

# ECOLOGY AND NATURAL HISTORY OF A STAND OF GIANT KELP, *MACROCYSTIS PYRIFERA*, OFF DEL MAR, CALIFORNIA

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## ABSTRACT

The assemblage of plants and animals living within a stand of *Macrocystis pyrifera* off the coast of southern California was studied from July 1967 through February 1973. *Macrocystis* is a perennial kelp, with some individuals living as long as 7 yr; however, the average life span in this bed was approximately 3 to 4 yr. Physical disturbances associated with storms were the major mortality causes of adult *Macrocystis* in this area. Once detached, these plants drift through the bed and become entangled with other plants which results in extensive mortality. The fact that germination was greatest after the surface canopy was thinned by natural attrition and commercial harvesting suggests that light is a critical factor influencing the recruitment of *Macrocystis*. There was little indication to show that sea urchin grazing contributed to kelp mortality.

Faunal species identified included 38 fish species and 98 invertebrate species. Of these, 14 species of macroinvertebrates were chosen for more intensive study as they represented common or characteristic species in the kelp bed. Patterns of distribution and abundance were recorded during the study period. Most species had aggregated distribution patterns and the populations of most remained reasonably constant over 4.25 yr. *Styela montereyensis* (ascidian) fluctuated annually and the *Muricea californica* (octocoral) population slowly decreased during this time. Conversely, *Diopatra ornata* (polychaete) displayed a numerical increase, such that in August 1972 it was the most abundant macroinvertebrate in the Del Mar kelp bed. A qualitative food web is presented based on limited trophic information.

Many large kelp stands historically have either undergone dramatic oscillations in areal cover and standing crop or completely disappeared (see North, 1971, for history and data). Nearshore kelp stands are found in many scattered locations along the mainland of California and fringe most of the state's offshore islands; in southern California kelps are often conspicuous when the dominant plant, *Macrocystis pyrifera* (Linnaeus) C. Agardh, forms a floating canopy or bed along the sea surface. This kelp community contains many plant and animal species which contribute aesthetic as well as diverse recreational and commercial resources. The loss and deterioration of these stands is correlated with many man-caused perturbations and natural events such as reduced water quality, the over-harvest of numerous important component animal populations, and fluctuations in seawater temperature.

There is widespread concern regarding effects of increasing human perturbations to these near-shore kelp communities which include increasing recreational and commercial usage as well as many projected sewer and thermal outfalls into or in the proximity of kelp beds. Despite this concern, there is little information regarding natural temporal variation of populations inhabiting these assemblages. Furthermore, natural history data such as food web interactions critical to a functional understanding of this community are in a very rudimentary state. This information is obviously vital to the proper management of this resource.

The objectives of this paper are to: 1) describe patterns of distribution and abundance, 2) record long term population fluxes, and 3) note food web and other natural history observations of conspicuous members of a relatively undisturbed kelp association. Such data are essential to the growth of a functional understanding of this community.

The study site (Figure 1) was located in a bed of *Macrocystis pyrifera* about 1 km offshore from Del Mar, Calif. (lat. 32°57'N, long. 117°16'W). The majority of the observations were made at

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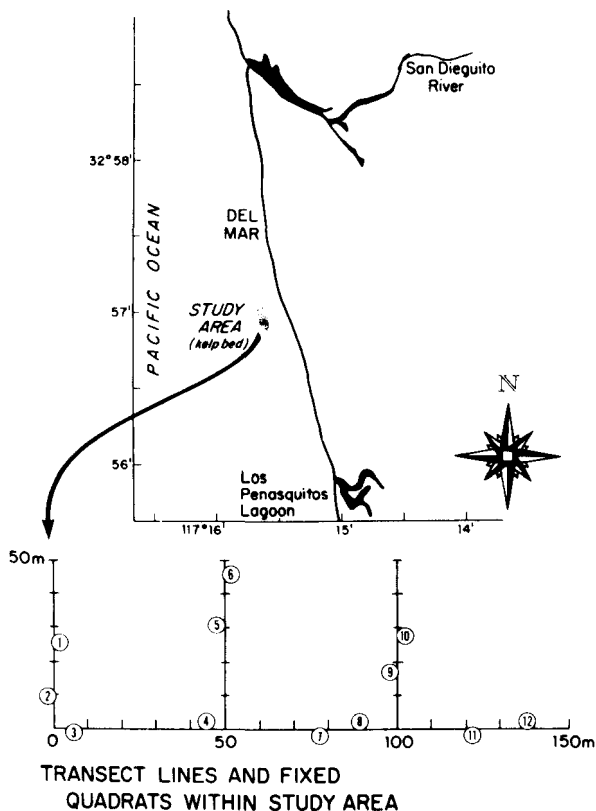


FIGURE 1.—Location of the subtidal study area off Del Mar, Calif. The drawing shows the layout of the transect lines and the position of each fixed quadrat.

depths between 14 and 20 m in the most seaward *Macrocystis* stand directly off 8th Street in Del Mar. These continuing studies were begun in June 1967.

Within the perimeter of the study area the substratum is composed primarily of sedimentary mudstones and siltstones, coarse sand, and silt. The sea floor is somewhat flat in appearance, although low (<1.5 m) consolidated mounds and shallow ledges break up the overall visual uniformity of the bottom.

The monthly mean surface water temperatures recorded off the pier at Scripps Institution of Oceanography, approximately 24 km south of the study site, varied from a minimum of 10.1°C to a maximum of 24.6°C between June 1967 and December 1971 (Scripps Institution of Oceanography, 1968-1971). The annual mean temperature during this same period was 16.3°C. Since the water column in this area is thermally stratified, it is essential to consider bottom temperatures

as well. To this end, 70 bottom temperatures were recorded at a depth of 17 m in which the mean temperature was 13.0°C with the minimum recorded temperature being 10.5°C, and the maximum being 16.0°C.

A great deal of water movement is typical to this environment (Inman and Brush, 1973) and water transparency or underwater visibility is greatly affected by the resulting sediment disturbance. Over the 5.7-yr study, the underwater visibility ranged from 0 to 20 m, the average visibility being about 3 to 4 m. However, on many dives the underwater visibility was so reduced that it was impossible to see along the bottom in the vicinity of the kelp bed.

## METHODS

The study was initiated in June 1967 after several months of exploratory observations. All of the in situ observations were made while scuba diving and more than 300 h were spent underwater in this location. Most observations were made during daylight hours, however about 5 h were spent in this location between 2000 and 2200 h. The observations reported in this paper span more than 5 yr, from June 1967 through February 1973.

Initially a 100-m transect consisting of 20 brass stakes (75 cm in height) was placed along the sea floor in June 1967. One stake was placed every 5 m, and the entire array was perpendicular to the shoreline. During July 1967 the position of each attached *Macrocystis* plant growing within 1 m on either side of the 100-m transect was recorded. The condition (i.e., number of living stipes, appearance of the holdfast, etc.) of each plant was noted at various times from the beginning of the study until the plant disappeared. Also, juvenile *Macrocystis* were recorded as they appeared along the 2 m × 100 m strip.

In the fall of 1967, the main transect was extended 50 m shoreward, and during March 1968 three additional lines running parallel to the coastline were added (Figure 1). Sectioned 25-m polypropylene lines (0.60 cm in diameter) were staked into the bottom alongside of the brass stakes. The lines were sectioned so that fouling or detachment of any part would not necessitate replacement of the entire transect. All lines were marked at meter intervals with tape, and the brass stakes were numbered with line and plastic

tags. This marking system made it possible to sample any point on the transect and return to the same position even during days of marginal underwater visibility.

The entire transect area was stratified into six  $2 \times 50$  m areas. Two sample points were randomly selected per stratum; at each of these 12 locations a 4-m<sup>2</sup> quadrat was placed in September 1968. Each quadrat consisted of polypropylene line, arranged in a square 2 m on a side, and held in place at each corner with galvanized spikes. Two additional 4-m<sup>2</sup> quadrats (no. 13 and 14) were added in August 1969, but in this case the locations were selected by the presence of juvenile *Macrocystis* in this part of the kelp bed. The latter two quadrats were not included in the evaluation of density or aggregation.

During September 1968 a drawing or map of each fixed quadrat was made underwater on a sheet of plastic recording natural history information and the position of each individual macroorganism. A brass meter square quadrat divided into 0.25-m<sup>2</sup> sections was used while mapping the quadrats in order to reduce the visual area being examined. Quadrats were examined at irregular intervals (i.e. monthly, bimonthly, or quarterly) by the same observer.

Data regarding density, frequency of occurrence, and distribution patterns were calculated from observations in the 12 4-m<sup>2</sup> fixed quadrats and from 48 1-m<sup>2</sup> quadrats placed at randomly chosen points along the transects. All quadrat analyses are from observations taken in August 1972. The distribution patterns of the conspicuous species were analyzed with the index of dispersion, variance/mean  $\times$  (number of observations - 1), described by Greig-Smith (1964). If the variance to mean ratio is significantly less than 1.0, the distribution is considered even, while an index significantly greater than 1.0 indicates an aggregated pattern of distribution. Significance is tested in a Chi square table with  $n - 1$  degrees of freedom. Lack of significance indicates a random distribution. Since the results of most such indices depend upon quadrat size, we compared independently the 4-m<sup>2</sup> quadrats and the 1-m<sup>2</sup> quadrats. The only differences in the two analyses of pattern were minor and involved slight loss of significance in three of the 4-m<sup>2</sup> quadrat analyses; in each case this was a result of small numbers of individuals in the 12 larger samples. The results of the pattern analysis are given in Table 5 and are based on the 48 1-m<sup>2</sup> quadrats.

## THE ALGAL ASSOCIATION

The floristic components of southern California kelp beds have been described by Limbaugh (1955); Dawson, Neushul, and Wildman (1960); North (1971); and Neushul (1971). Many of the mainland and insular kelp stands that we have surveyed in southern California appeared dissimilar with respect to the algal species present or their relative abundances. Therefore a generalized list of the algae known to inhabit these kelp communities is inadequate when describing a particular stand or comparing two or more kelp stands (Dawson, Neushul, and Wildman, 1960). The one characteristic of all mainland southern California beds appear to share is the overall domination of *Macrocystis*, in terms of both biomass (McFarland and Prescott, 1959) and apparent competition for the available light. The kelp bed at Del Mar is two layered, with the floating portion of *Macrocystis* suspended over an algal turf composed primarily of encrusting corallines. There is also a thinly scattered undergrowth of *Pterygophora californica*, *Laminaria farlowii*, and *Rhodymenia pacifica*. These species are taller than the corallines, but they occur so sparsely in this area that they cannot be considered a separate canopy. The algal association at Del Mar consisted of only a few species of attached macroalgae (Table 1); most of these plants were found along the margins of the *Macrocystis* bed.

TABLE 1.—The attached macroalgae found in the Del Mar kelp bed.

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<i>Bossiella orbigniana</i> (Decaisne) Silva
<i>Corallina officinalis</i> var. <i>chilensis</i> (Harvey) Kutzing
<i>Cystoseira osmundacea</i> (Turner) C. Agardh
<i>Desmarestia munda</i> Setchell and Gardner
<i>Desmarestia tabacoides</i> Okamura
<i>Laminaria farlowii</i> Setchell
<i>Lithophyllum</i> sp.
<i>Lithothamnium</i> sp.
<i>Macrocystis pyrifera</i> (Linnaeus) C. Agardh
<i>Pterygophora californica</i> Ruprecht
<i>Rhodymenia arborescens</i> Dawson
<i>Rhodymenia pacifica</i> Kylin
<i>Tiffaniella snyderae</i> Farlow

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## OBSERVATIONS ON *MACROCYSTIS PYRIFERA*

The giant kelp was the most abundant and conspicuous species of brown algae within the study area. It is perennial and usually grows attached to solid substratum anchored into place

by the holdfast. In July 1967, 35 attached *Macrocystis* plants which contributed fronds to the surface canopy were recorded along the  $2 \times 100$  m transect band (Figure 2). For convenience we have arbitrarily lumped all plants with fronds (stipe and blade) reaching the sea surface into a category as canopy adults. With the passage of time, the number of adult *Macrocystis* growing within this 100-m transect band was gradually reduced from 35 plants to a single survivor in June 1970. In addition to the plants along this part of the transect we followed 14 adult *Macrocystis* that grew along the 50-m shoreward extension of the transect (Figure 3). This shallower portion of the kelp bed displayed a similar reduction in the number of adult *Macrocystis*. In April 1968, 14 plants were recorded along this  $2 \times 50$  m belt, however by April 1970 the last survivor had disappeared.

The dramatic fluctuations in the number of adult *Macrocystis* within this kelp stand can be detected from both in situ counts and kelp har-

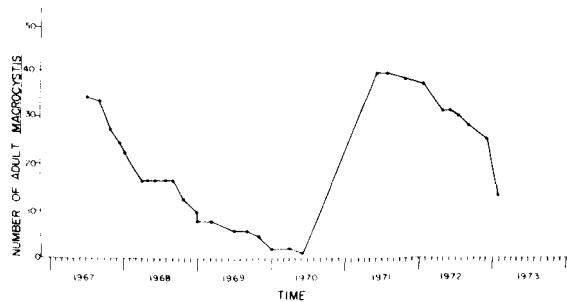


FIGURE 2.—Occurrence of adult *Macrocystis pyrifera* in the  $2 \times 100$  m transect (0-100 m).

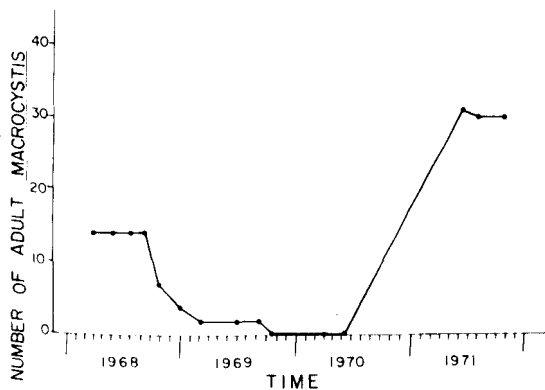


FIGURE 3.—Occurrence of adult *Macrocystis pyrifera* in the  $2 \times 50$  m transect (100-150 m).

vesting records over the past 32 yr (Figure 4). North (1971) stated "that beds five and six, lying between Del Mar and Oceanside, California have often fluctuated in this manner. These beds actually consist of approximately eight major kelp areas along about 15 km of coastline. They flourish and disappear more or less in unison, typically but not invariably with a four year period."

The general pattern for the Del Mar *Macrocystis* population seemed to be gradual attrition of the adult plants with little or no replacement over a 3-yr period, followed by recruitment after most of the adult plants had disappeared. With the addition of 40 young adult *Macrocystis* along the 100-m transect (Figure 2) during the summer of 1971 the study area again supported a density of kelp plants similar to July 1967.

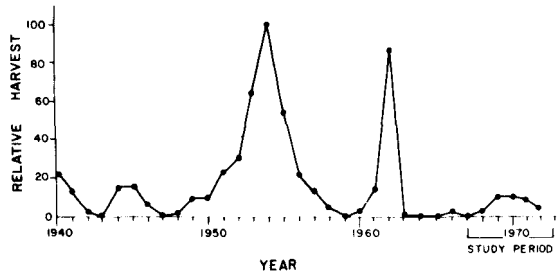


FIGURE 4.—Relative kelp harvest from bed number 5 (Del Mar). After North (1971) and Kelco Company.

### Causes of Plant Mortality

Severe grazing of *Macrocystis* by sea urchins, as described by Leighton (1971) off southern California, has not been observed within this kelp stand. The two conspicuous sea urchins in this area, *Strongylocentrotus franciscanus* and *S. purpuratus* were usually observed on consolidated sedimentary mounds, under rocks, or within ledges. During both daylight and nocturnal hours the sea urchins remained in these locations, and in most instances their feeding was restricted to detritus and detached pieces of drift algae. However, *S. purpuratus* was occasionally noted within the deteriorating holdfasts of aging *Macrocystis*. In general, it appeared that there was enough drift algae for the sea urchin population to make foraging unnecessary, and we gathered no evidence that the urchins were exerting much grazing pressure on *Macrocystis*.

Fish damage to *Macrocystis* was minimal in mature plants. Most of the grazing by fishes was directed towards juvenile plants. Quast (1968b, 1971) investigated the stomach contents of fishes collected at Del Mar and found *Macrocystis* fragments in the stomachs of the labrid *Oxyjulis californica*, the kyphosid *Medialuna californiensis* and the embiotocid *Phanerodon furcatus*. He also found macroalgae as a predominant item in terms of frequency and volume in the stomachs of *Girella nigricans*. During daylight hours in this area *O. californica*, *Embiotoca jacksoni*, and *G. nigricans* were observed biting off portions of adult and/or juvenile *Macrocystis*. Some of the fish grazing may have been directed at the invertebrates associated with the algae, but for whatever reason, the plants were damaged by these feeding activities.

Most adult *Macrocystis* attrition recorded over the 5.7 yr was caused by detachment of the holdfast and thereby elimination of the entire plant. Plants with weakened or decaying holdfasts were particularly vulnerable to physical

stress. Three factors probably accounted for most of the plant mortality in this location: 1) storms and strong surge, 2) entanglement of drifting plants with attached *Macrocystis*, and 3) kelp harvesting. Many of the kelp stands in San Diego County have been greatly thinned or almost torn away by the effects of storms (Brandt, 1923; ZoBell, 1971). Brandt (1923) reported that the La Jolla and Pt. Loma kelp beds were reduced nearly 40% in area by storms in the late winter and early spring of 1915. When *Macrocystis* plants become detached they drift along in the water column, often becoming entangled with other kelps (Figure 5). Drifting or dislodged plants thus present a potential source of mortality for attached *Macrocystis*. The stipes, blades, and holdfasts of entangled plants become so entwined that separation becomes almost impossible. We have observed as many as 18 adult *Macrocystis* entwined in one cluster near the transect. In almost every case the entanglement resulted in the mortality of the attached plant. This is a partial explanation why *Macrocystis*



FIGURE 5.—A detached *Macrocystis* drifting through the kelp bed.

growing along the transect were frequently removed in clumps of two or three plants at a time (Table 2).

The effect of harvesting on individual plants is still inconclusive. ZoBell (1971) concluded from observations of drift seaweeds on San Diego beaches that there is no consistent relationship between kelp harvesting operations and the amount of seaweed on beaches. However, at Del Mar we found adult *Macrocystis* pulled free of the substratum following harvesting. On 6 January 1969, 10 marked plants were growing along the 100-m transect (Figure 2) and 4 plants remained in the 50-m extension (Figure 3). The seas were calm and there were no loose or drifting *Macrocystis* observed along the entire transect. The kelp bed was harvested on 7-8 January 1969. Returning to the study area on 9 January 1969 we found unattached *Macrocystis* which were either drifting in the water column or entangled with other attached *Macrocystis*. Two of the marked plants on the 100-m transect were detached from the substratum, and one plant from the 50-m extension was missing. Also, one adult *Macrocystis* from fixed quadrat number 1 was removed. These detached plants probably caused additional mortalities by entangling with other plants in the kelp bed. In summary, strong water movement, plant entanglement, and harvesting probably act in a synergistic manner on attached *Macrocystis*.

## Germination, Recruitment, and Survivorship

*Macrocystis* undergoes a life cycle that alternates between an asexual macroscopic stage termed the sporophyte, and a sexual microscopic gametophyte stage (Brandt, 1923; Neushul and Haxo, 1963). Because of the difficulties inherent in microscopic investigation underwater we recorded recruitment only when the young sporophytes became visible. Although *Macrocystis* spores and gametophytes were probably present at different times of the year (Neushul, 1959; North, 1964), we were primarily concerned with the plants when they visually became part of the epibenthic community. A few young plants (<1 m in height) were observed in the study area during the early summer of 1967, however by the fall of that same year all of these juvenile sporophytes had disappeared. For the next 23 mo, no *Macrocystis* recruits were observed in the vicinity of the transect. During this time the overlying canopy was expanding to a point when, in December 1968, it covered approximately 90% of the 150-m transect line. Thus, insufficient light penetration resulting from shading by adult plants and water turbidity may have been key reasons for the absence of juvenile *Macrocystis* during 1967 and 1968. However, the bed was harvested in January 1969, which apparently reduced the surface canopy to about 15% cover

TABLE 2.—Stipe counts of individually tagged plants through study period. Plant number 1 survived with 7-8 stipes until August 1972. "G" means that the plant was completely gone and "O" signifies that there were no stipes but that the holdfast was still attached. Note the tendency for groups of plants to disappear together; in each case this resulted from mutual entanglement.

Date	Plant number																													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
July 1967	18	34	20	30	22	36	18	16	53	9	34	20	30	54	28	11	55	97	90	—	30	—	71	25	30	41	74	—	58	22
Sept. 1967	21	38	20	12	22	44	13	2	54	7	27	15	40	60	30	14	67	108	98	53	37	34	64	27	58	40	93	80	53	24
Dec. 1967	22	34	26	G	O	43	13	O	57	O	22	6	30	56	32	6	67	96	86	62	42	41	58	22	52	39	80	81	68	O
Jan. 1968	28	38	O			64	17		64		23	6	37	72	35	6	75	88	106	O	48	45	63	23	52	34	71	72	68	
Apr. 1968	32	31				16			60		27	G	32	G	30	4	67	63	102		46	44	G	22	42	35	74	60	G	
May 1968	34	28				10			63		28		35		31	G	73	82	115		42	53	22	52	34	78	62			
June 1968	29	22				10			49		25		36		35		81	84	123		42	52		22	46	31	75	57		
Aug. 1968	25	17				11			58		30		34		34		70	64	116		43	40		22	44	37	77	54		
Sept. 1968	30	14				9			47		30		32		38		80	70	114		42	39		24	50	36	87	64		
Nov. 1968	29	11				G			G		29		23		42		93	27	114		43	43		26	G	G	92	62		
Jan. 1969	23	12									24		22		40		—	G	127		43	40		24			G	65		
Mar. 1969	27	6									14		15		24		65		108		50	G		G			G			
July 1969	23	G									17		22		G		77		130		51									
Sept. 1969	22										14		27				66		126		54									
Oct. 1969	21										13		30				G		90		50									
Jan. 1970	25										G		23						G		G									
Apr. 1970	20												34																	
June 1970	12												G																	

along the 150-m transect. In addition to the harvesting effect, the kelp bed was aging and the canopy was being reduced through the natural attrition of older plants. More areas of the bed were gradually opened to receive increased light penetration.

The first visible germination of *Macrocystis* sporophytes occurred during August-September 1969, when plants approximately 1 to 3 cm in height appeared on or near the survey lines. Although juvenile plants were found in scattered locations throughout the kelp bed, the most dense concentrations appeared around the shoreward (eastern) end of the transect, from about 100 m to 150 m (Figure 1). Only two adult plants remained within this 2 × 50 m band transect during the summer of 1969 (Figure 3); therefore, shading of the underlying sea floor was probably minimal. Also, this shoreward edge of the bed is approximately 5 m shallower than the seaward portion and there may have been more ambient light in this part of the kelp bed. Juvenile sporophyte density ranged from 0 to 32 plants/m<sup>2</sup> within the fixed quadrats. *Macrocystis* recruitment was especially pronounced in the 100- to 150-m area on the transect. For this reason two additional 4-m<sup>2</sup> quadrats (no. 13 and 14) were added in this location when the first sporophytes appeared in August 1969. In September 1969, a total of 387 single-bladed *Macrocystis* were counted within the fixed quadrats (Figure 6). After the first month only 156 plants survived, and by June 1970 the young sporophyte population was reduced to only 5 survivors.

Most of the juvenile plant mortality was believed to be caused by plant entanglement, fish

grazing, physical scouring, and/or actual burial of the plants by moving sand. Many of the young sporophytes were damaged, primarily in the region of the apical tip. These plants were inspected for invertebrate grazers, but none were found. It seems likely that the grazers were positioned in the water column because most of the grazing was located around the terminal ends of each blade. On two occasions the labrid *Oxyjulis californica* and the embiotocid *Embiotoca jacksoni* were seen nibbling on juvenile *Macrocystis*. However, because of marginal underwater visibility in this area, it was generally not possible to observe the grazing activities of fishes directly.

Physical scouring and burial is another cause of juvenile plant mortality. For example, one group of young plants ( $n = 36$ ) growing within a shallow depression along the sea floor became completely covered with sand during the late fall of 1969 and never reappeared. The stipes of *Macrocystis* are quite sensitive to being enclosed or covered (North, 1971), and apparently the young plants can not tolerate burial for any length of time. In kelp beds such as Del Mar, the juvenile *Macrocystis* appear to be highly vulnerable to this physical phenomenon.

The five surviving *Macrocystis* plants that grew within the fixed quadrats continued to mature and eventually the stipes reached the sea surface. One plant perished in September 1972; however, the other four were still present within the quadrats in December 1972, 3 yr and 3 mo after germination.

### Plant Longevity

At the present time there is little information available in the literature on the life span of *Macrocystis* because most of the data have been collected on the longevity of individual fronds. The maximum life span of a *Macrocystis* frond was found to be about 6 mo (Brandt, 1923; Cribb, 1954; North, 1961). North (1968) reported that 3 yr were required to totally eliminate tagged mature plants within a stand of kelp off La Jolla, Calif. Most of the plants were very large at the beginning of the study, "so they probably were at least 5 years of age when they vanished, or quite likely older." (North, 1968:224).

Of the 49 adult *Macrocystis* plants originally marked along the Del Mar transect no survivors

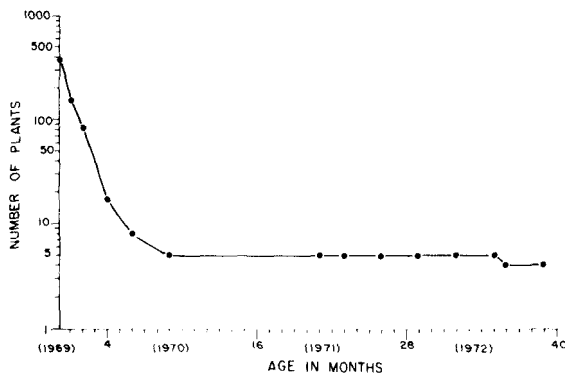


FIGURE 6.—Survivorship curve of individual *Macrocystis* which were observed to recruit in September 1969.

persisted in August 1972. The oldest surviving plant lived until July 1972, an elapsed time of 5 yr. During July 1967 this plant (number 1) had 18 living stipes (Table 2). The number of stipes growing from this plant reached a maximum of 34 during May 1968; thereafter, the number of stipes slowly decreased. Based on data derived from the fixed quadrats, a *Macrocystis* plant growing in this bed with 18 stipes is at least 2 yr old. Therefore, by July 1972 plant number 1 was probably at least 7 yr of age. In addition, three other tagged plants were believed to be more than 5 yr of age at the time of their dislodgement, and four of the *Macrocystis* that grew up within the fixed quadrats were still alive after 3 yr and 3 mo (Figure 6).

Counting the number of living stipes on selected *Macrocystis* plants does not necessarily indicate the age of a kelp bed or ages of plants within the bed. For example, the number of stipes found on individual plants at Del Mar usually fluctuated with the season and the condition of the plant (Table 2). Most of the adult *Macrocystis* displayed a period during which each plant maintained a maximum number of stipes, followed by a gradual decline in the total number of stipes. At some point in the life of a Del Mar *Macrocystis* the plant no longer appears to be able to actively support a peak number of stipes.

## FAUNAL ASSOCIATION

### Components of the Epifauna

Within the study area 38 species of fishes were sighted (Table 3), and 98 species of epibenthic invertebrates have been identified (Table 4). Many of the macroinvertebrates listed in the table were rarely observed, but 39 were seen on over half of the dives. A number of these species were numerically uncommon in this area, while other animals were infrequently seen because of differences in activity periods. For example, the gastropod *Cypraea spadicea* was rarely observed in exposed positions during daylight hours, but was one of the most abundant mollusks during the three nocturnal surveys made in this location. Of the 38 species of fish which we recorded, 20 species were collected in 1958 by Quast (1968a).

### Epibenthic Invertebrates

Invertebrates considered in this study consisted

TABLE 3.—A list of fishes observed in the kelp bed by Quast (1968a) and during this study. ++ signifies those species seen in both studies; — signifies those species seen in our study, but not reported by Quast (1968a).

<i>Anisotremus davidsoni</i> (Steindachner)	—
<i>Atherinops affinis</i> (Ayers)	++
<i>Brachyistius frenatus</i> Gill	++
<i>Chromis punctipinnis</i> (Cooper)	++
<i>Coryphopterus nicholsi</i> (Bean)	—
<i>Embiotoca jacksoni</i> Agassiz	++
<i>Engraulis mordax</i> Girard	++
<i>Girella nigricans</i> (Ayres)	++
<i>Gymnothorax mordax</i> (Ayres)	—
<i>Halichoeres semicinctus</i> (Ayres)	—
<i>Heterostichus rostratus</i> Girard	++
<i>Hyperprosopon argenteum</i> Gibbons	++
<i>Hypsurus caryi</i> (Agassiz)	++
<i>Leiocottus hirundo</i> Girard	++
<i>Medialuna californiensis</i> (Steindachner)	++
<i>Oxyulius californica</i> Günther	++
<i>Oxylebius pictus</i> Gill	—
<i>Paralabrax clathratus</i> (Girard)	++
<i>Paralabrax maculatofasciatus</i> (Steindachner)	—
<i>Paralabrax nebulifer</i> (Girard)	—
<i>Paralichthys californicus</i> (Ayres)	—
<i>Phanerodon furcatus</i> Girard	++
<i>Pimelometopon pulchrum</i> (Ayres)	++
<i>Pleuronichthys coenosus</i> Girard	++
<i>Pneumatophorus diego</i> (Ayres)	—
<i>Rhacochilus toxotes</i> Agassiz	++
<i>Rhacochilus vacca</i> (Girard)	++
<i>Scorpaena guttata</i> Girard	++
<i>Scorpaenichthys marmoratus</i> (Ayres)	—
<i>Sebastes atrovirens</i> (Jordan and Gilbert)	++
<i>Sebastes auriculatus</i> Girard	—
<i>Sebastes chrysomelas</i> (Jordan and Gilbert)	—
<i>Sebastes rastrelliger</i> (Jordan and Gilbert)	++
<i>Sebastes serriceps</i> (Jordan and Gilbert)	—
<i>Seriola dorsalis</i> (Gill)	—
<i>Sphyræna argentea</i> Girard	—
<i>Torpedo californica</i> (Ayres)	—
<i>Urolophus halleri</i> (Cooper)	—

of those species living along the sea floor that could be counted without disturbing the underlying substratum. Visually and numerically conspicuous macroinvertebrates were selected for study after data were collected on presence of species and their relative abundance in 1967. Of the 98 invertebrate species seen, only 14 species appeared to comprise the "characteristic" assemblage of epibenthic invertebrates in this kelp bed (Table 5). Characteristic epifauna were those "species that were always seen and that dominated the habitat, both numerically and in terms of their demand and impact on it." (Fager, 1968). Table 5 lists the frequency of occurrence, numerical density, pattern of distribution, and habit of each of the 14 species. Because of the importance of natural history information to an eventual synthesis of the organization of the kelp community, the following observations are presented for the 14 species. The species are discussed in order of their relative abundance.

The most abundant and frequently encountered epifaunal invertebrate in the study site during



TABLE 4.—Epifaunal invertebrates collected within the perimeter of the study area.

Porifera	Arthropoda—Continued	Mollusca—Continued
<i>Leucilla</i> (= <i>Rhabdodermlia</i> ) <i>nuttingii</i> Urban	<i>Hippolytina californica</i> Stimpson	<i>Leptopecten latiauratus</i> (Conrad)
<i>Leucosolenia</i> sp.	<i>Parapeleustes oculatus</i> Barnard	<i>Lima hemphilli</i> Hertlein and Strong
<i>Tethya aurantia</i> (Pallas)	<i>Balanus tintinnabulum</i> Pilsbry	<i>Saxidomus nuttalli</i> Conrad
<i>Verongia thiona</i> de Laubenfels	<i>Balanus pacificus</i> Pilsbry	<i>Octopus bimaculatus</i> Verrill
<i>Clypea celata</i> Grant	<i>Pachycheles rudis</i> Stimpson	<i>Penitella penita</i> (Conrad)
Cnidaria	<i>Idothea resicata</i> (Stimpson)	<i>Chaeceia ovoidea</i> (Gould)
<i>Aglaophenia</i> spp.	<i>Acanthomyxus sculpta</i> (Tattersall)	Bryozoa
<i>Corynactis californica</i> Carlgren	<i>Lophopanopeus frontalis</i> (Rathbun)	<i>Diaperocia californica</i> (d'Orbigny)
<i>Epiactis prolifera</i> Verrill	<i>Ampithoe humeralis</i> Stimpson	<i>Membranipora membranacea</i> (Linnaeus)
<i>Pachycerianthus</i> sp.	Mollusca	<i>Membranipora serrilamella</i> Osborn
<i>Tubularia</i> sp.	<i>Kelletia kelletii</i> (Forbes)	<i>Bugula neritina</i> (Linnaeus)
<i>Balanophyllia elegans</i> Verrill	<i>Mitra idae</i> Melville	<i>Antropora tinctoria</i> Osborn
<i>Paracyathus staarasi</i> Verrill	<i>Bursa californica</i> (Hinds)	<i>Thalamoporella californica</i> (Levinson)
<i>Lophogorgia chilensis</i> (Verrill)	<i>Conus californicus</i> Hinds	Echinodermata
<i>Muricea californica</i> (Aurivillius)	<i>Norrissia norrisi</i> (Sowerby)	<i>Dermasterias imbricata</i> (Grube)
<i>Muricea fruticosa</i> (Verrill)	<i>Astraea undosa</i> (Wood)	<i>Astropecten armatus</i> Gray
<i>Tealia coriacea</i> (Cuvier)	<i>Trivia californiana</i> (Gray)	<i>Astrometis sertulifera</i> (Xantus)
<i>Harenactis attenuata</i> Torrey	<i>Megathura crenulata</i> Sowerby	<i>Henricia leviscula</i> (Stimpson)
<i>Parazoanthus lucificum</i> Cutress and Peguegnat	<i>Cypraea spadicea</i> Swainson	<i>Patiria miniata</i> (Brandt)
<i>Sertularia</i> sp.	<i>Haliotis rufescens</i> Swainson	<i>Pisaster brevispinus</i> (Stimpson)
<i>Plumularia</i> sp.	<i>Haliotis corrugata</i> Wood	<i>Pisaster giganteus</i> (Stimpson)
<i>Anthopleura elegantissima</i> (Brandt)	<i>Shaskyus</i> (= <i>Jaton</i> ) <i>festivus</i> Hinds	<i>Ophioplocus esmarki</i> Lyman
Annelida	<i>Simnia vidleri</i> Sowerby	<i>Ophiotrix spiculata</i> Le Conte
<i>Diopatra ornata</i> Moore	<i>Maxwellia gemma</i> (Sowerby)	<i>Parastichopus parvimensis</i> (Clark)
<i>Salmacina tribanchiata</i> (Moore)	<i>Crassispira semiinflata</i> (Grant and Gale)	<i>Eupentacta quinquesemita</i> (Selenka)
<i>Phyllochaetopterus prolifica</i> Potts	<i>Acteon punctocaelatus</i> (Carpenter)	<i>Amphipholis</i> sp.
<i>Eudistylia polymorpha</i> Johnson	<i>Mitrella carinata</i> (Hinds)	<i>Ophioderma panamensis</i> Lutken
<i>Dexiospira spirillum</i> (Linnaeus)	<i>Crepidula adunca</i> Sowerby	<i>Ophiopertis papillosa</i> (Lyman)
<i>Spirobranchus spinosus</i> Moore	<i>Anisodoris nobilis</i> (MacFarland)	<i>Strongylocentrotus franciscanus</i>
Arthropoda	<i>Glossodoris californiensis</i> (Bergh)	(A. Agassiz)
<i>Paguristes ulreyi</i> Schmitt	<i>Dendrodoris tulva</i> (MacFarland)	<i>Strongylocentrotus purpuratus</i>
<i>Loxorhynchus grandis</i> Stimpson	<i>Cadlina flavomaculata</i> MacFarland	(Stimpson)
<i>Talipes nuttallii</i> Randall	<i>Flabellinopsis iodinea</i> (Cooper)	Chordata
<i>Synalpheus</i> spp.	<i>Hinnites multirugosus</i> (Gale)	<i>Styela montereyensis</i> (Dall)
<i>Alpheus dentipes</i> Guerin	<i>Platyodon cancellatus</i> (Conrad)	<i>Polyclinum planum</i> (Ritter and Forsyth)
<i>Panulirus interruptus</i> (Randall)	<i>Parapholas californica</i> (Conrad)	<i>Pyura hauster</i> (Stimpson)
<i>Betaeus hartfordi</i> (Kingsley)	<i>Adula</i> (= <i>Botula</i> ) <i>taicata</i> (Gould)	<i>Eudistoma diaphanes</i> Ritter and Forsyth
<i>Cancer anthonyi</i> Rathbun	<i>Lithophaga plumula</i> (Hanley)	

TABLE 5.—The conspicuous macroinvertebrates in the Del Mar kelp bed.

Species	Habit	Frequency <sup>1</sup>	Density <sup>2</sup>	Distribution pattern	Probability <sup>4</sup>
<i>Diopatra ornata</i>	Sessile	87/96	12.95	Aggregated	$P < 0.001$
<i>Styela montereyensis</i>	Sessile	79/96	3.40	Aggregated	$P < 0.001$
<i>Muricea californica</i>	Sessile	67/96	2.53	Aggregated	$P < 0.001$
<i>Kelletia kelletii</i>	Motile	35/96	0.62	Aggregated	$0.001 < P < 0.01$
<i>Parapholas californica</i>	Sessile	22/96	0.47	Aggregated	$P < 0.001$
<i>Paguristes ulreyi</i>	Motile	9/96	0.39	Aggregated	$P < 0.001$
<i>Muricea fruticosa</i>	Sessile	18/96	0.27	Aggregated	$0.05 > P > 0.02$
<i>Strongylocentrotus franciscanus</i>	Motile	2/96	0.16	Aggregated	$P < 0.001$
<i>Tealia coriacea</i>	Sessile	11/96	0.16	Aggregated	$0.001 < P < 0.01$
<i>Tethya aurantia</i>	Sessile	10/96	0.14	Random <sup>3</sup>	$0.05 < P < 0.10$
<i>Astrometis sertulifera</i>	Motile	12/96	0.13	Aggregated	$0.05 > P > 0.025$
<i>Lophogorgia chilensis</i>	Sessile	4/96	0.04	Random <sup>3</sup>	$0.70 > P > 0.50$
<i>Strongylocentrotus purpuratus</i>	Motile	2/96	0.03	Aggregated	$0.001 < P < 0.01$
<i>Pisaster giganteus</i>	Motile	3/96	0.01	Random <sup>3</sup>	$0.30 < P < 0.50$

<sup>1</sup> Occurrence in 96 1-m<sup>2</sup> quadrats.<sup>2</sup> Per m<sup>2</sup>.<sup>3</sup>  $n$  is small — index of dispersion inadequate.<sup>4</sup> Probability of a random distribution.

August 1972 was the tubicolous polychaete *Diopatra ornata* (Table 5). *Diopatra* was seen along the transect during the early years of the study (1967-68) however, it was not until the summer of 1971 that the species was considered to be common. During August 1972, *Diopatra* occurred in all 12 of the fixed quadrats, and quadrat number 7, which contained only a few

individuals in 1968, had many clumps of *Diopatra* tubes. The tubes covered an estimated 25-30% of the total area (4 m<sup>2</sup>) in the quadrat. Unpublished work of Ray Emerson (pers. commun.)<sup>4</sup> demonstrates that approximately 90%

<sup>4</sup>Emerson, R. In preparation. Reproductive biology and population dynamics of the polychaete *Diopatra ornata*. Ph.D. thesis, Univ. of Southern Calif.

of *Diopatra* tubes represent living worms. Emerson considers *Diopatra* a selective but omnivorous deposit feeder. We have seen fragments of *Macrocystis* attached to its tube apparently serving a dual function of camouflage and food reserve. The gastropod *Kelletia kelletii* and the sea star *Pisaster giganteus* were the only invertebrates seen eating *Diopatra* in this area. *Kelletia* was frequently observed penetrating either the sides or opening of the *Diopatra* tube with an extensible proboscis, and *Pisaster* was found with its stomach everted into the opening of the tube.

The solitary ascidian *Styela montereyensis* usually grows attached to rocks, shells, and *Macrocystis* holdfasts. *Styela* was found to live approximately 12 to 20 mo; however, one individual lived for more than 30 mo. Usually there is a heavy recruitment in the late summer and heavy mortality late the next spring (Figure 7). The fall *Styela* population remained reasonably constant over 4 yr (1968-72), despite the fluctuations in the population during a calendar year. A major cause of mortality in the fixed quadrats was sediment movement and strong water motion that either buried or detached the ascidians from the substratum. Three predators of *Styela* were observed: *Pisaster giganteus* and *Kelletia kelletii* frequently were seen feeding on *Styela*. On five occasions these two species were encountered feeding simultaneously on the same *Styela* (Rosenthal, 1971). In addition, we found the sea star *Astrometis sertulifera* eating *Styela* in this location.

The gorgonian *Muricea californica* was the most

visually conspicuous and the third most abundant (2.53/m<sup>2</sup>) macroinvertebrate in the assemblage (Table 5). It is a colonial animal usually found growing erect from solid substratum. *Muricea californica* recruits become visible to the unaided eye when the colony is approximately 1 cm high; at this stage they appear to be at least several months old (Grigg, 1970). A decline in the *M. californica* population was recorded during the time period of this study. A total of 192 individual colonies were living within the 48-m<sup>2</sup> area in September 1968, but by December 1972 the population had declined to 119 colonies. During this time interval there were 147 mortalities and 74 recruitments recorded in the fixed quadrats (Figure 8). Grigg (1970) found a similar decrease in the *M. californica* population off Del Mar in which he recorded a relatively heavy mortality with no replacement or recruitment during a 1-yr period of observation in 1968. There are several physical factors contributing to the mortality of *M. californica* in this area. Scouring, holdfast detachment, and burial by sand are important examples. Grigg (1970) felt that two-thirds of the mortality recorded at Del Mar during 1968 resulted from physical abrasion by suspended particles, and one-third from colony detachment. Occasionally, *M. californica* growing either between the holdfasts of adult *Macrocystis* or in close proximity to an established plant died when the plant became detached and drifted away. In such cases the *M. californica* were entangled and pulled from the sea floor or were

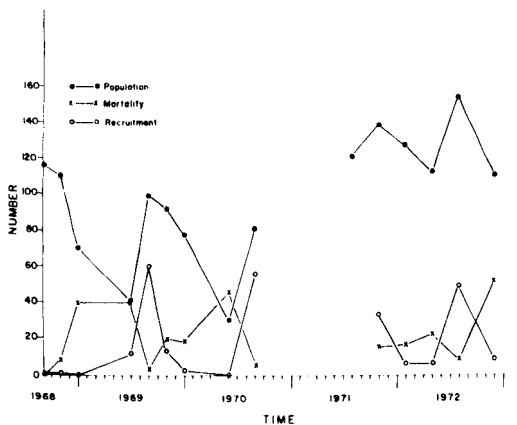


FIGURE 7.—*Styela montereyensis* in the 12 fixed quadrats (48 m<sup>2</sup>).

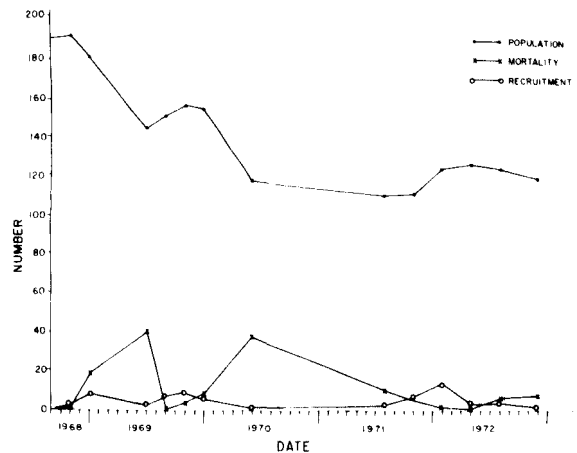


FIGURE 8.—*Muricea californica* in the 12 fixed quadrats (48 m<sup>2</sup>).

killed by increased scouring and sediment burial in the absence of the large *Macrocystis* holdfast.

The Kelle's whelk, *Kelletia kelletii*, is usually found on rocky substrata or in sand areas adjacent to more solid substratum. During August 1972 we observed a mean density of 0.62/m<sup>2</sup> in the combined samples (Table 5). On other occasions the density along the transect ranged from 0.42 to 0.75/m<sup>2</sup>. Movement off Del Mar is apparently not random, for individual snails were often found in aggregated patterns of distribution. Such aggregations may reflect feeding and reproductive behavior. For example, during the height of the April-May spawning period (Rosenthal, 1970), mixed aggregations of both male and female *Kelletia* were repeatedly encountered. A few of these spawning aggregations contained between 200 and 300 individuals; however, the average spawning cluster was about 15 to 20 snails.

*Kelletia* is basically a carnivorous scavenger; however it does feed on live sedentary polychaetes and solitary ascidians. It has been observed eating 22 species of invertebrates and 3 species of dead or moribund fish in the subtidal waters off San Diego County (Rosenthal, 1971).

Predators of *Kelletia* include the asteroids *Pisaster giganteus*, *P. brevispinus*, and *Astrometis sertulifera*, and the cephalopod *Octopus bimaculatus* (Rosenthal, 1971). Few other predators are known, although Limbaugh (1955) reported finding juvenile *Kelletia* in the stomachs of pile perch, *Rhacochilus vacca*.

*Parapholas californica*, a bivalve clam, was the most conspicuous terrigenous borer off Del Mar. It primarily bores into sedimentary rocks consisting of consolidated mudstones and siltstones. Within the 12 fixed quadrats the *Parapholas* population density was 0.54/m<sup>2</sup>. During the monitoring period there were two recruitments and three mortalities recorded in these quadrats. *Pisaster giganteus* and *P. brevispinus* occasionally prey upon *Parapholas* in this location, as they do in other nearshore areas off San Diego County (Rosenthal, 1971). Predation by sea stars often has the additional effect of breaking the substratum surrounding the clam.

*Paguristes ulreyi* is a relatively large, pubescent hermit crab. Almost all were found in discarded *Kelletia* shells; however, a few crabs were also seen in the shells of *Bursa californica*. *Paguristes* was seen throughout the study area, although its

most frequent habitat appeared to be the siltstone ledges and consolidated sedimentary mounds located towards the seaward edge of the bed. Each year large aggregations (to 220/m<sup>2</sup>) of *Paguristes* were observed in this area from August through October, the crabs often being stacked several layers thick. *Paguristes* is a scavenger (Pequegnat, 1964), a conclusion supported by our observations of it feeding upon dead invertebrates and pieces of detached algae. *Octopus bimaculatus* was the only known predator of *Paguristes* in this location. On two occasions, *O. bimaculatus* was observed moving shells inhabited by *Paguristes* and one individual was encountered while feeding on a *Paguristes*.

*Muricea fruticosa* is similar in appearance to *M. californica*, but is usually bushier with a rusty-brown coenenchymal layer and white polyps. Both species of *Muricea* were observed growing on similar or identical substrata. The mean of 0.27 colonies/m<sup>2</sup> in this area (Table 5) is in agreement with the estimate of 0.25 colonies/m<sup>2</sup> of Grigg (1970). The *M. fruticosa* population was almost balanced with respect to mortality and recruitment. Fourteen *M. fruticosa* were recorded in the fixed quadrats during September 1968, and 13 individual colonies were found in these same quadrats during December 1972, but during this period 17 mortalities and 16 recruitments were noted. No predators of *M. fruticosa* were observed in the study area, and causes of mortality are believed to be similar to those reported for *M. californica*.

*Tealia coriacea* is a solitary, medium sized (4 to 7 cm) sea anemone. It attaches to solid substratum and usually the column is partially buried or enclosed by sediment. Two mortalities and three recruitments were recorded in the fixed quadrats. One *Tealia* was eaten by a leather star, *Dermasterias imbricata*, and the other died from an unknown cause. *Dermasterias* has been reported to eat *Tealia* spp. and other sea anemones in the Pacific Northwest (Mauzey, Birkeland, and Dayton, 1968), and may on occasion be an important source of mortality in California kelp beds.

The largest and most conspicuous sea urchin seen off Del Mar was *Strongylocentrotus franciscanus*. Individual test diameters ranged from 5.5 to 18.2 cm. Most of these animals inhabited the sedimentary mounds and boulders located towards the seaward edges of the kelp stand.

The trophic role displayed by *S. franciscanus* in southern California kelp communities has been adequately described (Limbaugh, 1955; Leighton, 1971; North, 1971). *Strongylocentrotus franciscanus* is important because it often overexploits its algal resources in areas of high sea urchin density. Despite the fact that this species is highly motile, foraging movements on attached kelps were not witnessed in this kelp bed. The *S. franciscanus* population appeared to be sustained by snagging detached pieces of macroalgae that drifted along the sea floor. The only predator we observed feeding upon live *S. franciscanus* in this area was the labrid *Pimelometopon pulchrum*.

*Tethya aurantia*, a hemispherical shaped sponge, attains a circumference of at least 25 cm and is usually found attached to rocks and consolidated sediments. There were two mortalities and three recruitments recorded in the fixed quadrats. One mortality was attributed to sediment burial, and *Dermasterias imbricata* was observed feeding on *Tethya* in the vicinity of the transect. Rosenthal and Chess (1972) reported *Dermasterias* to be a predator of *Tethya* in the sublittoral zone off Pt. Loma, Calif.

*Astrometis sertulifera* was the most abundant (0.13/m<sup>2</sup>) sea star encountered off Del Mar (Table 5). This estimate of abundance is probably conservative because *Astrometis* is relatively small (4 to 6 cm in radius) and individuals are somewhat cryptic in habit. The most frequent habitat of *Astrometis* off Del Mar was the undersides of rocks and the interstices of *Macrocystis* holdfasts. It appears to be ideally suited for preying upon the assemblage of organisms found associated with the holdfasts of *Macrocystis*. *Astrometis* was observed eating juvenile *Kelletia kelletii* (gastropod), *Conus californica* (gastropod), *Mitrella* sp. (gastropod), *Styela montereyensis* (ascidian) and juvenile *Strongylocentrotus purpuratus* (echinoid) in this study. Leighton (1971) mentioned that *Astrometis* feeds heavily on juvenile sea urchins off southern California. No predators of *Astrometis* were observed in the study area; however, Rosenthal and Chess (1972) found that 4% of 437 feeding *Dermasterias* were eating *Astrometis*.

The gorgonian *Lophogorgia chilensis* is one of the most exquisite macroinvertebrates in this region. It usually grows in an upright manner attached to solid substratum. A few small colonies

were found growing attached to *Muricea californica*. *Lophogorgia* was not nearly as abundant as *M. californica* or *M. fruticosa*; the mean density during August 1972 was 0.04/m<sup>2</sup> (Table 5). There was one mortality and one recruitment recorded in the 48-m<sup>2</sup> quadrat area during 1968-72. No predators of *Lophogorgia* were observed in this kelp bed and causes of colony mortality are probably similar to those of *Muricea* spp.

The purple sea urchin, *Strongylocentrotus purpuratus*, ranged in size from 15 to 68 mm, with a median size of 42 mm ( $n = 82$ ). In contrast to the low density in this location (0.03/m<sup>2</sup>), other kelp stands off southern California have been found to contain as many as 77 *S. purpuratus*/yd<sup>2</sup> (Leighton, 1971). The most frequent habitat of *S. purpuratus* off Del Mar was the undersides of rocks; however, individuals were also found on consolidated mounds and siltstone ledges. A few individuals were noted within the holdfasts of adult *Macrocystis*; however, we believe the incidence of holdfast infestation is low in comparison to other San Diego County kelp beds. *Strongylocentrotus purpuratus* is a herbivore well known to overexploit its algal resources (Leighton, 1971; North, 1971). In the Del Mar area most of the purple sea urchins were observed eating detritus and drift algae; rarely were the attached macroalgae grazed upon.

*Dermasterias imbricata* (Rosenthal and Chess, 1972), *Astrometis sertulifera* (Leighton, 1971; pers. observation), and *Pimelometopon pulchrum* (Limbaugh, 1955; pers. observation) are three known *S. purpuratus* predators which inhabited the study area.

*Pisaster giganteus* is one of the most abundant and widely distributed sea stars found off southern California. Although visually conspicuous at Del Mar, *Pisaster* was not nearly as abundant (0.01/m<sup>2</sup>) as it was in some of the other kelp beds (i.e. Pt. Loma, La Jolla, Catalina Island) we surveyed between 1968 and 1972. The diet of *Pisaster* has been partially quantified (Rosenthal, 1971). Although it was occasionally observed scavenging, it primarily feeds on live animals which, in this area, include *Astraea undosa* (gastropod), *Conus californicus* (gastropod), *Kelletia kelletii* (gastropod), *Botula falcata* (pelecypod), *Hinnites multirugosus* (pelecypod), *Lithophaga plumula* (pelecypod), *Parapholas californica* (pelecypod), *Pennitella penita* (pelecypod),

*Diopatra ornata* (polychaete), and *Styela montereyensis* (ascidian).

## DISCUSSION

During the years of this study (1967-73) there was a pronounced oscillation in the number of adult *Macrocystis* in the study area. Partially concurrent with these in situ observations has been a fluctuation in the amount of kelp harvested in this area since 1940 (Figure 4). The disappearance or detachment of adult *Macrocystis* along the transect was usually related to physical stress from an increase in water motion and/or entanglement with detached, drifting kelp plants. Storms, particularly during the months of October through April, seem to be the major cause of plant mortality in this bed. For example, during a 2-mo period (December-February 1973), 46% of the adult *Macrocystis* were lost along the transect (Figure 2). There is historical evidence of severe storm mortality as Brandt (1923) reported the La Jolla and Pt. Loma kelp beds were severely diminished in area by storms in 1888-89 and 1915. Doty (1971) also reports that storms have important effects on the standing crop of algae in Hawaii.

Another cause of plant attrition was commercial harvesting. Four tagged *Macrocystis* representing 21% of the marked plants in the study area were detached from the substratum during a kelp harvesting operation in January 1969. However, this rate of mortality could be higher than the harvesting attrition rate in other beds because of the relatively unstable substratum of the north San Diego County kelp beds. Certainly a preharvest consideration should be given to the actual cutting technique best suited to each individual stand of kelp.

The vulnerability of adult *Macrocystis* to entanglement and detachment would appear to result in the development of a multiage class kelp bed in which there are patches of cohorts or plants of the same age class. That is, the drifting and entanglement is rather localized and results in distinct patches of the canopy being cleared. Thus, germination and recruitment take place not only around the periphery of the bed, but also within central portions. This spatial heterogeneity of different aged *Macrocystis* may add stability to a particular kelp bed as mature, perhaps more secure plants are growing adjacent

to both young and senile plants. During February 1972, it was estimated that the Del Mar bed was composed of at least four age classes of *Macrocystis*.

The paucity of juvenile *Macrocystis* sporophytes during the first 23 mo of the study was believed to be related to the establishment of a well-developed adult canopy, turbidity of the water column, and the relatively unstable substratum. These factors are interrelated since they contribute to the absorption and scattering of the available light necessary for germination and sporophyte development. A layer of fine sediment (silt) remained along the bottom during the entire study period, and this silt was usually suspended by increased water motion. The Los Penasquitos salt marsh located approximately 2 km southeast of the study site could be a source of much silt. Whatever the source, this sediment layer seems to be a general feature of most north San Diego County kelp beds, and as it contributes to a reduction in the submarine light and physically scours the substratum, it probably has a strong negative effect on *Macrocystis* recruitment. Despite these limiting factors, young *Macrocystis* sporophytes appeared in the Del Mar bed during August 1969. The reduction of the kelp canopy from natural attrition and harvesting probably paved the way for the late summer germination and recruitment. Following recruitment of these young plants there continued to be a strong attrition as only 4 of the original 387 sporophytes growing within the fixed quadrats survived the 3.25 yr (to December 1972).

Many of the same physical parameters that influence the *Macrocystis* population at Del Mar appear to effect the distribution, frequency of occurrence, and abundance of the fauna. Quast (1968a) determined from three fish collection sites off Del Mar, Bathtub Rock (San Diego County), and Papalote Bay, Baja California that Del Mar was lowest in fish species diversity, despite the fact that it covered the greatest area. He concluded that the differences between the three areas were due to differences in the amount of shifting sediment and the durability of the rocky substratum. Furthermore, he found a positive correlation between the degree of bottom relief and the abundance and species diversity of fish.

The epibenthic invertebrates are similarly affected by the physical characteristics of the habitat. The aggregated distribution patterns of

such sessile species as *Muricea californica*, *Styela montereyensis*, and *Parapholas californica* (Table 5) probably reflect physical heterogeneity within the Del Mar study site. The aggregated distribution patterns of motile species (*Kelletia kelletii*, *Paguristes ulreyi*, and *Strongylocentrotus franciscanus*) are probably related to aspects of their foraging and/or reproductive behavior as well as to the physical heterogeneity of the habitat.

The species composition of the epifauna was reasonably constant, however, the abundances of some species has undergone change during the 5.7 yr. The most pronounced population change occurred with the tube dwelling polychaete *Diopatra ornata*. Although this species was recorded within the study area during 1967-68, it was somewhat rare and individuals were not noted within the 12 fixed quadrats until 1971. By August 1972 however, *Diopatra* was the most abundant and most frequently encountered macroinvertebrate in the Del Mar kelp bed (Table 5). Reasons for the *Diopatra* population increase are unknown at this time.

During the same time period the *Muricea californica* population decreased from 192 to 119 colonies during 4.25 yr (Figure 8), despite considerable recruitment of small identifiable colonies. In contrast to the decline in the *M. californica* population at Del Mar, Grigg (1970) studied a population of *M. californica* off La Jolla which was relatively stable with respect to mortality and recruitment. Differences between these two sea fan populations were believed to be due to the physical characteristics of each habitat (Grigg, 1970).

The *Styela montereyensis* population had a reasonably predictable seasonal oscillation, usually reaching a peak during the late summer and fall (Figure 7). The maximum annual population ranged from 81 to 153 individuals. The average life span of *S. montereyensis* is shorter (12 to 20 mo) than some of the other members of this community such as *Muricea californica*, which is thought to reach at least 50 yr of age (Grigg, 1970). Three species: *Pisaster giganteus*, *Astrometis sertulifera*, and *Kelletia kelletii* feed upon *Styela* in this area; however, natural predation is slight in proportion to the heavy mortality caused by strong water motion and sediment burial. Other Del Mar invertebrate populations were somewhat more constant. For example, the *Muricea fruticosa* population re-

mained relatively constant over the monitoring period (changing from a total of 14 to 13), despite 17 mortalities and 16 recruitments recorded in the fixed quadrats.

There is sufficient evidence of trophic interaction to present a very qualitative food web (Figure 9). Two of the predators, *Pisaster giganteus* and *Astrometis sertulifera* feed upon living members of the community; the diet of the former species is probably better understood (Rosenthal, 1971), because it is seen more often. While both asteroid species attack a variety of prey, mollusks appear to be the major food items off Del Mar. In addition, *Dermasterias imbricata*, *Pisaster brevispinus*, *Octopus bimaculatus*, and *Pimelometopon pulchrum* have been added to this food web. We have only qualitative data on the diets of these four species. Two other carnivores, *Kelletia kelletii* and *Paguristes ulreyi*, generally feed upon moribund or decaying animal matter, but they occasionally eat live organisms (Rosenthal, 1971). The rest of the generalized food web represents lower trophic levels.

The biotic components and temporal population changes recorded off Del Mar should not be interpreted as "characteristic" of all southern California kelp beds. Although the Del Mar bed closely resembles kelp stands off northern San Diego and Orange Counties, it appears to be different from those at La Jolla and Pt. Loma.

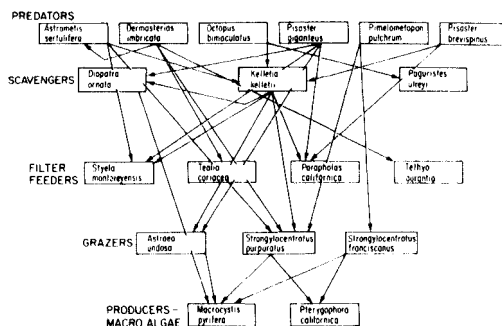


FIGURE 9.—A qualitative food web that depicts trophic interaction in the Del Mar kelp bed.

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