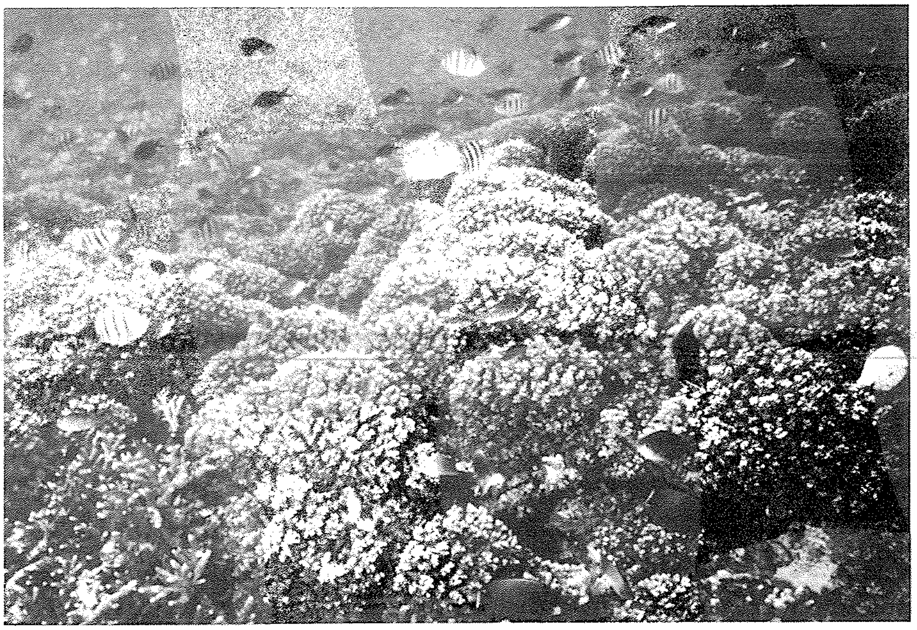

Figure 9. Underwater view of a dominantly *Pocillopora damicornis* build-up, Musandam Peninsula, site 8 (Fig. 2), 4 m depth (21 September 1982). This patch reef was approximately 0.5 ha and had a maximum reef frame thickness of 3-4 m.

micrantha (Ehrenberg), and other azooxanthellate corals, were abundant on partially shaded limestone boulders at 1-3 m depth. Numerous species of reef corals continued down slope to a sand bottom at 10-12 m depth.

No *Pocillopora* spp. were seen at sites 1-6, but numerous colonies of *P. damicornis* were present in several coral communities at sites 7-12. Several of the latter displayed conspicuous bleached (whitened) branch tips. Occasionally a few colonies of *Pocillopora verrucosa* (Ellis & Solander) with stout branches and distinct verrucae also were found.

Coral communities at sites 7, 9, 11 and 12 appeared to have been subject to repeated rock slide disturbances. Large sections of steep limestone cliffs bordering the shoreline often collapsed, resulting in rock piles that covered the adjacent submarine shelf. Inspection of the undersides of rocks revealed crushed corals. Some of the older blocks were overgrown by corals, indicating successful recolonization and growth following rock slide events.

Schools of herbivorous fishes (e.g., scarids, acanthurids and kyphosids) or large invertebrate predators (e.g., tetraodontids, diodontids and balistids) were conspicuously absent. Large numbers of small predators, e.g. labrids, pomacentrids and haemulids, were abundant (Figures 8 and 9). A few large *Eucidaris metularia* (Lamarck) occasionally were observed on the live branches of *Acropora* corals, but there was no indication that they were feeding on coral tissue. Microfilamentous algae comprised the chief epibenthic plant cover, which are characteristic of reef habitats with reduced herbivory and low nutrient levels (e.g., Hatcher, 1983; Littler and Littler, 1984; Berner, 1990).

Daymaniyat Islands. *Acropora, Montipora, Pocillopora* and *Porites* species occurred abundantly at most sites in the Daymaniyat Islands (Figure 3). *Acropora cytherea*, 1-2 m diameter colonies, were prominent yet all of these large colonies were dead (Figures 10-13). The majority of these corals were in normal growth position and were overgrown with microfilamentous algae, hydroids, alcyonaceans and bryozoans. *Pocillopora damicornis* often was observed growing on the upper surfaces of dead *A. cytherea* (Figures 10 and 13). Also seen on dead *Acropora* were small (< 30 cm diameter) colonies of *Stylophora* sp., *Porites* sp., *Acropora* sp. and *Symphyllia radians*. The only notable large colonies that still exhibited patches of living tissue were *Porites*, which were tentatively identified as *Porites solida* (Figure 10). Where *Acropora* corals predominated, live cover was low (≤ 1%). Most bottom areas where *Pocillopora* and *Porites* predominated exhibited relatively few dead colonies and showed high live coral cover (≥ 50%, Figure 13). Mixed *Acropora-Pocillopora* communities, with nearly all *Acropora* dead and all

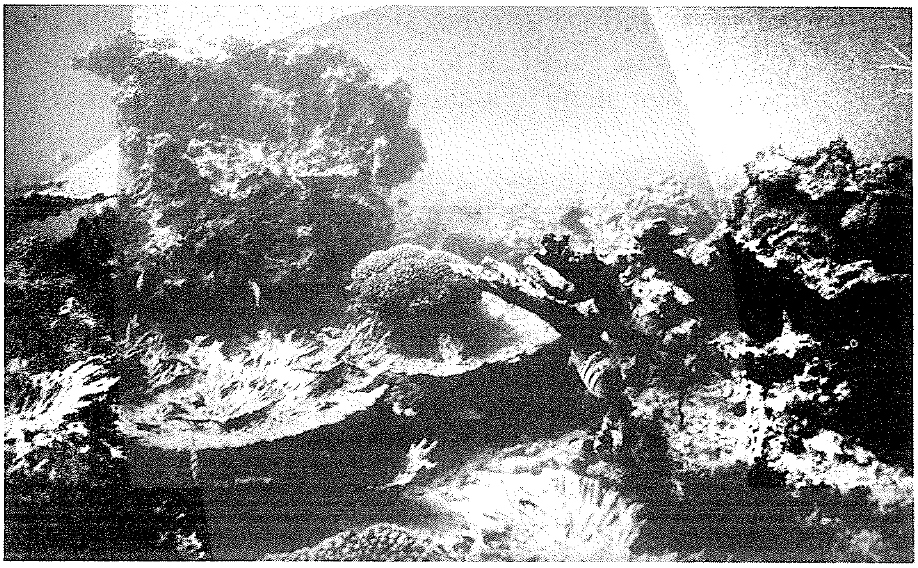

Figure 10. Underwater view of a dead, predominantly *Acropora* spp. coral community, Daymaniyat Islands, site 58 (Fig. 3), 4 m depth (20 October 1982). Note live *Pocillopora damicornis* colony resting on top of a dead *Acropora* coral (center of photograph).

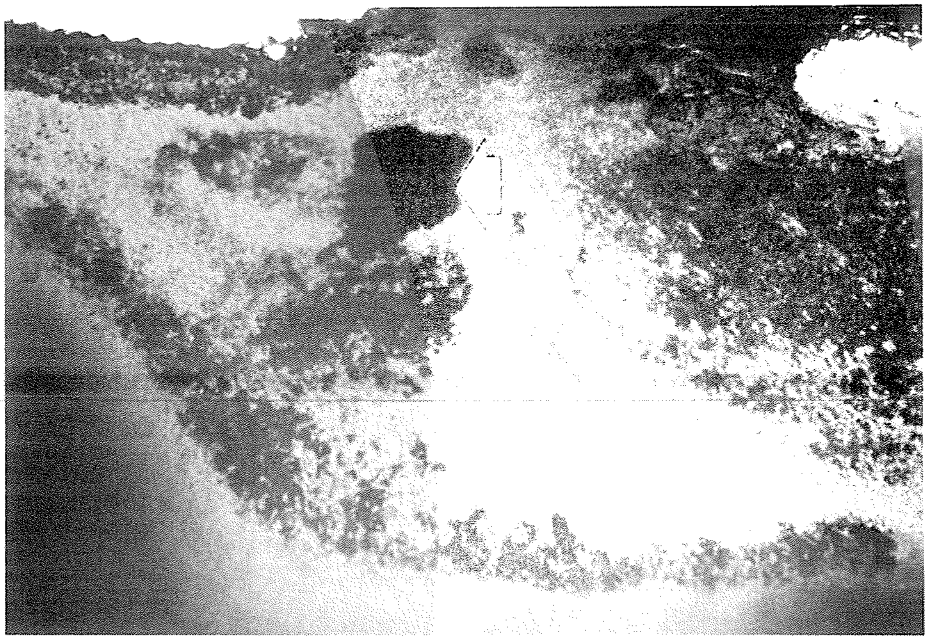

Figure 11. Near-vertical aerial view of leeward side of Jun Island, site 58 (Fig. 3), Daymaniyat group (ca. 600 m elevation, 18 October 1982). Dark, broken patches along shelf edge (bottom) and elsewhere represented mostly dead *Acropora* spp. communities. Dark, solid, trapezoidal patch (arrow) was a live *Pocillopora damicornis* build-up.

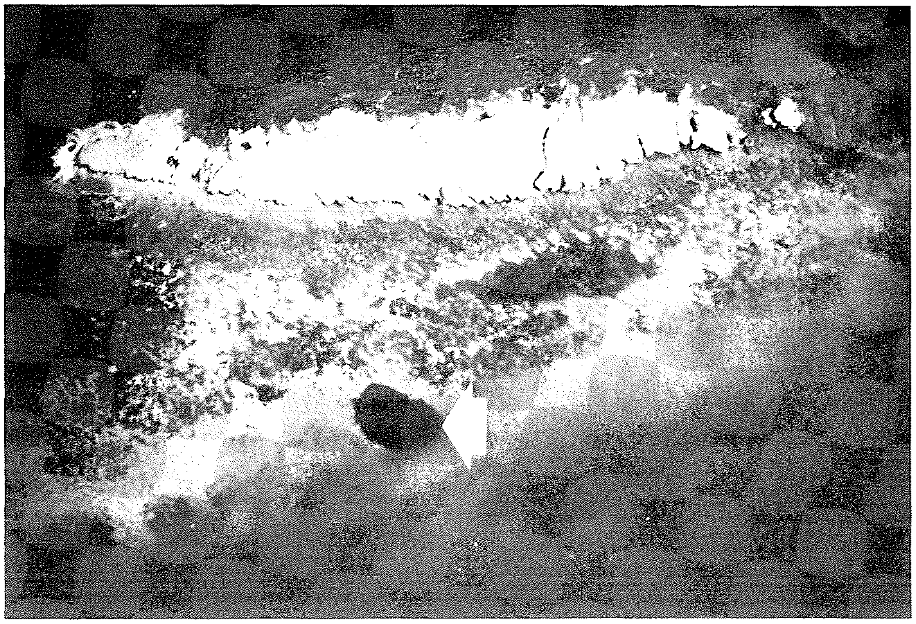

Figure 12. Near-vertical aerial view of island east of Jun Island, site 59 (Fig. 3), Daymaniyat group (ca. 600 m elevation, 18 October 1982). Dark patch on shelf edge (arrow) was a live *Pocillopora damicornis* build-up, dark patches on shelf consisted predominantly of dead *Acropora* spp. communities.

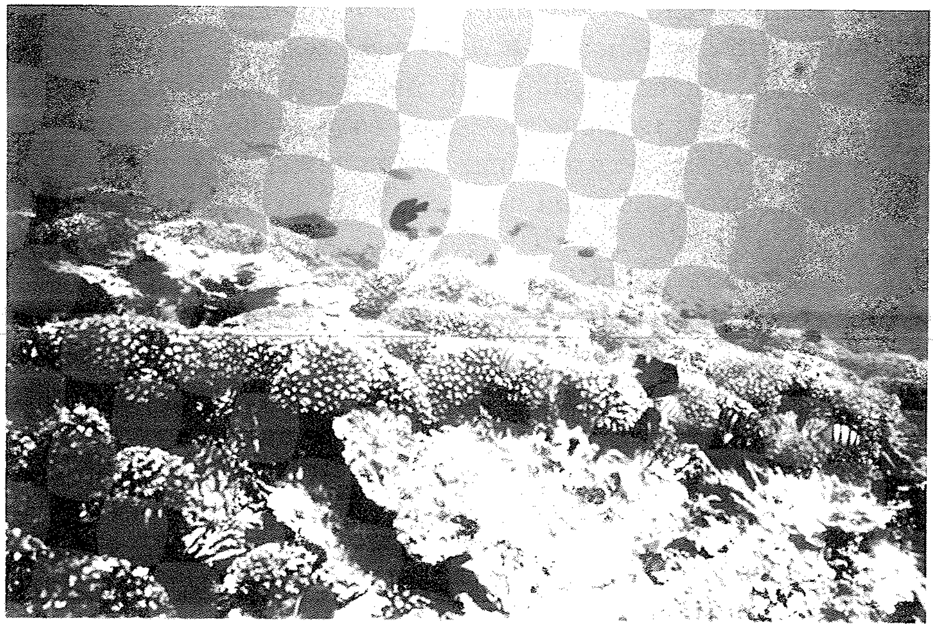

Figure 13. Underwater view of live *Pocillopora damicornis* colonies adjacent to dead *Acropora* spp., Daymaniyat Islands, site 60 (Fig. 3), 5 m depth, 19 October 1982. The line of *Pocillopora* colonies in the foreground is overlapping slightly (overgrowing) the dead *Acropora* colonies.

Pocillopora alive, indicated a marked disproportionately higher mortality of acroporid species.

Live corals occurred at a maximum depth of about 15 m, where light levels were high. Underwater visibility was high at all sites, approximately 20 m laterally. Patch and fringing reefs were well developed along the lee (south) sides of the island chain (Figures 11 and 12). Fringing reefs were present at sites 58 and 70. Massive *Porites* sp. were most abundant on the reef flats and shallow sections of these reefs, whereas *Pocillopora damicornis* tended to predominate on the deeper slopes to a calcareous sand bottom at 5-6 m depth. A shallow (1-2 m depth) moat between the leeward reef flat and shoreline was populated with *Platygyra, Stylophora,* branching *Porites, Montipora,* and *Acropora* at site 58. The framework relief of fringing reefs was approximately 4-5 m.

The dead *Acropora* patch reefs were present at shallow depth (2-5 m). Their vertical framework construction was slight, from about 1 to 3 m only, suggesting a youthful stage of development. These dead reefs, each covering several thousands of square meters of bottom, were observed at sites 58, 60, 63 and 65. *Porites* fringing reefs showed a vertical relief of 4-5 m, and the larger pocilloporid patch reefs appeared to have a relief of 6-7 m. The pocilloporid reefs, virtually monospecific stands of *Pocillopora damicornis,* were present on insular shelves (Figure 11) or at shelf-slope boundaries (Figure 12). Some of the pocilloporid reefs were elongate and paralleled the leeward shelf 4-5 m isobath. Such reefs were well developed at sites 59, 61, 66, 67, 68 and 69. Some pocilloporid reefs were elongate and appeared to follow the 4-5 m isobaths along the shelf edge. The shelf-edge pocilloporid reefs descended gradually into deeper water where they stopped abruptly on a gently sloping calcareous sand plain at 10-12 m depth. The black balistid *Melichthys indicus* Randall & Klausewitz was abundant where holes were present in the deeper sections of pocilloporid reefs.

Although reef building was not observed, coral communities were well developed at sites 57, 62 and 71. Scattered coral knolls constructed by massive *Porites* occurred at site 57. Numerous species occurred at sites 62 and 71 on the north sides of the islands. Wave action there stirred up sediments and reduced lateral visibility to about 10 m. Site 64 was a flat rock bottom with scattered dead coral cover.

Capital area. Nearly all of the reef-building coral species present in the Musandam and Daymaniyat Islands also were found in the Capital area (Figure 4). The chief reef frame builders also were similar in the three regions.

A group of rocky islands located immediately offshore of Ra's as Sawadi, about 85 km west of Muscat on the southern Al Batinah coast, was the location of site 24 (Figure 1). The abundant genera in this turbid (2-5 m lateral visibility) environment were *Acropora*, *Pocillopora* and *Porites*. *Acropora cytherea* and *Platygyra* also were observed. Patch reefs composed of branching *Acropora* and *Pocillopora damicornis* were present around some of the small islands. The maximum depth of these reefs reached only about 8 m, and maximum vertical relief was 1-2 m. A drying reef flat was present on the mainland coast, composed mainly of massive *Porites* colonies.

Pocilloporid reefs were well developed at Fahal Island (site 13) and near Muscat (sites 21 and 22), where they were present in areas relatively sheltered from direct wave assault. Lateral water visibility ranged between 10-20 m during the surveys. These reefs demonstrated high live coral cover (80-100%), were constructed primarily of *Pocillopora damicornis*, and had maximum relief of 6-8 m (Figures 14 and 15). Maximum reef depths ranged between 9-10 m.

The pocilloporid reef on the south side of Fahal Island was at least 1 ha in planar view. The shallowest reef summits, with 100% live coral cover, were 3-4 m below sea level and appeared not to have been exposed at low water. Massive *Porites* sp. colonies, 2-3 m high, were intermingled with *P. damicornis* framework in some areas. The basal margins of some of the *Porites* sp. were overgrown by *P. damicornis*, and a few colonies were nearly completely overtopped by pocilloporid framework. Several large *Diadema setosum* Leske were present at the reef base. The mainland pocilloporid reefs were approximately 0.5 (site 21) and 0.8 (site 22) ha in planar view. The reef flats on both reefs revealed considerable dead coral, mostly in growth position, probably indicative of exposures at low tides. Much of this dead coral was overgrown by crustose coralline algae and microfilamentous algae. This was reflected in the relatively low percent live *Pocillopora* cover on reef flats compared with the seaward slope zone (Figures 16 and 17). Coral species diversity was highest at the reef base at site 21 (H' = 0.91), due to the occurrence of species of *Montipora*, *Acropora*, *Goniopora*, *Porites*, *Psammocora*, *Favites*, and *Astreopora* (Figure 16). The highest H' index at site 22 (H' = 0.77) was observed on the reef flat, where a few *Acropora* colonies were present (Figure 17). In general, these reefs revealed sparse pocilloporid rubble at the reef base or on adjacent sand plains. Large *D. setosum* were common at the reef base.

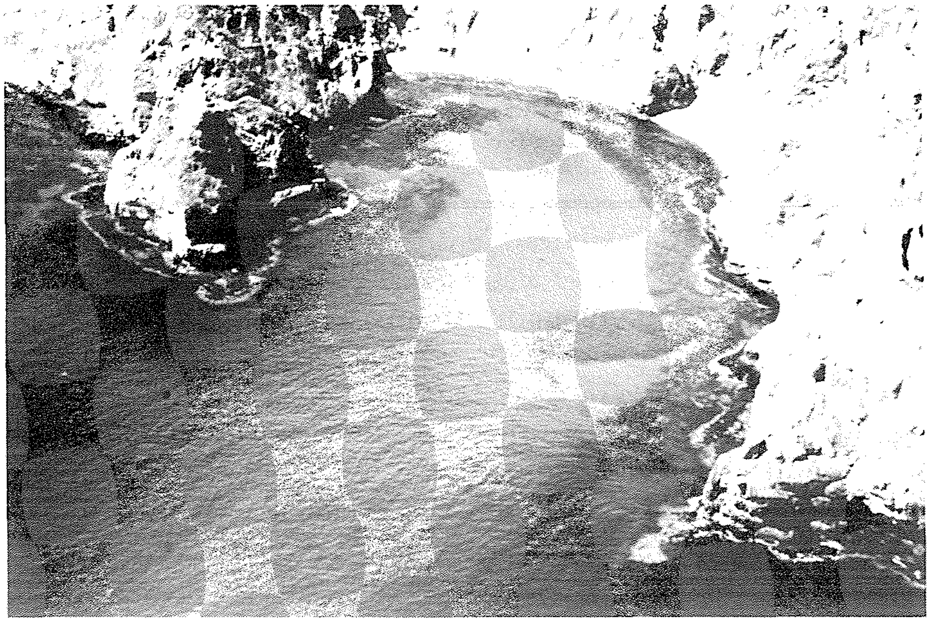

Figure 14. Oblique aerial view of the Christian cemetery embayment, site 21 (Fig. 4) (ca. 600 m elevation, 18 October 1982). Dark patch (right of center) is the same pocilloporid patch reef shown in Fig. 15. Other linear patches skirting the shoreline are incipient fringing reefs composed of a variety of coral species.

Figure 15. Underwater view of fringing pocilloporid reef, Capital area, near Christian cemetery, site 21 (Fig. 4), 2 m depth, 15 October 1982. A school of the Arabian Butterflyfish, *Chaetodon melapterus*, is visible in the foreground feeding on live *Pocillopora damicornis*.

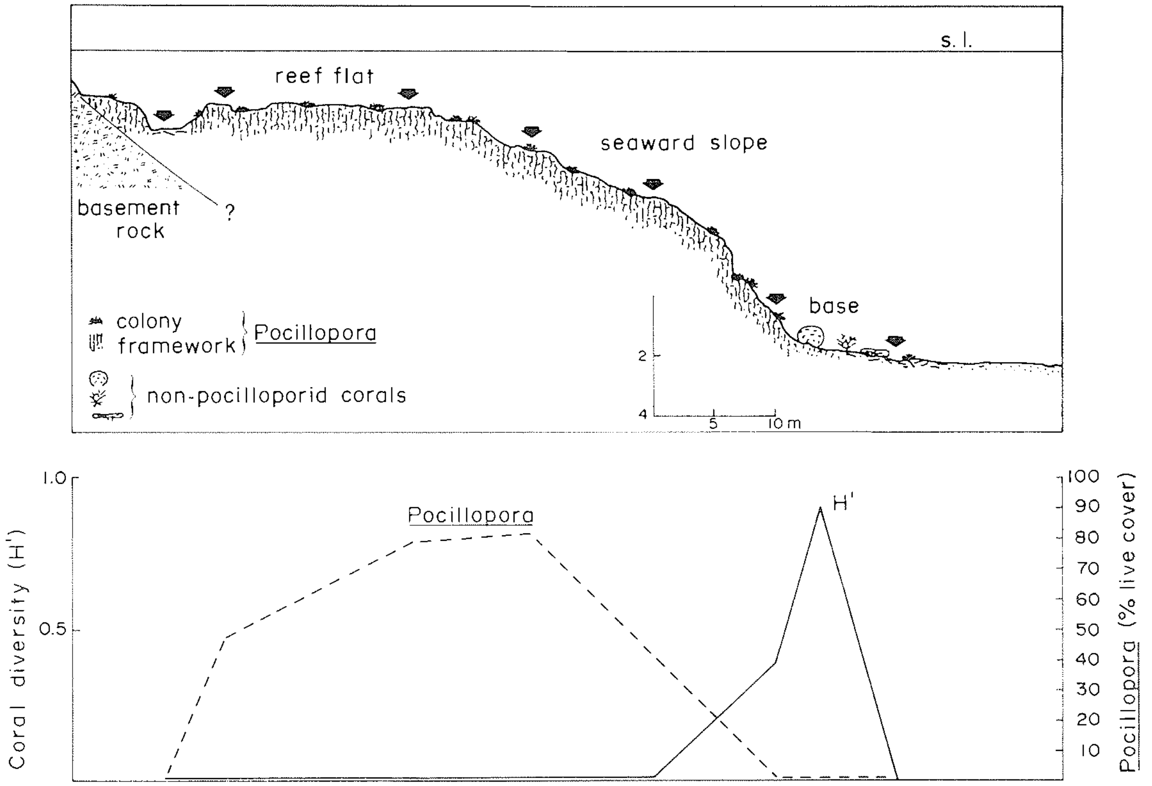

Figure 16. Cross-section sketch of a pocilloporid reef near the Christian cemetery (site 21, Fig. 4) from shoreline to off-reef sand plain (above). Sampling areas across the reef are denoted by arrows, and the corresponding percent live *Pocillopora damicornis* cover and coral species diversity (H') are indicated on the graph (below). S.l. is approximately mean sea level. Data from chain transect sampling performed on 15 October 1982.

Chaetodon melapterus Guichenot, the Arabian Butterflyfish, often was observed feeding on live *P. damicornis* colonies on mainland pocilloporid reefs (Figure 15). They appeared to be removing polyps as do other butterflyfishes in different areas of the Pacific Ocean (Hourigan et al., 1988). Only two porcupinefish, *Diodon hystrix* Linnaeus, were seen during the entire survey (at site 21). Several other fishes that commonly frequented pocilloporid reefs included: unidentified benthic pomacentrids and schools of *Abudefduf saxatilis* (Linnaeus) (Pomacentridae); *Cephalopholis miniatus* (Forsskal) and *Cephalopholis argus* Bloch & Schneider (Serranidae); *Ostracion tuberculatus* Linnaeus (Ostraciontidae); *Rhineacanthus aculeatus* (Linnaeus) (Balistidae); *Zebrasoma xanthurum* (Blyth) (Acanthuridae); *Carangoides fulvoguttatus* (Forsskal) (Carangidae); *Heniochus acuminatus*

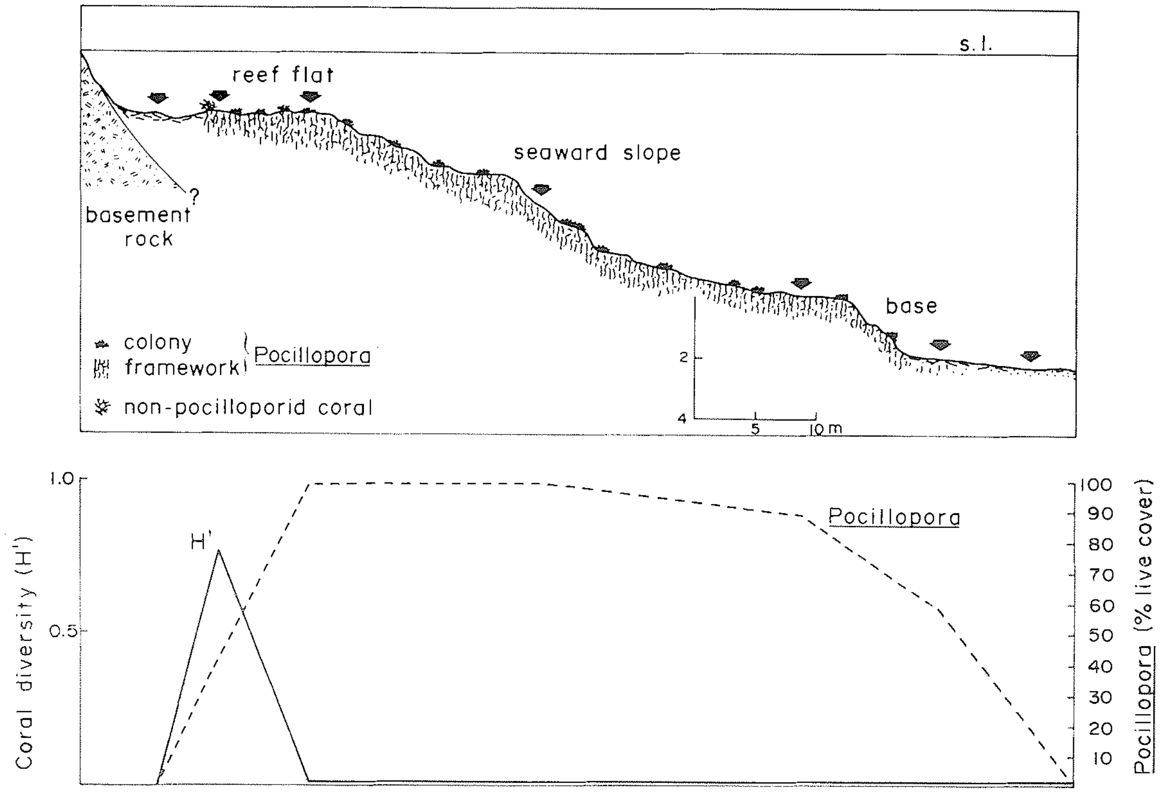

Figure 17. Cross-section sketch of a pocilloporid reef off Jazirat Muscat near the Sultan's Palace (site 22, Fig. 4) from shoreline to off-reef sand plain (above). Sampling areas across the reef are denoted by arrows, and the corresponding percent live *Pocillopora damicornis* cover and coral species diversity (H') are indicated on the graph (below). S.l. is approximately mean sea level. Data from quarter meter quadrat sampling performed on 24 October 1982.

(Linnaeus) (Chaetodontidae). However, large schools of herbivores (e.g., parrotfishes, acanthurids, kyphosids) were not seen.

Small patches (5 X 20 and 10 X 20 m) of live *P. damicornis* were present at Bandar Khayran (site 16). These patches were thin with maximum vertical buildups of 1-2 m. Two dead pocilloporid formations were observed at Bandar Jissah. The larger of these (site 19, between north island and the mainland, see Map 1 in Salm, 1985), about 0.8 ha and 3-4 m high, was broken apart with coral rubble widely scattered. Large sections of this reef were overgrown with microfilamentous and macroalgae, and alcyonaceans. The second dead pocilloporid patch (site 74, south side of island in the central branch of the main bay, Salm, 1985) was in growth position. Another dead pocilloporid formation, observed by B. Speck (pers. comm.) in a bay to the south of Bandar Khayran, was not visited during this study.

Small *Acropora* patch reefs, usually with a maximum vertical buildup of 1-2 m, were observed immediately west of Qantab (site 14), inside Bandar Khayran (site 16), and in the central branch of the main bay at Bandar Jissah (site 17). Lateral water visibility was about 10 m at these sites. *Acropora cytherea*, with larger colonies 2-2.5 m in diameter, predominated at sites 14 and 17. Most of these corals were dead with several colonies observed being eaten by *Acanthaster planci* (Figure 18). *Goniopora* sp., about 1 m diameter colonies, were also present and did not show signs of predation by *Acanthaster*. *Acropora* thickets, with up to 100% live cover of branching species, were present at site 16.

Coral reefs with other than acroporid and pocilloporid species predominant were seen at four sites. A fringing reef composed of numerous

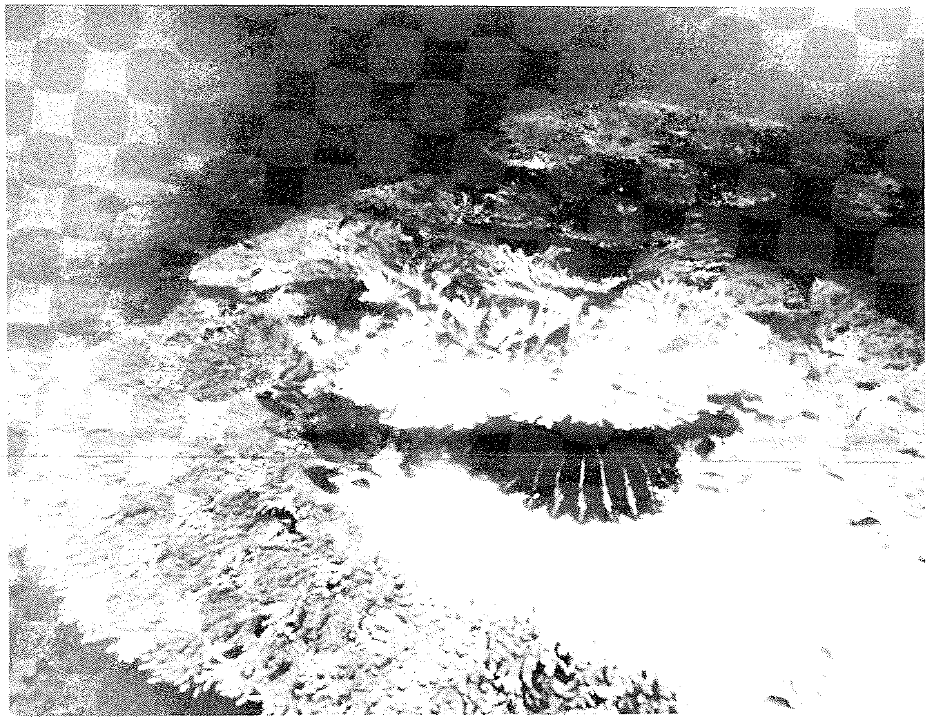

Figure 18. Underwater view of *Acanthaster planci* resting on a tabular colony of *Acropora cytherea*, 5 m depth, Bandar Jissah, site 17 (Fig. 4), 15 October 1982. Approximately one-third of this 1.5 m diameter colony had been eaten by the three *Acanthaster* present between the tabular branches.

genera, e.g. *Stylophora, Pocillopora, Acropora, Goniopora, Porites* and *Pavona,* extended along the western shore of the large island at Bandar Khayran (site 15). This reef displayed a vertical buildup of 2-3 m, but the framework ended abruptly at 5-6 m depth. Several aggregations of *Diadema,* with 25 to 50 individuals each, were present at the reef base. Thickets of branching *Montipora* sp. covered 10s of square meters inside Bandar Khayran at site 16. A *Porites* sp. fringing reef was developed in turbid water (1-2 m lateral visibility) at Khawr Yenkit (site 18). This reef had a relief of 2-5 m. Most of the coral was dead at 1 m depth. A small, monospecific *Goniopora* sp. patch reef was present in a sheltered cove at site 23. This reef covered a 50 X 20 m area, exhibited 100% live cover, and had a maximum reef frame relief of 3-4 m.

No reef development was observed at sites 20, 56, 72, 74 and 75. However, species rich coral communities characterized sites 56, 74 and 75, all of which were subject to different levels of *Acanthaster* predation. The most abundant genera at site 56 were *Pocillopora, Stylophora, Porites* (including both dendritic and massive species), and an encrusting *Montipora* sp. *Acropora* were predominant at site 74, and *Pocillopora* and *Porites* at site 75.

<u>Ra's Abu Da'ud to Ra's al Hadd</u>. Lateral water visibility was only 3-6 m at sites 25-31 (3-4 October 1982). Plankton blooms were evident at most sites, including large numbers of brown, stinging jellyfish. Few corals were seen at sites 25-27, northwest of Sur (Figure 5). Species belonging to the genera *Pocillopora, Stylophora, Acropora, Porites* and *Platygyra* were observed scattered on cobbles and boulders at site 25.

A small patch reef was present just inside the west bay entrance at Khor al Hair (site 28). This reef was only 2-3 m deep, and was constructed dominantly of massive *Porites* and, to a lesser degree, *Goniopora.* Alcyonaceans dominated sites 29-31. A few corals belonging to the genera *Pocillopora, Stylophora, Acropora, Porites, Goniopora* and *Platygyra* also were seen. Large encrusting alcyonacean colonies were observed overgrowing and killing some of these corals (Figure 19).

Environmental conditions changed dramatically at Ra's Abu Da'ud with clear water (10-12 m visibility) and well developed coral communities prevalent, similar to those reported in the Capital area. *Pocillopora damicornis* reef building was evident in two areas between an island and the mainland shore. Maximum framework development ranged between 1-3 m. Both of the pocilloporid reefs contained large dead sections with surfaces that appeared to have been planed. These leveled surfaces were colonized mostly by *Acropora* spp. and *P. damicornis,* but small colonies of *Stylophora,*

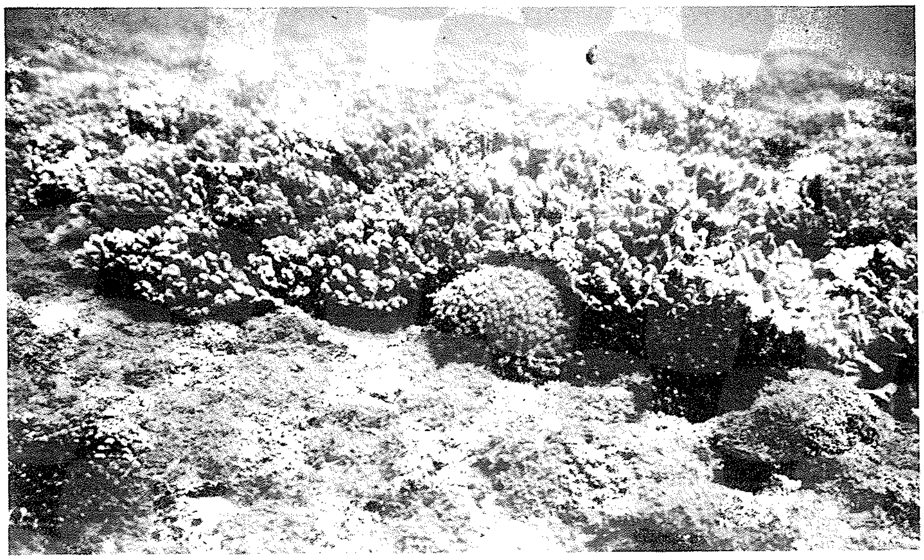

Figure 19. Underwater view of 'soft corals' (alcyonaceans) in the process of spreading over the substratum and overtopping reef corals, including *Goniopora* sp., 4 m depth, east of Sur, site 30 (Fig. 5), 4 October 1982.

Montipora and *Platygyra* also were present. *P. damicornis* dominated large sections of the dead reef frame with 100% live cover. In other areas, *Acropora* spp. were predominant with many examples observed of branching and table *Acropora* overtopping *Pocillopora* and *Stylophora.* Some 20-30 cm diameter pocilloporid colonies were underneath and completely shaded by the acroporids.

Masirah Island. Reef corals were abundant at Masirah Island and the best developed coral communities were found along the northwestern coast (Figure 6). *Pocillopora damicornis* and *Montipora foliosa* were among the more abundant species with the following genera also well represented at several sites: *Stylophora, Porites, Favia, Favites, Leptoria, Platygyra,* and *Acanthastrea.* Relatively few *Acropora* spp. were seen at Masirah compared with the Musandam, Daymaniyat Islands and Capital area. The water was highly turbid, with 1-3 m visibility, at most sites. This was caused by SW winds that continued for several days (maximum velocity 7 knots during site visit), and wave action over the shallow shelf, which resuspended fine carbonate sediments.

Few corals were present at sites 43 and 44, which were inhabited more by macroalgae (e.g., *Padina* and *Caulerpa*) and zoanthids (*Palythoa*). While a species rich coral community was found at site 45, most of this patch that is designated as a coral bottom on the nautical chart (Figure 6) contains few corals. On the west side of Masirah, corals also were sporadically abundant at sites 47, 48 and 55, but seagrasses and macroalgae (e.g., *Caulerpa* and *Sargassum*) predominated.

Fringing coral reefs dominated the coastline from site 49 north to site 54, including sites 46, 50 and 51 (Figure 6). These reefs were shallow, ranging between 1.5-5 m depth, with maximum vertical framework relief of 3-4 m. *Pocillopora damicornis* and *Montipora foliosa*, either alone or together, were the chief reef-building species (Figure 20). *Acropora* reefs were not observed at Masirah Island as erroneously attributed by Sheppard et al. (1992) to Glynn (1983a). On reef exposures where internal structures were visible, *P. damicornis* contributed disproportionately to the framework with mostly live colonies of *M. foliosa* populating the dead pocilloporid framework at the surface. *M. foliosa* contributed predominantly to the live

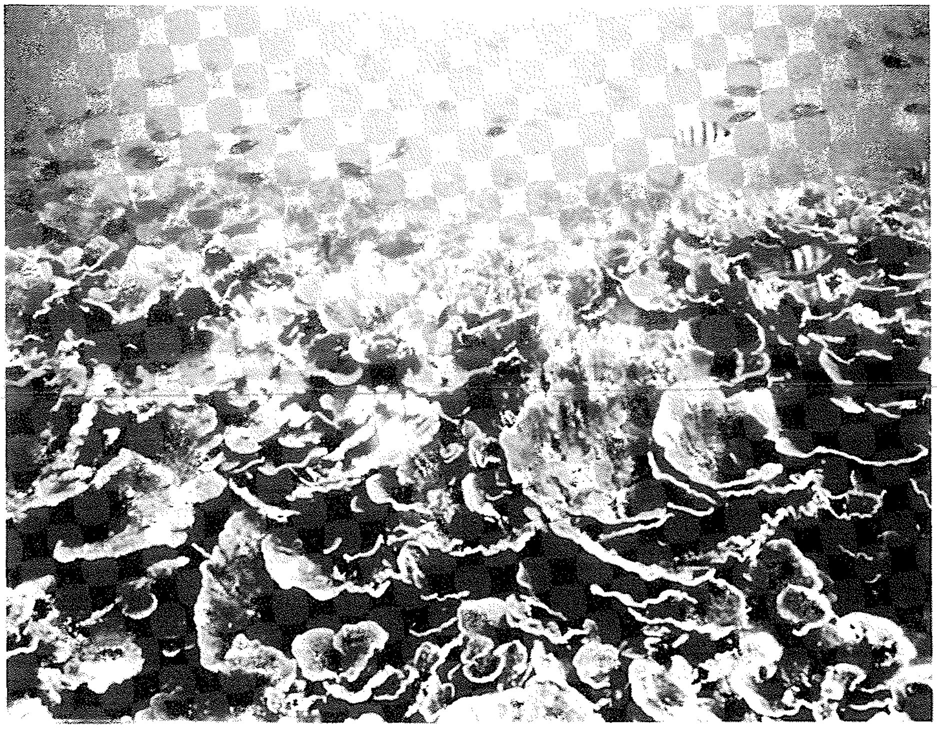

Figure 20. Underwater view of live *Montipora foliosa* buildup, incipient fringing reef, 3 m depth, Masirah Island, site 54 (Fig. 6), 12 October 1982.

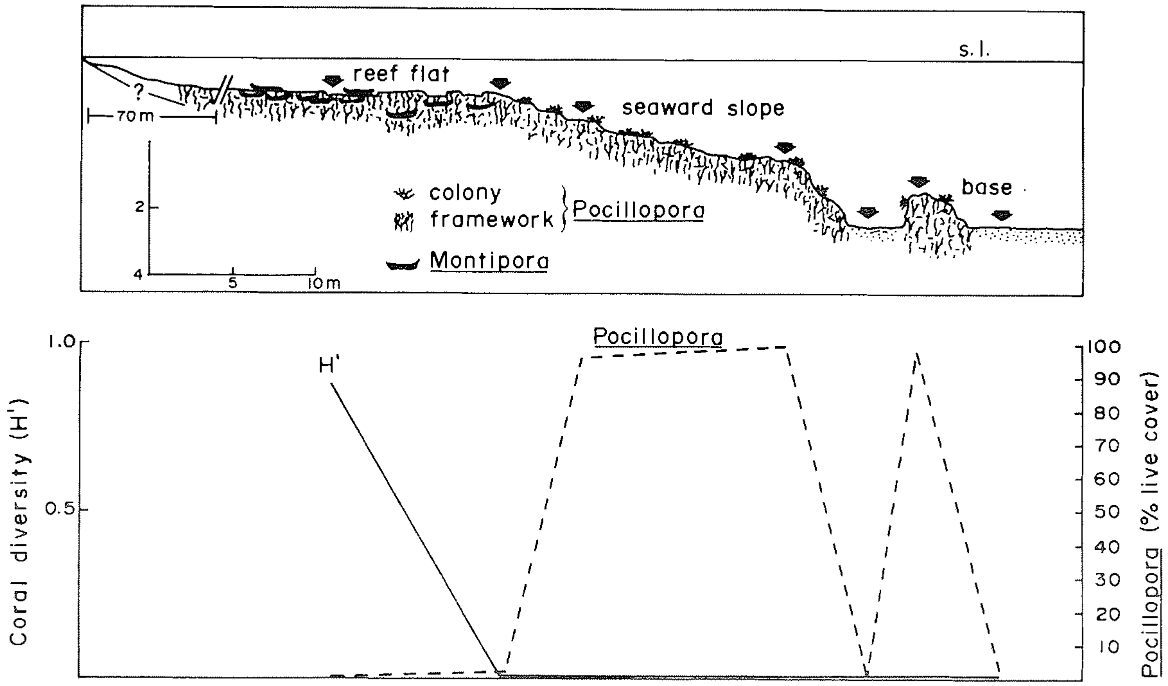

Figure 21. Cross-section sketch of a dominantly pocilloporid reef off the west side of Masirah Island (site 46, Fig. 6) from shoreline to off-reef sand plain (above). Sampling areas across the reef are denoted by arrows, and the corresponding percent live *Pocillopora damicornis* cover and coral species diversity (H') are indicated on the graph (below). S.l. is approximately mean sea level. Data from quarter meter quadrat sampling performed on 12 October 1982.

cover at sites 49, 50 and 51. At sites 46 and 54, *P. damicornis* also was abundant, especially on the seaward slope (Figure 21). Other coral genera (e.g., *Stylophora, Acropora, Cyphastrea, Favia, Favites,* and *Acanthastrea*) were largely restricted to reef flats where pocilloporid and montiporid cover was low. The reef flats in this area are exposed during extreme low water (M.A. Al-Barwani, pers. comm.). Large numbers of rock scallops were attached between the basal branches of live *Pocillopora* in the slope zone at site 50 (Figure 6). The reef framework abruptly ended in a thick carbonate sand bottom with few live, intact corals or broken fragments and rubble at the reef base (Figure 21).

Chaetodon melapterus were observed on most fringing reefs and were seen feeding on live *Montipora foliosa*, although it could not be determined what the butterflyfish were feeding on (e.g. mucus, coral tissues). Schools of large fish grazers or large invertebrate predators were not observed at Masirah Island.

At site 55, *Sargassum* spp. occurred as dense beds at 0.5-1 m depth, with 1-1.5 m long blades forming a thick canopy. Numerous scattered corals were attached to the dead coral boulders beneath the canopy, including *Psammocora, Stylophora, Montipora, Goniopora, Porites, Cyphastrea, Favia, Favites, Galaxea, Acanthastrea,* and *Turbinaria.* At 1.5-2 m depth, between 100-200 m from the shoreline, the mixed macroalgal/coral community was replaced by crustose coralline algae, which were growing on a thin (0.5-1 m) framework of *Montipora.* This fringing reef was only sparsely populated by corals, chiefly *Montipora foliosa.* Farther seaward the unbroken fringing reef became separated into isolated blocks, which eventually thinned out and disappeared.

Coral communities intermixed with macroalgae and seagrasses were observed at sites 47 and 48. Among the common genera observed were *Stylophora, Montipora, Porites, Favia, Favites, Leptoria, Platygyra* and *Acanthastrea.* The summits of many large colonies of the massive genera (e.g., *Porites, Leptoria,* and *Platygyra*) were partially covered with carbonate sand. SST and water visibility decreased markedly around the north end of Masirah, from site 53 to site 52. Only scattered colonies of *Stylophora pistillata* were observed at site 53 and *Favia* and *Favites* at site 52. Macroalgae were predominant at these sites.

Dhofar. The rocky coast from Marbat to slightly east of Sadh was populated with lush communities of frondose macroalgae (Figure 7). Species of Sargassaceae (Phaeophyta) were especially abundant, their buoyant blades forming a canopy with a dampening effect on approaching swells. Other abundant brown algae included *Bifurcaria* sp., *Cystoseira* sp., the kelp *Ecklonia radiata* (C. Ag.) J. Agardh, *Padina* sp. and *Turbinaria* sp. The red alga *Hypnea musciformis* (Wulfen) (Rhodophyta) also was abundant along with the green algae *Caulerpa* spp. and *Ulva* sp. (Chlorophyta). For more information on the algal communities and rocky shore fauna in this area, consult IUCN/ROPME/UNEP (1984).

Water visibility was only 3-5 m at sites 32-34 near Marbat. Macroalgal cover was near 100% from the mid-intertidal zone to 3-5 m depth. Associated with the algae were abalones (*Haliotis mariae* Wood), sea urchins (*Echinometra, Stomopneustes, Echinostrephus*) and unidentified starfish. Only a few corals were seen shallower than 5 m (Figure 22). Corals increased in abundance between 5 and 10 m with a concomitant decrease in macroalgal cover. Most colonies were small. However, some large colonies

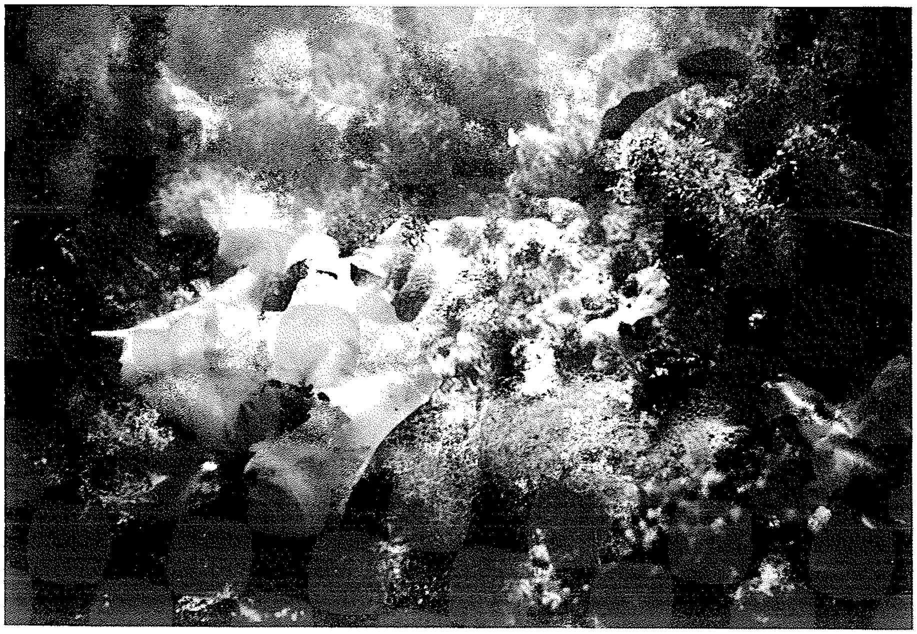

Figure 22. Underwater view of macroalgae surrounding a reef-building coral (*Platygyra*, center), 3 m depth, east of Marbat, site 32 (Fig. 7), 6 October 1982.

were present including species from the genera *Acropora* (40 cm diameter tables), *Astreopora* (80 cm diameter), *Porites* (35 cm high massive colonies), *Favites* (50-60 cm, longest dimension), and *Turbinaria* (75 cm diameter). *Stylophora pistillata* was common, but *Pocillopora* was rarely seen.

The water conditions and shallow marine community composition near Sadh (sites 35-39) were similar to those at Marbat. Quantitative sampling of the epibenthos to 11 m depth (sites 35 and 39) revealed primarily macroalgal communities. At site 35, *Ulva* was the predominant alga with occasional *Sargassum* plants also present. Both crustose and articulate coralline algae were often present under the macroalgal canopy. Corals (*Acropora* and *Stylophora*) occurred only between 8 and 11 m depth. *Sargassum* spp. were the most abundant macroalgae at site 39. Corals were more common below 5 m with *Acropora*, *Favites* and *Cyphastrea* present to 11 m depth.

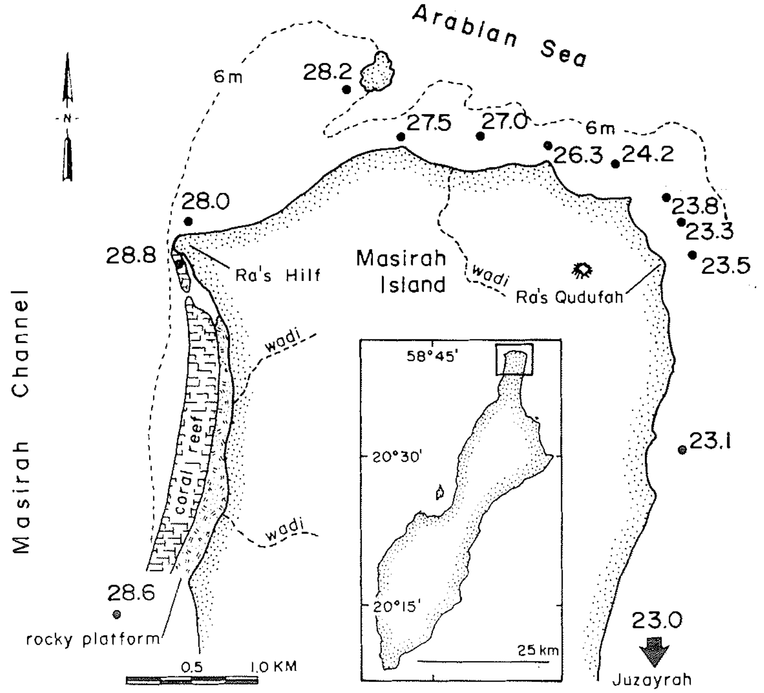

Figure 23. SST (°C) gradient around the north end of Masirah Island. Measured between 0850-1140, 12 October 1982. The southernmost temperature was measured at Juzayrah, about 15 km south of Ra's Qudufah. Base map from Everts et al. (1983).

Thermal Environments and Seasonal Variations

<u>Shore-based sea temperature observations (1982)</u>. Sea water temperatures were measured at various sites on the Arabian Sea coast during a transitional warming period following the 1982 SW monsoon season. SSTs ranged between 28.2°C and 30.8°C (10-12 October) at all sites on the west side of Masirah Island. The high temperature (30.8°C) was measured nearshore at Qa' ad Kalban (site 55) at 1415; 20 m offshore SST was 28.8°C at 1422.

A well defined thermal front was evident along the north end of Masirah (Figure 23). SST was 28.8°C over a fringing reef off the NW corner of the island. A steady decline in SST occurred around the north end of the island with a 3°C difference (26.3°-23.3°C) evident over a 1.2 km stretch off the NE corner of the island. The lowest SST (23.0°C) was observed at Juzayrah Island (site 52), about 12 km south of Ra's Qudufah.

SSTs observed off the Dhofar coast (6-9 October) generally were similar to those reported for the east coast of Masirah. Relatively high SSTs occurred nearshore at two sites between Marbat and Sadh: 27.0°C (site 32) and 25.0°C (site 37). These temperatures, measured in bays in the late morning and early afternoon, probably reflect some surface warming that occurred in areas with heavy macroalgal canopies. The bottom (4 m) temperature at site 32 was 24.5°C. SSTs offshore (about 1 km) of site 37 ranged between 22.8° and 24.0°C. The lowest nearshore temperatures occurred at site 35, where SST was 22.5°C; 22.0°C was recorded at 8 m depth. SSTs were somewhat higher west of Ra's Rayzt with nearshore temperatures that ranged between 25.5°-26.7°C.

Nansen cast data (1933-1979). To amplify the temperature records obtained in 1982, a long-term data base from Nansen casts was analyzed for geographic and seasonal trends. During the NW monsoon (December-February), characterized by onshore water movement and downwelling along the Arabian Sea coast, SSTs are relatively high (24°-25°C) (Figure 24). SSTs are low in the Gulf of Oman in the winter season and high in the summer (Figure 24). In contrast, summer SW monsoon SSTs were low along the Arabian Sea coast, a reflection of strong upwelling in this season (Figure 25).

SST isotherm plots along the Arabian Sea coast of southern Oman similarly reveal relatively warm conditions during the NW monsoon (Figure 26) and cool upwelling conditions during the SW monsoon (Figure 27). A strong SST gradient (19°-23°C) is evident along the SE side of Masirah Island in July with the lowest temperatures nearshore. Lower SST isotherms (21°-22°C) also are closest to coastal areas near Marbat, suggesting that active upwelling occurs very close to shore and/or upwelled water is preferentially retained there.

The synoptic seasonal variations in SST illustrate well the contrasting thermal environments in the Gulf of Oman and Arabian Sea (Figure 28). In both regions, SST increases from March through June with maximum annual mean temperatures in June. Notably high extreme SSTs of 36°-37°C occurred in June in both regions. In the Gulf of Oman, mean SST remains high (30°-31°C) through September and then decreases through February. Monsoon-induced upwelling in the Arabian Sea causes summer temperatures to fall suddenly in July with mean SST remaining relatively low (24°-25°C) through September. A 2 month post-monsoon increase in SST occurs in the autumn, to be followed by lower mean temperatures from December through February. Extreme low SSTs were nearly 2°C lower in the Arabian Sea (July) than in the Gulf of Oman (February).

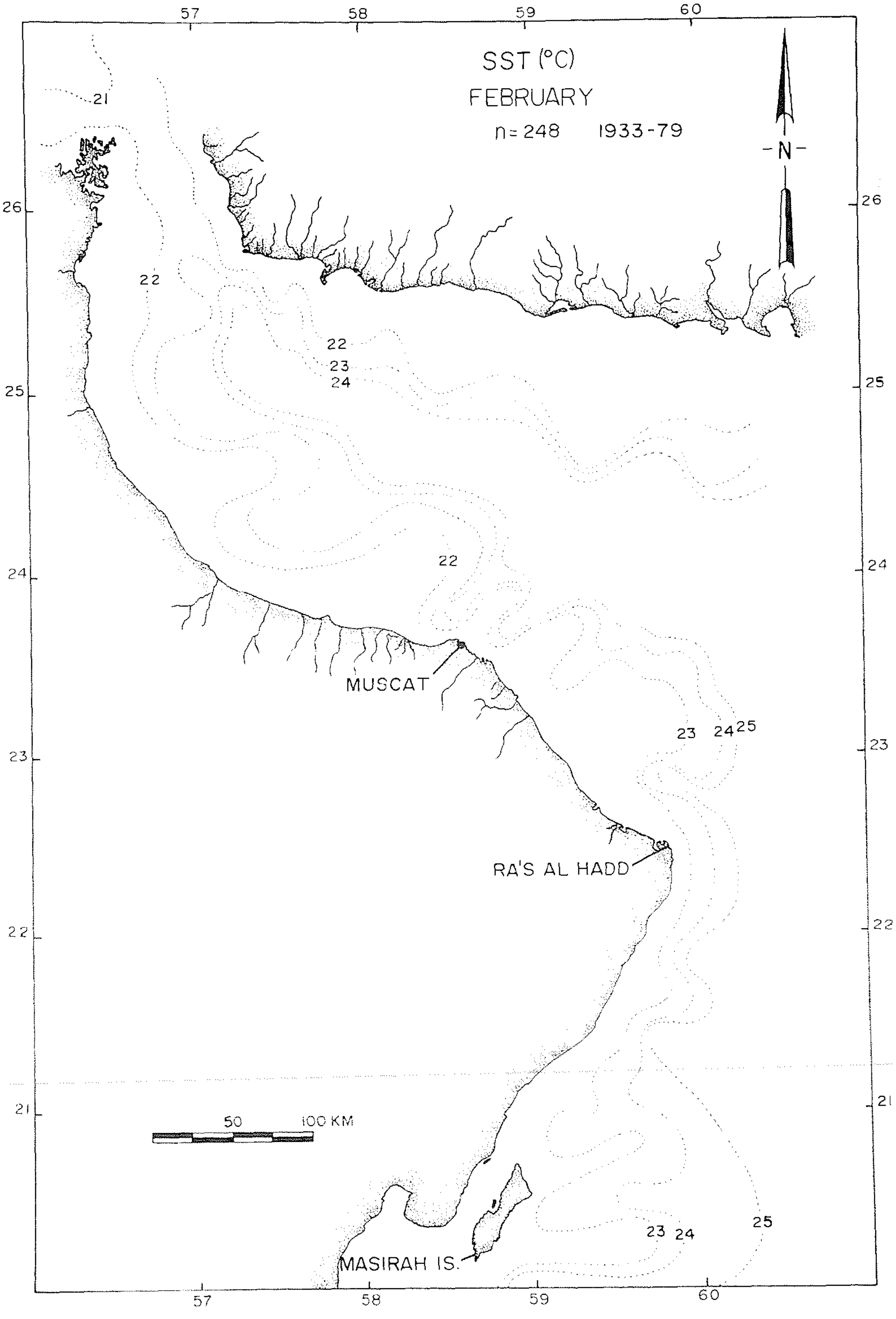

Figure 24. Mean monthly isotherms constructed from Nansen cast data from Gulf of Oman and Arabian Sea waters, northern region of Oman, February (1933-1979).

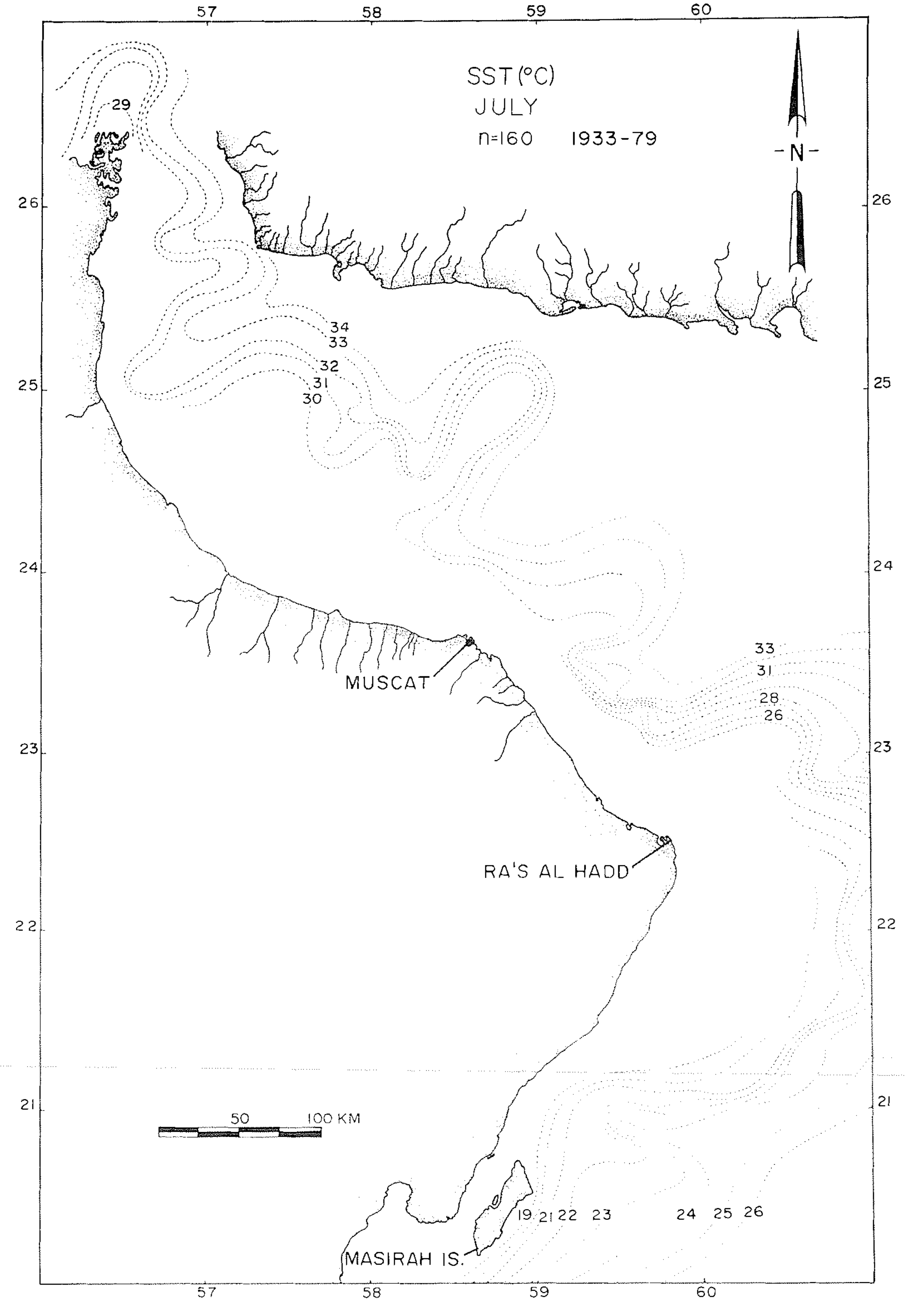

Figure 25. Mean monthly SST isotherms constructed from Nansen cast data from Gulf of Oman and Arabian Sea waters, northern region of Oman, **July** (1933-1979).

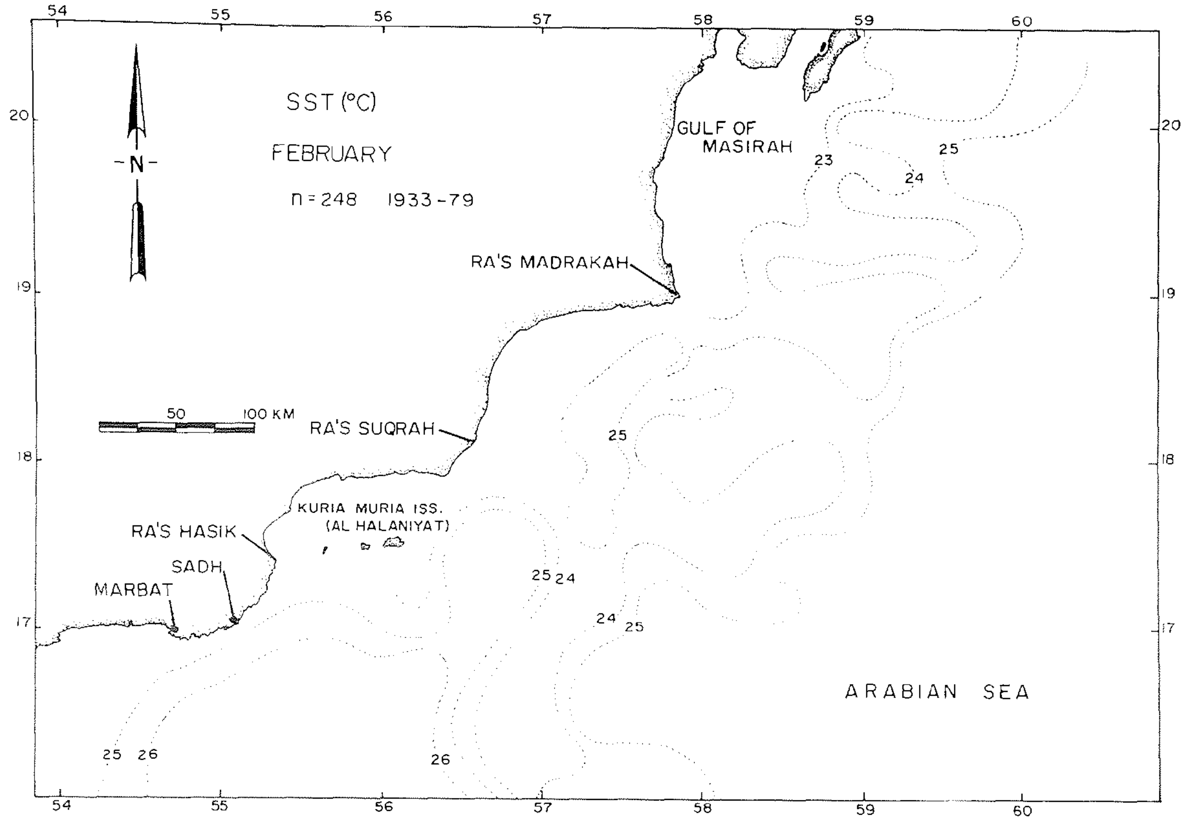

Figure 26. Mean monthly SST isotherms constructed from Nansen cast data from Arabian Sea waters, southern region of Oman, February (1933-1979), NE monsoon.

Because the Nansen cast measurements typically were made in shipping lanes, these data did not reveal information on nearshore temperature structures that influence coral communities.

Remote sensing data (1988, 1989). Analysis of SST fields from satellite imagery provided details of nearshore temperature conditions and variations during the SW monsoon. The grids analyzed are shown in Figure 29. The images in Plate 1 reveal a thermal front off Ra's al Hadd in July 1989 (a), and warm pools on the NW side of Masirah Island and at Barr al Hikman, across Masirah Channel on the mainland coast, in August 1988 (b). SSTs on the south side of Ra's al Hadd were 24°-25°C, and increased to 27°-28°C around the point towards the NW (near Sur). The temperature change was more abrupt at Masirah Island, with SSTs of 23°-24°C at easterly exposures and 27°-28°C towards the west.

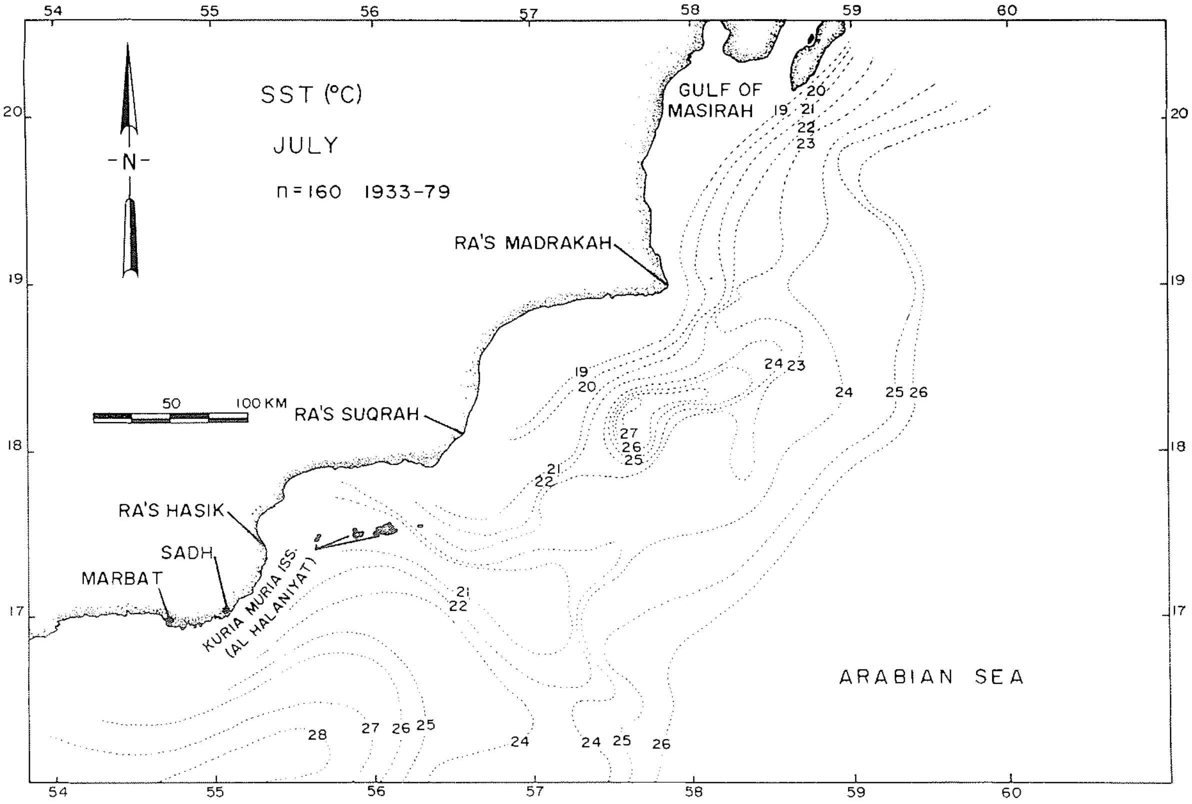

Figure 27. Mean monthly SST isotherms constructed from Nansen cast data from Arabian Sea waters, southern region of Oman, July (1933-1979), SW monsoon.

The Muscat and Masirah Island areas are compared in Figure 30 in terms of seasonal upwelling activity and persistence of the warm pool respectively. Only a single, weak upwelling plume was detected off Muscat in 1988 (Figure 30 A), in early July, whereas large areas experienced upwelling in 1989, most notably in August and September (Figure 30 B). Warm pools covered extensive areas along the west side of Masirah Island and at Barr al Hikman in 1988 (Figure 30 A; Plate 1). The mean area of the warm pool in 1988 was 1,001 square nautical miles (= 1,855 km^2). Warming was not as evident in 1989 (Figure 30 B); the warm pool then had a mean area of only 738 square nautical miles (= 1,368 km^2).

The seasonal advection of cool, upwelled waters into the SW sector of the Gulf of Oman is indicated in Figure 31 for 1988 and 1989. In both years, the onset of cooling began in late May. Coastal cooling began as early as June-July in 1989, but not until August in 1988. The penetration of cool,

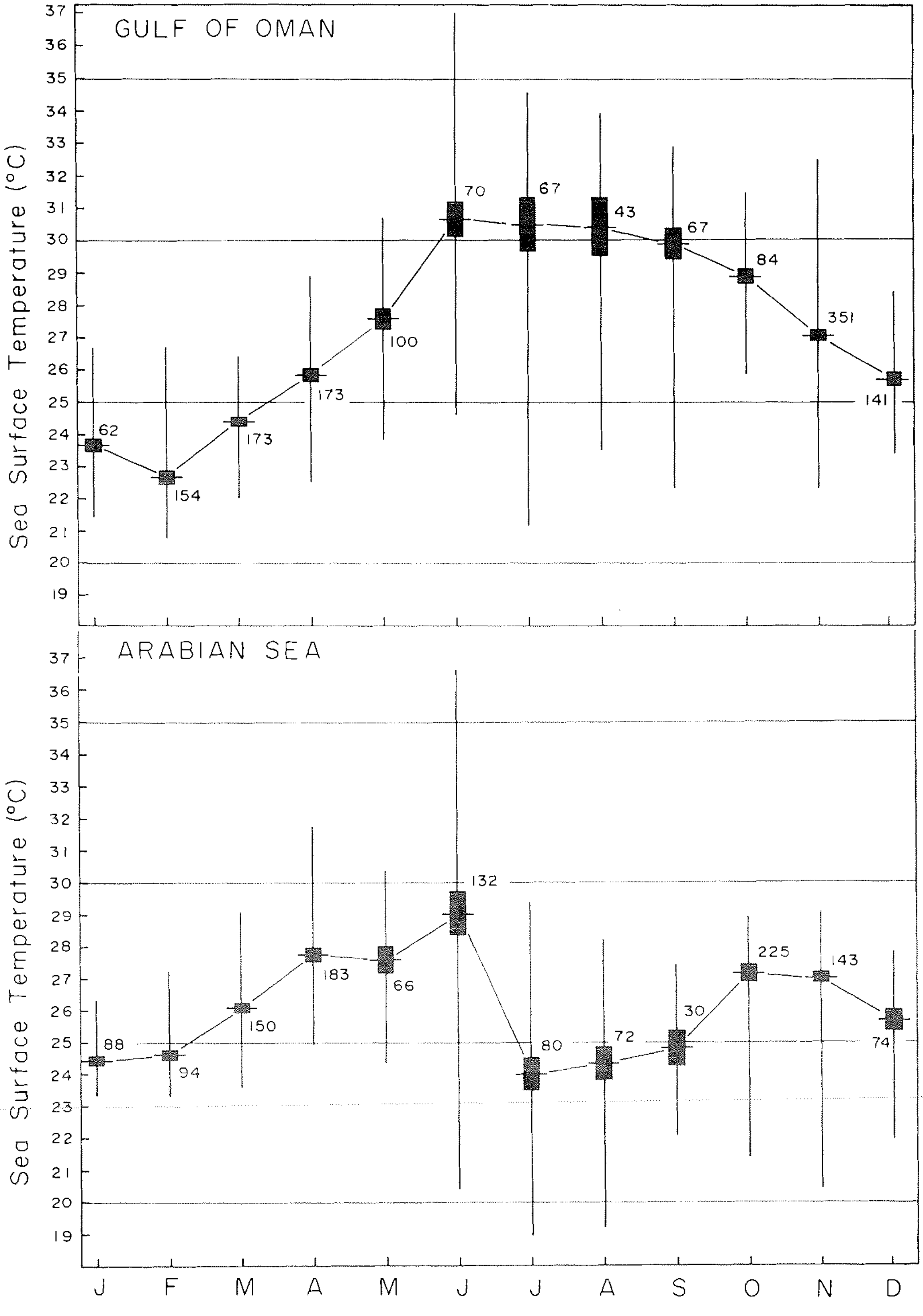

Figure 28. Seasonal SST variations in the Gulf of Oman (above) and Arabian Sea (below) constructed from Nansen cast data, 1933-1979. Horizontal lines denote monthly mean values, bars the 95% confidence intervals of means and vertical lines the maximum and minimum temperatures. Numbers of observations are indicated for each month.

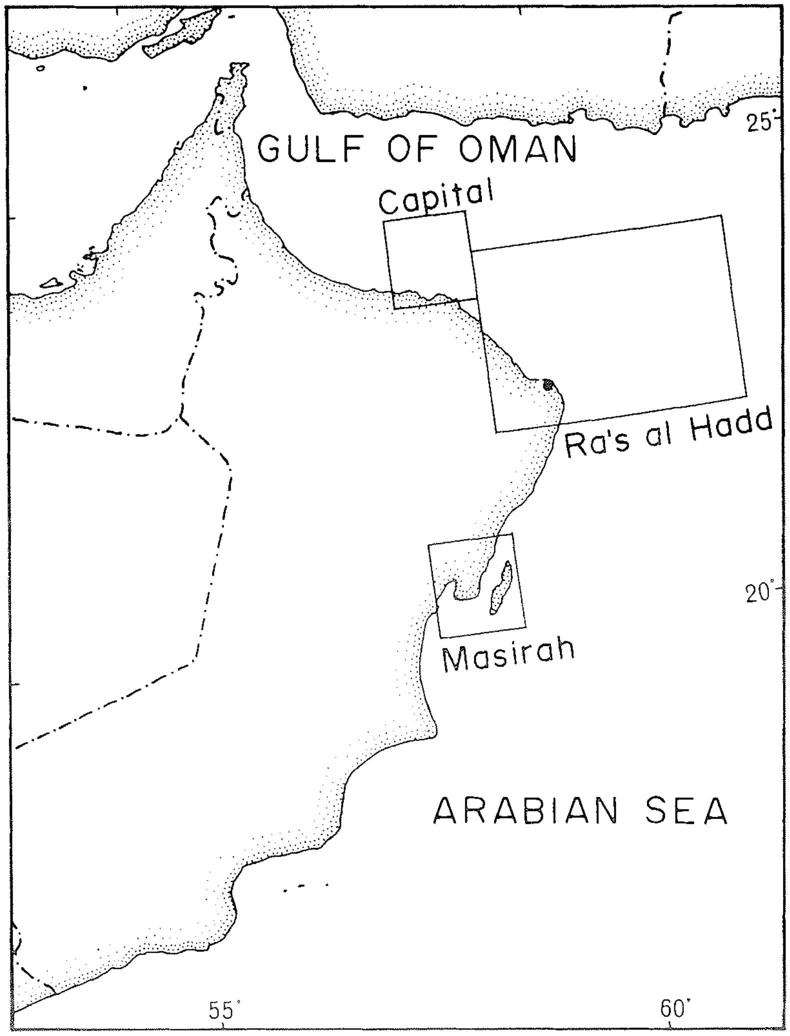

Figure 29. Areas studied for SST patterns from 1988 and 1989 (satellite infra-red data). Location of 1° grids over the Muscat-Daymaniyat Islands (Capital) and Masirah Island areas, and the 6° grid over the Gulf of Oman-Arabian Sea boundary off Ra's al Hadd.

upwelled water from the Arabian Sea into the Gulf of Oman was greater in 1989 than in 1988, and the cool front off Ra's al Hadd persisted 2-3 weeks longer in 1989 than in 1988. Synoptic plots illustrating the percentage occupancy of cool fronts also reveal a greater spatial penetration into the Gulf of Oman in 1989 compared with 1988 (Figure 32).

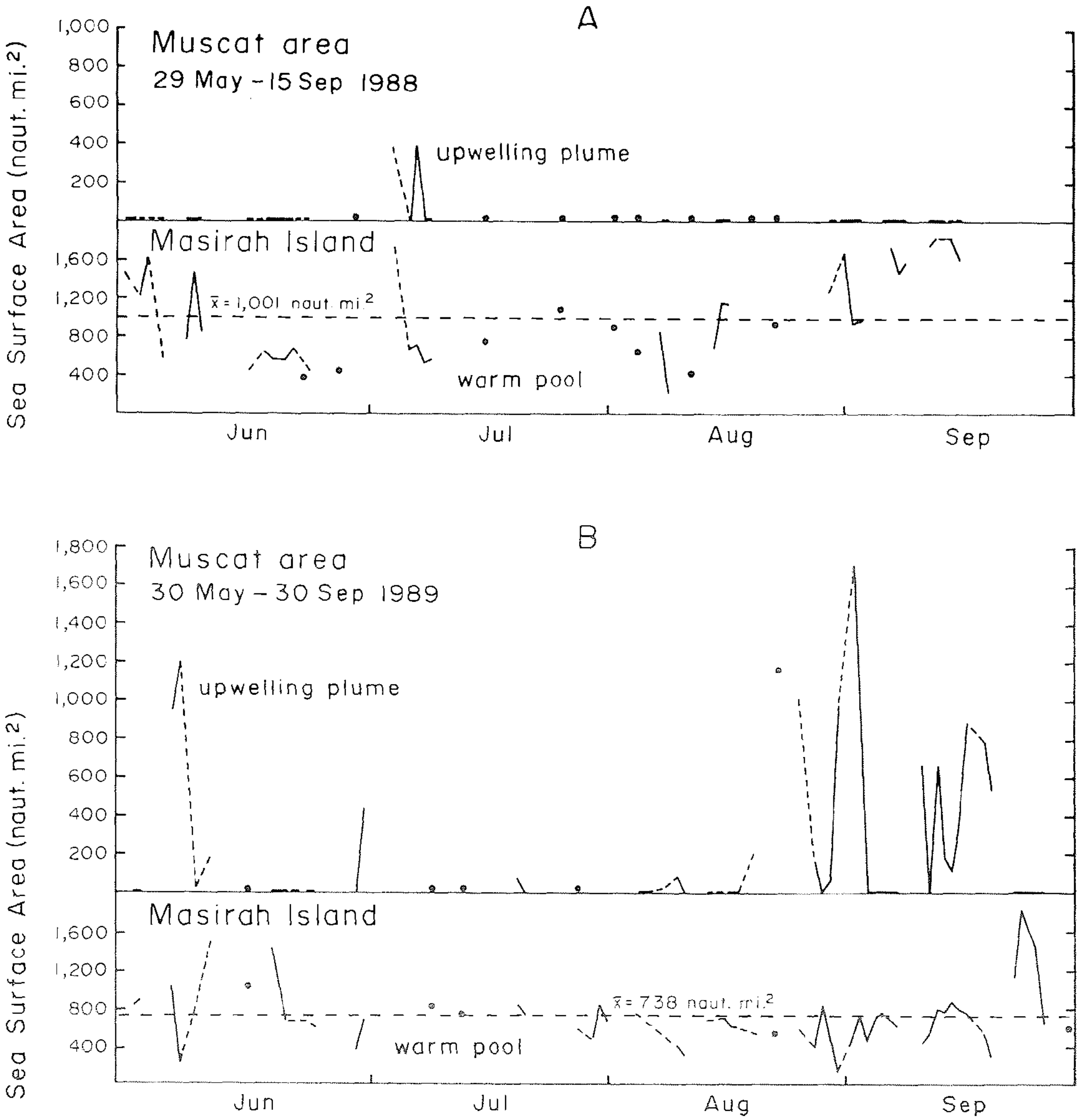

Figure 30. Upwelling activity in the Muscat area and persistence of a coastal warm pool along the lee side of Masirah Island during the monsoon season. The thermal changes are expressed in terms of sea surface area per 1° geographic quadrant for 1988 (A) and 1989 (B). Both plots in 1988 are based on 47 days each, and in 1989 on 58 days (Muscat) and 61 days (Masirah).

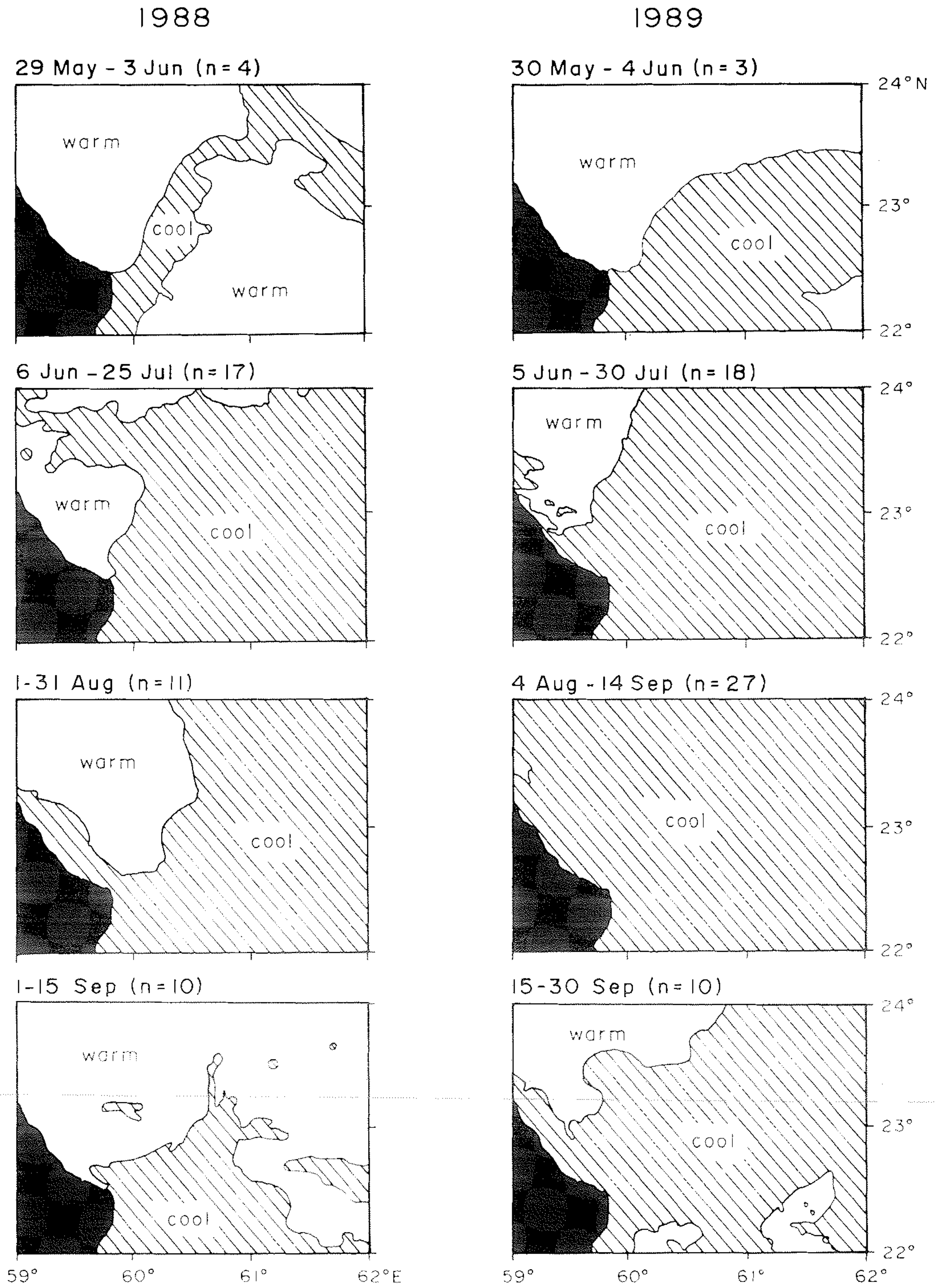

Figure 31. Development and spread of cold fronts near Ra's al Hadd during the summer monsoon periods in 1988 and 1989. Diagonal line patterns indicate the maximum penetration of cool Arabian Sea waters into the southern Gulf of Oman. Constructed from satellite SST images with observation dates and number of days examined indicated in each panel.

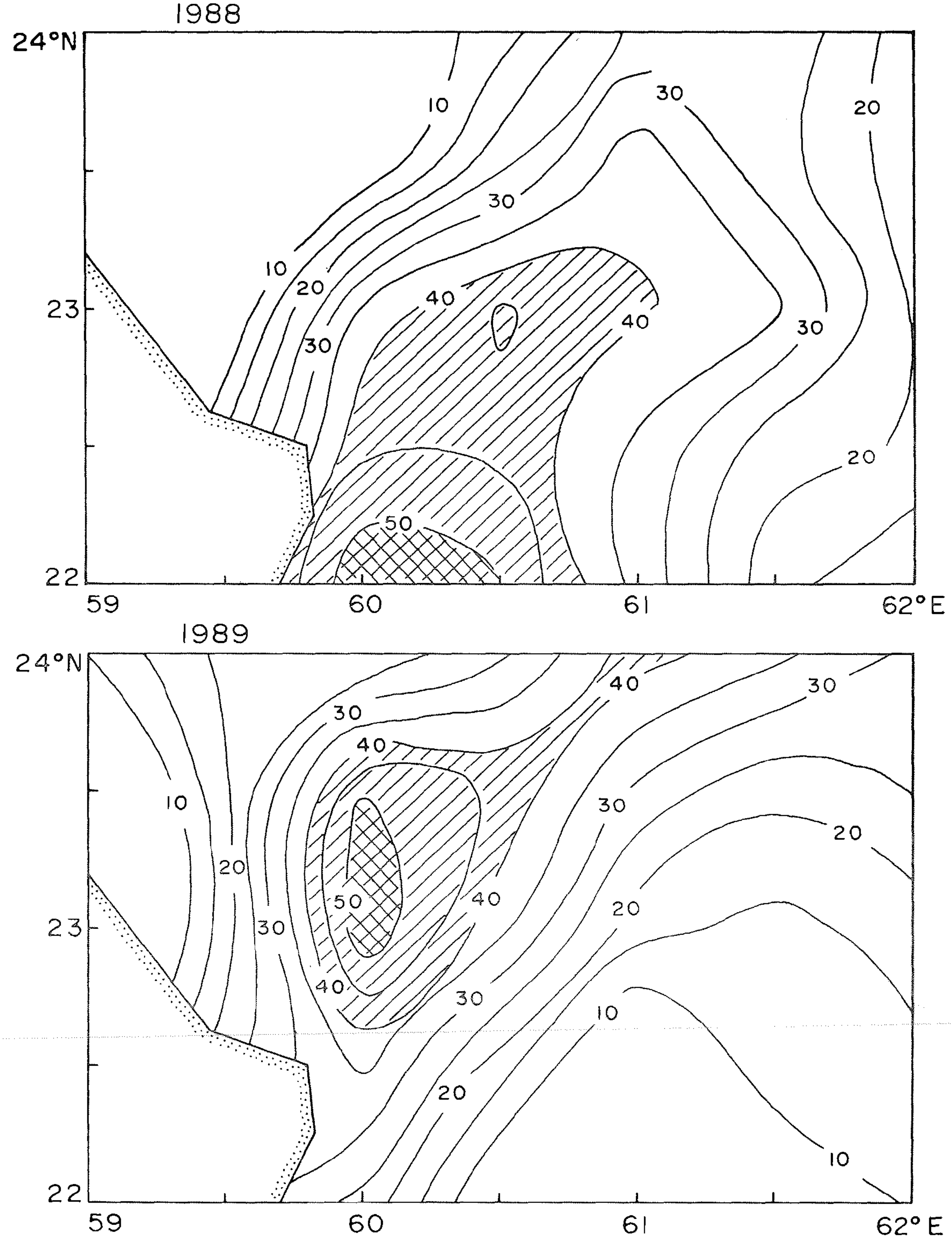

Figure 32. Percentage occupancy by area of the leading (northerly) SST cold fronts off Ra's al Hadd during the summer monsoon season in 1988 and 1989. Plotted in 0.5° quadrants from the minimum curve grid interpolation algorithm with a maximum absolute error of 0.005 and 500 iterations (Surfer, Golden Software, Inc.).

Status of the Crown-of-Thorns Starfish *Acanthaster planci*

Distribution and abundance. *Acanthaster planci* was observed only in the Gulf of Oman: at the Daymaniyat Islands, in the Capital area, at Ra's Abu Da'ud, and immediately west of Ra's al Hadd. *Acanthaster* occurred at 16 (41%) of the 39 sites surveyed in the Gulf of Oman. *Acanthaster* was present at 6 of 15 sites surveyed in the Daymaniyat Islands and demonstrated a median abundance of 60 ind/ha where present (Table 2). Population densities were high (70-140 ind/ha) at three sites (62, 70, 71). On the mainland coast, *Acanthaster* was present at 11 of 23 surveyed sites with a median density of 31 ind/ha (Table 3). The densest aggregation on the mainland, 63 and 84 ind/ha, occurred east of Sur (site 29) and at Bandar Jissah (site 17) respectively. A statistical comparison of the population densities in the Daymaniyat Islands with the mainland coast, at sites where *Acanthaster* was present, indicates that densities in the islands were significantly higher than on the mainland ($p = 0.05$, Mann-Whitney U test, 1-tailed test). However, when all sites are compared, including the 0 abundance observations (9 sites in the Daymaniyat Islands and 13 sites on the mainland), no significant ($p > 0.05$) difference was apparent.

Table 2. Abundance of *Acanthaster planci* in the Daymaniyat Islands (19 and 20 October 1982).

Locality	Site Number	Number *Acanthaster* Observed	Population Density (ind/ha)
W-most coral shoal	57	4	13
Jun (W-most island)	58	4	50
Small island E of Jun	59	16	49
Main group	62	7	70
Main group	70	14	140
Main group	71	3	100
		Median =	60

Table 3. Abundance of *Acanthaster planci* along the mainland coast in the Capital and Sur areas (20 September - 24 October 1982).

Locality	Site Number	Number *Acanthaster* Observed	Population Density (ind/ha)
Jazirat Muscat	22	3	30
Pillar rock (yacht club)	75	1	20
Qantab	14	16	32
Bandar Jissah	17	42	84
Bandar Khayran	15	7	35
	23	12	17
Bandar Khayran (south)	56	25	31
Ra's Abu Da'ud	73	6	20
		14	18
Sur (ca. 20 km east)	29	11	63
Khor al Hair	28	5	36
		Median =	31

Size measurements. *Acanthaster* disc diameters (cm) were measured at the following five localities with sample sizes indicated: Muscat, site 22 (n = 3 ind); Bandar Jissah, site 17 (n = 12); Bandar Khayran, sites 15 and 23 (n = 23); Ra's Abu Da'ud, site 73 (n = 20); Daymaniyat Islands, sites 57, 58, 62 and 71 (n = 16). Total diameter (TD) can be estimated from disc diameter (DD) according to the relation, TD = DD/0.56 (Glynn, 1982).

Statistical testing indicated a significant difference in *Acanthaster* sizes among the five localities ($p < 0.001$, Kruskal Wallis test). *A posteriori* testing (multiple comparisons procedure, $\alpha = 0.15$) indicated that starfish were significantly smaller at Muscat, Ra's Abu Da'ud and in the Daymaniyat Islands (Md DD = 16.0 cm) than at Bandar Jissah and Bandar Khayran (Md DD = 20.5 cm) (Figure 33).

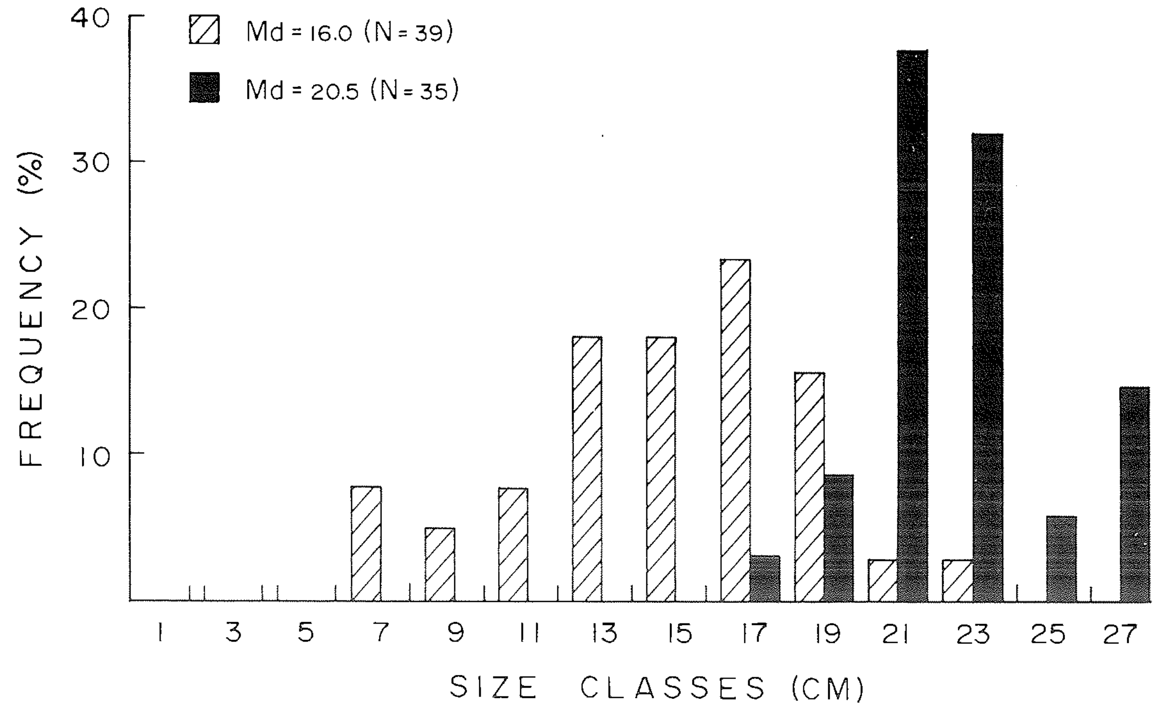

Figure 33. Size-class frequency distributions of *Acanthaster* sampled at Muscat, Ra's Abu Da'ud and the Daymaniyat Islands (cross-hatched bars), and Bandar Jissah and Bandar Khayran (solid bars). Combined median (Md) disc diameter and sample size (N) are noted for each distribution.

Search for juveniles. An effort was made to search for coral-feeding juvenile *Acanthaster* that could mature and impact coral communities later. Other than the 7-11 cm (12-20 cm TD) juvenile starfish found in the general censuses (Figure 33), no juveniles were seen in the various microhabitats searched in 8 areas, which involved a total effort of 8.7 man-hrs (Table 4). Small feeding scars occurred on corals in 3 areas (Sur, at a bay south of Bandar Khayran and in the Daymaniyat Islands), and it was assumed that *Acanthaster* caused these scars because they were observed near feeding starfish and other potential predators (e.g. gastropod corallivores) were not found.

Feeding observations. A quantitative assessment of the coral species attacked in the Daymaniyat Islands (site 62) revealed significant preferences for *Montipora* and *Acropora*, and an avoidance of *Pocillopora damicornis* (see Glynn, 1987). In the western Daymaniyat Islands (sites 57 and 58),

Table 4. Summary of search effort information for juvenile coral-eating *Acanthaster* (20 September - 20 October 1982). No *Acanthaster* juveniles were found during surveys.

Area	Sites	Microhabitats searched	Search time (man-hrs)
Musandam	4, 7	Basal branches of live and dead *Acropora*; undersides of dead *Acropora* slabs.	50 min
Bandar Khayran	15, 17	Basal branches of live and dead *Acropora* and *Pocillopora*; coral rubble bottom.	90 min
Suwadi	24	On live and dead ramose and massive *Porites*; basal branches of *Pocillopora* and in pocilloporid rubble.	40 min
Sur	28, 29	Among and under massive *Porites* colonies with small feeding scars1); under coral rock.	25 min
Marbat	32, 33	Basal branches of live and dead *Acropora*; among rocks and under boulders.	120 min
Masirah	44, 45 49, 55	Among basal branches of live *Montipora* and *Pocillopora*; under *Platygyra* colonies; under coral slabs.	55 min
Bandar Khayran (ca. 3 km south)	56	Among massive *Porites* colonies with small feeding scars1); among live and dead *Acropora* and *Montipora* corals.	30 min
Daymaniyat Islands	57, 58 60, 70	Basal branches of *Acropora* with small feeding scars1); under *Acropora* rubble; on live *Porites* and among basal branches of live *Pocillopora*.	110 min
		TOTAL EFFORT:	8 hrs 40 min
		TOTAL NUMBER JUVENILES FOUND:	0

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1) *Acanthaster* were feeding in the vicinity and the freshly dead coral was presumed killed by adult or juvenile sea stars.

Acanthaster was observed feeding on *Pocillopora, Porites* and *Goniopora* with a significant preference for the latter genus. No live *Acropora* or *Montipora* were seen in the areas where *Acanthaster* was foraging. The only evidence of *Acanthaster* predation on all pocilloporid patch reefs was an occasional, freshly killed small colony or broken fragment of *P. damicornis* near the reef base.

Feeding scars typical of *Acanthaster* were seen occasionally on the mainland (sites 13, 21 and 74). Mostly small and broken fragments of *P. damicornis* had been eaten, presumably by *Acanthaster*, along the reef bases of pocilloporid reefs at sites 13, 21 and 22. *Acropora cytherea* was abundant at site 74 and this was the only species, of many present, that had been attacked. *Acanthaster* attacks on *Acropora* and *Montipora* were common where live colonies of these genera were abundant (e.g. sites 14, 15, 17, 23, 56 and 73). At most of these sites, numerous colonies appeared to have been killed recently by *Acanthaster*. Quantitative sampling indicated that *Acanthaster* preyed preferentially on *Acropora* at Bandar Khayran (site 15) and on *Montipora* at Ra's al Khayran (site 56) and Ra's Abu Da'ud (site 73). *Acanthaster* was observed feeding on massive *Porites* colonies at Khor al Hair (site 28). The small reef there consisted predominantly of *Porites* and *Goniopora* corals. Some coral taxa were seldom, if ever, observed being preyed upon by *Acanthaster* (e.g., *Astreopora myriophthalma, Echinopora* spp., *Platygyra* spp., *Acanthastrea echinata, Symphyllia radians* and *Turbinaria* spp.) even when present beside corals that were being eaten. All *Acanthaster* that were feeding at site 29 (n = 10 ind) were eating alcyonaceans. Reef corals were uncommon to rare at this site.

DISCUSSION

Pocilloporid Reefs and Inter-regional Comparisons

All pocilloporid coral communities and coral reef frameworks observed in this study occurred in habitats sheltered from strong wave action. On some reefs with large holes and separated pocilloporid blocks, visual inspection revealed that the reef framework accreted vertically as a meshwork of interlocking *Pocillopora damicornis* branches. These frameworks were highly porous, contained few binding coralline algae, and revealed no obvious post-depositional cementation. They are very similar to eastern Pacific pocilloporid reef structures (Glynn et al., 1972; Porter, 1972b; Glynn and Macintyre, 1977; Glynn and Wellington, 1983). Both Omani and eastern Pacific pocilloporid reefs are fragile and typically develop under relatively calm-water conditions.

The *Pocillopora* assemblages described by Rosen (1971) at Mahe, Seychelles Islands, develop under markedly different conditions than those noted above. The Mahe pocilloporid assemblages were composed predominantly of colonies with an encrusting or robust growth form, which were tentatively identified as *Pocillopora danae-meandrina*. Moreover, the colonies were characteristically discrete, i.e. not forming contiguous patches, and generally increased in abundance under turbulent conditions such as shallow forereef habitats. These corals are closely allied, if not identical, to *Pocillopora verrucosa*, which is a well known Indo-Pacific species that typically inhabits exposed, reef front habitats (Veron and Pichon, 1976).

Although *P. verrucosa*/*P. meandrina* and *P. damicornis* communities develop under different conditions of water motion, they demonstrate similar cover/diversity relationships. Coral communities present in exposed habitats, e.g. at Mahe (Rosen, 1971) and also in Hawaii (Grigg and Maragos, 1974), tend to show decreasing coral species diversity as *Pocillopora* live cover increases. Grigg and Maragos (1974) suggested that increases in coral diversity were due to physical disturbances, which prevented the monopolization of space by competitively competent *Pocillopora* corals. This pattern also was observed in sheltered *P. damicornis* communities in Oman (present study) and the eastern Pacific (Glynn, 1976) with highest diversity on reef flats or in reef base zones. In Panamá, physical factors (e.g. extreme tidal exposures) were identified as diversifying agents at shallow depth and biological processes (e.g. predation, bioturbation) in deeper reef zones (Glynn, 1976).

Reef frames constructed by *P. damicornis* also occur at other outposts of reef development, i.e. in the western Arabian Gulf (Burchard, 1979), at several locations in the eastern Pacific region (Glynn and Wellington, 1983), and in western Australia (Veron and Marsh, 1988; Hatcher, 1991). Pocilloporid reef patches, occupying 100s of m^2 of bottom, were observed by Burchard (1979) in the western Arabian Gulf. The virtually monospecific stands of *Pocillopora* in the Arabian Gulf, which Burchard (1979) suggested might be of clonal origin, were present on current-swept reef knolls. Burchard (1979) did not comment on how clonal propagation might have occurred, but it is possible that water movement played some role. In the eastern Pacific, fragmentation of *Pocillopora* is caused by pufferfish that feed on colony branch-tips, incidental breakage by other foraging and nest-building fishes, bioerosion and wave action (Glynn et al., 1972; Wellington, 1982; Guzmán and Cortés, 1989). Since pocilloporid recruitment by sexually produced planula larvae is not frequent (Richmond, 1985; Glynn et al. 1991), the lateral spread of eastern Pacific *Pocillopora* reefs appears to be due mainly to asexual fragmentation (Highsmith, 1982). Stoddart (1983) found that asexual planula production was frequent in *P. damicornis* in western Australia (Rottnest Island). On the basis of a population genetic analysis and the growth morphology of post-juvenile colonies, he concluded that recruitment by asexual planulae was more important than fragmentation in reef growth.

The processes promoting the lateral growth of Omani pocilloporid reefs are not obvious. *P. damicornis* recruits were uncommon and relatively few *Pocillopora* fragments (dead or alive) were present. The general absence of large foraging fishes (herbivores and carnivores) or nest-building species, such as balistids and wrasses that often break and move corals in their building activities, suggests that this kind of disturbance may not be as important in Oman as it is in the eastern Pacific. Even on some pocilloporid reefs in the Daymaniyat Islands, where resident balistids (*Melichthys indicus*) were numerous, few broken coral branches were evident. In Hawaii, *Melichthys niger* (Bloch) feeds mostly on plankton, but occasionally eats coral (Hobson, 1974). Most reef base zones graded abruptly into sediment plains in Oman compared with extensive pocilloporid rubble slopes on eastern Pacific reefs. Possibly tropical cyclones play a role in coral fragmentation and horizontal reef growth (see below), however, the reefs that showed evidence of breakage in the Capital area were virtually devoid of live coral that would contribute toward reef recovery.

Upwelling Effects on Coral Reef Development and Distribution

This study revealed that coral communities and coral reefs were best developed in Arabian Gulf (Musandam) and Gulf of Oman (Daymaniyat Islands and Capital area) waters compared with the Arabian Sea coast of Oman, in general agreement with the findings of Green and Keech (1986), Sheppard (1988), Sheppard and Salm (1988), Sheppard et al. (1992) and Salm (1993). Coral cover and reef development were limited along the Arabian Sea coast except in a few areas sheltered from monsoon-induced upwelling. This difference is evident in the percent cover of coral and algal epibenthos in two areas (4 sites) on the Arabian Sea coast and one area (2 sites) in the Gulf of Oman (Figure 34). Macroalgae predominated at Sadh with only a few reef-building corals present below about 5 m. The most notable difference between Masirah and Muscat was the shallow occurrence of corals in the Arabian Sea area (to 4 m depth) compared with the Gulf of Oman (to 11 m depth). These results also agree with other studies that have

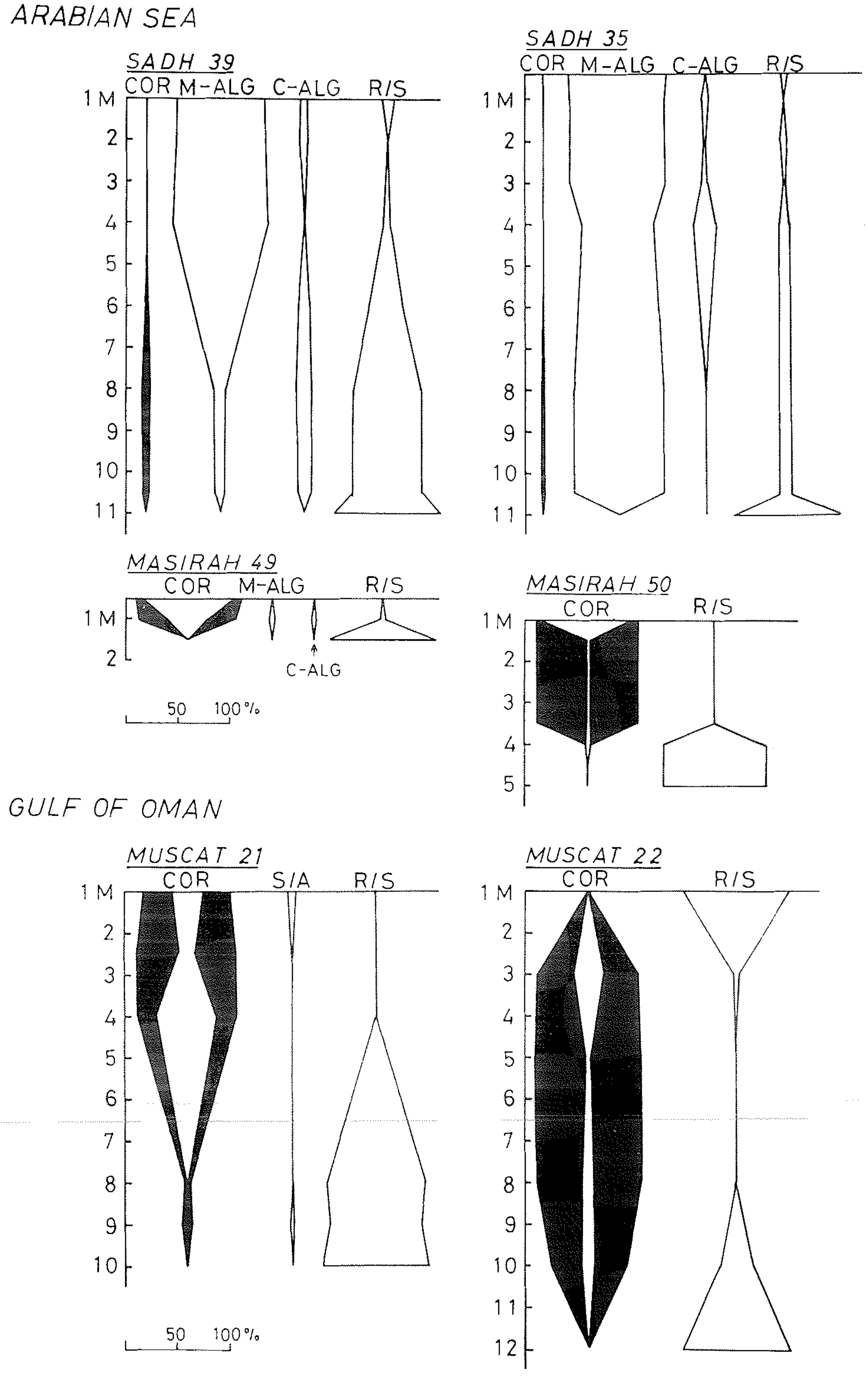

Figure 34. Percent cover with depth of major epibenthos at four sites in the Arabian Sea and two sites in the Gulf of Oman. COR, reef-building corals (solid = live, open = dead); M-ALG, macroalgae; C-ALG, coralline algae; R/S, rock and/or sand; S/A, sponges and/or sea anemones.

demonstrated a negative influence of upwelling on reef growth in the Indian Ocean (Scheer 1971, 1984; UNEP/IUCN, 1988) and elsewhere (Ladd, 1971; Glynn and Stewart, 1973; Sournia, 1976; Antonius, 1980; Glynn and Wellington, 1983).

Two areas in the Arabian Sea not investigated in this study, Barr al Hikman and the Kuria Muria Islands (Al Halaniyat), have been shown to support extensive reef development, and diverse and abundant coral communities (Salm, 1993). Most of the coral reefs off Barr al Hikman, Gulf of Masirah, are built chiefly of *Montipora foliosa*, occupy many square kilometers, and are the largest reef structures in the Sultanate (Salm, 1993). The distribution of the Barr al Hikman reef complex corresponds with the typically warm thermal conditions observed in the northern sector of the Gulf of Masirah.

In some bays on the mainland Dhofar coast and in the Kuria Muria Islands, maximum live coral cover was 99%, *Porites* colonies attained 12 m in diameter, and several reef associated cnidarians (e.g., *Tubipora*, *Millepora*, *Gardineroseris*, *Goniastrea*, *Euphyllia* and *Leptoria*) were found that are not known from other parts of the Sultanate (Salm, 1993). True reef development, with *Porites* constructing up to 3-m thick frameworks, also were observed at 17 sites in the Dhofar Province. Sheppard et al. (1992) noted the occurrence of coral reefs at Ra's Madrakah (Figure 27), but offer no information on location, size or species composition. The 8 sites I examined on the Dhofar coast revealed scant coral cover (≤ 10%), no reef frameworks, and no new coral genera. The bottom cover at all sites consisted of 80-90% macroalgae. The diverse and well developed coral formations reported by Salm (1993) were unexpected because of the active upwelling that occurs along the Dhofar coast. According to Savidge et al. (1990), the main upwelling area off the southern coast of Oman is likely localized in the immediate vicinity of the Kuria Muria Island chain. During the 1984 SW monsoon season, minimum SSTs of 16.2°C were recorded from a site approximately 1 km offshore in Kuria Muria Bay (Savidge et al., 1990). Several workers have reported the coldest upwelled water to occur on the downstream (eastern) side of headlands, off Ra's Hasik (approximately 40 km W of the Kuria Muria Islands), off Ra's Suqrah, and Ra's Madrakah, in the southern sector of the Gulf of Masirah (Currie et al., 1973; Weaks, 1983; Elliott and Savidge, 1990; Savidge et al., 1990; Brock et al., 1992; present study).

Exceptionally large coral colonies are known from upwelling regions, e.g. the 12 m diameter colony of *Pavona* in Urvina Bay, Galápagos Islands (Colgan, 1990). However, this colony was located on the lee side of Fernandina Island, which sheltered it from the most intense upwelling of the region (Colgan, 1991). In addition, the best developed coral formations in the Galápagos Islands and Pearl Islands (Panamá) are located on island shores that are not exposed to the most intense upwelling in these regions (Glynn and Stewart, 1973; Glynn and Wellington, 1983). Also, the occurrence of several tropical coral genera only in the upwelling Dhofar area (Salm, 1993) is inconsistent with known distributional patterns in upwelling eastern Pacific environments. For example, 3 species of *Millepora* are known from the non-upwelling Gulf of Chiriqui, Panamá, while none has been reported in the upwelling Gulf of Panamá (Glynn et al., 1972; Porter, 1972b). Clearly, detailed studies are now in order to determine fine-scale upwelling patterns and how these relate to coral community distribution and development in the Dhofar.

The occurrence of several tropical species of corals, echinoderms and fishes in the Dhofar and not elsewhere in Oman is intriguing. Salm (1993) briefly noted that some of the extant Dhofar coral species may represent Pleistocene relicts since they are also found as fossils in beach gravel deposits along the Gulf of Oman coast from Ra's al Hadd to Sur. It is also possible that such species represent ephemeral Holocene populations that experience relatively brief periods of invasion and extinction. Monsoon-driven currents could convey propagules from the east African coast during the SW monsoon and from northeastern Arabian Sea localities (e.g., Pakistan and India) during the NE monsoon (Bauer et al., 1991). Considering the strong upwelling conditions that accompany the SW monsoon, I believe that non-upwelling NE monsoon currents would offer a more suitable means for the conveyance of tropical larvae along the southern coast of Oman. Other examples of current systems that likely advect larvae into marginal reef environments from tropical source areas are the Leeuwin Current off western Australia (Hatcher, 1991), the Kuroshio Current off southern Japan (Tribble and Randall, 1986; Yamaguchi, 1986; Veron, 1992), and the North Equatorial Counter Current that flows into the eastern Pacific (Dana, 1975; Richmond, 1990; Glynn and Colgan, 1992).

Nutrient pulses that accompany upwelling promote the growth of benthic algae, which may interfere with coral growth and survivorship through increased competition (Glynn and Stewart, 1973). A similar argument has been advanced to explain the latitudinal limits of coral reef growth, which seem to be influenced by low water temperature, high nutrient levels and abundant macroalgal populations (Johannes et al., 1983; Hatcher, 1985, 1991). Dissolved nutrient concentrations increase dramatically along the Dhofar coast during the SW monsoon period. For example, NO^3-N demonstrated a 10-fold increase during upwelling, from 2-3 to 20-22 μg-at.l^{-1}, and PO^4-P a 2-3 fold increase, from 0.75-0.80 to 1.9-2.0 μg-at.l^{-1} (Savidge et al., 1990). The elevation in nutrient levels shows a high seasonal correlation with increases in benthic algal biomass (Barratt in IUCN/ROPME/UNEP, 1985; Sheppard et al., 1992). Unlike upwelling-dependent, macroalgal ecosystems elsewhere, the Dhofar kelp forests undergo a marked seasonal die-back. Barratt noted a "...total annual decline and recovery with the life cycles of the relevant species being completed in a time span of only six months." Thus, reef corals on the Arabian Sea coast of Oman can tolerate the seasonal proliferation of macroalgae as do corals in the Arabian Gulf (Coles, 1988).

Upwelling also occurs in the Gulf of Oman during the summer (June-September) monsoon season, but is more localized and sporadic compared with upwelling on the Arabian Sea coast. Green and Keech (1986) noted the high interannual variability of upwelling in the Capital area. This variability was evident in the present study as well: a single, spatially restricted upwelling pulse was observed in the Capital area in 1988 whereas several, widespread upwelling plumes occurred in 1989. Green and Keech (1986) reported a 15°C temperature drop (from 32° to 17°C) observed at 10 m depth in just under two weeks during an upwelling event in July 1983. It was speculated that such sudden temperature drops might be responsible for areas of dead coral observed on reefs in upwelling environments. The youthfulness of coral formations and the absence of certain coral genera in the Capital area also were attributed to upwelling disturbances (Green, 1983). In light of the many distinctive coral genera that are restricted to strong upwelling conditions along the Arabian Sea coast (Salm, 1993), the latter suggestion is not very convincing.

Acanthaster: Distribution, Abundance and Effects on Coral Communities

Surveys conducted through 1990, spanning a 7 year period since this 1982 study, have confirmed that *Acanthaster* is limited in distribution to the Gulf of Oman (Salm, 1993). *Acanthaster* was not found at any of the Musandam sites in the 1982 study. However, on the north coast of Musandam (Kumzar, site 10), the easternmost site surveyed in 1982, large adults of *Acanthaster* were locally abundant in 1989-90. No *Acanthaster* were found on the west or Arabian Gulf side of the Musandam in later surveys, but outbreak populations were seen at several sites along the north and east shores or Gulf of Oman side of the Musandam. Environmental conditions (i.e. warm thermal regime, abundant coral prey) appeared to be favorable for *Acanthaster* on the Arabian Gulf side, and its apparent absence there was unexpected. Salm (1993) has suggested that current eddies characteristic of areas of complex coastal terrain could be responsible for concentrating coral and *Acanthaster* larvae at Musandam sites bordering the Gulf of Oman. Modelling results of the larval dispersal of *Acanthaster* on the

Great Barrier Reef have demonstrated a focusing of recruitment from multiple sources by currents (Dight et al., 1990).

Acanthaster was not seen in two areas (Masirah and Dhofar) on the Arabian Sea coast in 1982 nor in later surveys, including the Kuria Muria Islands (Salm, 1993). Several factors could be responsible for the absence of the starfish from this region. Regarding the relatively high thermal conditions necessary for *Acanthaster* to reproduce and complete larval development (25°-32°C; Lucas, 1973; Moran, 1986) -- spawning typically occurs between May and August in the northern hemisphere when sea temperatures are high -- it is clear that the Arabian Sea coast of Oman would not offer suitable conditions during most of the summer (June-September) when the monsoon jet from northeastern Africa induces active upwelling (16°-19°C). If it were possible for *Acanthaster* to reproduce in the early summer (May and June), then it is likely that later developmental stages could be adversely affected by at least two factors. The high population abundances of suspension feeders inhabiting this upwelling environment would pose a risk to the larvae, and coral prey required by the young adults would generally be in low supply and highly dispersed. Still, high coral abundance and moderate thermal environments do occur along the Arabian Sea coast, e.g. in the northern Gulf of Masirah, indicating the presence of suitable conditions on local scales. A similar situation occurs off the eastern tropical Pacific coast where the southern limit of distribution of *Acanthaster* corresponds with a marked thermal front that separates non-upwelling and upwelling waters (Glynn, 1974). Certain areas to the south support vigorous coral reef development, e.g. Gorgona Island, Colombia (Glynn et al., 1982), yet *Acanthaster* has not been reported from these localities.

Although the MAF had received several reports of *Acanthaster* outbreaks in the Daymaniyat Islands and Capital area, these were largely unsubstantiated. Commercial fishermen and sports divers claimed that several hundreds of *Acanthaster* per hectare were feeding on reef corals at several sites in the Gulf of Oman. The only quantitative data that I could find reported two *Acanthaster* in a 100 m transect at Fahal Island (near site 13, Figure 4), and 0.5 ind/m^2 (25 ind/50 m^2) at Bandar Jissah (Interim Report, 1982; Glynn, 1983a). If the latter density could be extrapolated realistically to a larger area, then this would be equivalent to an outbreak population (100s of ind/ha; Moran, 1986).

The population densities reported in this study and the earlier survey at Bandar Jissah probably are oppositely biased by two effects: 1) the counts were made in restricted areas and represent starfish that had aggregated while feeding, and 2) the searches were conducted during daylight hours when some resting starfish were hidden from view. Fresh feeding scars attributed to *Acanthaster* were noted at three sites where no starfish were observed. I believe that these field procedures tend to inflate starfish abundances. If surrounding areas of coral habitat, with few or no starfish present, were added to the sampled areas then the starfish densities in many cases would surely be lower than reported.

After 1982, the highest abundances of *Acanthaster* were reported from the Gulf of Oman shores of the Musandam (Salm, 1993). In the Habalayn area (about 10 km SE of Khasab), 27 *Acanthaster*/0.4 ha were observed in 1986, and 117 ind/15 min (the largest number seen) were reported during the 1989-90 survey. Although highly variable abundances have been observed at various Indo-Pacific localities (Moran, 1986), the former density (68 ind/ha) is higher than any reported normal population, and the latter corresponds with most outbreaking populations. *Acanthaster* has remained relatively common in the Muscat area during the past decade (Salm, 1993).

On the basis of field studies in the western Pacific (Kenchington, 1977; Zann et al., 1987), *Acanthaster* can attain disc diameters of 14-20 cm in a period of 3-4 years. Therefore, it is probable that most individuals observed in late 1982 originated locally from the abundant populations reported during 1978-1980. The considerable range in starfish sizes may result from two effects: (1) populations composed of smaller individuals are relatively youthful; (2) the size differences reflect the abundance of coral food resources (Dana et al., 1972). In support of the food-abundance explanation, the largest starfish were present in areas with the highest abundance of *Acropora* corals, i.e. at Bandar Jissah and Bandar Khayran.

Much effort was spent in the 1982 survey searching for juvenile starfish that could mature and affect coral communities at a later time. Since very few juveniles (7-9 cm disc diameter) were found in the Gulf of Oman surveys, no large-scale outbreaks were predicted through late 1984 (Glynn, 1983a). Evidently, all areas of the Gulf of Oman south of the Musandam have been free of *Acanthaster* outbreaks since the 1978-80 episode (Salm, 1993).

Acanthaster fed disproportionately on *Acropora* and *Montipora* species at all sites in the Gulf of Oman where these corals were abundant (Glynn, 1987). However, where *Acropora* and *Montipora* were uncommon or absent -- in several areas only dead colonies of these genera remained after presumed earlier starfish attacks -- *Acanthaster* fed on *Porites* spp., *Goniopora* spp., *Stylophora pistillata*, *Pocillopora damicornis*, and other corals. Several field studies have shown that *Acanthaster* feeds preferentially on acroporid corals (e.g. Branham et al., 1971; Glynn, 1983b, 1987; Moran, 1986; Colgan, 1987; Faure, 1989; Keesing, in press). Pocilloporids also have been named as preferred prey in some studies (Porter, 1972; Ormond et al., 1976; Glynn, 1983; Faure, 1989; Keesing, in press). However, when the supposed preferred prey species is *P. damicornis*, this claim is usually based on qualitative evidence (Potts, 1982). That is, the number of consumed prey is not related to prey availability. Moreover, the spatial distribution of colonies, i.e. dispersed versus aggregated, is seldom mentioned. *P. damicornis* colonies within monospecific patches are seldom attacked by *Acanthaster* (Glynn, 1976). *Acanthaster* commonly feeds, however, on the broken branches of *P. damicornis*, which contain few if any crustacean guards, around the edges of pocilloporid patches.

Many *Stylophora* (Pocilloporidae) were eaten by *Acanthaster* in Oman despite the defensive maneuvers of their crustacean guards. *Acanthaster* also demonstrated a strong preference for both mature and juvenile *Stylophora* in American Samoa (Glynn, 1983b) and Okinawa (Keesing, in press) respectively. It is possible that the lower guard densities/colony and lower level alpheid guard defensive responses in *Stylophora*, compared with *Pocillopora* (Glynn, 1983b, 1987), is at least partly responsible for the different susceptibilities to predation in these genera. Another factor may relate to the spatial distribution of the prey taxa. That is, *Stylophora* colonies typically are dispersed whereas *P. damicornis* colonies frequently form thickets. Dispersed colonies could be more susceptible to predation than aggregated colonies.

Coral communities in many parts of the Gulf of Oman are recovering following high levels of *Acanthaster* predation and are in a nonequilibrium state (Connell, 1978). Where predation was severe coral cover and diversity demonstrated a notable decline. The recruitment of *Acropora* and *Pocillopora* has been observed in some affected areas (Salm, 1993), but the course of recovery cannot be predicted without knowledge of continuing *Acanthaster* predation and patterns of coral recruitment. In the western Pacific, rapid recovery (ca. 10 years) has occurred on some reefs that experienced intense and short-lived predation and high recruitment following *Acanthaster* outbreaks (Pearson, 1981; Colgan, 1987). However, if *Acanthaster* abundances remain relatively high in the Gulf of Oman, i.e. around 30 ind/ha, and coral recruitment is low, recovery of acroporid reefs could be prolonged (perhaps spanning decades).

This recovery scenario would be exacerbated if *Acanthaster* continues feeding selectively on remnant and recruiting acroporid corals (Keesing, in press) as occurred on an Okinawan reef subject to persistent *Acanthaster* predation since the early 1970s (Nishihira and Yamazato, 1974; Yamaguchi, 1986). Keesing (in press) found that medium population levels of *Acanthaster* (33-44 ind/ha) that continued feeding selectively on recruiting acroporid and pocilloporid corals interfered with recovery, resulting in a community dominated by non-preferred *Porites*, *Millepora*, and alcyoniid soft corals. The destructive grazing effects of high sea urchin [*Echinometra mathaei* (de Blainville)] densities on the Okinawan reef also were suspected of interfering with coral recruitment. This effect on Omani reefs has not been investigated.

The results of the 1978-80 *Acanthaster* outbreak, particularly in the Daymaniyat Islands, had a devastating impact on acroporid reefs. Virtually all acroporid corals were killed. In mixed coral assemblages, where acroporid, montiporid, pocilloporid, and poritid corals occurred side by side, only acroporid/montiporid taxa were killed in large amounts. Several reefs composed mainly of *Porites* and *Pocillopora* corals were still largely intact, exhibiting 80-100% live cover. This scale of predation would seem to affect the differential survival of reef types. Perhaps the prominence of poritid and pocilloporid corals in the Gulf of Oman is in large degree mediated by *Acanthaster* predation, both at outbreak and long-term moderate levels. The prominence of acroporid and montiporid communities and reef frameworks on the Arabian Gulf side of Musandam, and at sites protected from intense upwelling on the Arabian Sea coast, also may be related to the absence of *Acanthaster* in these areas.

Other Factors Affecting Omani Coral Reefs

Unlike the large stands of dead *in situ Acropora* observed in the Daymanyiat Islands and Capital area, the dead *Pocillopora* reefs from Bandar Jissah south to Ra's Abu Da'ud, a coastal stretch of 37 km, showed clear signs of mechanical destruction. The summits of these reefs were planed level and large amounts of coral debris were found nearby. Considering the large scale of this damage and lack of fishery-related artifacts, other sorts of disturbances should be considered. Since the Gulf of Oman and Arabian Sea are located within a center of tropical cyclones (Stoddart, 1971a), it is possible that these fragile pocilloporid reefs were damaged by a severe storm. It is also possible that the dead, *in situ* pocilloporid reef framework observed at Masirah Island could have resulted from a storm similar to that which crossed Masirah on 13 July 1977 (Everts et al., 1983). This storm had maximum sustained winds of 46.3 m/sec, maximum wind gusts of 61.7 m/sec, and resulted in 430.6 mm of precipitation over a 24 hr period. Some potential impacts from a storm of this magnitude that could kill corals yet not affect their growth position are (1) sea water dilution resulting from heavy rainfall and river flooding, (2) drop in water level due to altered reef geomorphology, and (3) deposition of sediment on live corals (Stoddart, 1971b).

Widespread and locally severe coral reef bleaching (zooxanthellae and/or chlorophyll pigment loss) was reported for the first time in the Gulf of Oman during the summer of 1990 (Salm, 1993). Reef corals, alcyonaceans and zoanthids were affected in the Muscat area and on the eastern shores of the Musandam Peninsula. The bleaching event revealed the following responses, which have been related to elevated SSTs in other regions (Brown, 1990; Glynn, 1990b, 1991; Williams and Bunkley-Williams, 1990): 1) severity greatest during peak summer temperatures; 2) shallow reef populations most affected; 3) populations in areas with reduced circulation most affected; and 4) duration of exposure, with SSTs in excess of 30°C, was critical.

Although near-shore temperature data are not available to assess the intensity and duration of elevated SSTs in 1990, the Nansen cast record reported in this study suggests that the June 1990 SSTs were exceptionally warm. For example, the 39°C SST reported near Muscat (Salm, 1993) was 2°C higher than the maximum June temperature recorded during the 46 year period of record. The 35°C SSTs recorded in the Musandam in August 1990 also were 1°C above the long-term maximum temperature for this month in the Gulf of Oman. Additionally, remote sensing SST data from the Muscat area in the summers of 1988 and 1989 showed that near-shore high temperatures were in the range 31°-33°C, which agree with earlier (1965 and 1966) summer maximum temperatures of 30°-32°C recorded at 1.8 m depth at Mina al Fahal (Green and Keech, 1986). Satellite SST data from 1990 were not analyzed.

Bleaching-induced mortality in the Muscat area was slight (<2%) and affected only *Acropora*. *Montipora* and *Porites* were severely bleached, but recovered when SSTs normalized. Mortality was greater in the Musandam, but highly variable, ranging from <1% to >95%. Many of the affected coral species (*Acropora* and *Stylophora*) were species also selectively preyed on by *Acanthaster*. *Platygyra daedalea* experienced high partial mortality and dead patches were invaded by algae and presumably later heavily bioeroded by sea urchins. Salm (1993) speculated that the many hollowed-out, live *P. daedalea* in this area might result from sporadic bleaching events such as that observed in 1990. Interestingly, Salm (1993) did not report bleaching in *Pocillopora damicornis*, a highly susceptible species in other regions (Brown, 1990; Glynn, 1990b). The upper branches of numerous shallow (0.5-1 m depth) *P. damicornis* colonies were bleached on the Arabian Gulf side of Musandam (site 12) on 21 September 1982. This was the only coral bleaching observed at that time.

The differences in severity of bleaching and mortality in the Muscat and Musandam areas were hypothesized by Salm (1993) to be related to local differences in circulation processes. Although higher SSTs were recorded in the Muscat area than at Musandam, temperatures dropped rapidly at Muscat, from 39°C to 24°C in less than one week at the end of June. This sudden temperature drop likely was due to upwelling. Upwelling has not been reported at Musandam, and there SSTs in 1990 remained above 30°C to a depth of 10 m for at least three months. In the Gulf of Panamá, upwelling moderated sea warming during the 1982-83 El Niño event, delaying coral bleaching and mortality by four months (Glynn, 1984).

Other factors impacting Omani coral reefs, such as coastal erosion, flooding, sedimentation, possible coral diseases, and several types of anthropogenic disturbances are enumerated by Salm (1993). Entangling fishing nets, anchor damage and other fishery-related impacts are prevalent in the Musandam and Capital areas. Fragile *Acropora* and *Pocillopora* assemblages in particular have been subject to widespread destruction during the past decade. Salm (1993) reported that litter and fishery activities have caused notable damage to coral communities at 72% of 111 sites surveyed in the Musandam, 61% of 43 sites in the Muscat area, and 35% of 20 sites in the Dhofar Province. I did not witness any obvious human-related damage to coral communities in 1982, during concentrated surveys at 75 sites distributed across the Sultanate. Besides the unfortunate degradation of numerous, formerly pristine, coral sites in recent years, in many damaged areas it will now be impossible to distinguish between natural and anthropogenic causes. This will greatly complicate management procedures because of the increasing difficulty in assessing the impact of human activities.

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