NUTRIENTS AND PRODUCTIVITY OF THE GIANT KELP, *MACROCYSTIS PYRIFERA*, IN THE NEARSHORE

Thesis by

George Anthony Jackson

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Low though the concentrations of nutrients may be in the water which bathes them, its continual renewal by tides and currents provides the sessile plants with an inexhaustable supply of these essential materials.

John Ryther, 1963

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During my time at Caltech I have learned to play basketball and therebye stay mentally healthy by being physical. I was helped by the coach, spider, cupcake,

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ABSTRACT

The growth of giant kelp, *Macrocystis pyrifera* was studied by field measurements of nutrients and other water parameters. Gross primary production of the kelp bed at Point Loma, California was calculated at 1.5 moles-O_2/m^2-day or 14.6 g-C/m^2-day. This represents one of the highest measured values of gross primary production. A rate of production twice as high might be attained under optimal conditions.

The condition most limiting *Macrocystis* production was the low concentration of dissolved nutrients, especially nitrogenous substances, near the surface. Kelp compensated for this limitation by translocating nitrogenous compounds from depths where nutrient concentrations were higher. Summer dieoff of the surface canopy may be caused by inability of plants to translocate nutrients due to low availability of nutrients in deeper water.

Nutrient concentrations varied seasonally. Surface nitrate concentrations were low for most of the year (usually less than 1 μM), higher during the winter. Nitrate concentrations at 6 and 9 meters depth usually exceeded 1 μM. They were highest during spring upwelling months, lowest during summer months.

Nutrient concentrations in the kelp bed were not depleted by the kelp or enhanced by sediment nutrient regeneration, implying relatively fast exchange of water in the bed with outside waters.

Nutrient concentrations varied at different longshore locations. Surface nitrate concentrations were more likely to be higher near the tip of Point Loma than 5 kilometers farther north. Localized upwelling caused this.

In the shallow nearshore (depth<5 meters) the nutrient concentrations were higher than those in the kelp bed at comparable depths. The cause remains unknown.

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CHAPTER 1

INTRODUCTION

Rich algal beds grow to form thick layers at the water´s surface along thousands of miles of the North American west coast. To the south the predominant alga is giant kelp, *Macrocystis*.

This brown alga grows off the southern California coast in vast beds extending to sea as much as a kilometer and along shore for as much as 5 kilometers. Productivity of these beds is presently harvested for organic extracts. Plans are being made to grow and harvest kelp for energy. Yet, little is known about kelp growth rates or requirements.

Biologists have shown that both on land and in the ocean plant growth rates are slowed by the lack of sufficient nutrients. In the ocean, the extensive work has been done on the growth of the microscopic phytoplankton. Little has been done on the macroalgae.

The benthic algae reside in an area distinctly different from the horizontally isotropic oceanic environment. The nearshore is the meeting place of the ocean and the land, where waves and tides dissipate against the edge of the continents, where the sea bottom approaches the surface and enters the euphotic zone.

In this thesis I examine the distribution of nutrients in the nearshore to see how their distribution differs from that of the oceanic environment and I look for the effect of kelp on nutrients and the effect of nutrients on kelp.

The kelp plant

The dominant seaweed of the southern California coast is giant kelp, *Macrocystis pyrifera* (Linnaeus)Agardh. This species is a member of the Phylum Phaeophyta, Class Heterogeneratae, Order Laminariales, and Family Lessoniaceae. Biology and ecology of the species have recently been summarized in a volume edited by North (1971a).

Macrocystis pyrifera usually grows in seawater of depth between two and twenty meters. Plants attach themselves to hard substrata by means of root-like holdfasts. Fronds grow upward to the sea surface from the top of the holdfast, intertwining to form a column between the hard bottom and the sea surface, diverging at the surface to form a canopy (Figure 1).

A frond is similar in appearance to a vine and is composed of a stipe, blades and sporophylls. The stipe serves as a stem to which the blades are attached and through which nutrients are distributed throughout the plant. The blades are leaf-like organs that serve as the main photosynthetic structures of the alga. A gas-filled bladder called the pneumatocyst connects the base of each blade to the stipe. The sporophylls are modified blades located near the base of the plant that serve as the reproductive organs of the plant. A frond may be longer than 25 meters and contain as many as 300 blades. It tends vertically toward the surface buoyed by the pneumatocysts but anchored basally to the holdfast.

A kelp frond develops from a growing tip formed at the holdfast by a basal meristem. This growing tip produces the stipe and the blades of the frond. Both the blades and the stipe separating the blades will grow some after they are produced. Distance between adjacent blades increases as the stipe lengthens. Consequently the frond lengthens and the growing tip is propelled upward. Growth of the frond slows or stops after a terminal blade is formed. After six to

Figure 1. Diagram of *Macrocystis pyrifera* (from Neushul & Haxo, 1968).

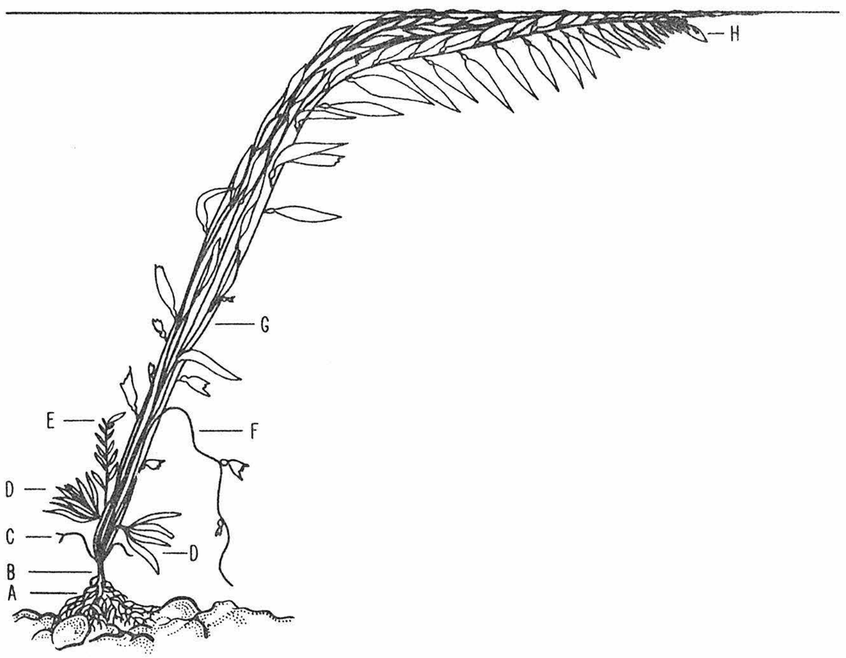


Diagram of a mature plant of the giant kelp, *Macrocystis pyrifera,* one to two years old, standing in 20 to 30 feet of water. A, holdfast; B, primary stipe; C, stub of an old frond; D, sporophyll clusters; E, juvenile frond; F, senile frond; G, stipe bundle; H, apical blade of mature frond, giving rise to additional blades.

eight months a frond will become decayed and eventually slough off at the holdfast.

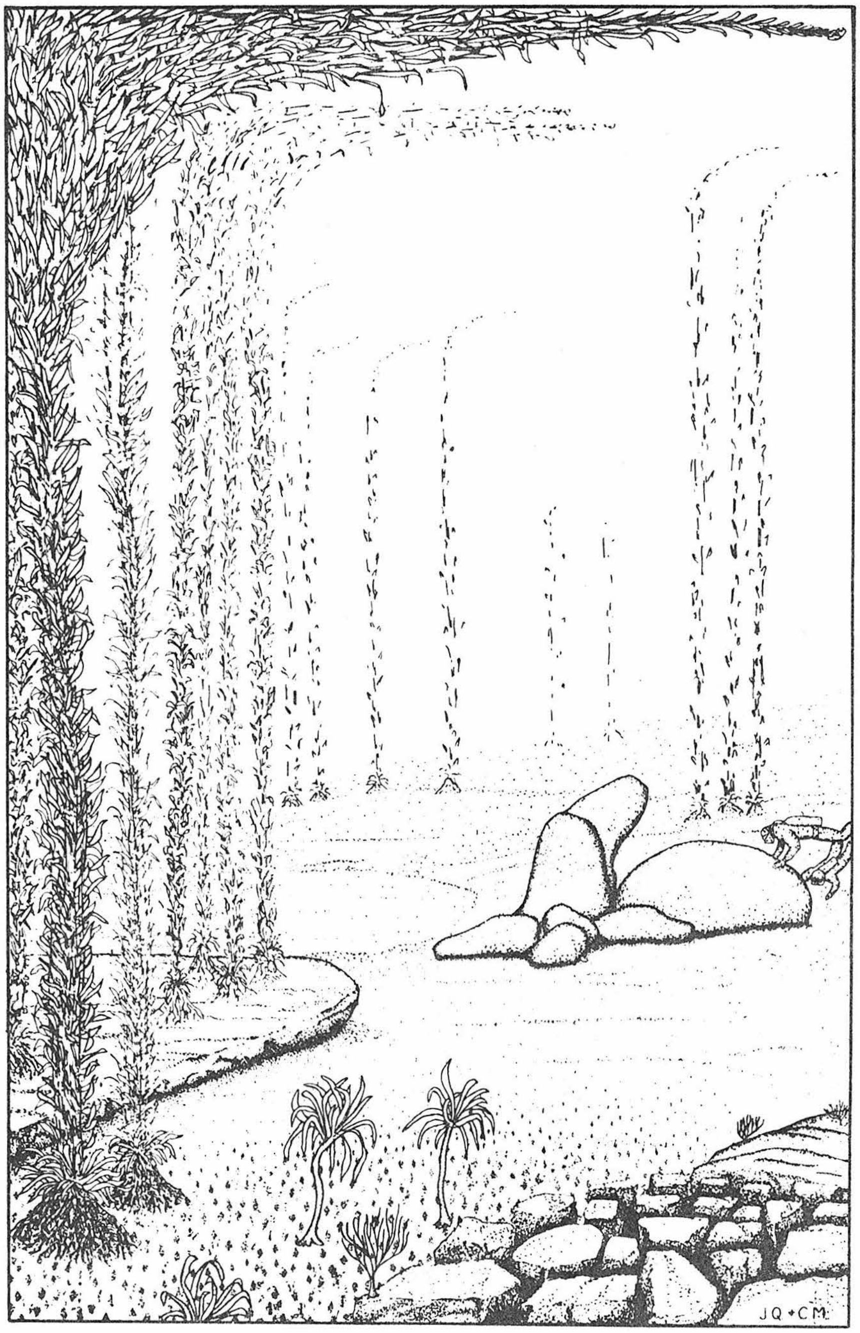
A mature plant will have forty or more fronds in various states of growth attached to one holdfast. Photosynthesis of new fronds on large plants is retarded by low light levels in the shadow of the thick canopy formed by mature fronds. However, the growth of a new frond is enhanced by the transport of photosynthetic products through a translocation system from mature fronds extending to the surface.

Kelp plants often occur in extensive stands, called kelp beds (Figure 2). One of the largest beds in southern California occurs off Point Loma, San Diego. The Point Loma bed extends seaward for about 1 km and along the coast for about 4 km.

Photosynthesis

Photosynthesis in *Macrocystis* has been studied by Clendenning (1963, 1971). He measured oxygen evolution by photosynthesis and oxygen utilization by respiration in different parts of the plant. Most parts of the kelp plant have chloroplasts and can photosynthesize but photosynthesis occurs predominantly in the blades. The maximum

Figure 2. Sketch of a kelp bed (from Quast, 1968).



Drawing of a representative kelp bed of the San Diego region. The rock formations depicted are fragmented rock (right foreground), pavement rock (center), a ledge (left center), and boulders (right background). Plants include columns of kelp *(Macrocystis pyrifera)*, the 2–4-foot *Pterygophora californica* (or the similar *Eisenia arborea)* and a short (2–4 inches) tufted coralline algae that clothes the pavement rock (center). A 1-foot gorgonian is represented on the fragmented rock (right foreground). Two divers are included for scale (right background). No fish are represented. A sand patch, common in some areas, is shown in the left background, behind the ledge.

photosynthetic rate per unit of blade surface area varies with distance of a blade from the growing tip. Clendenning combined the measured maximum photosynthetic rate per unit of surface area with the surface area as a function of distance along the frond to obtain a curve showing the photosynthetic capacity per meter of stipe (Figure 3). The curve clearly shows that the majority of the photosynthetic capacity is located in the upper portion of the frond. This is the end of the stipe that is nearest to the light source but also tends to be located in water with the lowest nutrient concentrations.

Clendenning also measured oxygen evolution of blades as a function of the light intensity (Figure 4). The photosynthetic rate for a mature kelp blade located at the surface was linear up to a light intensity of 400 foot-candles and saturated at about 1400 foot-candles. Blades taken near the bottom of kelp plants saturated at about 700 foot-candles. Sunlight above the sea surface has a maximum intensity of about 10,000 foot-candles. Saturating light intensity was higher at higher temperatures, lower at lower temperatures.

Algae commonly show a linear relation between photosynthesis and light intensity at low light intensities changing to a saturated system at high intensities (Yentsch,

Figure 3. Distribution of net photosynthetic capacity (from North, 1971a).

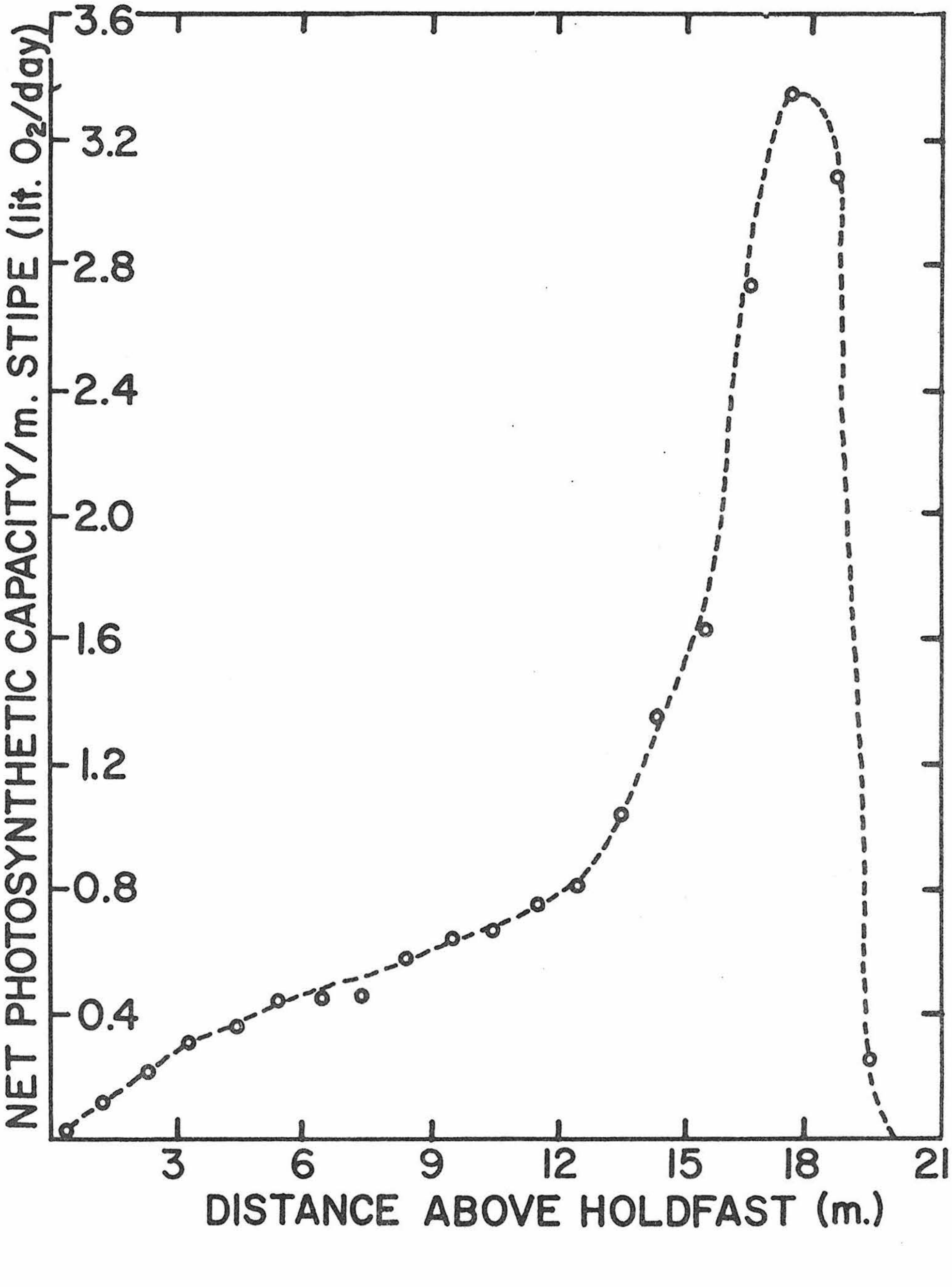
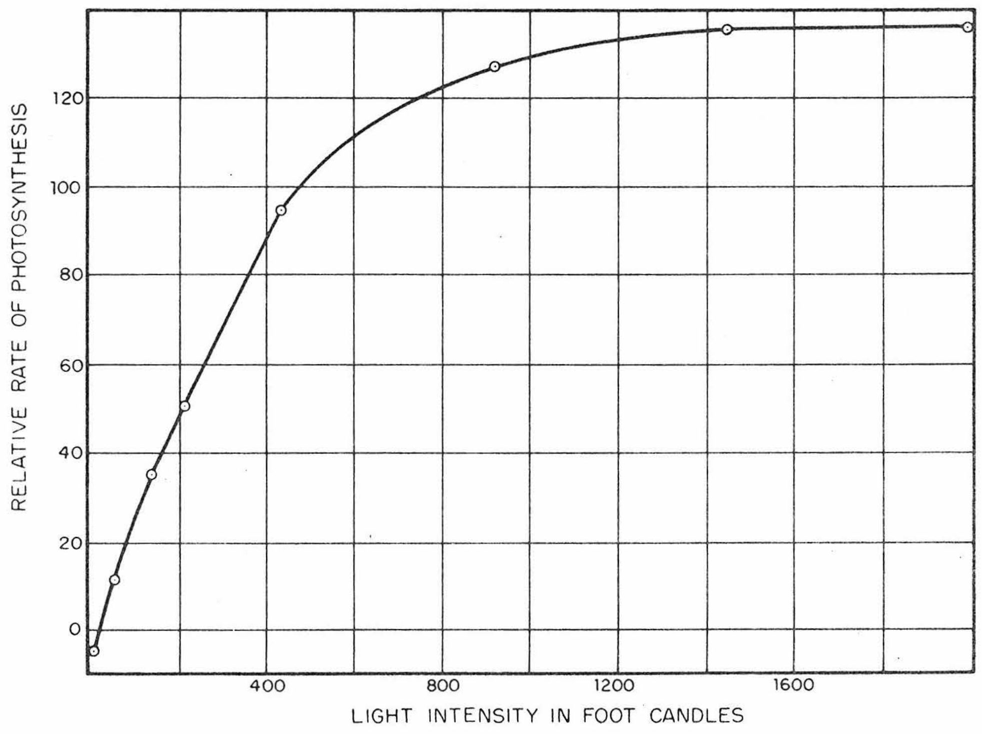


Figure 4. Photosynthesis in the mature kelp blade as a function of light intensity (from Clendenning, 1971).



1974; Steeman Nielsen,1974). Two types of reactions, the light and the dark reactions, are believed to cause this pattern. The light reactions absorb energy from incident photons and split water to produce high energy compounds. The dark reactions utilize the high energy compounds and fix CO_2. The rate of light reactions is limited by light intensity and is fairly insensitive to temperature; the rate of dark reactions is limited by enzyme kinetics and exhibits enzymatic temperature response. The photosynthetic rate is limited by the light reactions at low light intensities. The saturation of the enzymes involved in the dark reactions determines the maximum photosynthetic rate at high intensities. Algae can change their maximum photosynthetic rates by altering the concentrations of the enzymatic systems involved in the dark reactions.

Ability to control dark reaction rates explains how algae adjust seasonally to the different temperature regimes. Clendenning examined the maximum photosynthetic rates of kelp plants taken from the field at different times of the year. Plants coming from colder waters had higher photosynthetic rates then warm water plants when compared at the same laboratory temperature. Plants compared under conditions similar to those in the field (i.e., at the temperature of the water from which they came) showed essentially constant photosynthetic rates throughout the year. The ability that Macrocystis showed to acclimate to different temperatures also appears in other algae. Steeman Nielsen (1974) argued that algae increase the concentrations of the enzymes involved in the dark reactions to maintain a constant photosynthetic capacity.

Carbon fixed during photosynthesis goes predominantly to two carbohydrates: the storage sugar alcohol, mannitol; and the structural polysaccharide, alginic acid (Vaughan, 1959). Mannitol is also the major component of the fluid that is translocated within the plant (Parker and Huber, 1965).

North (1975) has reported values for the carbon and nitrogen content of Macrocystis pyrifera fronds. The highest C:N ratio was 40:1 at the end of summer time; the low value of approximately 15:1 was measured in late November, early December (Table 1). Values for springtime, during periods of high oceanic nutrient concentrations, have not yet been analyzed.

Translocation

Differentiation of tissues into specialized structures in higher plants requires a transport mechanism faster than diffusion. In the higher land plants this need is met

Date	# of Blades Sampled	Range of C:N	Average C:N
9/16/74	12	37-49	40
11/18/74	11	21-42	28
	10	12-28	17
	10	13-17	16
	7	16-20	17
12/16/74	10	14-22	18
	1 (tip)	20	--

Table 1. C:N ratios of *Macrocystis pyrifera* off of Corona del Mar, California. The ratios are for molar concentrations. Each line represents the information from one frond. The overall C:N ratio is the average over the whole frond, weighted for the biomass of the individual blades. Raw data came from North (1975).

through two types of conducting tissue. Xylem moves water and inorganic nutrients from roots to photosynthesizing leaves by a form of capillary action. Phloem carries the organic products of photosynthesis from leaves to non-photosynthesizing tissues as well as to growing shoots. Translocation in phloem consists of mass transport of the fluid present, driven by osmotic gradients (Crafts and Crisp, 1971).

There is no xylem in seaweeds. This is not surprising, since there is no need to translocate water from one part of the plant to another in plants that grow immersed in water. Tissue analogous to phloem, however, has been discovered in some of the kelps (Parker, 1971a). This phloem is very similar to that of the higher land plants, and consists of interconnecting tube cells which form a veritable pipe line between the different parts of the kelp plant. This system of tube cells is most highly developed in *Macrocystis*, extending through the stipes to include the growing tips, the mature blades and the holdfast of a plant. There is some evidence that translocation in *Macrocystis* might also occur in the medullary filaments, although at a slower rate than in the sieve tubes.

Sargent and Lantrip (1952) first showed that translocation is important for the growth of *Macrocystis* fronds. By comparing photosynthetic rates of different blades on a frond with their growth rates, they concluded that there must be translocation of fixed carbon. Young blades near the growing tip used more carbon in growth than they fixed in photosynthesis. Blades more than 15 blades away from the tip fixed more carbon than they used in either respiration or growth. Sargent and Lantrip explained the surpluses and deficits by postulating transport of photosynthate from the mature blades to the growing tip. Sargent and Lantrip could not account for all of the calculated organic matter produced. Hence, they postulated that large amounts of organics were being exported to the haptera (the holdfast region).

Photosynthesis was measured by enclosing different parts of the kelp plant (small discs cut out of the blades) in glass bottles. These bottles-with-discs were immersed in the ocean within 10 cm of the surface. Oxygen evolution in each light bottle and respiration in each dark bottle were measured. Oxygen evolution and respiration values were scaled to provide organic production of different parts of the plant. Only gross production of those parts of the kelp plant expected to be at the surface was included when they calculated total production of the whole plant.

There were several unappreciated factors which would have caused their estimated net production to be low. First, light does fall on lower parts of the plant and causes photosynthesis. Secondly, the blades in the lower part of the plant are normally in colder water than those at the surface . When such blades were brought to the surface, their respiration rates were raised by the effect of higher temperature. Respiration rates of the lower parts of the plant had been subtracted for the determination of net production overestimating respiration and underestimating the net rate of production. Thirdly, the nutrient state of the water or the state of mixing in the bed may have caused the kelp to photosynthesize at a lesser rate in the containers than in the environment, again leading to underestimation of the net production, especially as related to the lower parts of the kelp plant. Nonetheless, the principle conclusion was still valid, namely that the kelp plant must be translocating, based on a calculated surplus of organic matter in the budgets.

Clendenning (1963) repeated and validated the studies of Sargent and Lantrip.

North (1963) was the next worker in the kelpyard of translocation. He measured growth rates of juvenile fronds on plants from which he had severed connections to the mature fronds (those fronds reaching to the surface) and still shaded the holdfast. These rates were compared to the growth by juvenile fronds on unaltered plants. The comparisons showed that mature fronds must be enhancing the growth of juvenile fronds by translocating organic matter. This observation was interesting because it explains how juvenile fronds in a kelp bed with a heavy canopy can obtain the organic matter needed to grow to the highly illuminated surface. Such juvenile fronds are attached to plants with fronds already at the surface.

The physiological basis for transport was first examined by Parker(1963, 1965, 1966, 1971; with Huber, 1965). He illuminated blades still attached to their stipes and isolated in seawater containing $NaH^{14}CO_3$. This procedure yielded labelled organic matter produced in the blades during photosynthesis. By following the transport of the radioactive carbon away from the blades, he was able to determine translocation rates towards the tip and towards the holdfast. He found that translocation was from blades that were between 50 and 60 blades away from the apex (between 2 and 3 meters back). The predominant transport was toward the growing tip at the apex at rates as high as 80 cm/hr. This was equivalent to a volume flow rate of 1 cc/hr, if the cross sectional area of the sieve tube cells in the stipe is $1.4x10^{-2}$ cm^2 (a number obtained by estimating the number of sieve tube cells in the phloem of a stipe as 500-from Figure 33, North 1971a- and by assuming a sieve tube diameter of 60μ, Parker and Huber 1965). These studies have been confirmed by Lobban (personal communication, 1975).

Parker (1966) analyzed the composition of the fluid transported in the phloem. He collected fluid exuded by phloem at the face of cut stipes. Upon analyzing the exudate, he found that the dominant carbon compounds were the sugar alcohol, mannitol, and free amino acids (Table 2). From concentrations of carbon and nitrogen in the exudate we find that the C:N ratio was 9:1 on a molar basis. This represents a greater relative concentration of nitrogen than occurs in the whole plant.

In an effort to determine whether nitrogen is transported in the inorganic form of ammonia, I collected 1.5 ml of exudate from several cut stipes at the La Jolla kelp bed on May 6, 1975. I diluted the exudate with deionized, distilled water to 100 ml and analyzed the solution for ammonia, using the same method employed for analyzing ammonia in seawater. The exudate contained less than 100 μM ammonia. This concentration was insignificant compared to the 0.2 M nitrogen present in the amino acids.

	Concentration g/ℓ	Molecular Weight	Conc mM	#N/molec.	#C/molec.	Concentration N-mM	Concentration C-mM
Total Solids	148.9	-	-				
D-mannital	36.0	172	209	0	6	0	1254
protein	5.7	est. 125/aa	46	est. 1/aa	est. 4	46	184
lipid	.16						
total amino acids	19.1						
L-alanine	9.83	89	110	1	3	110	330
aspertic acid	2.63	131	20	1	4	20	80
glutamic acid	1.45	147	10	1	5	10	50
citrolline	.43	175	3	3	6	3	18
other	4.7	est. 125	38	est. 1	est. 4	38	152
Total						227	2068

C:N (molar) = 2068/227 = 9.11
C:N (weight) = 7.81

Table 2. Content of translocated kelp fluid. For protein and undetermined amino acid fractions, molecular weight assumed to be 125/residue, nitrogen content assumed 1/residue and carbon content assumed 4/residue.

Thus the flux of nutrients in the phloem was about 2 mmoles-C/hr and 0.2 mmoles-N/hr. This is equivalent to 24 mg-C/hr and 2.8 mg-N/hr.

Productivity estimates

Care must be taken in comparing various estimates of algal productivity because of the different experimental techniques and methods of calculation used. Primary production estimates are efforts to represent the amount of photosynthetic products accumulated by the plants. Because investigators are concerned with different aspects of the primary production process they assess the matter produced by several methods. The total amount of energy captured or total amount of carbon fixed is given as gross photosynthesis. Production that is ecologically important is obtained by subtracting respiration from the gross photosynthesis to obtain net photosynthesis. Net photosynthesis is thus an estimate of the net amount of organic matter produced after a day-night cycle. The amount of plant matter that can be harvested by man represents the production in terms of change of the standing stock over some time interval and is termed yield. This change in accumulated biomass will be the net production over that time period, less several types of losses that include losses from increased respiration during times less favorable than those when net production estimates were made, losses due to senility of the plant, losses to herbivores, and losses caused by physical factors, such as storm damage. That is, the yield is what is left over.

Methods used to measure organic production include: techniques involving the measurement of oxygen released and taken up by the isolated whole or parts of plants; the use of the radioactive form of carbon, ^{14}C, as a tracer to measure the amount of carbon fixed, also using isolated plants or plant parts; the measurement of oxygen concentrations in field situations where the water movement and plant biomass are known; the measurement of change of biomass of plants through time; and the collection and measurement of representative samples of the standing crop of a plant at different times. Each of these methods presents problems that affect interpretation of productivity.

Productivity measurements conducted on isolated pieces or whole parts of algae may not be applicable to field situations because mixing processes in the enclosed system are dissimilar to those in the field. Because diffusion in solution is relatively slow, the rate of transport of substance depends primarily on the mixing of the water around a macroalga. When nutrient transport limits the algal growth rate, then the mixing rate can determine productivity. The problem of mixing and transport is more fully discussed in the section on currents in the nearshore.

It is not always convenient to bring all of the parts of a plant into the laboratory. Such things as kelp holdfasts represent a considerable part of the biomass yet are seldom considered in the oxygen or carbon budget. Thus, laboratory measurements cannot necessarily be extrapolated to field conditions unless these problems are realized and dealt with.

Flow techniques require that the currents be well understood to allow interpretation of the results. This is a key problem in the kelp bed because the currents depend on such transient factors as internal waves as well as net currents. Extensive current measurements are needed in order to understand the current regime. Field measurements based on flow techniques give the net metabolic processes in the community, not just the primary production. When one primary producer is the predominant member of the community, as _Macrocystis pyrifera_ is in the kelp beds in San Diego, net metabolism is more clearly definable.

Results given by different measurement techniques are controversial (Yentsch,1974). Oxygen evolution and utilization methods raise the question whether respiration is the same in dark and in light. This knowledge is useful for converting gross to net photosynthesis. Radioactive carbon methodology involves uncertainty as to carbon uptake in the dark as well as uncertainty about the amount of photosynthesized organic matter released to solution, remaining unmeasured when radioactive carbon taken into the plant is counted.

Estimates of the productivity of kelp beds

Sargent and Lantrip (1952) estimated production by measuring oxygen evolution from parts of a kelp plant in small containers and extrapolating to the whole plant. They assumed that all of the photosynthesis occurred in the canopy and that the lower parts only respire. For a 31 kg plant, wet weight, with a crown of 15.2 kg, their results showed a gross production of 114 liters of oxygen/day, respiration of 30 l/day and a net production of 85 l/day. The net calculated production was 940 g-wet weight/day. Net production was thus 3% of plant biomass per day, and gross production was 4%/day. At a bed density of 0.3 plants/m^2, such as Dayton (personal communication, 1974) has found in the Point Loma kelp bed, gross photosynthesis amounts to 34 l-oxygen/m^2-day.

Clendenning(1963) determined photosynthetic capacity of Macrocysis pyrifera fronds by measuring oxygen evolution and demand of different tissues along the length of a frond in the laboratory (Figure 3). By integrating along the length of the frond he calculated that a frond 20 meters long could produce 19 liters of oxygen/day.

Towle and Pearse (1973) determined productivity of Macrocystis pyrifera in Monterey Bay, California by measuring the in situ carbon uptake of the plants. They enclosed individual blades, still attached to the plants, in plastic bags and measured uptake of the ^{14}C tracer by the enclosed blades. Carbon uptake rate among blades at 4 m depth was 20% of that of surface blades. Taking account of the measured vertical distribution of biomass, they calculated that photosynthesis at the surface accounted for 99% of the total. Their kelp bed, had a stipe index of 5.1 stipes/m^2, an average wet weight of 1.2 kg/frond and a resulting wet weight density of 5.9 kg/m^2. They reported a production value of 6.8 g-C fixed/m^2-day. This production value is probably closest to a gross production estimate. Using the conversion factors employed by Sargent and Lantrip (1952), I derived the relationship that 1 g-C is equivalent to 20.4 g of wet weight. Thus Towle and Pearse's production estimate is equivalent to a wet weight production of 105 g-wet weight/day-m^2 or a gross photosynthetic rate of 2%/day.

McFarland and Prescott (1959) estimated productivity of a kelp bed at Paradise Cove, California, by flow measurements coupled with oxygen measurements. For a kelp bed density of 4.4-5.8 kg/m^2, wet weight, they calculated a gross production of 22-25 liters of oxygen/m^2-day, and a respiration of 23-26 liters of oxygen/m^2-day. This implies that community production was 0 liters-O_2/m^2-day or, stated otherwise, there was no increase in standing crop. Converting gross primary production to wet weight using the factors of Sargent and Lantrip (1952) yields approximately 500 g/m^2-day, or approximately 10% of the standing crop.

These strange results may arise from several very serious flaws. They should have measured current and dissolved oxygen concentrations much more frequently than every three hours. In my experience, water flow directions derived from current measurements made ten minutes apart can differ by 180 degrees. Frequent current measurements are needed to combine with dissolved oxygen measurements to provide a basis for estimating kelp bed metabolism.

McFarland and Prescott also tried to compensate for any diffusion of oxygen vertically. Their compensation technique was developed for estuaries and lagoons (Odum and Hoskin, 1958), where the waters are vertically more mixed than in the stratified Pacific Ocean, and where there are no internal waves causing vertical water motion.

Because of these serious flaws, this study does not give an adequate estimate of Macrocystis production.

Nutrient-organism interaction

Nitrogen and phosphorus, along with the much more abundant elements of carbon, hydrogen and oxygen, are the major components of living matter. Richards (1965), using the average elemental composition of marine plankton and assuming the carbon was present in carbohydrate form and the nitrogen on amino groups, proposed a chemical reaction to express the elemental relationship:

$$(CH_2O)_{106}(NH_3)_{16}H_3PO_4+138O_2=106CO_2+122H_2O+H_3PO_4+16HNO_3$$

The various forms of carbon dioxide in sea water are CO_2(aq), HCO_3^- and CO_3^{2-}. They are present at total concentration of about 3 mM. Oxygen is present in surface waters in concentrations of about 0.2mM-O_2.

Three principal forms of phosphorus are usually measured in the sea: dissolved inorganic phosphate; dissolved organic phosphorus; and particulate phosphorus, inorganic and organic. Dissolved inorganic phosphorus occurs almost totally as orthophosphate. Solorzano and Strickland (1968) examined inorganic phosphorus as polyphosphates off California. They found that polyphosphates were only rarely present at concentrations above detectable levels.

The other form of dissolved phosphorus, dissolved organic phosphorus, has been found in amounts roughly equal to that of orthophosphate in surface waters. Dissolved organic phosphorus concentrations were highest when phytoplankton populations were large (Strickland and Austin, 1960). Strickland and Austin attempted to characterize organic phosphorus present as enzyme hydrolyzable phosphate esters, but found little present.

The only evidence that macroalgae can take up organic phosphorus comes from the experiments of Eppley (1962), who found that *Porphyra perforata* could hydrolyze the phosphate esters, ATP and ADP, but could not hydrolyze the non-ester, AMP. Watt and Hayes (1963) found no evidence of organic phosphorus uptake in *Fucus vesiculous* in sterile seawater.

Because most of the organic phosphorus does not occur as organic esters,the two sets of experiments suggest that organic phosphorus is not an important source of phosphorus for macroalgae.

Nitrogenous compounds are more numerous than those of phosphorus and their relative importances less well understood. The predominant form of nitrogen is the dissolved gas, N_2, present in seawater at a concentration of about 500 µM (Corner and Davies, 1971). Examination of nitrogen:argon ratios by Benson and Parker (1961) produced values that agreed with those of dissolved air within their 1% experimental error. This study , as well as direct measurements of nitrogen fixation (Dugdale and Goering, 1967) showed that while some nitrogen fixation occurs in the ocean, other forms of nitrogen are more important for the growth needs of algae.

The main inorganic forms of fixed nitrogen are the ammonium cation and the nitrate and nitrite anions. Concentration ranges of these chemical species in the ocean, expressed in units of micromolar (µM), are: $NH_3(aq)+NH_4^+$, 0.35-3.5; NO_2^-, 0.01-3.5; and NO_3^-, 0.1-43.0.

Because nitrogenous inorganic ions frequently occur in low concentration in surface waters during times of algal growth, phytoplankton biologists have started scrutinizing organic forms to determine their importance in providing nitrogen.

Amino acids have been observed in concentrations of up to 2.4 μM near a southern California sewer outfall and up to 1.6 μM away from it by Clark, Jackson and North (1972). North (1975) found concentrations of primary amines, presumably mostly amino acids, of up to 0.5 μM in nearshore waters of southern California. Approximately half of these amines could be used by an alga in culture. Wheeler, North and Stevens (1974) showed that amino acids could be used as a nitrogen source by nitrogen-starved cells to support moderate rates of growth. They were able to induce amino-acid uptake only by depriving the cells of other nitrogen sources for several days.

Recently concentrations of another organic form of nitrogen, urea, have been measured in the surface waters off southern California (McCarthy, 1971). Urea concentrations were similar to those of ammonia, usually less than 1.0 μM-N. Both Carpenter _et al._ (1972) and McCarthy cultured algae in media with urea to show that some phyotoplankton species are capable of taking up urea at rates comparable to ammonia and nitrate rates. Not all species, however, used urea as a nitrogen source. McCarthy showed that ammonia concentrations greater than 0.5 μM in a culture suppressed urea and nitrate uptake. Comparing the importance of urea to that of nitrate and ammonia as sources of nitrogen for oceanic phytoplankton, McCarthy found that an average of one-quarter of the nitrogen was taken up as urea.

Whitledge and Dugdale (1972) measured the concentration of another nitrogen form, creatine. Creatine is the major excretion product of fish and is found in areas such as off Peru where there are high concentrations of fish. It does not seem to be important in the nitrogen cycle off the coast of California.

All of these nitrogenous forms are inter-related by the various processes that cycle nutrients. The nitrogen cycle in the ocean starts with nitrate brought up from the deep waters to the euphotic zone. Nitrate is taken up by phytoplankton growing near the surface and converted mainly to protein. Some of the organics are released back to the water as amino acids. The phytoplankton are either swept away from the surface by water movement or eaten by the zooplankton. Zooplankton release amino acids during feeding, and excrete ammonia and small amounts of urea. Bacterial degradation of the amino acids produces further urea and ammonia. Fish eating the plankton excrete creatine. Ammonia oxidizes to nitrite and then nitrate.

Organic matter settling to the deeps oxidizes to nitrate. In the littoral zone organic matter will fall to the sediments, where the nutrients are regenerated or will be swept out to deeper waters, where it will reenter the oceanic nutrient cycle.

Concentration ratios of the elements in the plankton correspond to the changes of nutrient concentration in solution. The average changes for the world oceans have been observed to be in the relationship of $\Delta O:(\Delta C:\Delta N:\Delta P) = -276:(106:16:1)$ (Redfield,Ketchum and Richards, 1962). These nutrient ratios vary with time or location due to different processes of depletion and regeneration that include: loss of oxygen to the atmosphere when water is supersaturated with respect to the atmosphere; mixing of different water masses with different ratios; and differential regeneration of the different nutrients. Nonetheless, when concentrations of the different dissolved elements are plotted one against another, remarkably good fits to straight lines result.

Interaction of physical and biological processes produce definite spatial distribution patterns of nutrients. Phytoplankton deplete the nutrients near the surface where light intensity is high; vertical mixing replenishes surface waters with nutrients from the deeps while sweeping phytoplankton away from the light. In temperate oceans the summer sun produces a warm buoyant layer of water at the surface that resists vertical mixing. Surface waters are not well mixed and nutrient concentrations drop. Vertical mixing can occur during winter when surface waters cool and nutrient concentrations increase.

Coastal regions sometimes become enriched during the summer. Upwelling along the San Diego coast during late spring and early summer brings nutrient-rich waters to the surface. This vertical water movement makes the west coast of North America one of the most productive areas of the sea. Winds blowing from the correct direction with sufficient strength and duration transport the warm surface waters away from the land. Cold bottom waters flow up to replace the transported warm waters. Because these cold waters bring nutrients to confluence with the energy-providing rays of the sun, upwelling areas are characteristically very productive.

Despite much work through many years, physical oceanographers understand only the general patterns of upwelling along the southern California coast. Bakun (1973) modeled the process for the west coast of North America by using long-term wind data and knowledge of the coastal orientation. He predicted that upwelling should be most intense in southern California, decreasing farther north. The maximum transport should occur in May and June. Work done as part of the CalCOFI program, quoted in Jones (1971), showed that upwelling is most intense in southern California during April, May and June. The calculated vertical transport rate of bottom water was approximately 50 cm/day. Theoretical work by O´Brien (1972) suggested that upwelling takes place only in the first 10-20 kilometers from the coast. Unfortunately, this work was done for the simple geometry of an idealized straight coast. Complicated real coastal configurations react differently. However, the fact that upwelling occurs in such a narrow zone increases the importance of the littoral zone.

The most intense areas of upwelling are capes and points of lands, where the surface waters leave the shore in plumes (Walsh, 1972). Point Loma (the site of my studies) represents this kind of topography and the orientation of the coast line is correct for winds that cause upwelling along southern California. Hence, Point Loma should be an upwelling area. Biological evidence and temperature distributions support this conclusion. North (1972) has frequently observed animal species considered typical of the colder waters of northern California in Point Loma waters. Such species as the seastar, Pycnopodia helianthoides and the sponges, Tedania topsentia and Acarnus erithacus, are rarely found in such shallow water in other parts of the Southern California Bight. Presumably, it is the vertical transport of nutrients and cold water that makes the kelp beds of Point Loma so rich.

Nutrients and growth

Most work pertaining to nutritional influences on algal growth has involved growth and uptake measurements on phytoplankton at different nutrient concentrations utilizing both laboratory cultures and phytoplankton from the field. The relationships of algal growth rates to limiting nutrient concentration are often expressed by the Monod relationship (Eppley *et al*., 1969). For low concentrations the Monod equation gives a linear relation between growth rate and nutrient concentration when nutrient concentrations are low. Likewise growth rates are constant when the nutrient concentrations are high. Typical concentrations near the upper limit of the linear range are) 0.1-6. μM for ammonia and 0.1-4. μM for nitrate (Eppley,*et al.*, 1969).

Extensive analyses of the growth rates of marine macro-algae as a function of a limiting nutrient are few. Laboratory measurements of the nutrient uptake rates of macrophytes as a function of nutrient concentration under field conditions are difficult because of transport problems discussed below.

As expected, increased nutrient concentrations do lead to increased algal growth in culture (Henkel, 1959; Kinne-Diettrich, 1955). Waite and Mitchell (1972) recently examined effects of very high concentrations of ammonia (between 3.6 and 77 µM) and phosphate (between 1.3 and 25. µM) on photosynthetic rate of the green alga, Ulva lactuca. Increasing the concentration of nutrients enhanced the rate of carbon fixation. These authors were primarily concerned with the fertilization of estuaries by municipal sewage. Hence they did not examine growth rates of Ulva at low, more environmentally meaningful concentrations.

Because of the importance of the culture of seaweeds for human consumption in Japan and China, there has been work on increasing yields by fertilization (Cheng, 1969; Tamura, 1970). The fertilizers most frequently reported had some form of nitrogen as the active component. Scientists were able to harvest as much as 4 kilograms of dried Laminaria japonica for each kilogram of fertilizer that they applied. Their plants apparently stored nitrogen, since periodic immersions in concentrated solutions of nitrogen adequately supplied nutrients.

Dawes, Mathieson and Cheney (1974) studied seasonal growth of several species of Eucheuma along the Florida coast, monitoring dissolved nutrient concentrations in the water. The authors noted: "the period of maximum growth coincided with low temperatures, reduced light intensities, and maximum nutrients." These authors concluded that higher nutrient concentrations were responsible for high winter growth rates and the lower carbohydrate concentrations of the plants.

There is thus evidence that relationships exist between nutrient concentrations of growth solutions and growth rates of seaweeds. Beyond this there is little knowledge yielding insights into the workings of the coastal marine seaweed systems. It is difficult to relate the growth rates measured in the laboratory with rates occurring in the field. There are differences in the transport rates from the bulk solution to the plant surfaces. There are also unknowns involving the ability of the algae to store nutrients and to change their nitrogen contents. There is however, every indication that nutrients play an important role in the ecology of the nearshore. Distribution, supply, and effect of nutrients in the highly productive area of the the coastal nearshore have been little studied. This thesis describes one of the first systematic studies of the nutrient ecology the California nearshore.

Nutrients in the nearshore

Almost all work relating algal production to nutrients has been done by phytoplankton ecologists working from large ships that do not dare venture too near to shore. The record of nearshore nutrient distributions is thus scanty.

Kamykowski (1973) was interested in the spatial and temporal scale of planktonic phenomena, and therefore examined distribution of several biologically important water properties both along and perpendicular to the shoreline between La Jolla and Oceanside, California. Phytoplankton concentrations decreased rapidly in the direction perpendicular to shore. Chlorophyll a fluorescence was used to estimate phytoplankton concentrations on one transect. Flourescence decreased by a factor of 10 between that station closest to shore at 1 kilometer and a station 13 kilometers from shore. Between La Jolla and Oceanside there were few differences among stations comparable distances from shore over a distance of up to 10 kilometers. Thus the nearshore differs from the oceanic environment farther out. Presumably edge or bottom effects must be important.

Armstrong and LaFond (1966) measured the vertical distribution of the temperature and the nitrate concentration as part of a study of the vertical motion of water associated with the internal waves propagating at the thermocline. Both nutrients and temperature were stratified at the Naval Electronics Laboratory Tower (NEL tower), located in 18 meters of water on a sand bottom off the coast of Mission Beach, San Diego. The nitrate concentration during one sampling was close to 0.1 μM at the surface, 14 μM at the bottom. The sharpest nitrate gradient (the nitrocline) was at 9 meters while the thermocline was at around 7 meters depth. Nineteen hours later, the surface and bottom concentrations of nitrate were nearly unchanged, but the thermocline had risen to 4 meters below the surface and the nitrocline to 6 meters. When Armstrong and LaFond monitored the nitrate concentration at a constant depth of 9 meters for a period of three hours, the nitrate concentration of the water at that spot varied by as much as 6 μM in ten minutes (from 1 to 7 μM) caused by fluctuations in the thermocline depth. Vertical movement of the nutrients associated with internal-wave-induced motion was also observed by Kamykowski (1973) in his studies of temporal and spatial scales in phytoplankton production.

My data also showed the pattern of vertically varying nutrient concentration (see Chapter 3). Its consequences are different for a phytoplankter drifting with the water and for a macroalga, such as Macrocystis, anchored to the bottom: the phytoplankter will be exposed to a relatively constant nutrient concentration but also varying light intensity; the macroalga will be exposed to temporally constant light but nutrient concentrations will vary with time. Parts of the same plant will be bathed by different nutrient concentrations. Thus the nutritional strategy of the macroalga may well be different than that of the single-celled alga.

The nearshore also differs from the pelagic environment because the potential exists for recycling of nutrients in the sediments that are in contact with the euphotic zone. Hartwig (1974) studied rates of nutrient regeneration in a sand bottom at a depth of 18 meters off La Jolla, California. Nutrient release rates to the water were extremely variable. The average release rates from the sediments were: oxygen, -56 mmoles/m^2-day; nitrate, -77 moles/m^2-day; nitrite, +34 moles/m^2-day; ammonia, +872 moles/m^2-day; phosphate, +77 moles/m^2-day. Ammonia was the only important form of nitrogen release. Nutrient ratios were O(-366):N(11):P(1), equivalent to a C:N ratio of 34:1. This carbon to nitrogen ratio was quite high relative to ratios in phytoplankton but was very similar to that of the dominant alga in the region, <u>Macrocystis pyrifera</u>. Hartwig calculated that the measured release rates were insufficient to change appreciably the nutrient concentration of an 18 meter column of water. Significance of the sedimentary contribution to nearshore nutrient concentrations region depends, however, on factors that Hartwig did not investigate, including thickness of the layer of water mixing immediately above the sediments, the residence time of that water, and the initial nutrient concentration of the surrounding water.

Discharged sewage constitutes another possible source of nutrients for the Point Loma kelp bed. Municipal effluent from the city of San Diego is discharged through a submarine outfall 3.2 kilometers in length through a diffuser structure at a depth of 64 meters (S.C.C.W.R.P., 1975). The outfall discharges 3.8×10^8 l/day of primary treated effluent containing 1.3×10^4 kg of nitrogen, 59% of it present in the form of ammonia, and 1.4×10^4 kg/day of phosphate. Stated otherwise, effluent has concentrations of 2.5 mM-N, 1.5 mM-P (SCCWRP, 1975). When this effluent is diluted 200:1 by seawater through by the outfall diffuser, there is a mass of water enriched by 7.5 µM ammonia and 0.7 µM phosphorus. If the phosphorus is in the form of phosphate then the enrichment ratio in the sea water would be 10:1, ammonia:phosphate.

Currents in the nearshore

Water motion providing nutrients to macroalgae for growth can be important in two ways: by minimizing boundary effects and by renewing water depleted of nutrients.

Munk and Riley (1952) analyzed the importance of boundary layers to the movement of nutrients by diffusion to plants. Next to any object in a flowing medium there is a thin region (or boundary layer) where the medium moves very slowly. Nutrients move from the bulk medium to the object by the relatively slow process of diffusion through the boundary layer. Boundary layer thickness diminishes when velocity of the water flowing by the object increases or when the turbulence in the medium increases. Munk and Riley compared effects of the geometries and habitats of macroalgae and of phytoplankton on nutrient transport to algal surfaces. They noted that macroalgae are usually attached to the bottom, experience high velocities relative to the water, hence should have relatively thin boundary layers. This permits fast transport rates to the plant surface. The individual phytoplankton cell drifts with the water, has little relative velocity and therefore a thick boundary layer. A phytoplankter, however, has a smaller biomass to support for a given amount of surface area. Single cells thus transport less nutrient across their surfaces than do the macroplants. Water motion is consequently important for supplying nutrients to attached plants and small size is important for phytoplankton.

Conover (1968) explored the relationship between standing crop and current velocity regime for several marine plant species in tidal lagoons and estuaries. He found a strong correlation between a measure of the water motion and the standing crop. The relationship between the two parameters was similar to the relationship between carbon particle transport to a plant surface and a measure of the water velocity. Conover interpreted this similarity as proof that standing crop was determined by the nutrient transport. This is obviously simplistic because the standing crop is an expression of competition between growth and loss processes. Conover´s work does suggest, however, that nutrient supply can be important in benthic processes.

The importance of water motion in delivery of nutrients to plants makes it difficult to estimate primary production and nutrient dynamics on the basis of laboratory studies. Attempts, such as those of Towle and Pearse (1973), to measure the *in situ* carbon uptake of a kelp blade by putting it in a bag will give values that are too low if rates of transport of the various dissolved gases and nutrients are critical. Wheeler (1974) has shown that the rate of oxygen production of a blade of Macrocystis sp. increases as the velocity of water passing by it increases.

There can thus be no doubt of the importance of water motion to the growth of attached algae. For the adult giant kelp plant, with its canopy thick with fronds lying on top of fronds, with its column of stipes and blades intertwined in a tight mass, standing in an environment where the water moves as the wind- and tide-driven currents, pushed by surface waves and internal waves, it will not be easy to quantify or understand the precise role of water motion.

There is one certainty about the water motion: nutrients that do not flow into a kelp bed are not extracted by the kelp. A knowledge of the currents that exist in the region of a kelp bed is essential for the complete understanding of the nutrient regime.

Because of the importance of the currents in the fate of a sewage field, the City of San Diego contracted for current studies of the area off of Point Loma. In a report to the city, San Diego Marine Consultants (1959) described the results of drogue studies carried out near the present location of the sewer outfall. Effects of wind-induced currents were minimized by using only those observations gathered during periods of low wind speed. Surface currents moved in a clockwise direction with a net motion to the southeast of about 2 km/25 hr tidal cycle. Because the drogues were easily entangled by kelp none of the drogue information came from the kelp bed. During one three-hour period, however, currents were measured at the surface and at 12 meters depth for two stations, one of which was in the kelp bed at a bottom depth of 15 meters. The other station was approximately 170 meters offshore from the outer edge of the kelp bed. A surface current toward the northeast at a velocity of 9.2-11.7 cm/sec occurred in the kelp bed. There was a northwest flow of 12.7-15.2 cm/sec at the second station, noticeably faster than the current in the bed. Currents at 12 meters flowed northerly and were approximately 8 cm/sec at both the kelp bed station and at a third station farther from shore. Thus currents can vary with depth and surface currents can differ between stations. The average net motion along shore was approximately 2 cm/sec.

Recent data indicate that nearshore water movements off San Diego are strongly influenced by motion of the water caused by internal waves. Properties of the thermocline and of internal waves have been unusually well studied off Mission Beach, San Diego. The work has been conducted at the NEL tower (Cairns, 1967; Cairns,1968; Cairns and LaFond, 1966; Cairns and Nelson, 1970; Lee, 1961; Summers and Emery, 1963). The vertical thermal gradient was weakest from late November to early March. During summer when thermal gradients were strongest, the water was essentially a two-layered system. A power spectrum analysis of variations in thermocline depth showed that the dominant periods were semidiurnal and diurnal (12.5 and 25 hours, respectively). Internal waves responsible for thermocline fluctuations were primarily correlated with the tides and secondarily the winds. Typical wave speeds were approximately 20 cm/sec. Calculated wave lengths were 9 km for the semidiurnal and 17.3 km for the diurnal waves. Internal waves propagating shoreward formed bores with vertical faces as high as 10 meters in water 20 meters deep. The semidiurnal waves are believed to originate at the continental shelf, when passage of the surface tide excites the thermocline, causing an internal wave to propagate shoreward. This wave can be detected passing at widely spaced points along the shore, although phases occur at different times at various locations.

Such strong thermocline motion should have strong effects on water circulation in the nearshore. When to a first approximation the water is stratified into two layers, the passage of an internal wave with a characteristic length of 10 kilometers should cause the surface layer and the bottom layer to move in opposite directions, on and off shore. That is, raising of the thermocline depth from 10 meters to 5 meters when the bottom is 20 meters would cause outward flowing surface water and inward flowing bottom water. The onshore-offshore components of the two currents should show that the two have the same periodicity but are out of phase by 180 degrees.

Current measurements were made and analyzed at the NEL tower at 4, 8, 12 and 16 meters from the bottom by Winant and Olson (1975). There were two current systems in the nearshore, driven by two different sets of tidally linked forces. The onshore-offshore currents were driven by internal waves colliding with the shore. These currents had strong diurnal and semi-diurnal periods that resemble tidal phenomena but showed no fixed phase relationship to surface tides at San Diego. Water motion direction at the surface and at the bottom were 180 degrees out of phase with each other; the water motions at the intermediate levels of 8 and 12 meters were sometimes in phase, sometimes out of phase, depending on whether or not the thermocline was between them. Winant and Olson proposed a three-layered model as a better description than a two layer one. The third layer was a thermocline of smoothly varying density. Despite differences between their three layer model and my two layer model, the essentials of their data are valid for my previous inferences about an internal wave driven current system.

A longshore current system was also found. Phase and magnitude of these currents were uniform throughout the water column. High velocity winds occasionally caused surface waters to flow much faster than bottom waters. These were rare instances, however, and Winant and Olson found no significant correlation between winds and properties of the overall data set. They did find correlations between longshore currents and tides, with a defined phase lag. Thus when the ocean is thermally stratified, the longshore currents are the same throughout the water column, while currents perpendicular to shore are opposite in phase at the surface and at the bottom.

The study area

Point Loma is the peninsula forming the western boundary of the San Diego Harbor entrance (Figure 5). The bottom on the offshore side is a rocky shelf extending out 2 kilometers to a depth of 20 meters before dropping off rather sharply. Interspersed on the shelf are rocks rising up to 10 meters off the bottom and patches of sand. There are more sand and rock outcrops inshore.

The kelp bed extends from 1.5 kilometers south to 7 kilometers north of the tip of Point Loma (Figure 5). North of Point Loma lie Mission Bay, the NEL tower and La Jolla

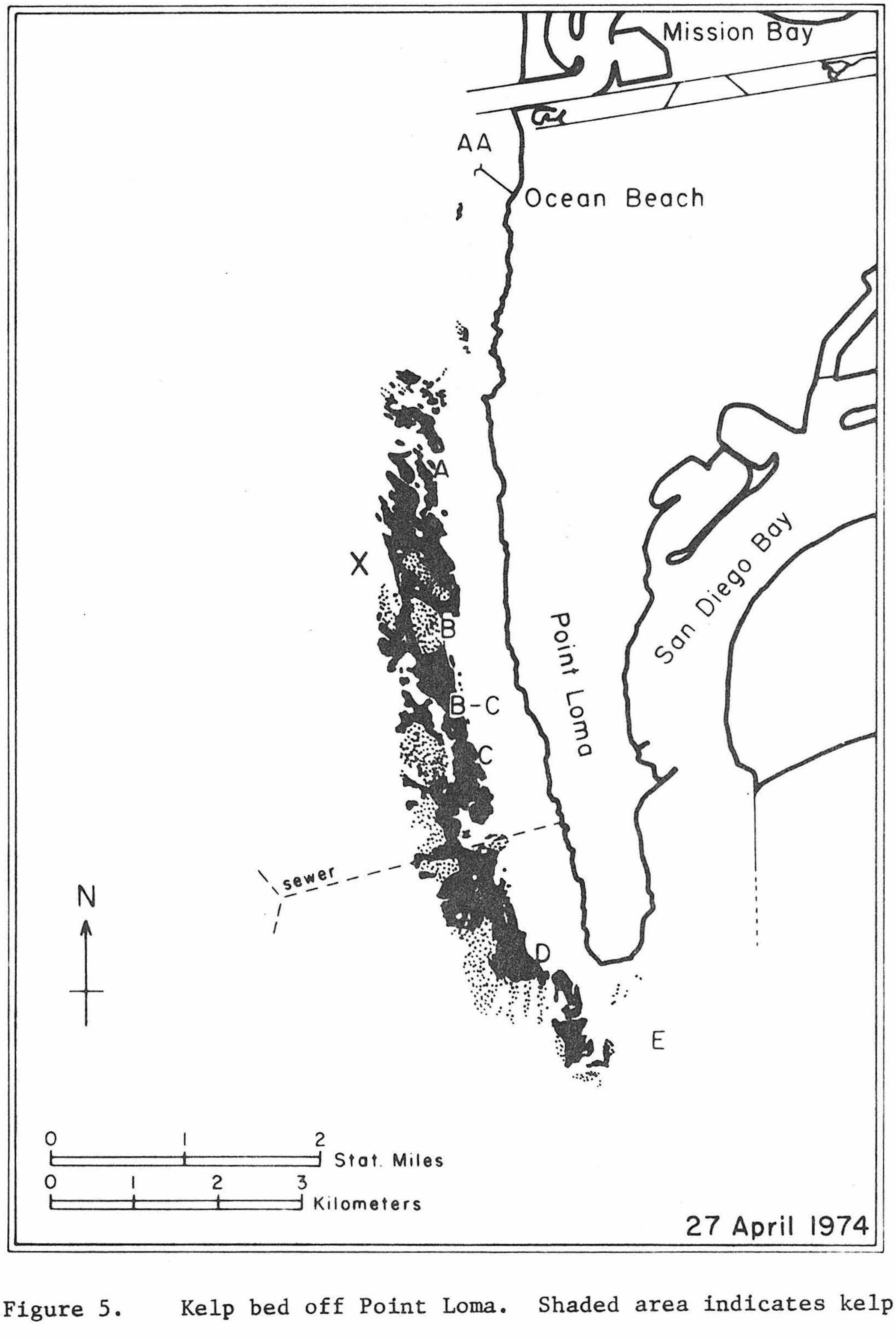


Figure 5. Kelp bed off Point Loma. Shaded area indicates kelp.

(Figure 6).

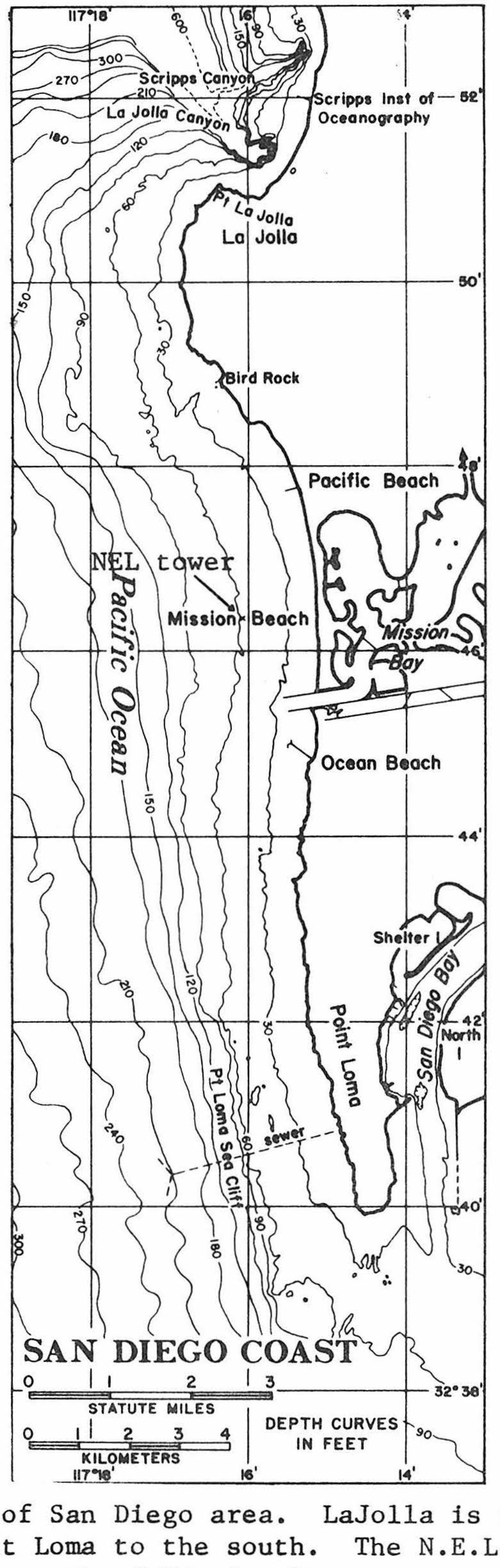


Figure 6. Map of San Diego area. LaJolla is to the north, Point Loma to the south. The N.E.L. tower is just north of Mission Bay entrance.

CHAPTER 2

METHODS

Field sampling

I did my sampling from the decks of small power boats. Station positions were determined by measuring angles between three or more prominent points on shore. These bearings were plotted on a 1:24,000 topographical map with a three-armed protractor to establish station locations. Stations in line on a heading towards shore formed a transect. It usually took two to three hours to complete a transect of four or five stations through the kelp bed. An exception was during a continuous twenty-four hour sampling period. Transects then took a half hour when no water samples were collected and one hour when they were.

Surface nutrient samples were collected at the side of the boat at a depth of about one foot (0.3 meters) below the surface. Deeper samples were either collected by a diver in polyethylene sample containers subsequently used for storage or in 1.5 liter van Dorn water samplers. Samples to be analyzed for nutrients were stored in acid-washed polyethelene bottles and frozen in the field with dry ice.

Samples to be analyzed for alkalinity were stored in 100ml polyethylene bottles and kept cool, but not frozen.

Data from the probe were collected either by dropping the probe slowly through the water or by dropping the probe to the appropriate depth and allowing equilibration. Data were recorded on a four-channel Rustrak recorder.

Water probe measurements

The probe was a Martek Mark II Water Quality Analyzer, with sensors to measure temperature, pH, dissolved oxygen concentration (DO), and depth. This unit was battery-powered and equipped with *in situ* electrical and electrochemical sensors.

Temperature sensing was done with a precision thermistor calibrated to an accuracy of 0.3 degrees over a range of 8-25 degrees centigrade.

The depth sensing unit used a pressure-sensing diaphragm and had an accuracy of ±4%.

The dissolved oxygen sensing unit used a gold/silver polarographic sensor with a teflon membrane. Water next to the membrane was kept constantly renewed by a battery-powered stirring pump. The unit included a thermistor and an electronic circuit to compensate for temperature changes in response of the electrode (Carey and Teal, 1965; Carritt and Kanwisher, 1959; Kanwisher,1962). The dissolved oxygen unit was calibrated in the laboratory before a sampling run (usually the night before) by standardizing the unit in seawater saturated with atmospheric oxygen at a temperature within the range of temperatures expected in the ocean. The concentrations of the standards were determined from tables from Whipple and Whipple (1911). When the calibration was rechecked after sampling runs readings were within 0.1 ppm of being correct (1 ppm=0.70 ml= 0.031 mM-O_2).

The pH unit used a set of temperature-compensated glass electrodes to give outputs on an expanded scale meter of 1.2 pH units, full scale. The reference electrode was a pressure-equalized Ag-AgCl electrode. The unit was calibrated with Beckman standard pH 4 and pH 7 buffers of low ionic strength. As a result, the sensor measured hydrogen ion activity rather than hydrogen ion concentration in the high ionic strength medium of seawater. Using the appropriate equations and stability constants given in Stumm and Morgan (1970) ($pK_1=6.11-0.006(T-5)$, $pK_2=9.34-0.011(T-5)$) and a constant alkalinity of 2.3 milliequivalents/liter, I calculated the total inorganic carbon in solution (C_T). This quantity is the sum of the carbonate species: CO_2(aq),

HCO_3^- and CO_3^{2-}.

Laboratory measurements

Alkalinity measurements were made according to Takahashi et al.(1970). A standard amount of acid is added to a seawater sample, super-saturated CO_2 (aq) is generated and driven off, the resulting pH is measured, and total alkalinity calculated. Using the total alkalinity, I calculated the carbonate alkalinity by the method given in Strickland and Parsons (1968). Corning digital 110 and Orion model 801 pH meters were used. Alkalinities measured on two different occasions showed no systematic trends. The mean measured carbonate alkalinity for 25 samples taken on July 8, 1975 was 2.17 milliequivalents/liter, with a standard deviation of 0.03 meq/l.

Subsamples were drawn for nutrient measurements from thawed samples collected at sea. The remainder of the original samples were then refrozen. All measurement techniques involved spectrophotmetric determination of light absorbances on a Beckman DU spectrophotometer with cells of 1 or 10 cm path length or a Gilford 300 sampling spectrophotometer with a 1 cm path length.

Phosphate concentrations were determined by the technique of Strickland and Parsons (1968) for reactive phosphorus. Phosphate reacts with a reagent containing molybdic acid, ascorbic acid and trivalent antimony to form a complex. The absorbance of this complex was measured at 885 nm.

Silicate was measured by the method given in Strickland and Parsons (1968) involving the formation of a silicomolybdate complex which is subsequently reduced by a metol addition. Because this method does not measure polymerized silicate, Strickland and Parsons referred to the substance measured as "reactive silicate." They indicated that the technique measured that silicate involved in diatom growth.

The nitrite measurement technique was that of Strickland and Parsons (1968). Concentrations of nitrite in the first two sets of samples were quite small (the greatest concentration measured being 0.15 μM). The method used for determining the concentration of nitrate also measures the concentration of nitrite. Consequently I discontinued nitrite measurements and analyzed solely for nitrate plus nitrite.

The nitrate measurement method of Strickland and Parsons (1968) was modified to take samples of 50 ml (Checkley, 1972). This technique reduces nitrate to nitrite on a copper-coated cadmium column. Water passing through the column is then analyzed for nitrite. Hence, the method measures nitrate plus nitrite. Nitrate is almost always present in much greater concentrations than nitrite. Results thus primarily reflect the concentration of nitrate. Whenever I refer to the concentration of nitrate in this thesis, I will be referring to the concentration of nitrate plus nitrite.

Ammonia was measured by the method of Solorzano (1969) modified by allowing samples to react with the reagents for times longer than two hours.

The quantity called "total nitrogen" was calculated by summing concentrations of ammonia and nitrate in a sample. It is thus a measure of the amount of ammonia plus the nitrate plus nitrite in solution. These are the dissolved inorganic forms of nitrogen.

Data analysis

Contour plotting is a convenient way to examine patterns of nutrient concentrations and other water parameters taken on a transect. The contour trace was determined by interpolating between points of known value. The value of the parameter being plotted was calculated along the sides of polygons defined by the sampling points at the corners. Contour lines occasionally cross each other in this method.

Relationships in the data were computed using multiple regression analysis with either one or two independent variables. The assumed relationship was:

$$z=a+bx+cy$$

where z was the dependent variable, x and y the independent variables. The method estimates the regression coefficients, b and c, that minimize the variance of the difference between the predicted and actual z.

CHAPTER 3

SPATIAL AND TEMPORAL PATTERNS

Typical patterns

I have sampled the kelp bed from 1972 to 1975 at different times of the year for a variety of parameters(Table 3).

Figures 7-14 show the results for a transect taken during the diurnal sampling on May 27-28, 1975. The figures show water parameter isopleths for a slice through the kelp bed. The transect ran perpendicular to shore 2 kilometers north of the tip of Point Loma. The outermost station was at the outer edge of the kelp bed, the inner station was near the inner edge but still inside the bed.

These data resemble my other results in several ways. The samples were taken early in the afternoon, while the sun was still high. Photosynthetic rates should have been maximal. Almost all of my various samplings were similarly around noon, sun time.

Date	Quantities Measured	Type of Sampling
3/30/72	- - - NO_3, NH_4, PO_4, -	Surface Sampling Throughout Bed.
4/20/72	- - - NO_3, NH_4, PO_4, -	" " " "
5/23/72	T, DO, pH, NO_3, NH_4, PO_4, -	" " " "
		Vertical Probe Sampling.
7/9/72	T, DO, pH, NO_3, NH_4, PO_4, -	Vertical Samples on Transect to Shore.
11/21/72	T, DO, - NO_3, NH_4, PO_4, -	" " " " " " "
2/24/74	T, DO, pH, NO_3, NH_4, PO_4, -	" " " " " " "
4/16/74	T, DO, pH, NO_3, NH_4, PO_4, -	" " " " " " "
5/21/74	T, DO, pH, NO_3, NH_4, PO_4, Si, alk	" " " " " " "
8/8/74	T, DO, pH, NO_3, NH_4, PO_4, Si, alk	" " " " " " "
9/20/74	T,DO, - NO_3, NH_4, P, Si	" " " " " " "
11/14/74	T, DO,- NO_3,NH_4, P, Si	" " " " " " "
5/6/75	T, - - NO_3, NH_4, P , Si	Transect along shore at 20 m depth, Pt. Loma to Pt. La Jolla.
5/27/75	T, DO, - NO_3, NH_4, P, Si	Transects to shore for 24 hours, vertical probe samples every 3 hours, vertical nutrient sample every 6 hours.

Table 3. Summary of kelp bed sampling.

The temperature map (Figure 7) shows the stratification that was almost always present. Although the water was stratified, there was no sharp, well-defined thermocline. This pattern was common for samplings near the tip of Point Loma. Likewise the depth of an isotherm was not constant through the bed and sometimes varied by as much as 5 meters at the different stations. The vertical fluctuation was caused by internal waves with periods shorter than half a day moving through the kelp bed. This vertical motion of the isopleths has often been observed at the NEL tower (Lee, 1961) as well as in my studies.

The dissolved oxygen contours (Figures 8, 14) show some features similar to the temperature contours. Isopleths oscillated vertically at the different stations and there was vertical stratification. The vertical displacement of the isopleths of oxygen is partially the result of the same processes that cause depth variations in the temperature contours (i.e., the physical movement of the water moves the iso-concentration lines of these parameters and of any other stratified constituent in the water up and down). The vertical stratification of the oxygen in the water originates from two causes: oxygen is stratified in the water before entry to the kelp bed due to production patterns of the phytoplankton; oxygen production in the bed is stratified by the the nonuniform distribution of light

Figure 7. Temperatures for Transect 1 (1400 PST), May 27, 1975. Crosses represent sampled points.

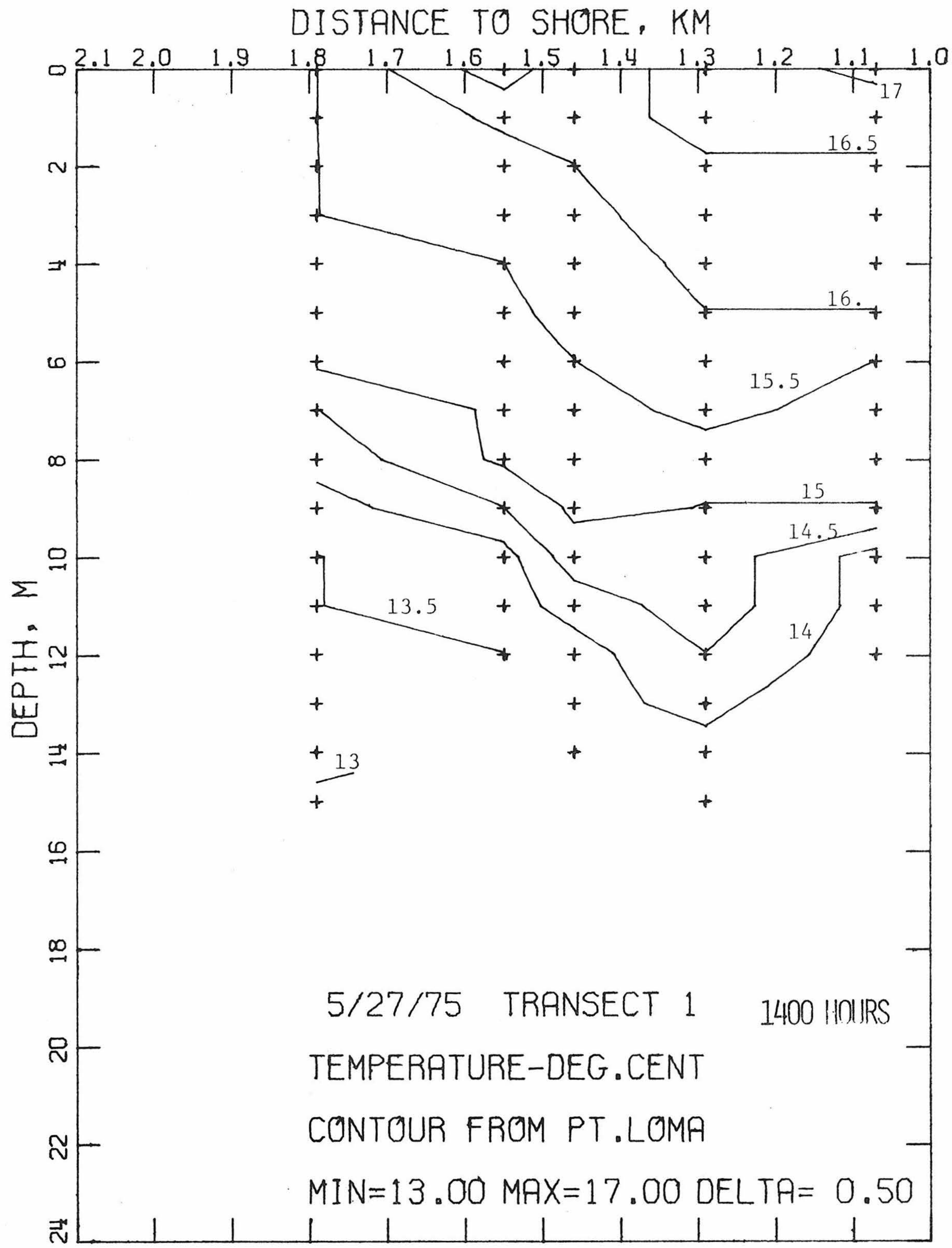
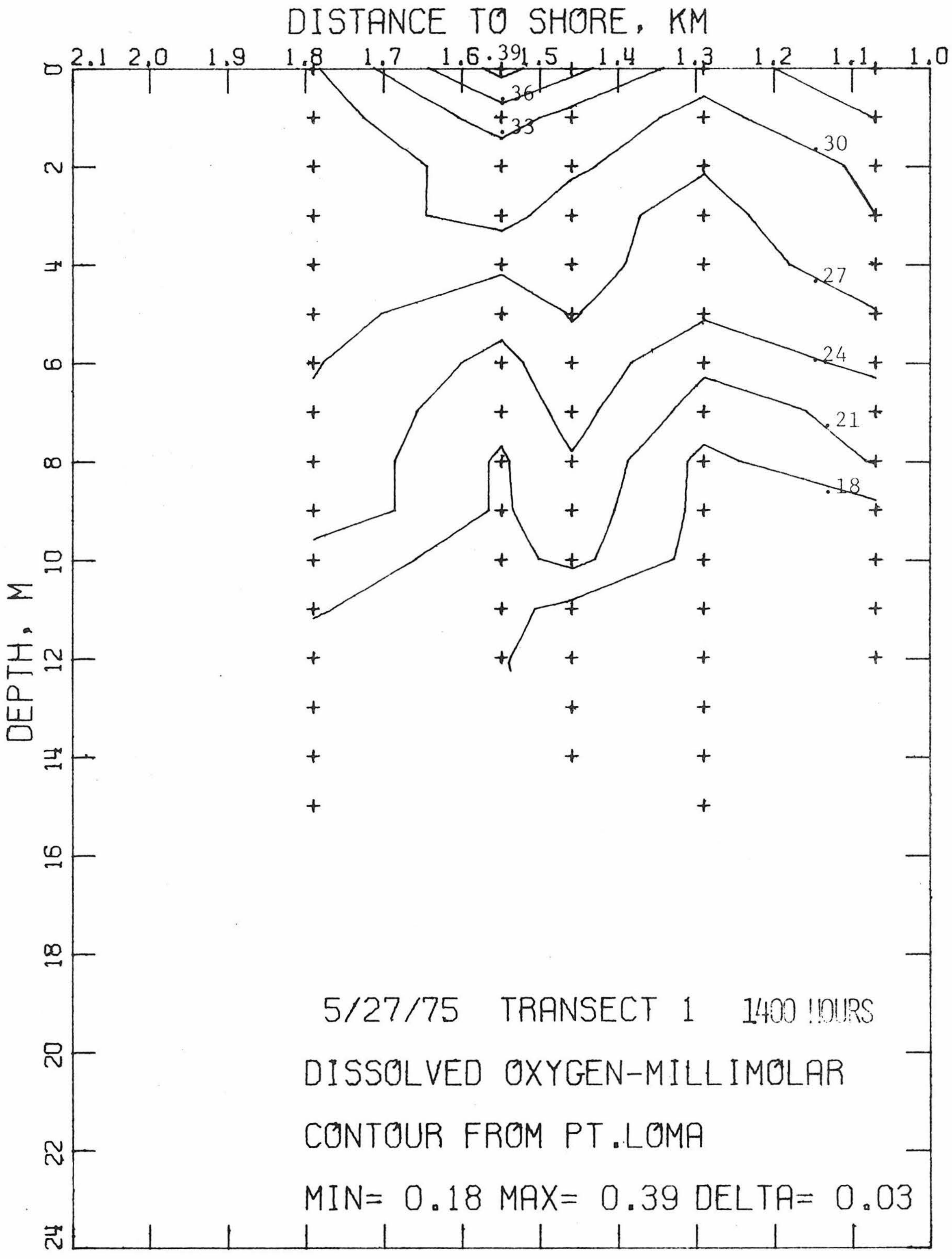


Figure 8. Dissolved oxygen concentrations for Transect 1 (1400 PST), May 27, 1975.



and photosynthetic tissue in the bed. As kelp photosynthesizes, the concentration of oxygen near the surface increases. It is possible that the oxygen could supersaturate here and come out of solution.

Phosphate contours (Figure 9) for the diurnal sampling show significant gradients in nutrient concentration even in the relatively shallow bottom depths of the kelp bed, less than 15 meters in depth. Phosphate concentration at the surface was less than 0.3 μM but was 0.8 μM at the bottom. Despite the strong gradient, amounts of phosphate at the surface were still significant. Phosphate was also always present in my other samplings.

The dominant form of inorganic nitrogen in the bed was nitrate. Nitrate concentrations for the diurnal sampling also showed a very strong vertical gradient (Figure 10- less than 0.5 μM at the surface and more than 4.5 μM at the bottom). Nitrate concentrations were very low at the surface. Nitrate was relatively more depleted than phosphate considering that approximately eight times as much nitrogen as phosphate is required by organisms. It was not uncommon for the surface concentration of the nitrate to be less than 0.1 μM during the four years of this study.

Figure 9. Phosphate concentrations, Transect 1 (1400 PST), May 27, 1975.

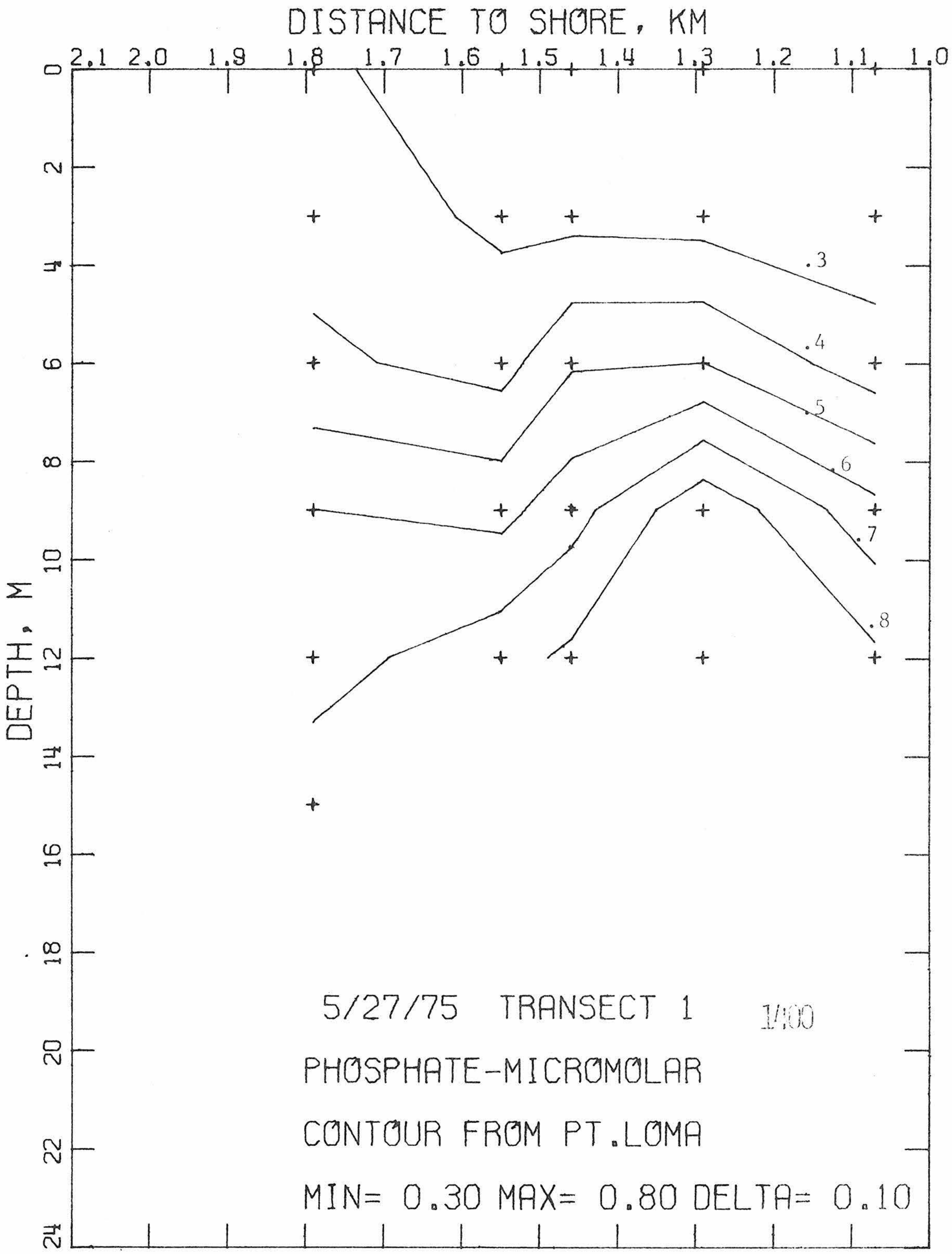
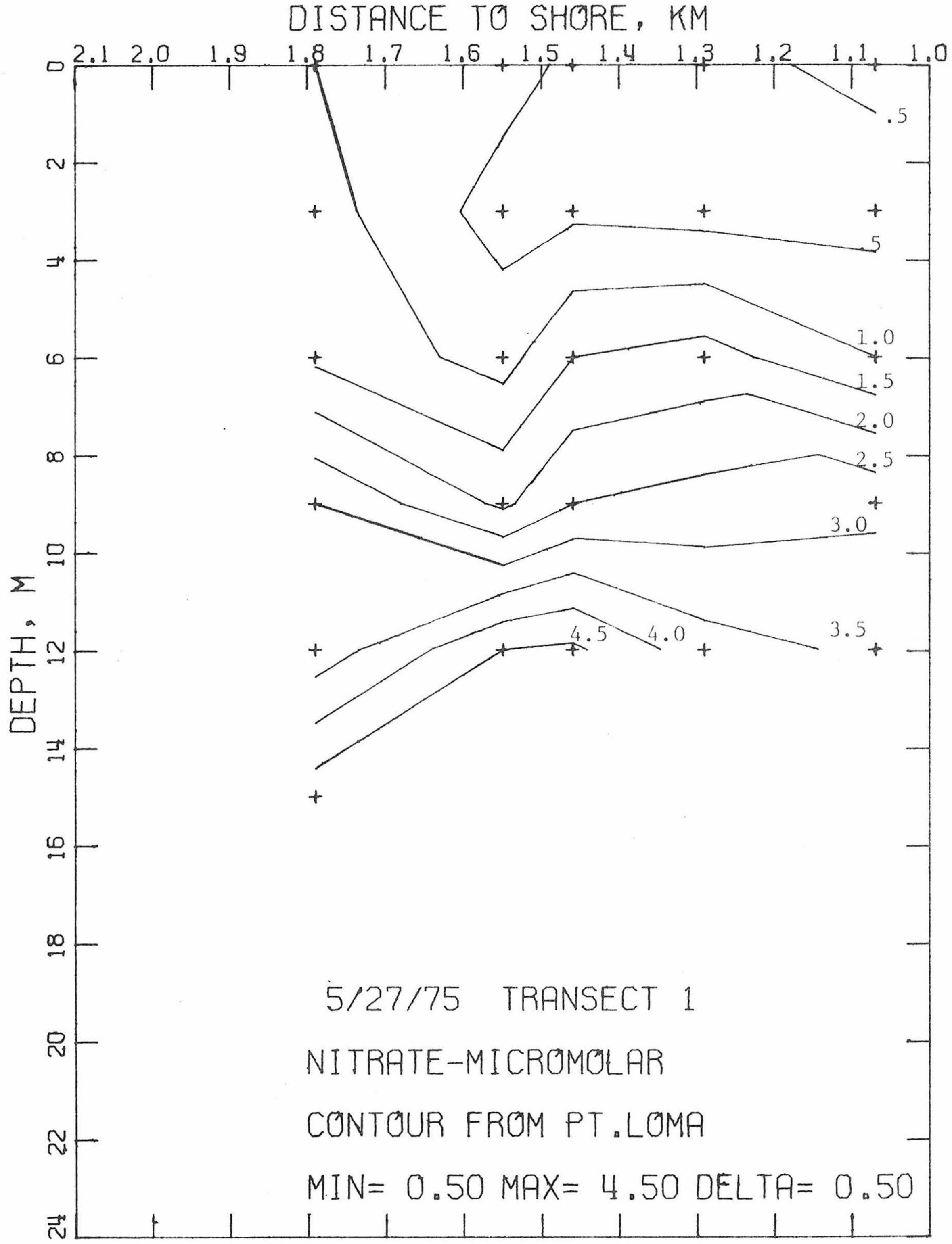


Figure 10. Nitrate concentrations, Transect 1 (1400 PST), May 27, 1975.



The other form of inorganic nitrogen, ammonia, also displayed vertical concentration gradients. Ammonia concentrations were never as high as those of nitrate (Figure 11). Ammonia sometimes was a significant fraction of the nitrogen in the upper meters of the kelp bed, where the nitrate concentrations often went to zero. Measured ammonia concentrations rarely surpassed 1. μM in the bottom waters.

Silicate concentrations displayed vertical gradients similar to the phosphate, nitrate, and ammonia (Figure 12). Silicate should not be taken up to any significant degree by Macrocystis pyrifera. It is thus a convenient tracer to distinguish between changes of nutrient patterns caused by open ocean phytoplankton and nearshore benthic plants.

There did not seem to be marked effects by the kelp bed on the measured parameters except for dissolved oxygen concentrations. It was therefore of interest to determine effects of the large kelp biomass during the night and evaluate whether oxygen content of the water in the bed would fall significantly. Temperature and dissolved oxygen contours at the end of the night that started May 27, 1975 show the effect of internal waves (Figures 13 and 14). The water in the bed during the previous day should all have left by the time of this transect. Therefore, it is

Figure 11. Ammonia concentrations, Transect 1 (1400 PST), May 27, 1975.

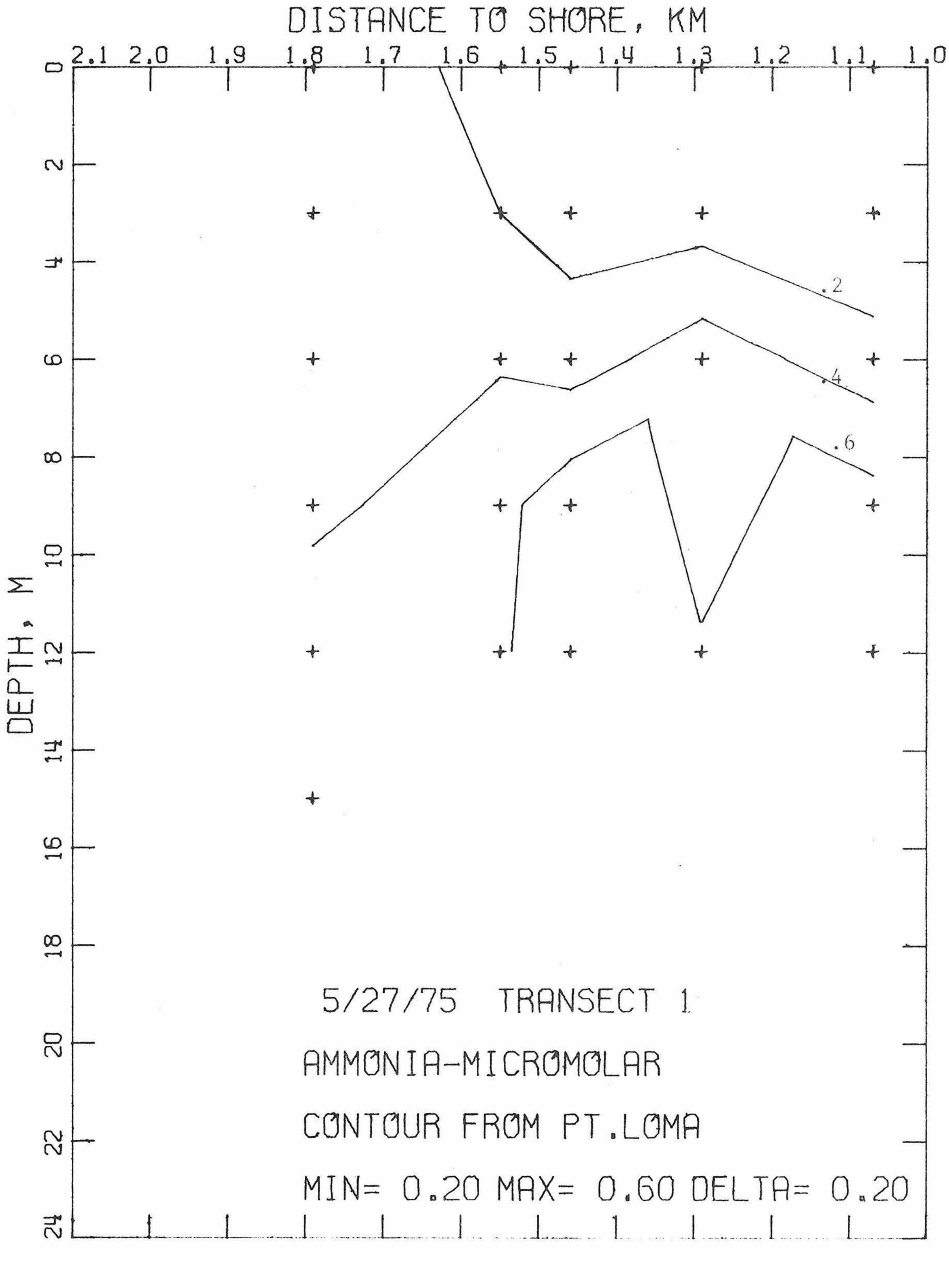


Figure 12. Silicate concentrations, Transect 1 (1400 PST), May 27, 1975.

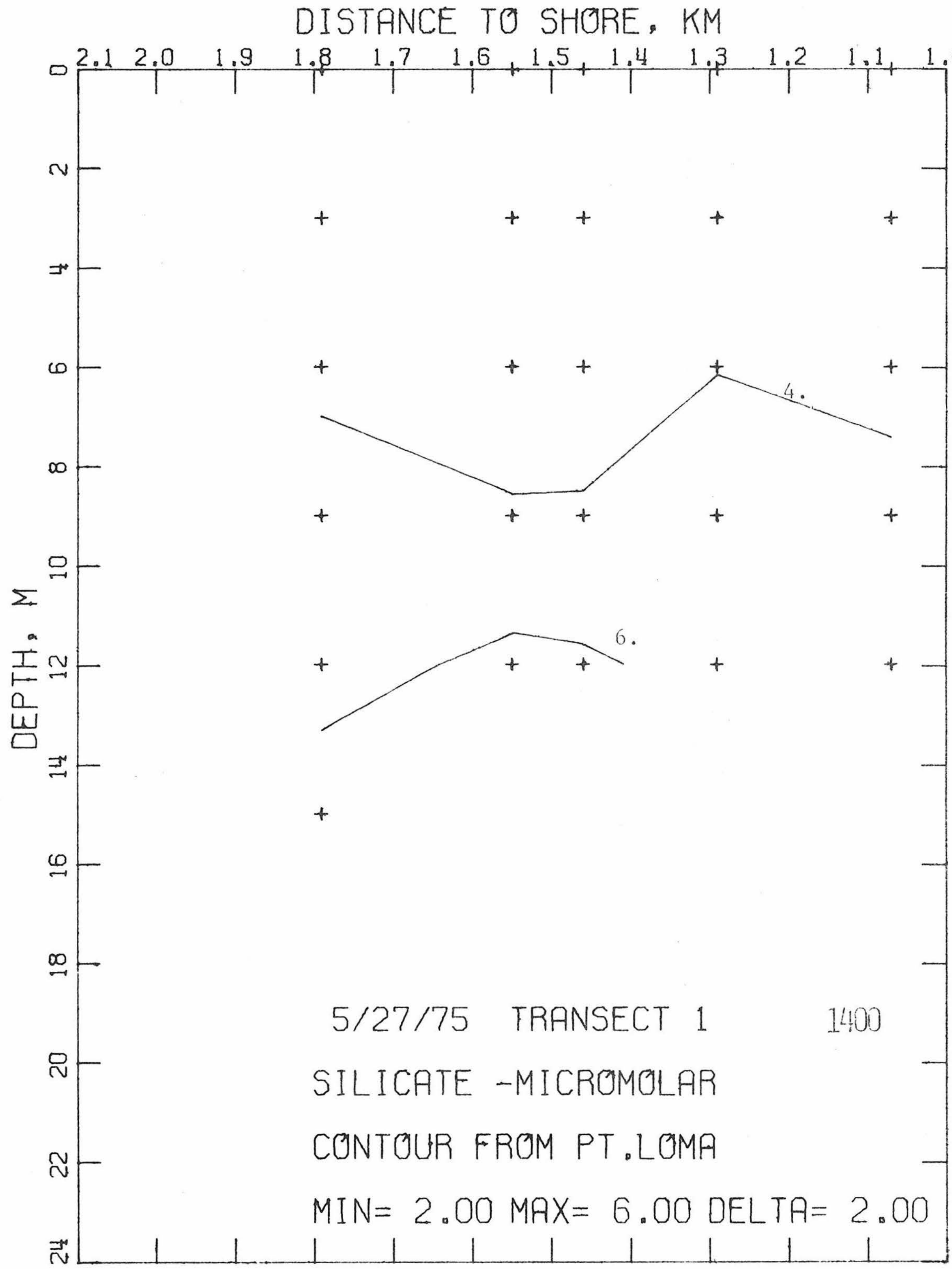


Figure 13. Temperatures for Transect 6 (0500 PST), May 27, 1975.

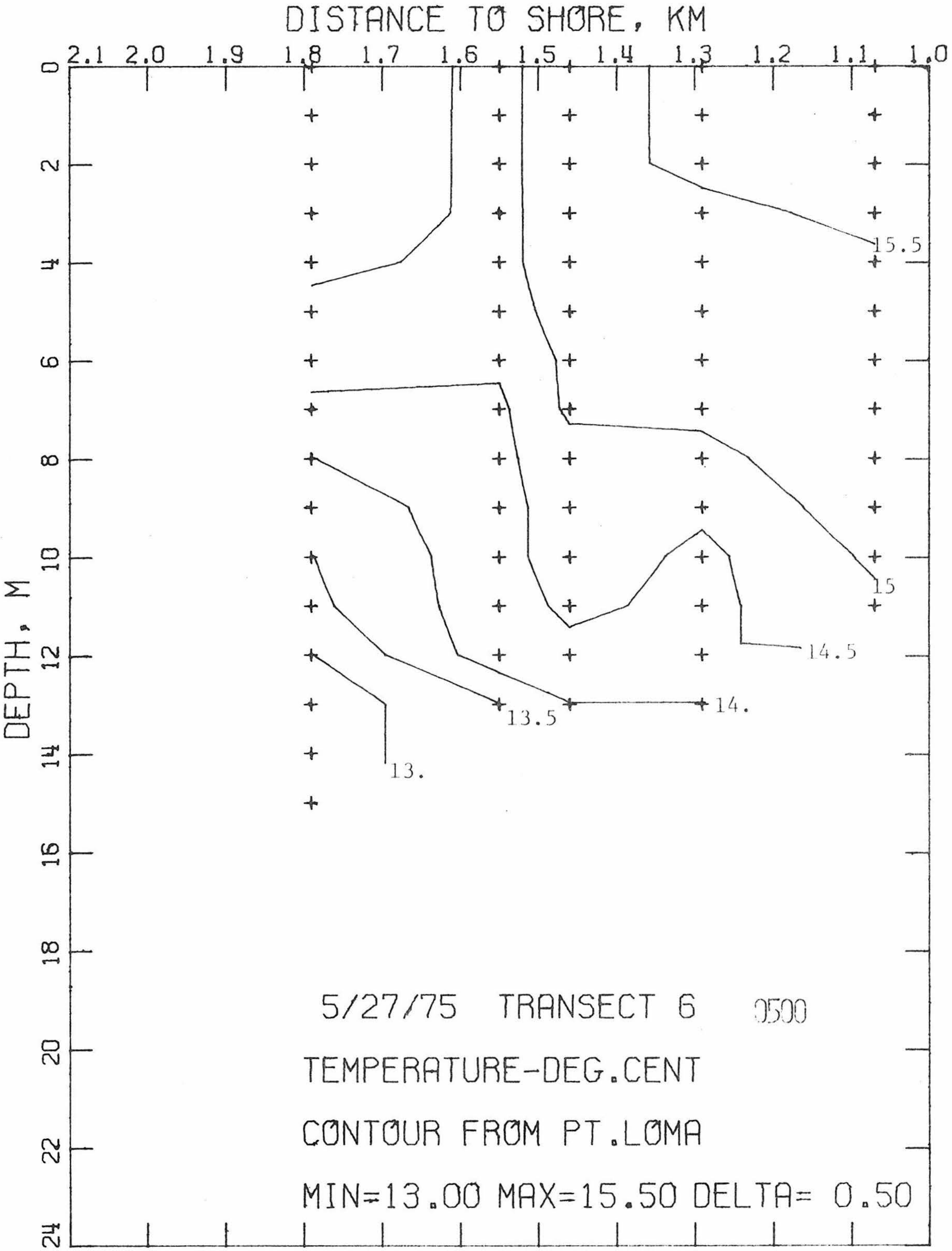
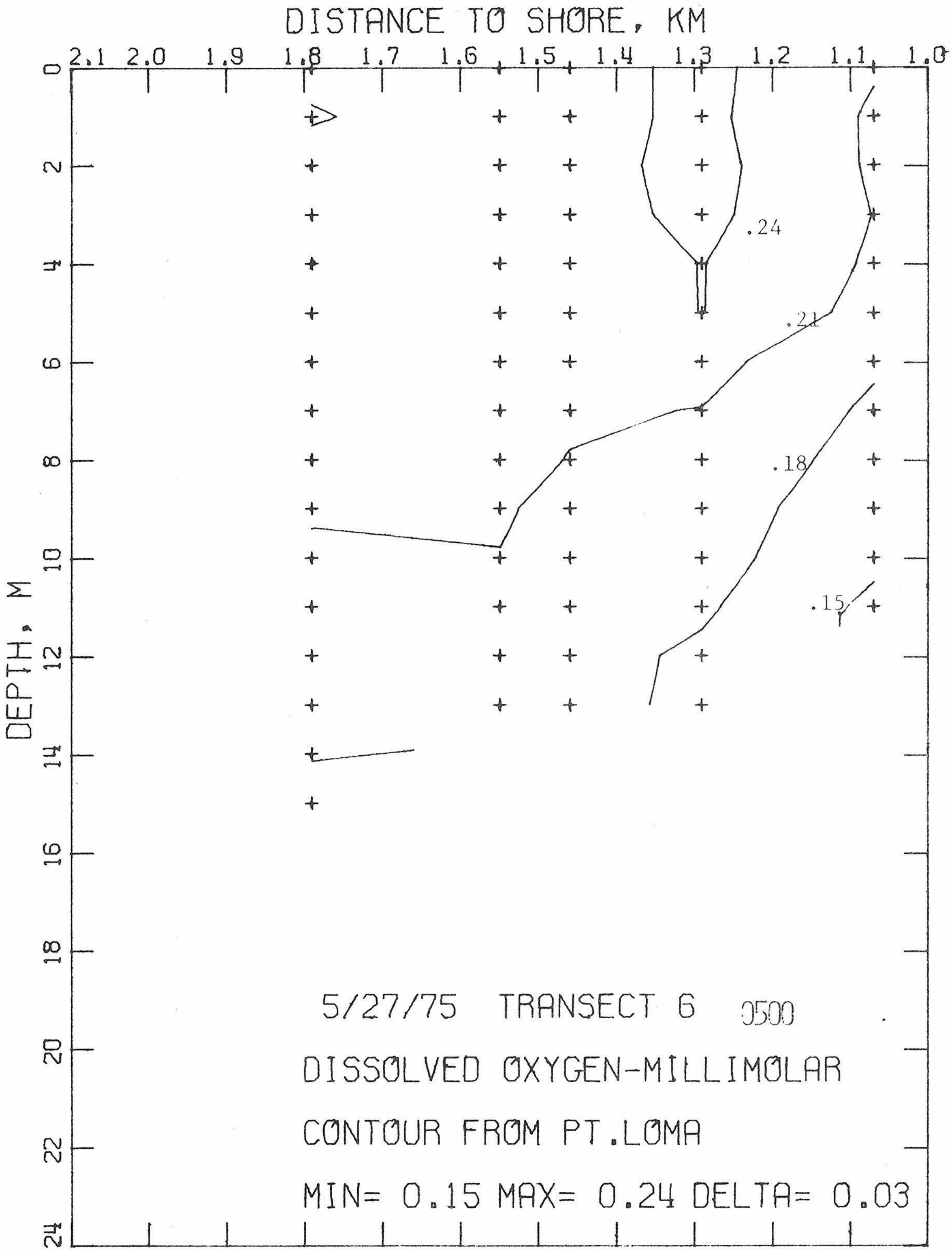


Figure 14. Dissolved oxygen concentrations, Transect 6 (0500 PST), May 27, 1975.



necessary to compare the oxygen concentrations in the bed to those outside to determine the extent of oxygen depletion by kelp respiration. There was no appreciable depression of oxygen levels.

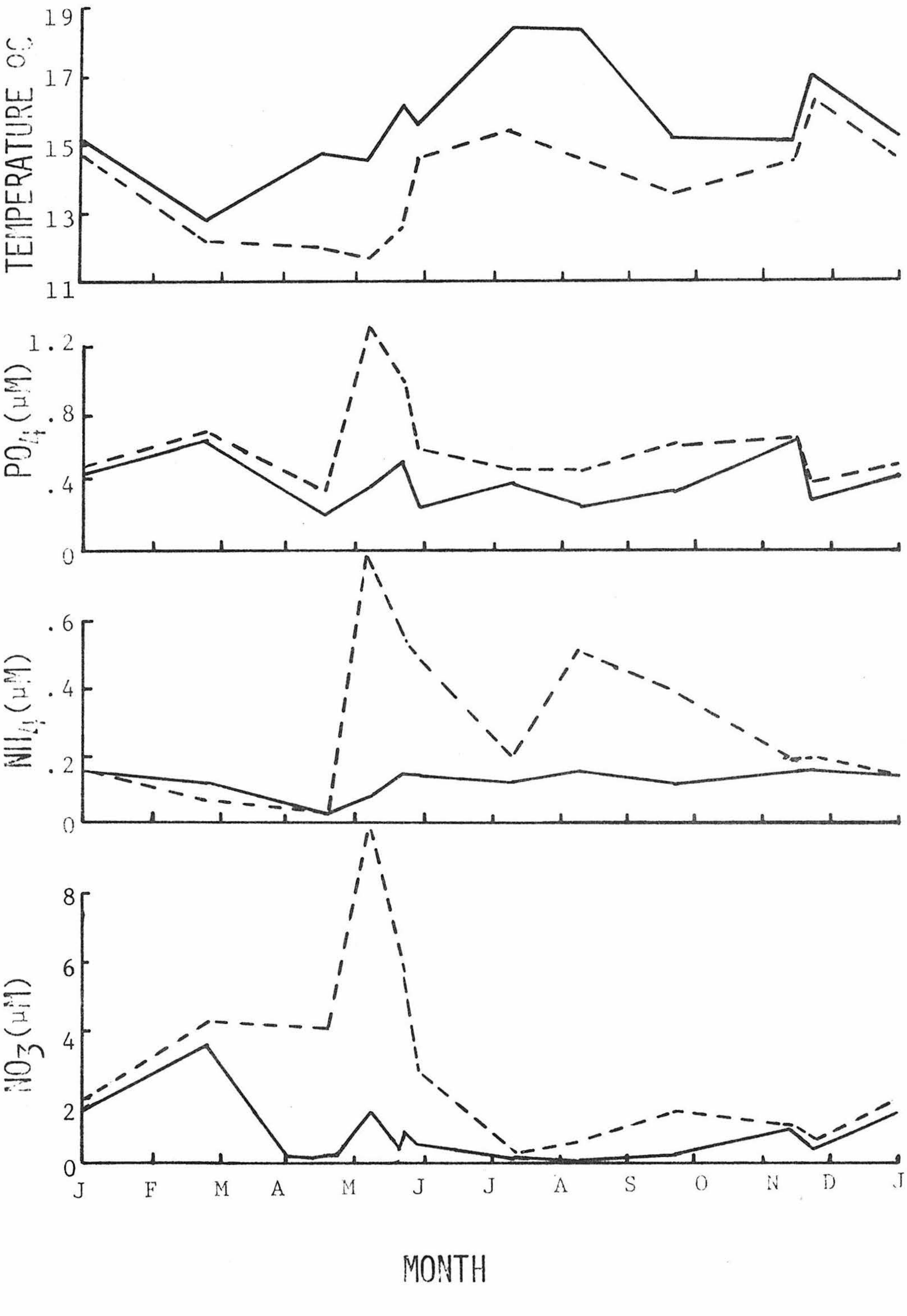
Seasonal nutrient patterns

Nutrient distributions in the kelp bed were typically stratified (low concentration at the surface and high on the bottom). This pattern did vary seasonally. The annual cycle is shown by comparing the median value of the nutrient samples taken at 0 and 3 meters depth to the median value of the samples taken at 6 and 9 meters for all of the data sets (Figure 15).

The temperature at the surface and below shows the pattern that Cairns and Nelson (1970) found: there is stratification between March and November. Amount of stratification varied with the season but is not clearly apparent from this display of the data.

Because nitrate is especially important as a limiting nutrient, its annual cycle is particularly significant to the kelp. There are several conclusions. Surface concentration of nitrate was low for most of the year. Median concentrations in the upper 3 meters of the water

Figure 15. Annual cycle of nutrient concentrations. Solid lines represent median concentrations of samples gathered from 0 and 3 meters depth. Striped lines represent median concentrations of samples gathered from 6 and 9 meters depth.



column were less than 1 μM from April to November, with the exception of an upwelling event on May 9, 1975. During winter, the surface nitrate concentrations did rise, but there were other factors possibly hindering the growth of algae during that period (December, January and February are times of winter storms, short days, and the sun is low on the horizon).

Nitrate concentrations at 6 meters and below were higher than at the surface, although for much of the year the concentrations in the water at 6 and 12 meters were less than 2 μM. The major exceptions were the months of March, April and May (the upwelling months). During these months nitrate concentrations were low at the surface and high below. That is, during the time of maximum kelp growth, nitrate concentrations were low at the surface where most of the photosynthesis is presumed to occur. The high concentrations of this vital nutrient lay below 6 meters. This suggests that either nitrate was taken up by tissue lower in the water column and translocated to the surface or that most of the photosynthesizing takes place lower in the water column.

The other nutrients also showed higher concentrations in the lower parts of the kelp bed. Ammonia, however, never achieved the high concentrations displayed by nitrate. The highest median concentration of ammonia measured was 0.8 µM on a day when the median nitrate concentration was 10. µM. Even then ammonia was far less abundant than nitrate. There was little evidence of large inputs of ammonia from the San Diego sewer outfall, because there were no anomolously high ammonia concentrations.

During the instances that I sampled, the median concentration of phosphate never dropped below 0.2 µM. During the upwelling months phosphate concentration did rise in the deeper parts of the bed.

Thus there was a seasonal distributional pattern common to all the nutrients. Concentrations were always higher in non-winter months at depths of 6 meters and deeper, although the difference was not always very large between surface and deeper waters. The sharpest vertical changes occurred during the period which has historically been the time of greatest kelp growth and of strongest upwelling. During much of the rest of the year, concentration differences between the surface and the deeper waters were not large. The nutrient that seemed to be in shortest supply was nitrogen. During winter the vertical gradients were small and the surface concentrations of nitrogen and phosphorus were higher than in the summer.

Longshore patterns

To determine whether differences in nutrient distribution occurred along the coast and whether patterns at the NEL tower were the same as those at Point Loma, I ran a transect parallel to shore along the 20 meter depth contour on May 6, 1975.

The temperature contours (Figure 16) showed no stratification of the water at the tip of Point Loma where the water was cold from the surface to the bottom. Stratification appeared between 3.5 and 4.5 kilometers north of the tip.

At the NEL tower, 11.8 kilometers north of the tip, the water was markedly stratified with a vertical temperature gradient as large as 1 degree-C/m. The nutrient distibution was affected by this upwelling. High surface nitrate concentrations occurred at the tip of Point Loma (Figure 17) while at the same time there were low surface and high bottom concentrations of nitrate around La Jolla.

Localized occurrence of upwelling was observed previously by Armstrong, Stearns and Strickland (1967) while studying phytoplankton growth off Baja California. They found upwelling at a cape, in accordance with the observation that upwelling tends to take place near points

Figure 16. Temperature distribution longshore during upwelling, May 6, 1975. Samples taken from Point Loma to LaJolla.

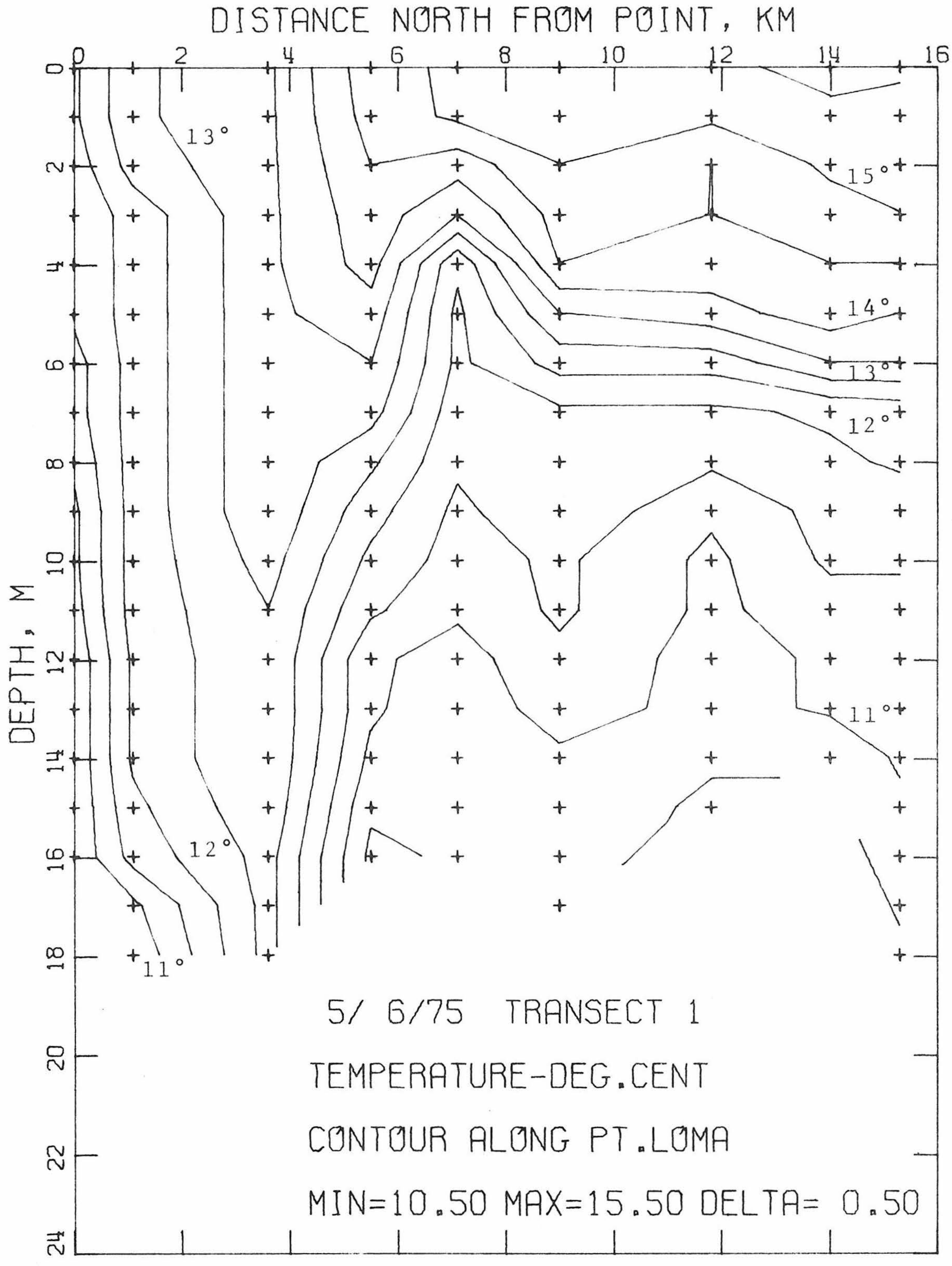
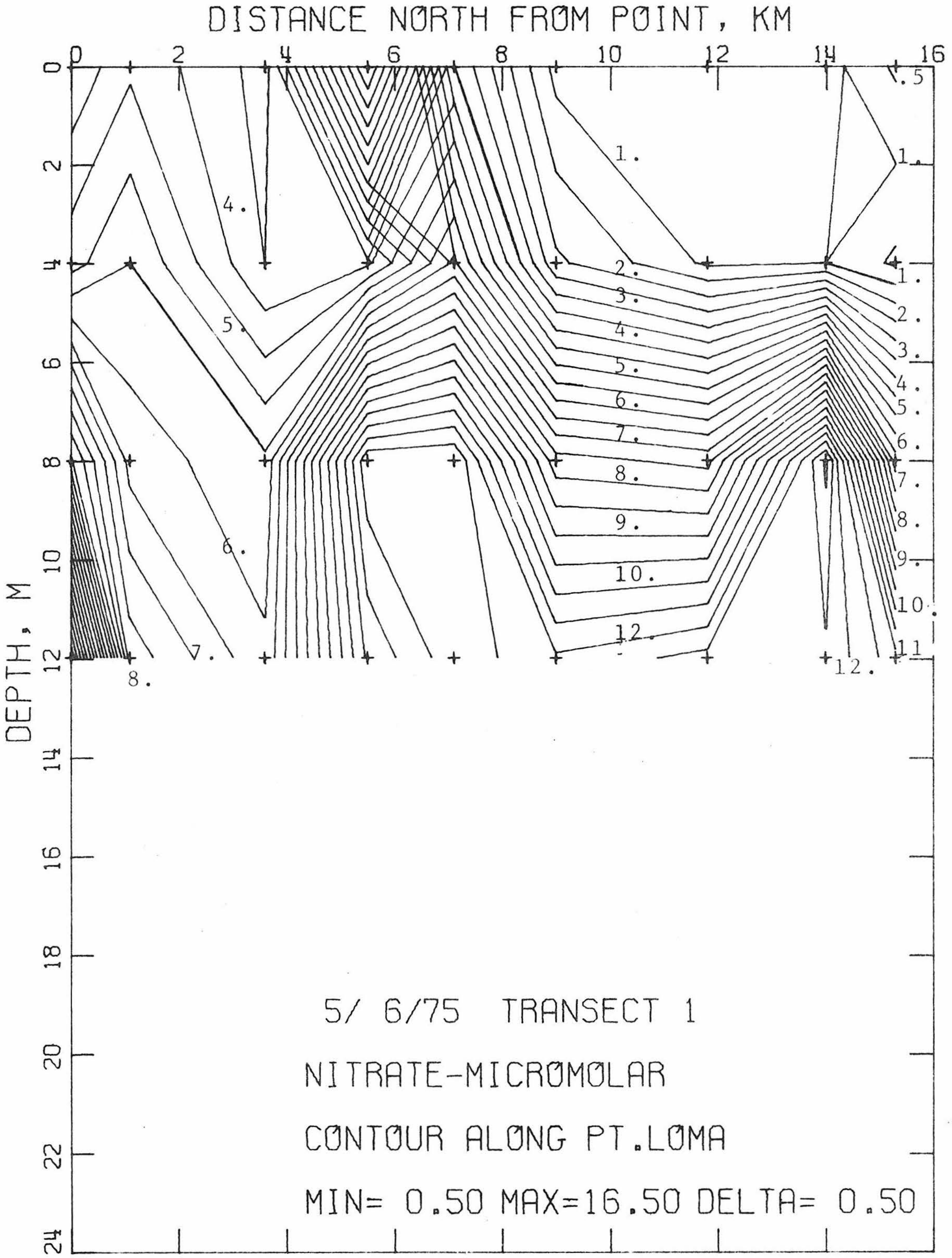


Figure 17. Nitrate distribution longshore during upwelling, May 6, 1975.

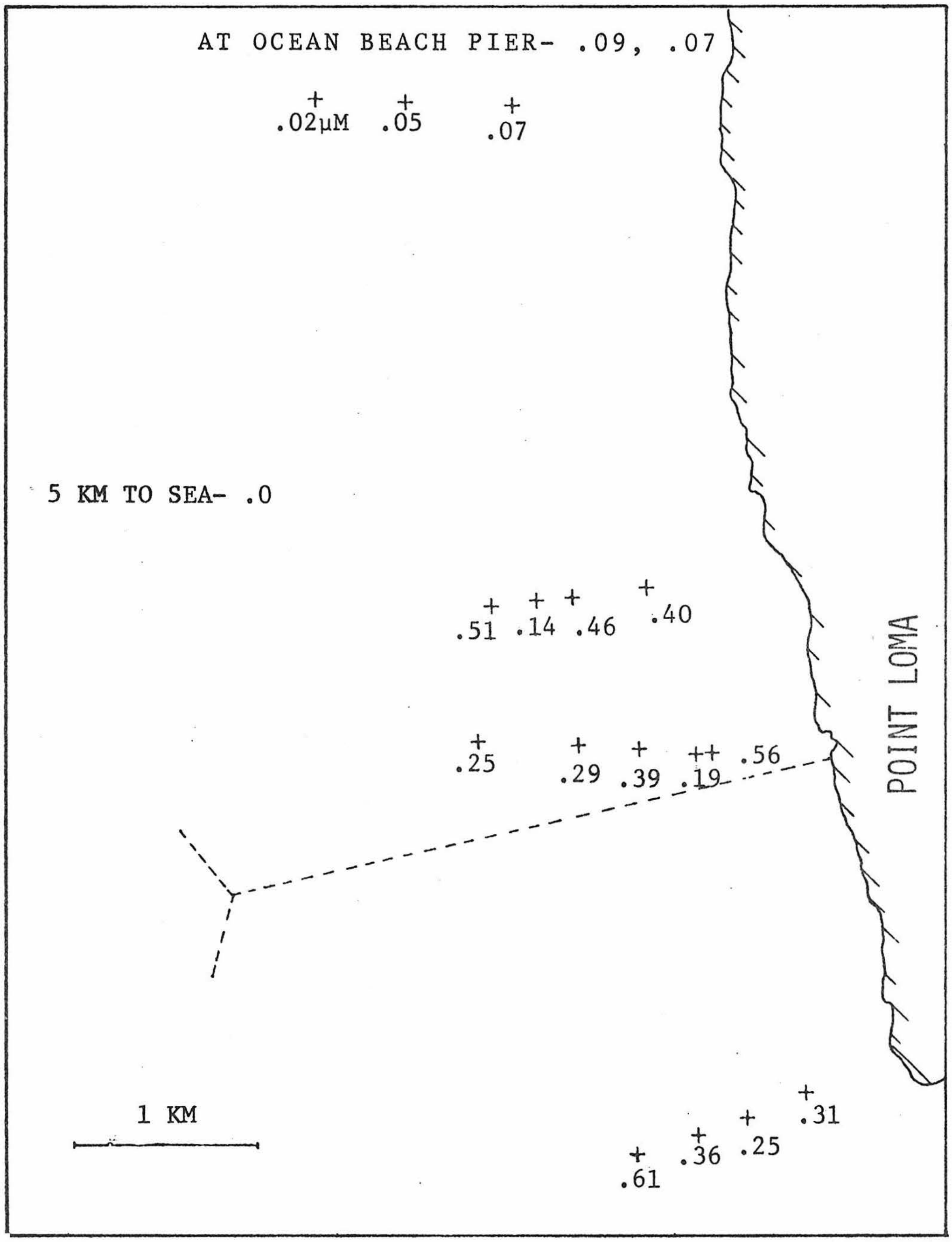


and capes.

The role of upwelling in establishing high nutrient concentrations in the the waters north of Point Loma is an important but unanswered question. My data commonly showed very high concentrations of nutrients below the thermocline. If upwelling at Point Loma caused enrichment of bottom waters at La Jolla, then there may be areas farther away that were not so enriched. There would thus be several different types of spring nutrient regimes along the California coast. These areas should be different ecologically.

On May 23, 1972 there were also higher surface nutrient concentrations to the south then to the north of Point Loma. Surface nitrate concentrations within three kilometers of the tip were almost all between 0.6 and 0.2 μM (Figure 18). Nitrate concentrations at all northern stations (5 kilometers from shore, in the kelp bed 5 kilometers north of the tip of Point Loma and at the Ocean Beach Pier) were all less than 0.1 μM. While these were not great differences on an absolute scale, the nitrate concentrations to the south were frequently more than five times as great as those farther up the coast.

Figure 18. Surface concentrations of nitrate, May 23, 1972.



Data from April 20, 1972 indicated that nutrients near the tip of Point Loma are not always higher (Figure 19). On that date there were no significant longshore differences between the different kelp bed areas sampled along the Point Loma peninsula.

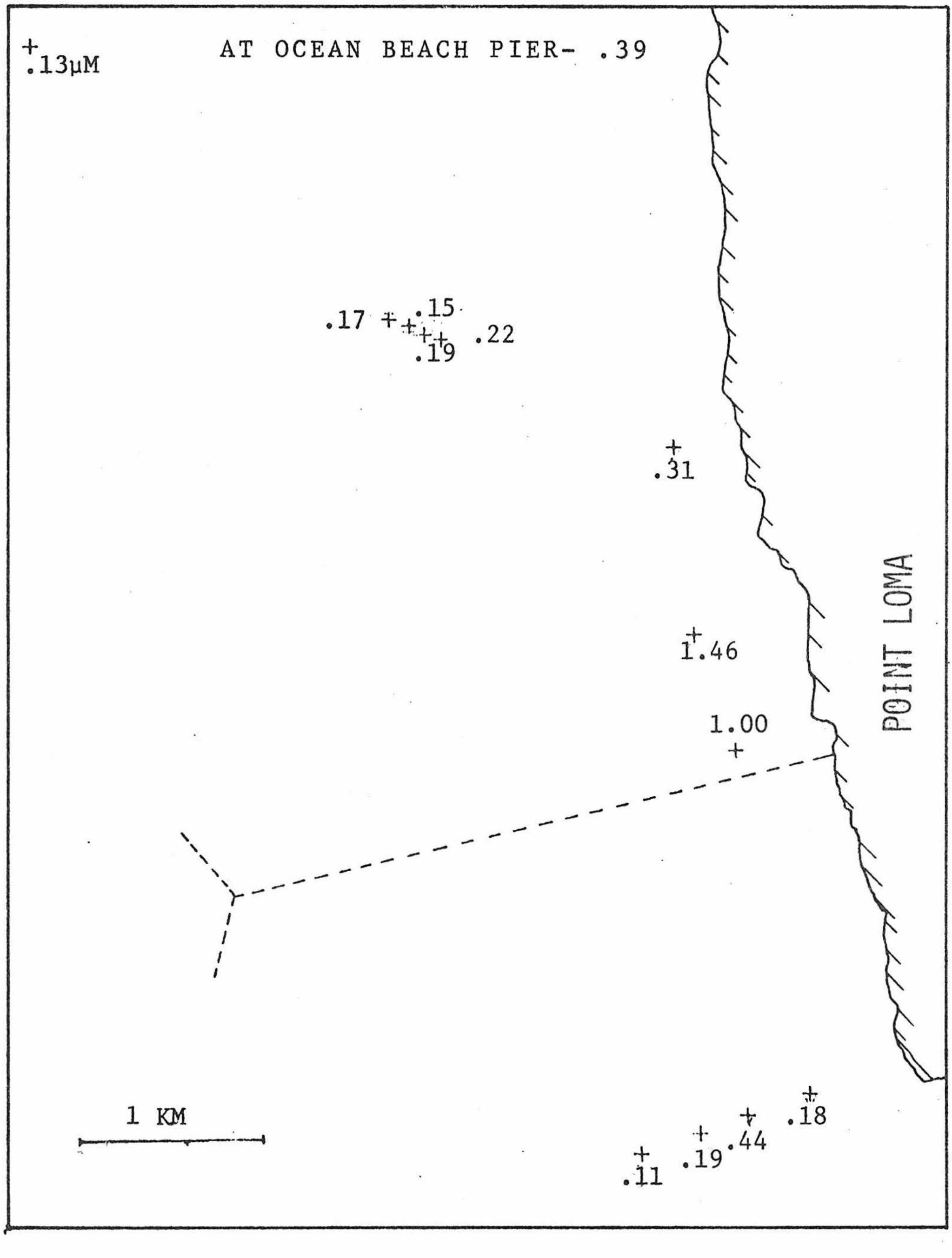
Onshore variations

Variation in nutrient concentrations might occur perpendicular to the shoreline. Changes could be caused during mixing by breaking waves in the shallow nearshore. Breaking waves would mix water throughout the water column from shoreline to bottom depths of 5 meters (Inman and Brush, 1973). If high nutrient bottom waters extend into appropriate shallow areas mixing would form a water with characteristics intermediate between surface and bottom. The result would be higher nutrient concentrations in the surface waters at shallow depths.

Nutrients regenerated in the sediments might appear in the shallow areas. This process would yield increased ammonia rather than nitrate.

A third possibility would be longshore flow in shallow water from a high nutrient water located around the tip of Point Loma.

Figure 19. Surface concentrations of nitrate, April 20, 1972.



The highest surface nitrate concentrations taken on April 20, 1972, 1.46 and 1.0 μM, were among those samples taken nearest to shore (Figure 19). The ammonia concentrations at those two high-valued stations were both less than 0.1 μM. Thus they were not caused by regeneration in the sediments but were possibly the result of wave-induced mixing or shallow water transport.

Further relevant data come from samples taken on July 19, 1972, when the transect extended from 0.2 to 2.8 kilometers offshore (Figures 20, 21,22,23 and 24). The shallowest station was in water approximately 6 meters deep in an area of intense wave surge. The nutrient concentrations at the innermost station at the surface and at the bottom were: for nitrate, 4.2 and 5.3 μM; for ammonia, 0.4 and 0.4 μM; and for phosphate, 0.48 and 0.42 μM. This contrasted sharply with the other stations, which had a maximum concentration of nitrate at the surface of 0.13 μM. There were, however, high nitrate concentrations below 10 meters, with the maximum measured being 9.5 μM.

If there were vertical mixing contributing to replenishment of surface nitrate at the shallow stations, it would have had to occur sporadically. High nutrient water in the kelp bed during this sampling was at a depth of

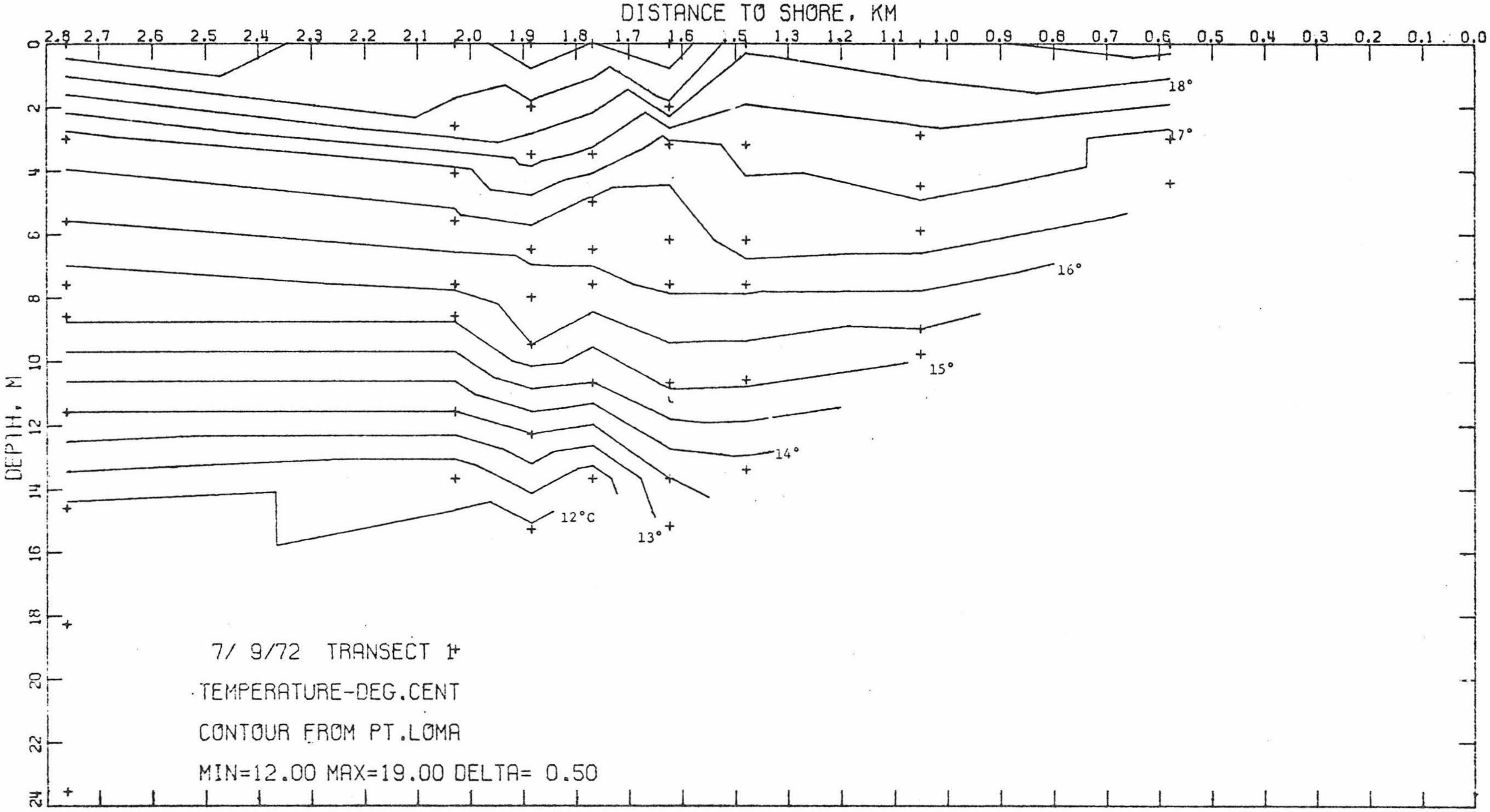


Figure 20. Temperatures for Transect 1, July 9, 1972.

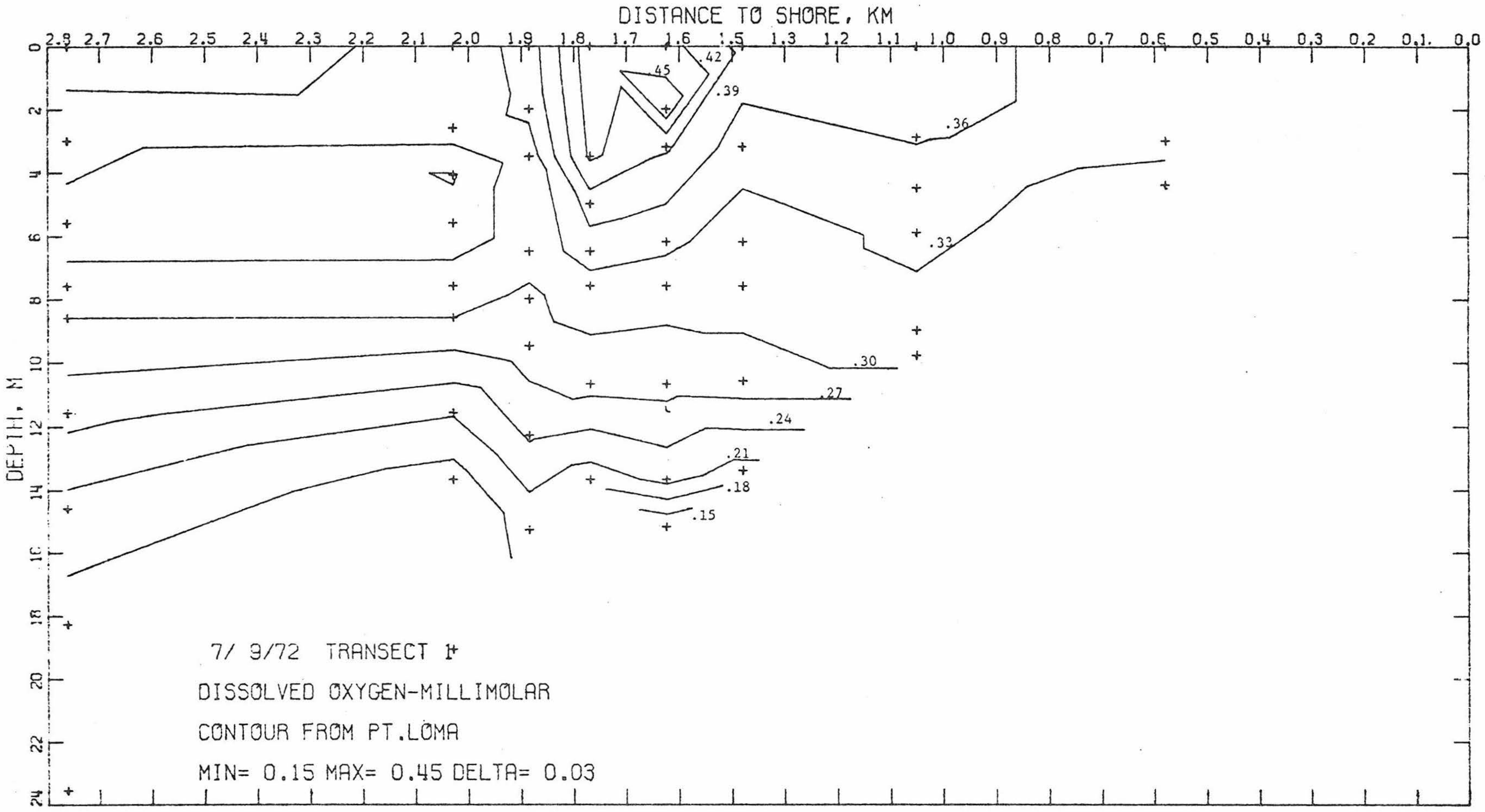


Figure 21. Oxygen concentrations for Transect 1, July 9, 1972.

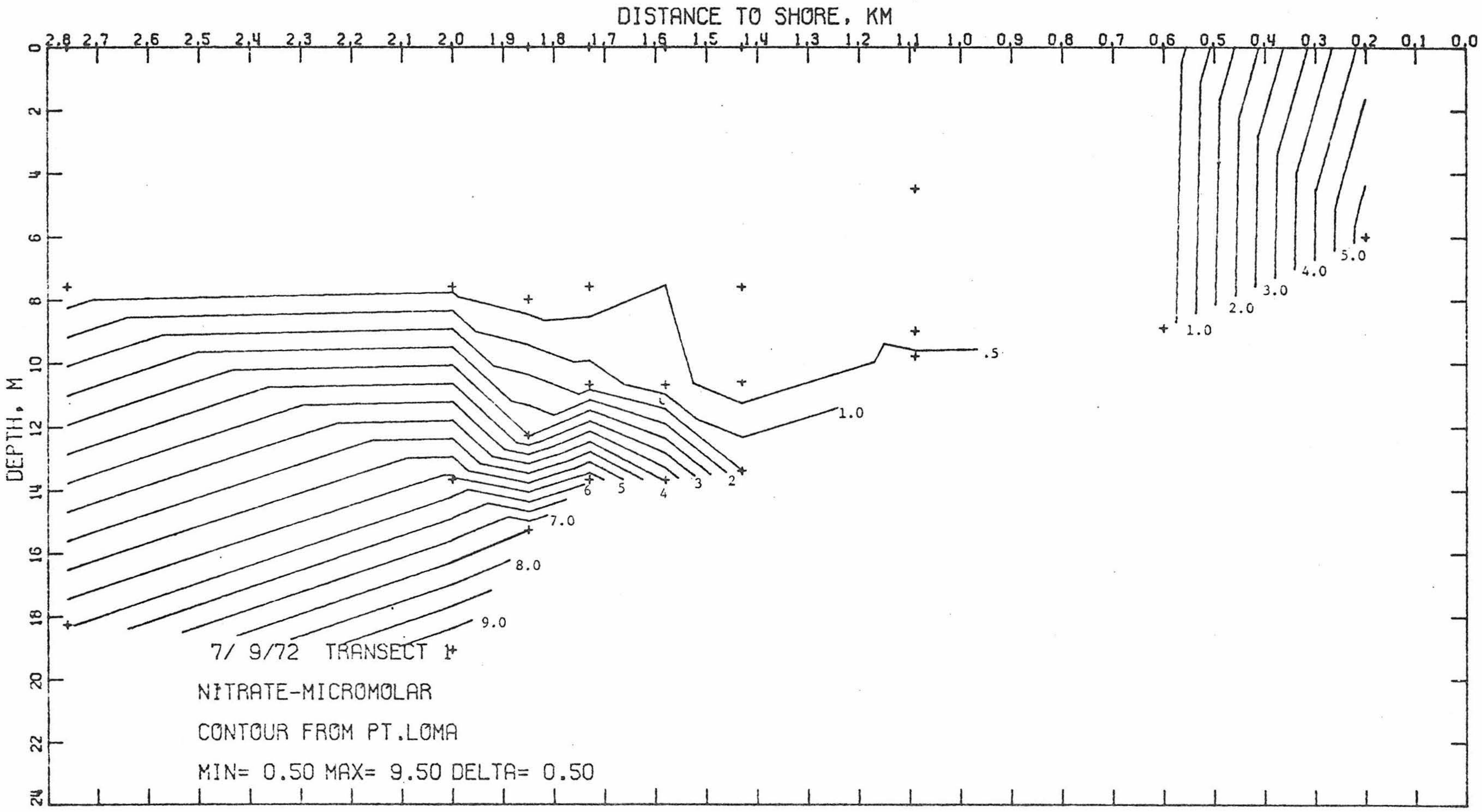


Figure 22. Nitrate concentrations for Transect 1, July 9, 1972.

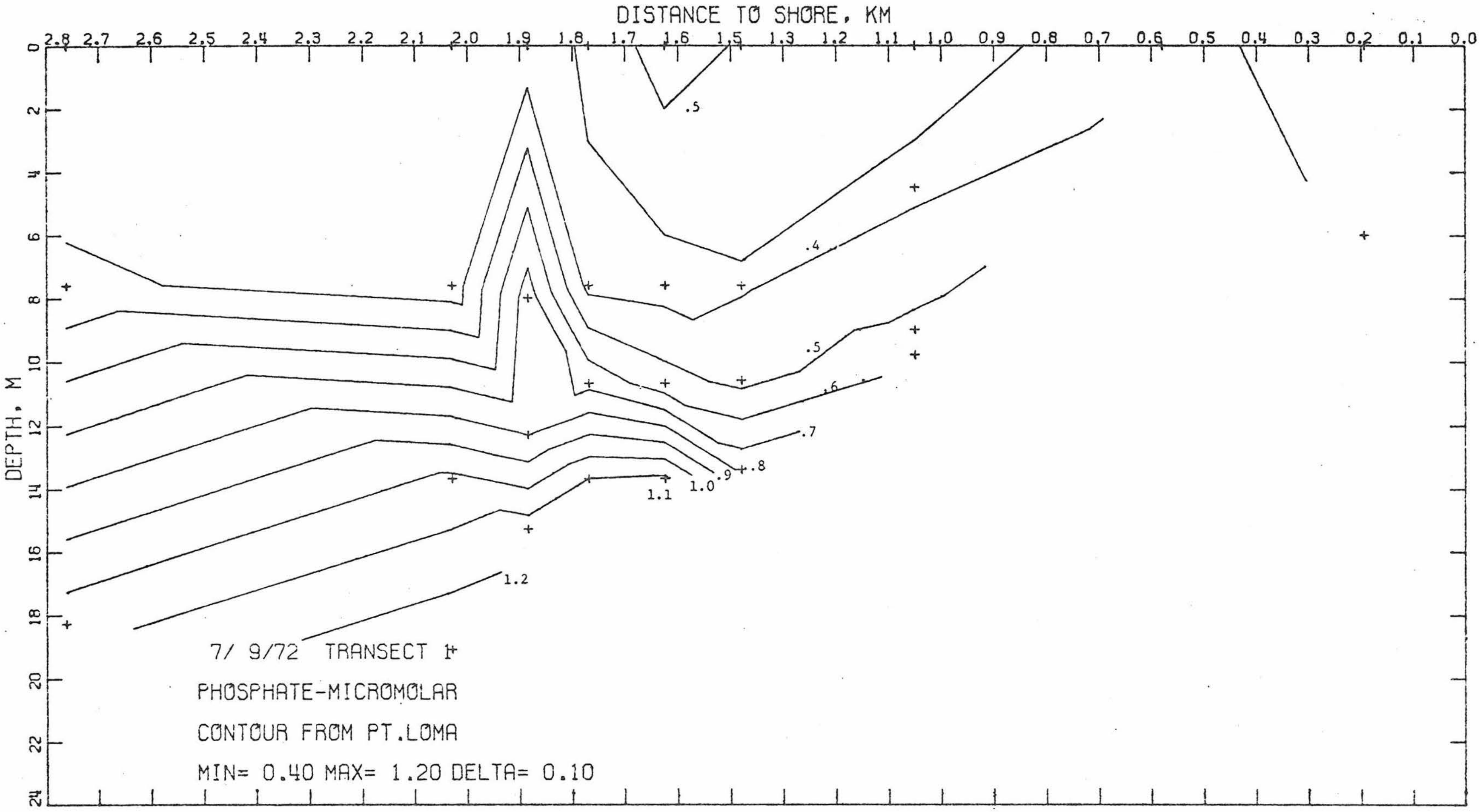


Figure 23. Phosphate concentrations for Transect 1, July 9, 1972.

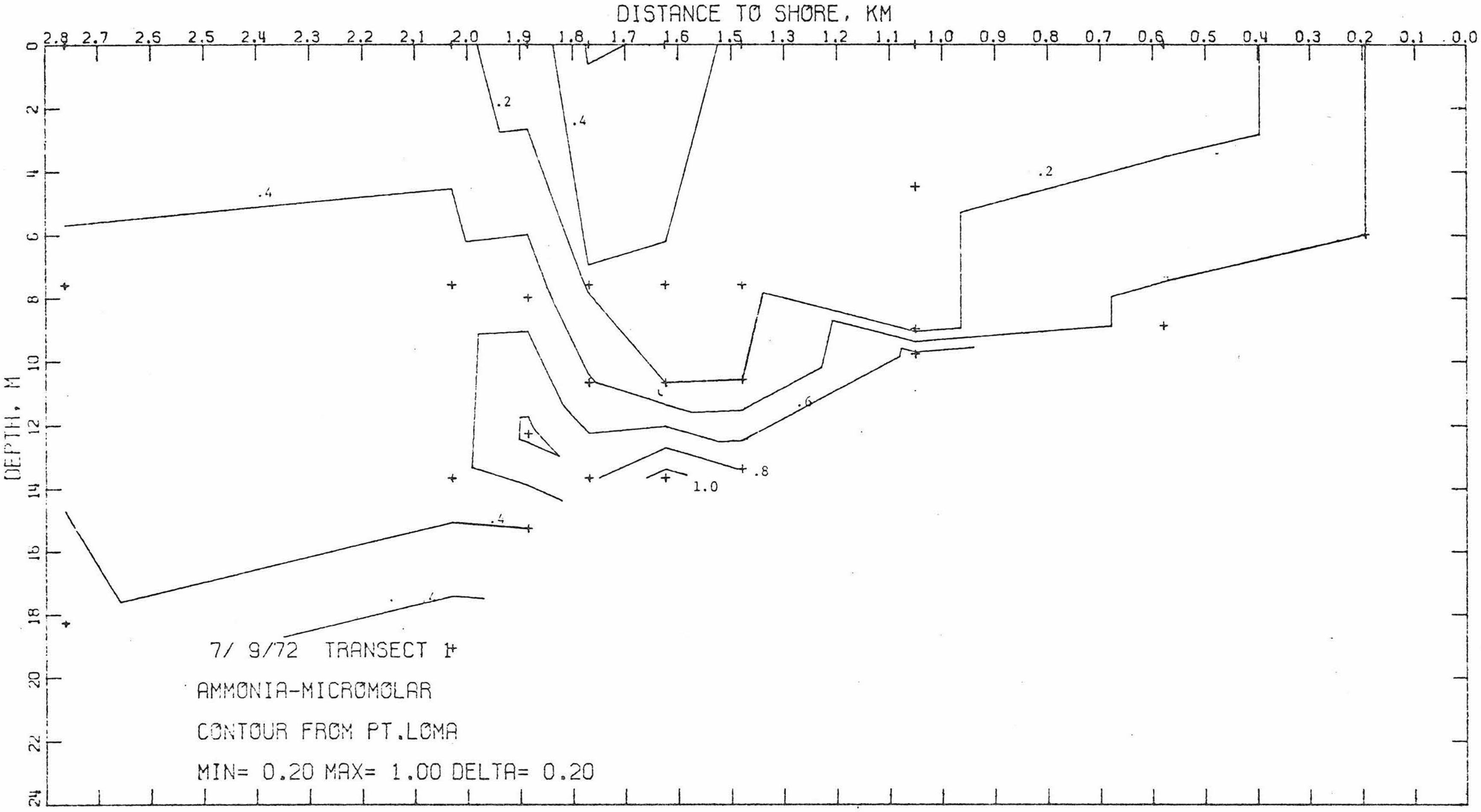


Figure 24. Ammonia concentrations for Transect 1, July 9, 1972.

approximately 10 meters. If the high nutrient and low nutrient waters mix they must both be shallow enough to be in the mixing zone. At the time of the sampling they were not. The ever present internal waves, however, could have raised the chemocline so that the two waters could have mixed, and the resulting mixture remained in the shallow area until it was sampled.

Discussion

The distribution of nutrients in the nearshore is similar to that of the deeper oceanic areas. The thermocline may be shallower in the nearshore but there are still large vertical gradients in nutrient concentrations. The nearshore exchanges water with the oceanic zone faster than the kelp can decrease or sediments increase nutrient concentrations. Thus the nearshore nutrient regime is closely linked with the oceanic. Differences involve the position of the nearshore in the coastal upwelling zone.

Along the coast there are differences in nutrient regimes. These differences involve localized upwelling effects.

The importance of upwelling-related effects in the nearshore implies that the large scale wind patterns are very important to the nearshore.

The very nearshore (depth less than 5 meters) seems to be different than the nearshore. My data are not extensive enough to define the extent or mechanism of the higher nutrient concentrations in shallow water. Possible mechanisms involve wave mixing or longshore transport.

CHAPTER 4

ECOLOGICAL EFFECTS

Measurements in kelp bed surface waters of those macronutrients known to be essential for plant growth have typically yielded very low concentrations of inorganic nitrogen, as well as low concentrations of orthophosphate. These same surface waters are the site of most of the photosynthetic tissue of the kelp plants. Does the low concentration of nutrients at the surface limit organic production by *Macrocystis* or can the alga overcome the lack of surface nutrients by translocating nutrients from deeper waters where the nutrients are more abundant?

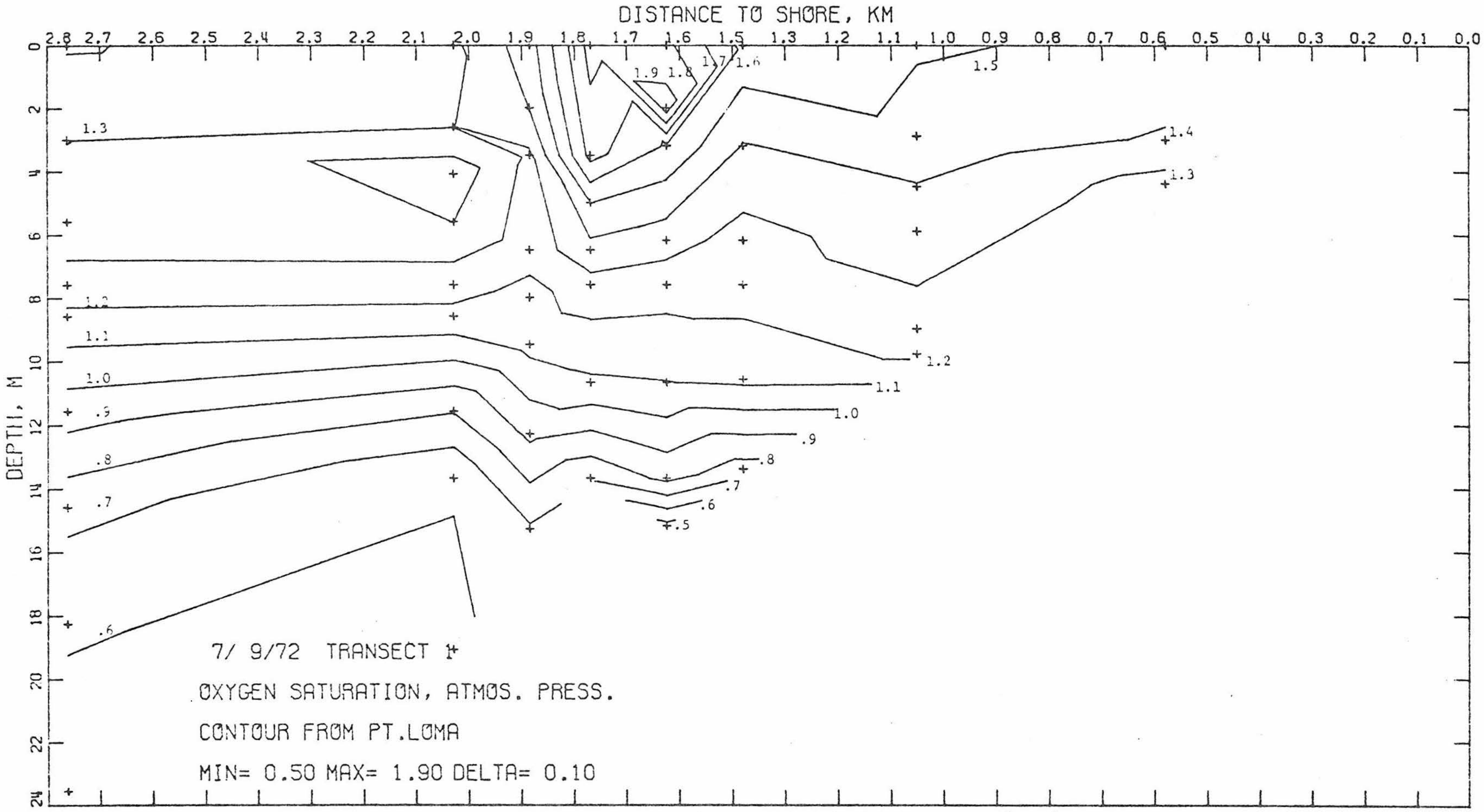
Oxygen-carbonate interactions

Thus far, I have tacitly assumed that the changes in the concentrations of O_2 and inorganic carbon in the seawater occur in a 1:1 ratio. This assumption makes it convenient to compare the oxygen and nutrient concentrations of the water with the published data on the elemental composition of kelp. There are, however, several possible processes that will change either the oxygen or the carbon concentrations that do not involve the metabolic process. If these are important, changes in the dissolved oxygen concentration or pH will not suffice to define the metabolism of the large kelp stands.

Precipitation of carbonates, such as calcium carbonate, will affect the concentration of inorganic carbon as measured by the pH. Calcium carbonate formation changes the alkalinity and lowers pH. As mentioned earlier (Chapter 2), alkalinity remained constant within the precision of measurements on the two different occasions on which it was measured. We can conclude there was no significant change in the inorganic carbon concentration of the water due to precipitation of carbonates in the bed.

Concentrations of dissolved oxygen and carbon dioxide in solution involves the exchange with the atmosphere. This exchange can take place by diffusion across the air-water interface or can occur when a gas (in this case, oxygen) supersaturates and forms bubbles that rise to the water surface and escape. The first process, which could involve both carbon dioxide and oxygen, is slow and should not be important on the time scale of hours that a water mass is in the kelp bed (Owens *et al.*, 1964).

Oxygen concentrations could change due to supersaturation and removal by bubble formation. Traditionally, supersaturation has been examined relative to the saturation concentration of oxygen in equilibrium with the atmosphere at one atmosphere total pressure (Odum and Hoskin, 1958; McFarland and Prescott, 1959). At one atmosphere, the partial pressure of oxygen is approximately 0.20 atmospheres, neglecting the vapor pressure of water. The saturation of a sample of water is expressed as the ratio of the concentration of oxygen in the sample to the saturation concentration of oxygen at that temperature and salinity. When the ratio is greater than one, the solution is supersatured. Equations to generate the Henry's Law constant have been developed by Green and Carritt (1967). I have calculated the equilibrium oxygen concentrations and compared them with the oxygen concentrations in the kelp bed. The oxygen concentrations measured on July 9, 1972 have been expressed in terms of the saturation of water with the salinity of 33‰ at the ambient water temperatures for one atmosphere of total pressure (Figure 25). The oxygen concentration down to approximately ten meters was above atmospheric saturation, with the oxygen reaching concentrations of 1.9 times saturation.



7/ 9/72 TRANSECT 1

OXYGEN SATURATION, ATMOS. PRESS.

CONTOUR FROM PT.LOMA

MIN= 0.50 MAX= 1.90 DELTA= 0.10

Figure 25. Oxygen saturation relative to atmospheric pressure, Transect 1, July 9, 1972.

The high supersaturation of oxygen in the kelp bed, relative to the atmosphere, suggests that there may be substantial losses of oxygen through bubble formation. However, this analysis neglects the fact that the hydrostatic pressure is higher than atmospheric below the surface. Because the water is density stratified, most of it will not come into contact with the low atmospheric pressure near the surface. Any oxygen that comes out of solution must be in the form of a bubble with a pressure at least as high as that of the hydrostatic pressure in the surrounding water. For a given depth, z (meters), the hydrostatic pressure, P_h (atmospheres), of seawater with a specific gravity of 1.025 (Neumann and Pierson ,1966) will be approximated by:

$$P_h = 1. + 0.1 \ z.$$

The total pressure of a bubble is the sum of the partial pressures of the gases inside the bubble. The predominant gases of the bubbles formed from solution will be nitrogen and oxygen. Since there are no processes in the kelp beds that will greatly change nitrogen concentration from equilibrium with the atmosphere, the nitrogen partial pressure in a bubble will be the same as that of the atmosphere, 0.8 atmospheres. The remainder of the pressure will come from the oxygen, P_{O_2}.

Should the bubble be at a pressure lower than hydrostatic, it will collapse. For a bubble with the same pressure as the water the oxygen partial pressure and the depth can be related

$$\begin{aligned} P_{bubl} &= P_{N_2} + P_{O_2} \\ &= P_h \\ &= 1. + 0.1\ z \qquad (1) \end{aligned}$$

$$P_{O_2} = 0.2 + 0.18\ z \qquad (2)$$

For a bubble at equilibrium with seawater at a given depth, the concentration of oxygen in solution is given by

$$\begin{aligned} [O_2(aq)] &= K_H P_{O_2} \\ &= K_H (0.2 + 0.1\ z) \qquad (3) \end{aligned}$$

where K_H is the Henry's Law constant , which is a function of temperature.

In order to determine whether oxygen is supersaturated at a given depth and hence can potentially bubble out of solution, the oxygen concentration should be compared with the depth-compensated saturated oxygen concentration. Note that the depth-compensated oxygen saturation concentration is identical to the traditional oxygen saturation concentration when the depth is zero, at the surface.

When examined this way, it can be seen that on July 9, 1972 the only supersaturated water was above the depth of 2 meters (Figure 26). We conclude that if oxygen were being lost to the atmosphere, it could only have been lost in the upper 2 meters.

If oxygen were coming out of solution, a scatter plot of dissolved oxygen as a function of inorganic carbon concentration for July 9, 1972 should show low inorganic carbon concentrations that do not correspond to higher dissolved oxygen values. Such points do not exist (Figure 27). There are no anomalously high oxygen points, nor are there any anomalously high carbonate points, as there would be if there were large amounts of carbonate precipitation occuring. There were also no anomalous points in the scatter plot for April 4, 1974, another day when there were high dissolved oxygen concentratons in the bed (Figure 28).

We conclude that oxygen produced by photosynthesis in the kelp bed remained in solution. Hence, oxygen concentrations are indicative of the amount of photosynthesis that has taken place in a parcel of water.

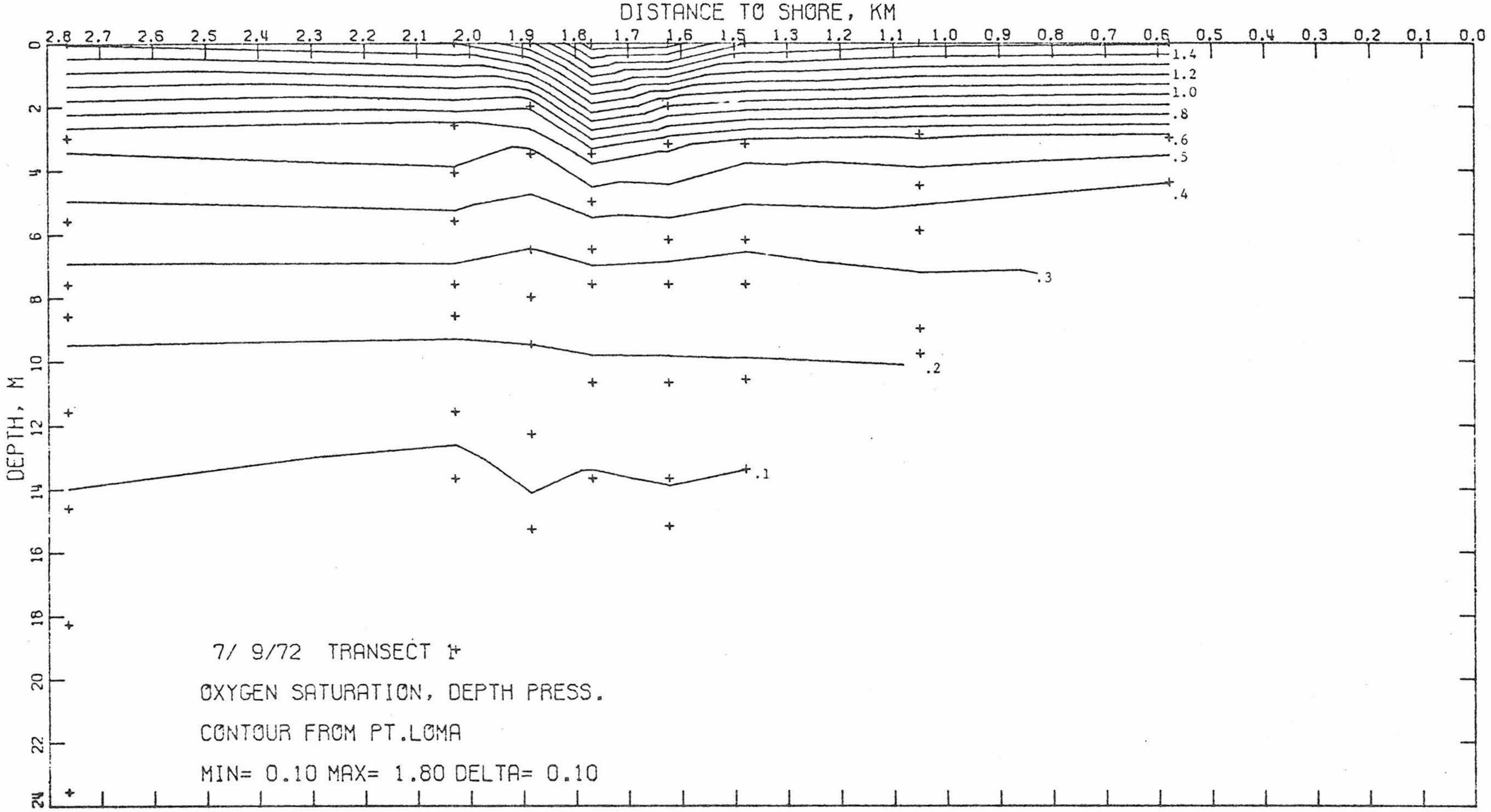


Figure 26. Oxygen saturation relative to hydrostatic pressure, Transect 1, July 9, 1972.

Figure 27. Oxygen as a function of total carbonate, July 9, 1972. For 27 sample points, the least square fit line was y = .95 (±.07) x +2.35.

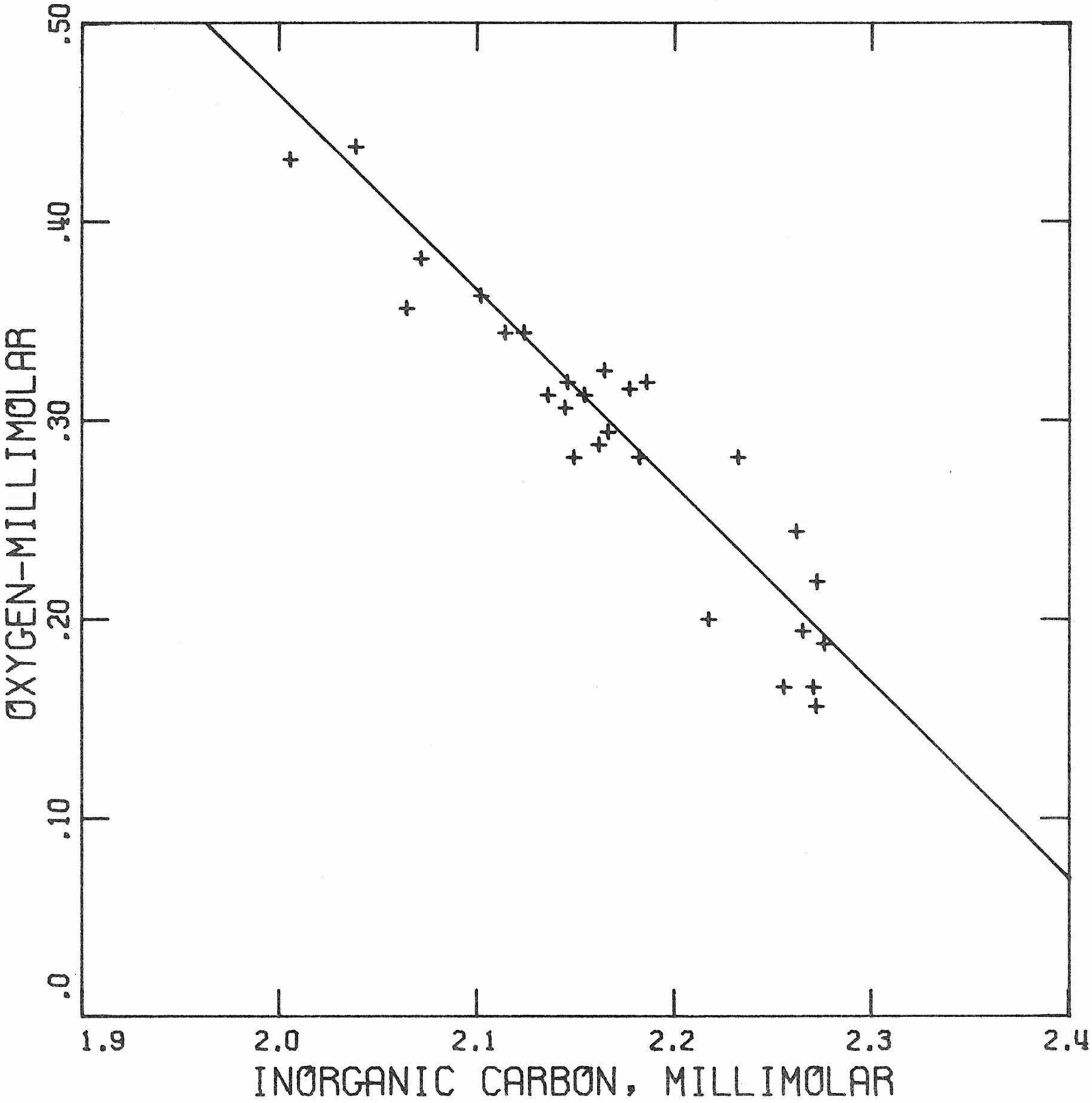
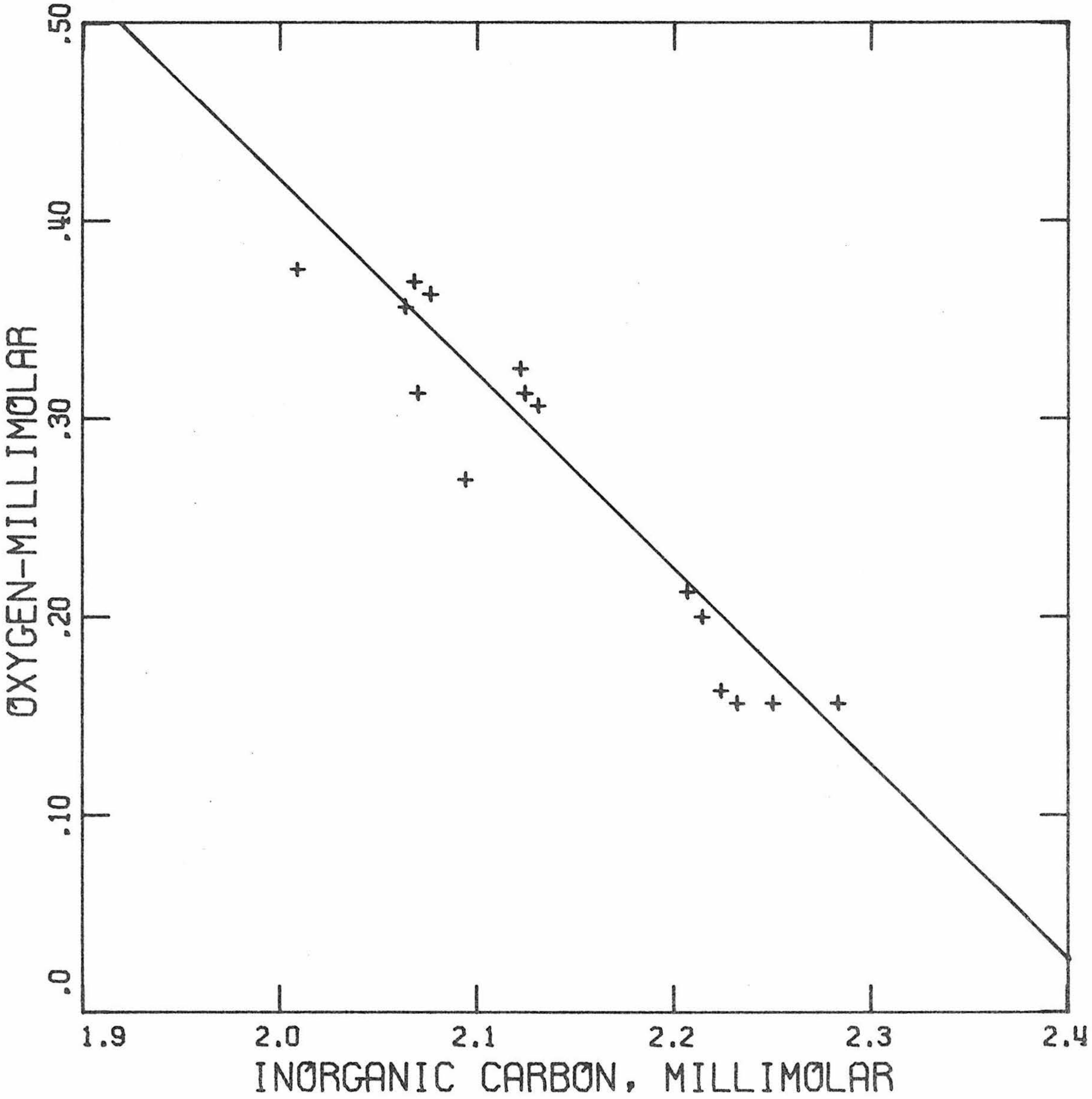


Figure 28. Oxygen as a function of total carbonate, April 16, 1974. For 15 sample points, the least square fit line was y = -.98 (±.09) x + 2.38.



Relationship between inorganic carbon and dissolved oxygen

The amount of oxygen produced by marine algae has been related to the amount of carbon and nitrogen that they incorporate during their growth. Redfield, Ketchum and Richards (1963) have observed that for every atom of carbon incorporated, two oxygen atoms are produced and for every atom of nitrogen, four of oxygen are produced. As a result, changes in dissolved oxygen concentration in water can be related to the changes in total carbonate and in nitrate:

$$\Delta O_2 = -\Delta C - 2\Delta N \qquad (4)$$

Hence the ratio of change in oxygen to change in nitrogen in the water can be related to the ratio of change in total carbonate to the change of nitrogen in the the water:

$$(\Delta C/\Delta N) = -(\Delta O_2/\Delta N) - 2 \qquad (5)$$

This is an important relationship because the dissolved oxygen sensor on the Martek probe proved more durable than the pH sensor and the calculated oxygen concentrations more precise than the calculated total carbonate concentration. Since the oxygen and carbon ratios can be related, it is possible to compare the changes in oxygen and nutrient concentrations in the water with the known carbon:nitrogen values of *Macrocystis pyrifera*.

Furthermore low $\Delta O_2:\Delta C$ ratios of about -1 should be indicative of low nitrate uptake. For those days for which data are available this relationship holds moderately well (Table 4). As always, there is the anomalous case, which here is the set of regressions for August 8, 1974. The oxygen to carbon ratio was -1.58, which should indicate high nitrate uptake. But the carbon to nitrogen ratio was 37, indicative of low nitrogen uptake.

Changes in nutrient and oxygen concentrations

The extent of the nutrient uptake during kelp photosynthesis should be mirrored in the ratios between the oxygen and nutrient concentrations of the nurturing seawater. The ratios between the dissolved nutrients and oxygen are determined not only by kelp growth but also by any previous growth of phytoplankton. The assumption that the oxygen- nutrient relationship is determined by the kelp, not by the phytoplankton can be tested by a tracer taken up by the oceanic algae and not the benthic algae. Silicate is an important macronutrient for diatoms, a very important group of phytoplankton. Thus, it makes a convenient tool to distinguish between the growth of the kelp and the phytoplankton. A relationship for the change in the concentration of a nutrient as a function of a change in the

	7/9/72	2/24/72	4/16/72	5/21/74	8/8/74
Regression of D.O.(mM) fn C_T(mM)					
Correlation	-.94	-.93	-.95	-.90	-.90
Regression coefficient ± std. err.	-.95±.07	-1.31±.14	-.98±.08	-1.25±.11	-1.58±.15
Intercept	2.35	3.08	2.38	2.94	3.61
Standard error of estimate	.027	.007	.027	.028	.034
Regression of ΣN(μM) fn D.O.(mM)					
Correlation	-.67	-.74	-.93	-.87	-.58
Regression coefficient ± std. err.	-29.0±6.	-82.4±21.	-62.7±7.	-64.0±7.	-14.5±4.
$\Delta O_2:\Delta\Sigma N$	-34.5	-12.1	-15.9	-15.6	-69.0
$-(\Delta O_2:\Delta\Sigma N) - 2$	33.	10.	14.	14.	67.0
Regression of ΣN(μM) fn C_T(mM)					
Correlation	.63	.74	.91	.93	.62
Regression coefficient ± std. err.	29±7.	122±30.	66.±8.	100.±7.	27±7.
$\Delta C:\Delta\Sigma N$	34.6	8.2	15.1	10.0	36.8

Table 4. Comparison of oxygen (DO) and inorganic carbon (C_T) regression ratios. Note that the regression coefficients are in units of micromole/millimole. The $\Delta O_2:\Sigma N$ and $\Delta C:\Delta\Sigma N$ are in units of mole/mole.

concentration of oxygen was expressed by a regression coefficient from multiple linear regressions of the nutrient concentration against the concentrations of silicate and oxygen. The O_2: nutrient ratio was the inverse of the regression coefficient against oxygen. The $\Delta C:\Delta N$ ratio was the $\Delta O_2:\Delta N$ ratio corrected by the use of equation 5.

The importance of different inorganic forms of nitrogen in supplying growth needs of the kelp bed can be determined by comparing changes in the nitrogenous concentrations as a function of the oxygen concentration changes. The $-\Delta O_2:\Delta NH_4$ ratios, corrected for phytoplankton effects, had a median of 490 (n=5; range, 300-750) (Table 5). Uncorrected, the median ratio was 300 (n=9; range, -280 to 1492). The changes in nitrate concentration were much greater, with the corrected $-\Delta O_2:\Delta NO_3$ ratio having a median of 130 (n=4; range, 27 to 256), and the uncorrected ratio having a median of 36 (n=7; range, 13 to 89) (Table 6). We conclude that the nitrate was more important than ammonia as a nitrogen source to the kelp.

The corrected ratios, having had the lower 8:1 C:N phytoplankton ratios factored out, are higher than the uncorrected ratios, but the patterns are similar.

	7/9/72	11/21/72	2/24/72	4/16/74	5/21/74	8/8/74	9/20/74	11/14/74	5/27/75
Number of points	31	29	15	16	31	28	32	22	112
Ammonia (μM) <u>fn</u> Oxygen (mM)									
Correlation	-.41	-.097	-.63	-.72	.84	-.80	-.66	-.38	-.73
Regression coefficient	-1.5±.6	-.7±1.4	-4.1±1.4	-4.8±1.2	3.6±.4	-3.4±.5	-2.2±.5	-1.3±.7	-3.4±.3
$-\Delta O_2:\Delta NH_4$	685.	1492.	244.	208.	-278.	299.	459.	781.	294.
Ammonia (μM) <u>fn</u> Silicate (μM), Oxygen (mM)									
Multiple correlation									
Regression coefficient	-2.0±.6				-2.0±.6	-3.4±.5	-2.1±.5	-1.3±.8	-3.2±.3
$\Delta O_2:\Delta NH_4$					508.	295.	488.	752.	316.

Table 5. Relationships between ammonia and dissolved oxygen, both uncorrected and corrected for phytoplankton-induced relationships. The regression coefficients are presented with ±the standard error of the estimate. Note that the regression coefficients are in units of micromole/millimole. The $\Delta O_2:\Delta NH_4$ ratios are in units of mole/mole.

	7/9/72	11/21/72	2/24/72	4/16/74	5/21/74	8/8/74	9/20/74	11/14/74	5/27/75
Number of points	31	29	15	16	31	28	32	22	112
Nitrate (μM) fn Oxygen (mM)									
Correlation	-.65	+.07	-.72	-.93	-.87	-.49	-.65	-.01	-.47
Regression coefficient	-2.8±6.	+9±26	-78±20	-58±6	-60±7	-11±4	-13±3	-.12±6	-22±4
$-\Delta O_2:\Delta NO_3$	36.	-	13.	17.	17.	89.	78.	-	45
Nitrate (μM) fn Silicate (μM), Oxygen (mM)									
Multiple correlation									
Regression coefficient					-37±8	-4±1	-7±2	-2±7	-9±1.6
$-\Delta O_2:\Delta NO_3$					27	256	151	-	112

Table 6. Relationship between nitrate and dissolved oxygen, both uncorrected and corrected for silicate effects. The regression coefficients are presented with the standard error of the estimate. Note that the regression coefficients are in units of micromole/millimole. The $-\Delta O_2:\Delta NO_3$ ratios are in mole/mole units.

The regression coefficient relating concentration of total inorganic nitrogen to dissolved oxygen concentration is an estimate of dNO_3/dO_2. This is a parameter that gives the relationship between the amount of nitrogen taken up and oxygen released by plants in the process of photosynthesis. This factor is the inverse of the oxygen:nitrogen ratio which ultimately is used for understanding carbon:nitrogen ratios of material being incorporated into plants.

The slope, $d\Sigma N/dO_2$, shows a seasonal variation that resembles the previously discussed median nitrogen concentration (Figures 15 and 29). $d\Sigma N/dO_2$ values are most negative during early spring. We infer from nutrient concentration ratios that the plants have their highest nitrogen concentrations during those times when the nutrient concentrations are the highest. During times of low nutrient concentrations, the nitrogen contents drop, possibly slowing the growth rates. The dependence of $d\Sigma N/dO_2$ can be assessed by examining correlations with median nutrient concentrations in different depth ranges. Such calculations show that the correlation of $d\Sigma N/dO_2$ is highest for the median concentration of total inorganic nitrogen that is between 4.5 meters and 10.5 meters below the surface (n=9, correlation=-0.83). The correlation is lowest for the median nitrogen concentration at depths between the surface and 4.5 meters (Figure 30; n=9,

Figure 29. Annual cycle of nutrient uptake ratios.

a. $\frac{d\Sigma N}{dO_2}$ as function of time of year.

b. $\frac{dPO_4}{dO_2}$ as function of time of year.

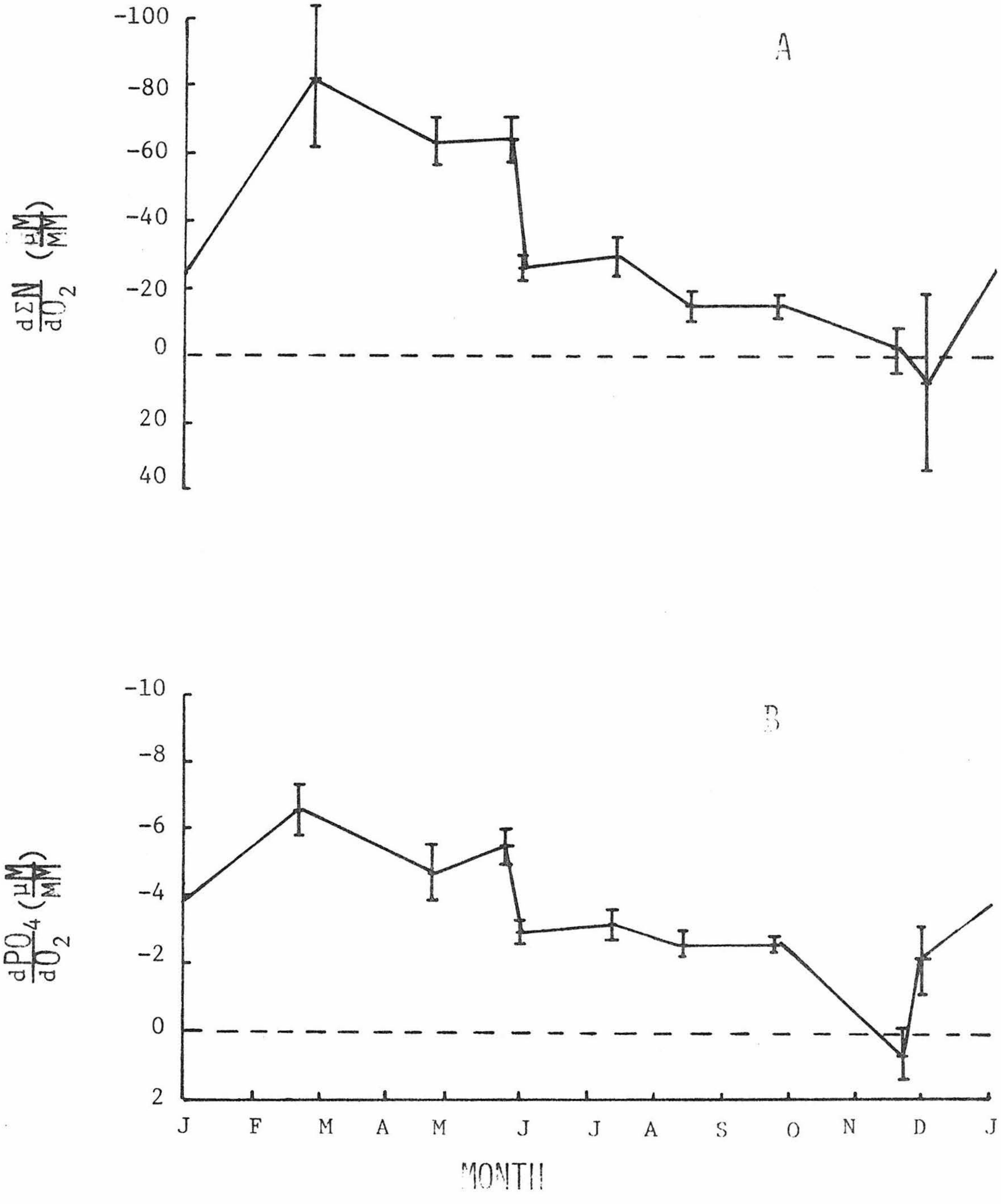
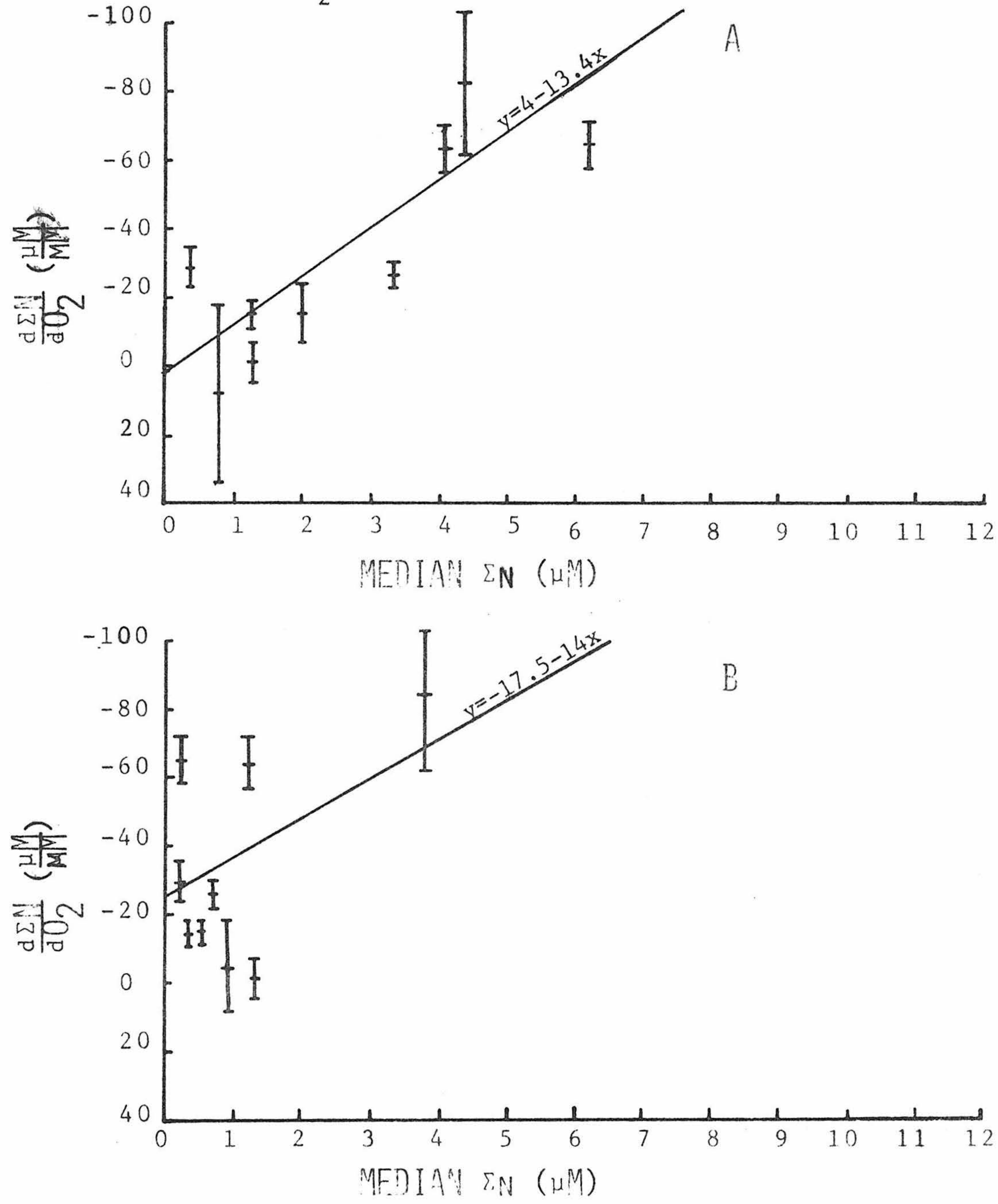


Figure 30. Nitrogen uptake ratios (with standard errors) as a function of median inorganic nitrogen concentration.

a. $\frac{d\Sigma N}{dO_2}$ vs median ΣN concentration at 6 & 12 meters.

b. $\frac{d\Sigma N}{dO_2}$ vs median ΣN concentration at 0 & 3 meters.



correlation=-0.51). Correlation was intermediate for the median nitrogen concentration in the water from the surface to 10.5 meters depth (n=9,correlation=-0.65).

Thus far the discussion has mentioned, quite often, that photosynthesis depends on the total inorganic nitrogen concentration. Are the organic forms, the most important of which seems to be urea, important to the growth of kelp? The evidence suggests that urea, at least, is not. McCarthy (1971) found that the concentration of urea was usually less than 1. μM. This is the magnitude of the concentration of ammonia in the kelp at Point Loma. It is doubtful that urea serves as an unknown, highly significant source of nitrogen for *Macrocystis* at Point Loma because ammonia, which is taken up preferentially to urea by algae, was not an appreciable nitrogen source for the kelp, and was not totally depleted in the surface.

Gross production estimates

Because they lack a time dimension, most of my data cannot be used to compute any measures of kelp bed production. Oxygen measurements were made more than once in a day on two occasions. In one instance, May 27, 1975, the water was quite stratified and as a consequence, there were extensive vertical and horizontal motions of the water.

This is established by the large variation isotherm depths (Figures 7 and 13) and in the great fluctations in the nutrient concentrations (Figures 9-12). On the other occasion, May 21, 1975, the water was weakly stratified. There was little evidence of internal waves moving parcels of water around (Figures 31, 32).

Gross production of the bed can be estimated by comparing total oxygen contents in a column of water before and after plants have been photosynthesizing therein. I integrated oxygen concentration from the surface to 12 meters as a function of depth to obtain the total oxygen content beneath a square meter of surface, using a linear interpolation to estimate dissolved oxygen at points between sampling depths. I assumed that all of the water beneath a square meter moved together when comparing the total integrated oxygen beneath the surface at two different times. When water is not well-stratified and shows no evidence of internal wave motion, as on May 21, 1975, Winant and Olson´s (1975) model of water motion in the nearshore coastal zone suggests that the water column should move as a unit.

The oxygen concentrations from the first transect of May 21, 1974 (Figure 33) were taken between 0730 Pacific Standard Time (PST) and 0900 PST. Total oxygen beneath a

Figure 31. Temperatures for Transect 1, May 21, 1974.

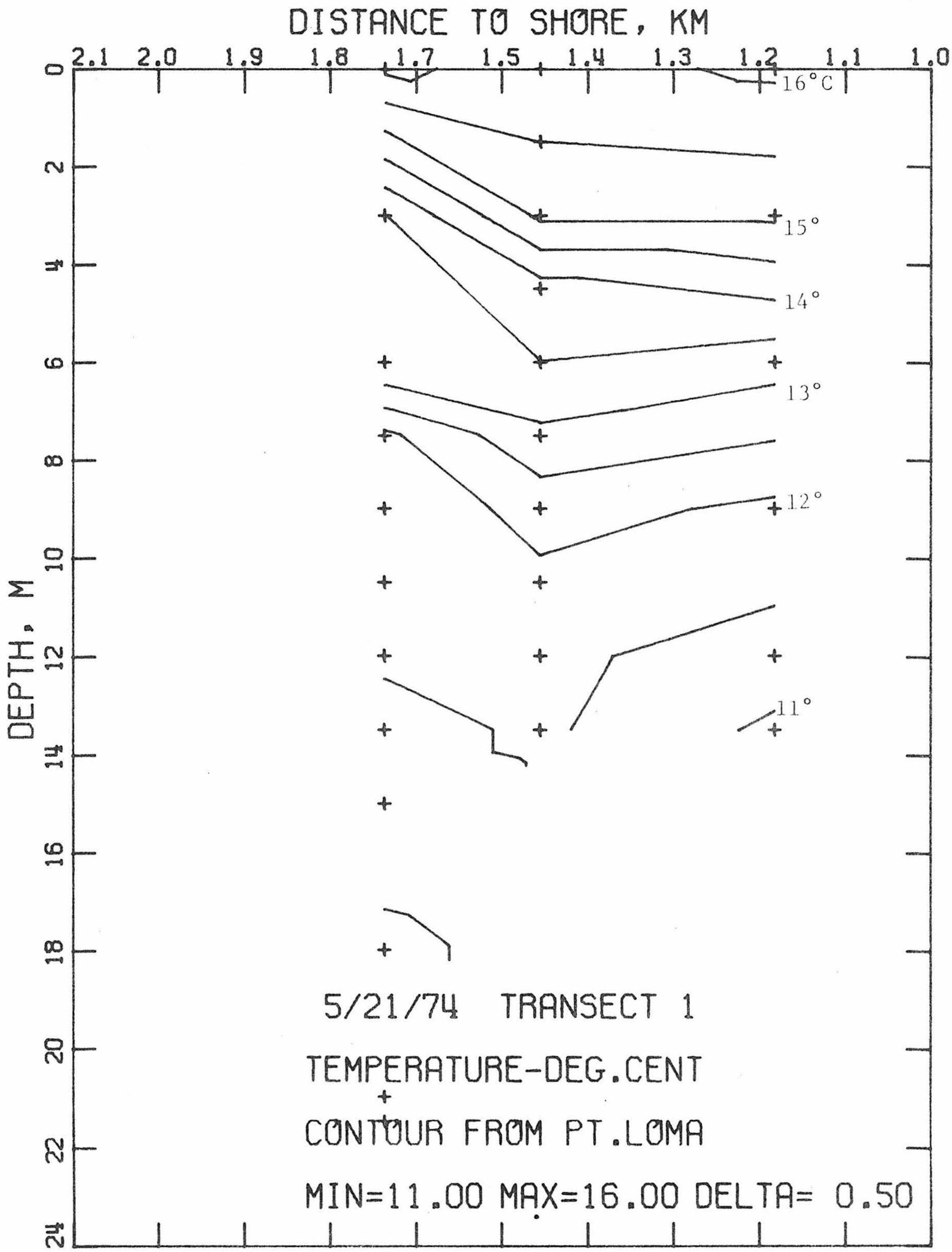


Figure 32. Temperatures for Transect 2, May 21, 1974.

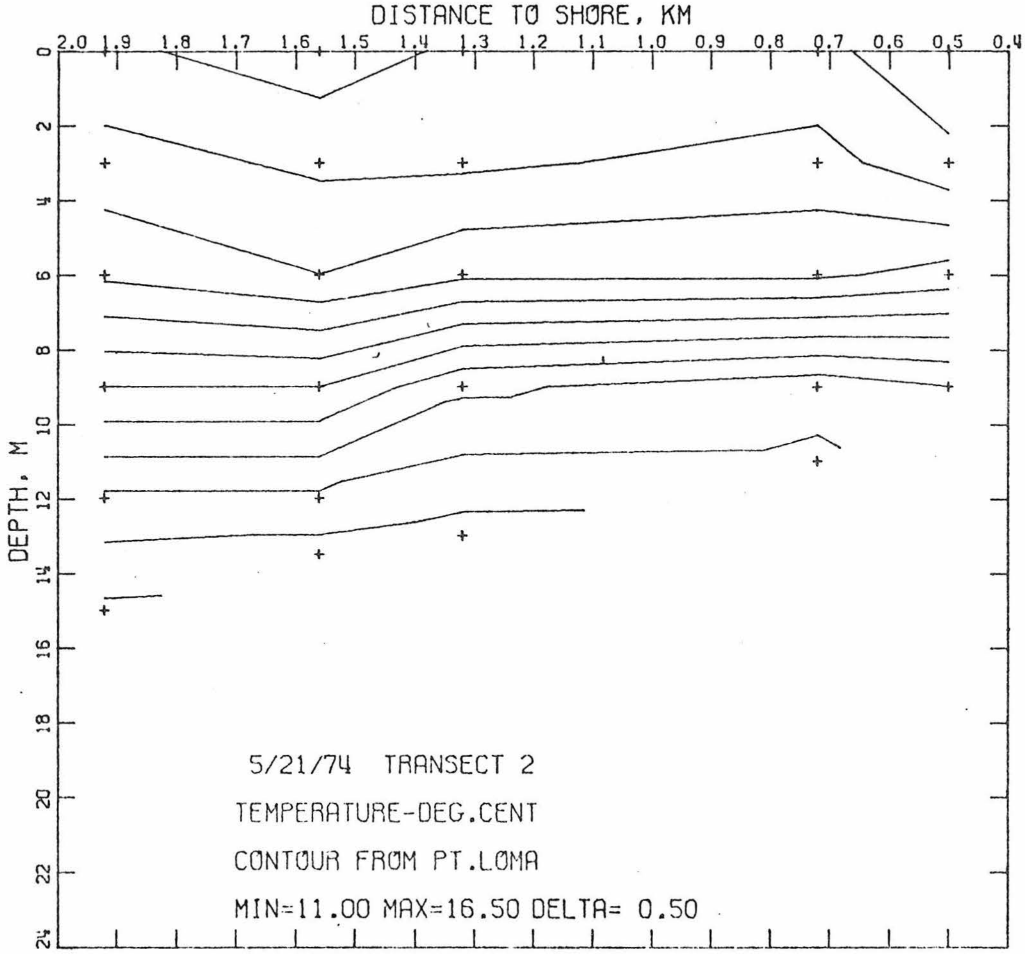
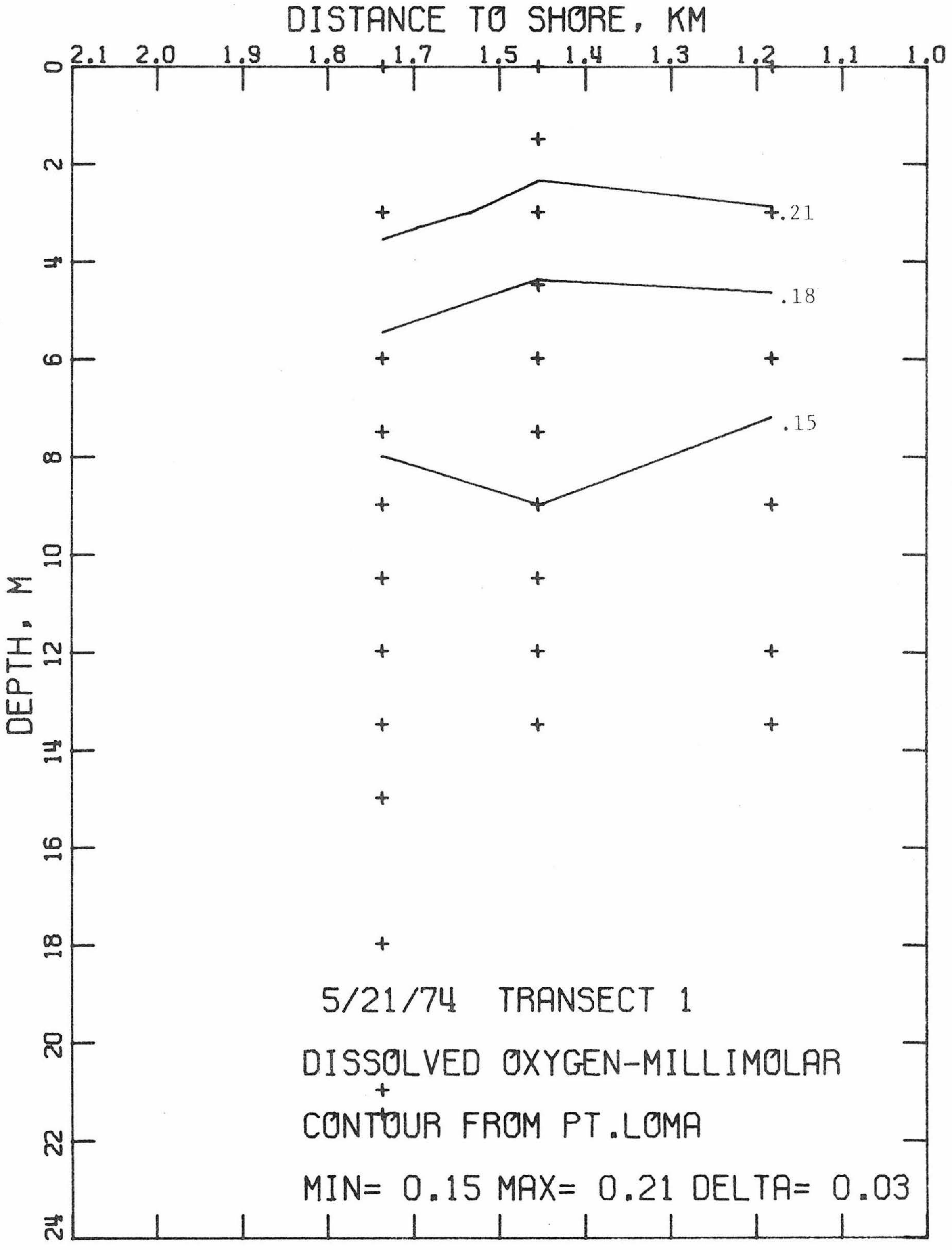


Figure 33. Oxygen concentrations for Transect 1, May 21, 1974.

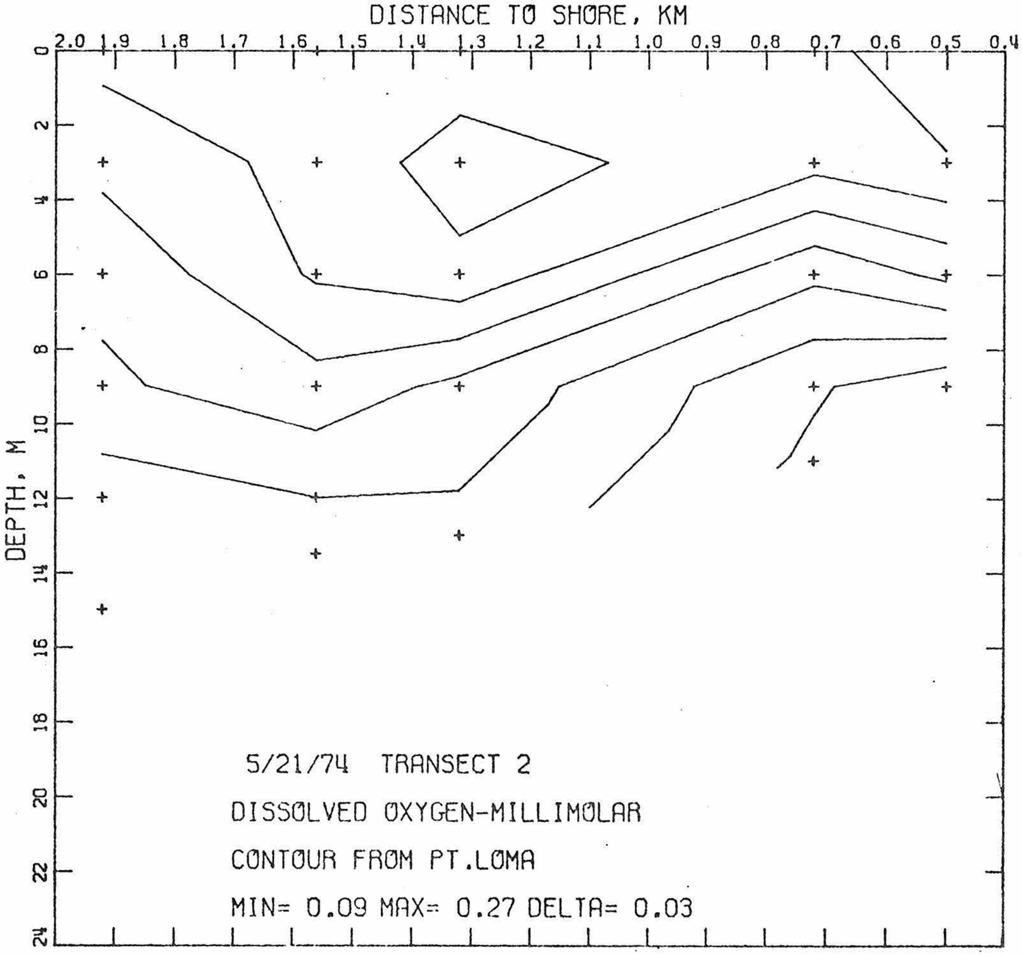


square meter of surface ranged from 2.14 to 2.05 moles-O_2/m^2, with an average of 2.09 moles-O_2/m^2. The average oxygen content, assumed to be at 0830 PST, was 2.09 moles-O_2/m^2. The highest integrated oxygen concentration during the second transect (Figure 34) was 2.74 moles-O_2/m^2 at 1130 PST. The amount of oxygen thus increased by 0.65 moles-O_2/m^2 in three hours. Assuming that this represents the general oxygen production of the bed and that the rate of oxygen production remained at the same rate between 0830 and 1530 hours as it was between 0830 and 1130, gross production would have been 1.52 moles-O_2/m^2-day or 34.1 liters-O_2/m^2-day. After converting by using the $-\Delta O_2:\Delta C$ ratio of 1.25 previously derived for this date, we obtain 14.6 g-C/m^2-day.

The gross production rate measured by Towle and Pearse (1973) was 6.8 g-C/m^2-day while that measured by McFarland and Prescott (1959) was approximately 1 mole-O_2/m^2-day. Both rates are lower than the rate presented here for the Point Loma kelp bed.

In the process of measuring the carbon uptake of Macrocystis pyrifera Towle and Pearse found that 99% of the photosynthesis took place at the surface. The results of my studies certainly do not agree. The maximum dissolved oxygen concentration was several meters below the surface

Figure 34. Oxygen concentrations for Transect 2, May 21, 1974.



for several of my transects (Figures 21, 34). The data collected on May 21, 1975 have provided quantatitative estimates of the rates of photosynthesis at different depths, assuming all water at a station was in the kelp for the same length of time. Such a calculation shows that the maximum rate of photosynthesis took place at the depth of approximately 6 meters (Figure 35). This is also approximately the depth at which the total inorganic nitrogen concentration increased to nearly 4 μM, contrasting with a surface median concentration of 1 μM. We infer that photosynthetic rate depends on the nitrogen supply available to the plant.

Discussion

Correlation of high nitrogen concentration with high oxygen production implies that much of the nitrogen used for growth by the kelp plants is primarily taken up at the sites of photosynthesis. Because the relationship between nitrogen uptake and oxygen release depends on the concentration of nitrogen below 4.5 meters more highly than it does on the nitrogen concentration above 4.5 meters we conclude that much of the photosynthesis takes place below the thermocline. That the changes in the oxygen concentration are greatly a function of depth strengthens

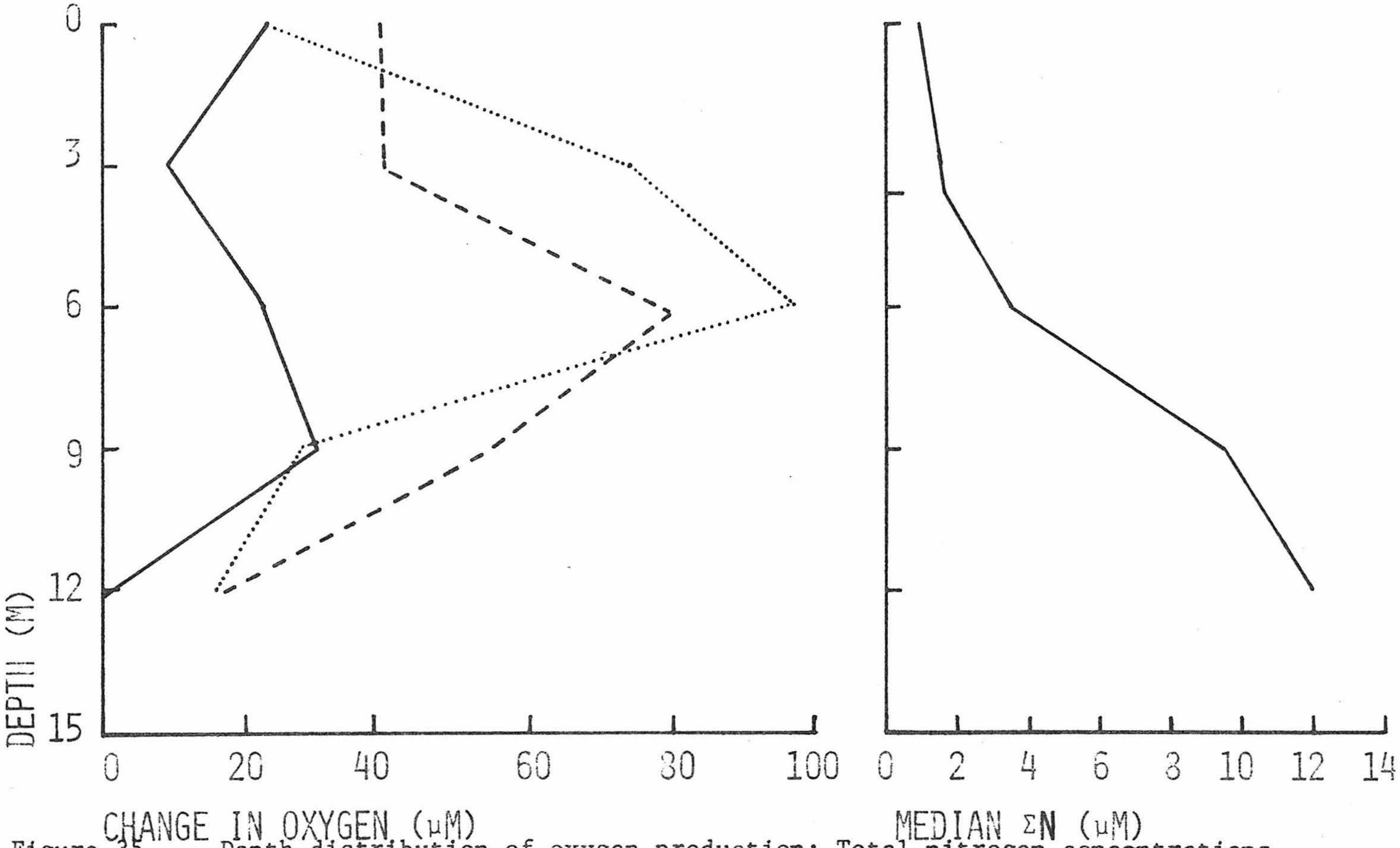


Figure 35. Depth distribution of oxygen production; Total nitrogen concentrations.

a. Changes in oxygen concentration from median of oxygen concentrations of Transect 1. Station 4 was the outermost station of Transect 2. Station 4 is represented by solid line, station 5 by dashed line, station 6 by dotted line.

b. Median total inorganic nitrogen as a function of depth.

this conclusion.

Other possibilities can explain the increased oxygen concentrations in deeper water, but they do not seem reasonable. For example, oxygen produced at the surface might escape to the atmosphere. The relationship between the oxygen and the inorganic carbon, however, showed that this dissolution did not happen. Perhaps the water moved through the kelp much faster at the surface than at the depths of 3 to 6 meters. A very large current, however, would be needed if the oxygen increase at 3 and 6 meters were twice as high as those at the surface. High wind speeds needed to generate the high surface current were not present on that day. Hence, increased oxygen concentrations could not have been caused by the faster movement of water at the surface. The most reasonable explanation is that the photosynthesis was predominantly taking place where the nutrients were, not where the light was.

CHAPTER 5

DISCUSSION

It should not be surprising that the photosynthetic production by *Macrocystis pyrifera* is strongly influenced by the nutrient concentration of the surrounding water. Fluctuations in growth patterns of the alga could be explained by spatial and temporal variation in distribution of nutrients. McFarland and Prescott (1959) have previously noted that during the month of June between 35 and 50 per cent of the blade surface was in the surface canopy, but the depth of the maximum photosynthetic rate was 3 meters. They were unable to explain this result. Their result is consistent with my finding that the rate of oxygen production is a function of the nitrogen concentration.

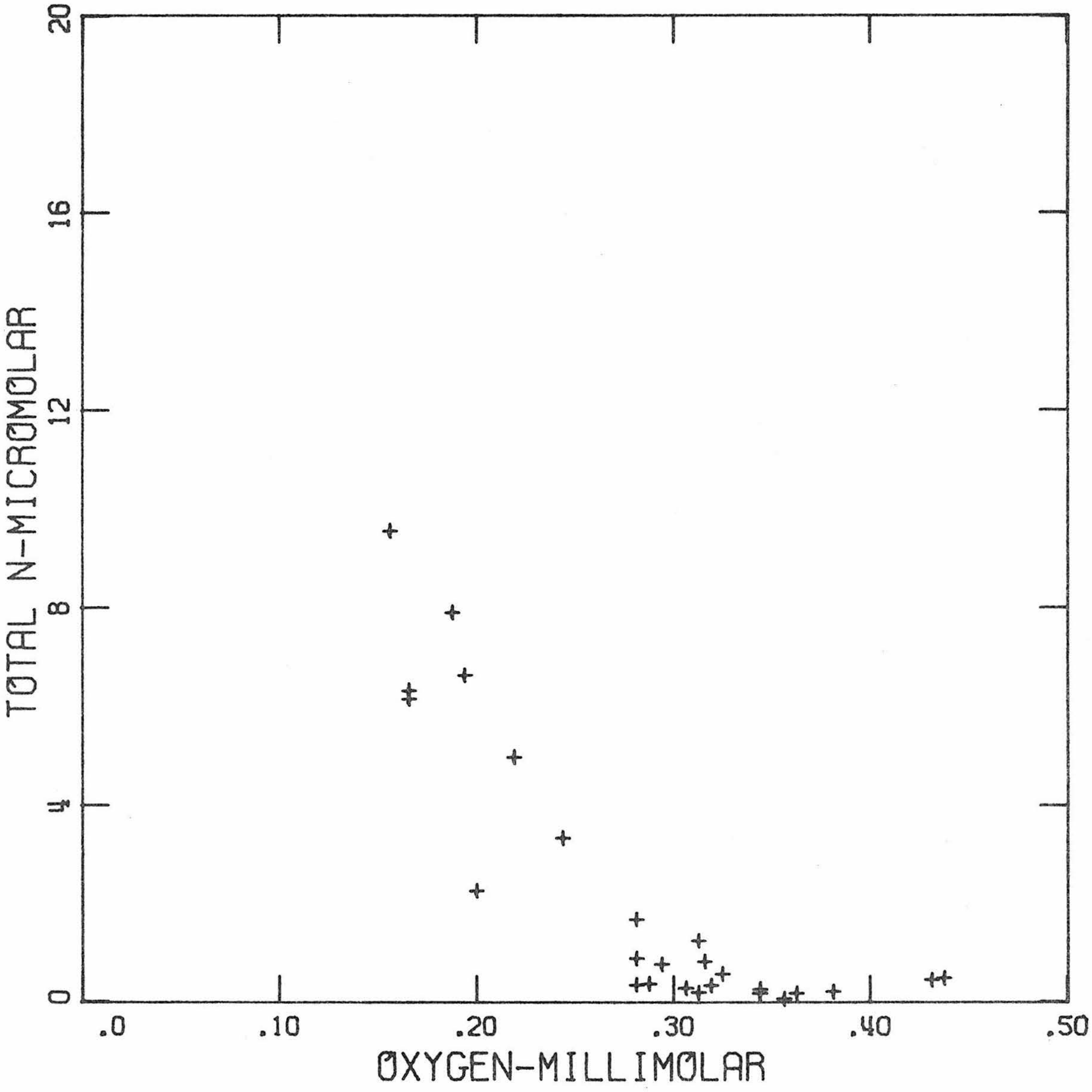
North (1971b) has often observed that surface parts of kelp fronds deteriorate during summer months. The parts of the kelp bed below the thermocline usually remain healthy. Clendenning analyzed the effect of temperature on photosynthesic and respiration rates of kelp blades. He found that increased temperature increased the net production of blades. He concluded that the temperature-linked die-off of the surface canopy was not due to an adverse change in the photosynthesis:respiration ratio among surface blades. The canopy's summer die-off is associated with high temperatures, suggesting a cause-and-effect relation. The die-off could also result, in part at least, from low nitrogen concentration in the water above the thermocline and possible temperature-nutrient interactions. Evidence that the die-off is caused solely by high temperatures is presently insufficient.

The gross production of the kelp bed on May 21, 1974 was quite high, especially considering that relatively little of it came from the canopy. On that occasion there was an extensive, healthy canopy at the surface. If 40 percent of the photosynthetic tissue of the plants was in the canopy (corresponding to the canopy that McFarland and Prescott measured) the gross photosynthetic capacity might well double if those blades could be supplied with nitrogen. Such a supply process would occur during the winter or during an upwelling event. A case in point was the upwelling event when the surface nitrate concentrations reached 4 μM . Gross production might reach 30 g-C/m^2-day during such a period. By comparison the tropical rain forests provide the often quoted high values for gross productions of up to 16 g-C/m^2-day (Odum, 1971).

If the canopy die-off is caused by the low nitrogen content of the surface waters in the summer, there is an important question about what allows the canopy to grow during the other months. It is, however, only during the summer that the concentrations at the deeper parts of the kelp bed drop.

The probable explanation involves the translocation of nitrogen from those parts of the plant bathed in higher nitrate water. When surface blades are not taking nitrogen from solution, they could be using the nitrogen being translocated from below. The relationship between oxygen and total nitrogenous substances shows that tissues in the low nutrient surface waters do not always obtain nitrogen in amounts corresponding to their oxygen production (Figure 36). The decrease in total inorganic nitrogen corresponding to the 0.15 mM dissolved oxygen increase would have been 3. μM for a plant producing tissue with a C:N ratio of 50:1. The surface water did not have that high a concentration at any point that day. The implication is that the surface tissues depend on translocated nitrogen for their growth. Because the C:N ratio of the translocated fluid is 8:1 and the C:N ratio of summer surface blades is 40:1, at least a fifth of the growth at the surface would have had to come from tissue in deeper water. Thus, the tissues below have to have enough light and enough nutrients if the system is

Figure 36. Total N **vs** dissolved oxygen, July 9, 1972. Note that at the low inorganic nitrogen concentrations, there was oxygen evolution without corresponding nitrogen uptake.



to work.

Presumably, the lower parts of the plant cannot translocate enough nitrogen to the surface and the canopy dies back if the nitrogen concentration or the light intensity becomes too low. This dieback would increase the photosynthesis of the lower parts of the kelp and also any other species below. Perhaps there are other algae that are adapted to grow during that time when the canopy die-back has allowed increased amounts of light to reach the bottom, where they reside in seawater with higher nutrient concentration than the surface.

Those times that the canopy inhibits the photosynthesis of the lower parts of the plants, the harvesting of the canopy could increase the growth of the kelp in the under story.

Nutrients and algal growth in the North Atlantic

Algal growth in other parts of the world shows strong seasonality suggesting regulation by nutrient supply. Studies done on brown algae, such as *Laminaria digitata*, *L. hyperborea* and *Cystoseira granulata* (Chapman, 1974; Mann, 1972; Hellebust and Haug, 1972), and on red algae (Dawes *et al.*, 1974) show a common pattern. Most growth occurs in winter and early spring when light is low and storm-caused turbulence the highest. C:N ratios are low during the winter; C:N ratios increase during the summer as the carbohydrate concentrations in the algae increase and growth slows and stops. Dawes, Lawrence, Cheney and Mathieson (1974) noted that increase in carbohydrate concentration in Eucheuma was paralleled by a decrease in dissolved nitrogen concentration. They speculated that the low nutrient concentration probably caused the higher carbohydrate concentration.

Nutrient concentrations decrease to low levels during late spring and do not increase again until the beginning of winter in the North Atlantic (Ryther, 1963). Mann (1972) observed that the brown algae Laminaria digitata, Laminaria longicruris and Agarum cribosum, display maximum growth from January to May, during the period of maximum nutrient concentrations.

Correlation of maximum algal growth with periods of maximum nutrient concentrations, and not with maximum light intensity in May, June, July, emphasizes the importance of nutrients to macroalgae in the nearshore. Stationary algae are probably unable to filter all the nutrients they need from the flowing water at concentrations normally occurring in the open ocean. Macroalgae could undoubtedly achieve much faster growth rates if they encountered high nutrient concentrations during the high light-flux season.

Spatial considerations

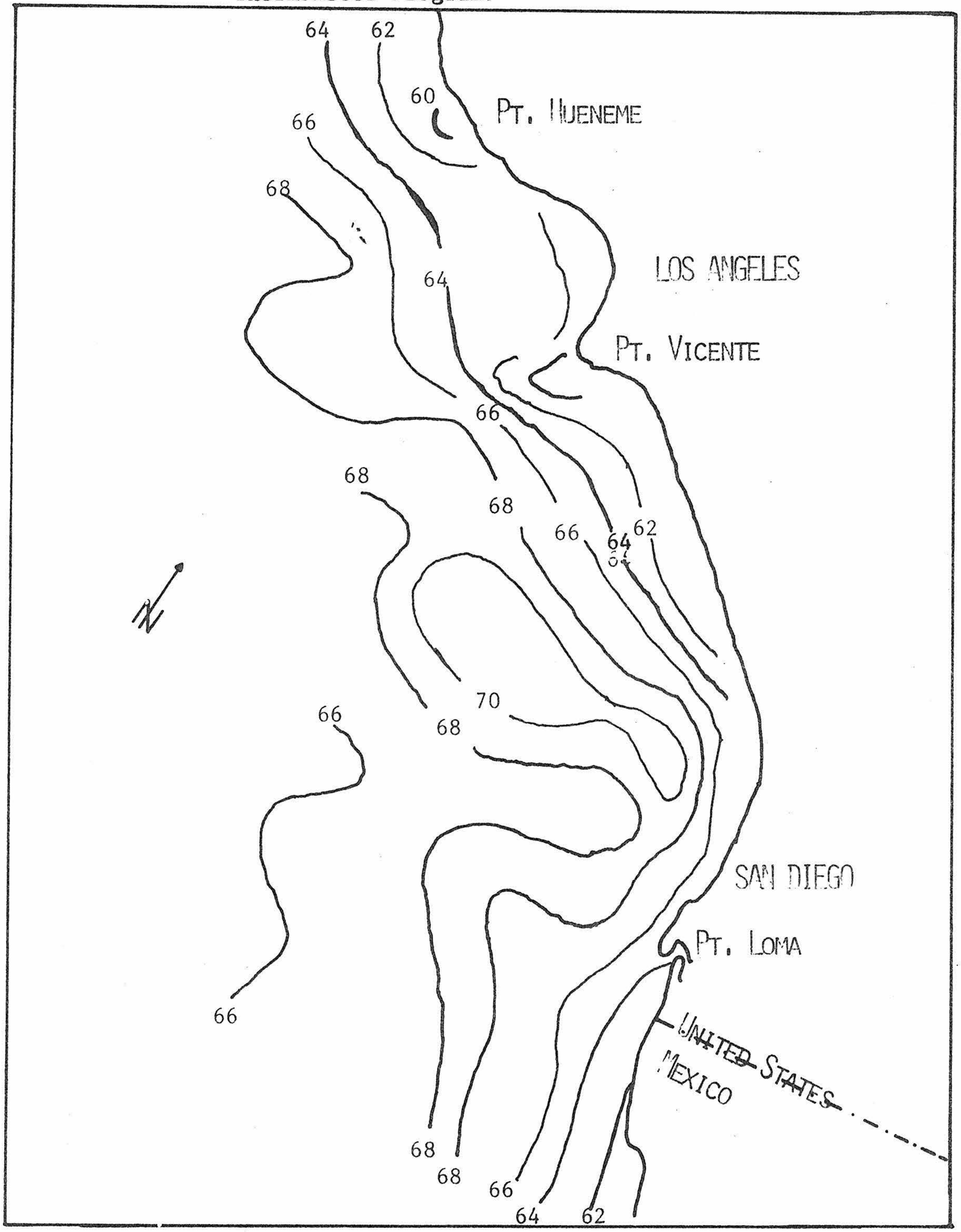
Some species undoubtably grow more efficiently under low nutrient conditions than others. Thus, nutrient regime is an important factor determining species abundance and dominance. Physical processes, such as the intense localized upwelling at the tip of Point Loma provide strong local gradients in nutrient conditions.

Because temperature typically inversely correlates with nutrient content, nutritional effects are closely associated with water temperature. Effects of nutrients on algal distribution may have been mislabeled as temperature effects. Studies of temperature effects on algal distribution and abundance should also include nutritional monitoring.

The inverse correlation between temperature and nutrient concentrations, with waters of higher temperature generally having lower nutrient concentrations, provides a convenient method for locating areas that may have different nutrient regimes. Temperature is an easily and widely measured parameter of oceanic surface waters. The U. S.

Coast Guard has been conducting aerial bimonthly surveys of the surface water temperature off California using remote sensing. Results of the surveys frequently showed localized upwelling at the tip of Point Loma (Figure 37). Coast Guard charts also showed localized low surface temperatures south of other points in southern California, most notably Point Vicinte and Point Hueneme. Presumably these are areas of increased nutrient concentration and benthic algal productivity.

Figure 37. Surface isotherms for Southern California Bight, August 21, 1969. Temperatures are in degrees Fahrenheit. Redrawn from survey of the U.S. Coast Guard, Oceanographic Branch, Airborne Radiation Thermometer Program.



CHAPTER 6

SUMMARY AND CONCLUSIONS

Gross primary production of the kelp bed at Point Loma, California was calculated at 1.5 moles-O_2/m^2-day or 14.6 g-C/m^2-day. This represents one of the highest measured values of gross primary production. A rate of production twice as high might be attained under optimal conditions.

The condition most limiting Macrocystis production was the low concentration of dissolved nutrients, especially nitrogenous substances, near the surface. Kelp compensated for this limitation by translocating nitrogenous compounds from depths where nutrient concentrations were higher. Summer dieoff of the surface canopy may be caused by inability of plants to translocate nutrients due to low availability of nutrients in deeper water.

Nutrient concentrations varied seasonally. Surface nitrate concentrations were low for most of the year (usually less than 1 μM), higher during the winter. Nitrate concentrations at 6 and 9 meters depth usually exceeded 1 μM. They were highest during spring upwelling months, lowest during summer months.

Nutrient concentrations in the kelp bed were not depleted by the kelp or enhanced by sediment nutrient regeneration, implying relatively fast exchange of water in the bed with outside waters.

Nutrient concentrations varied at different longshore locations. Surface nitrate concentrations were more likely to be higher near the tip of Point Loma than 5 kilometers farther north. Localized upwelling caused this.

In the shallow nearshore (depth<5 meters) the nutrient concentrations were higher than those in the kelp bed at comparable depths. The cause remains unknown.

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