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HYDROGRAPHY DURING AN UPWELLING SEASON OFF OREGON

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Biological and hydrographic data were collected off Oregon during six cruises between May and October 1969 to relate the spatial and temporal distributions of phytoplankton, herbivores, and primary carnivores to both coastal upwelling and the Columbia River plume.

Relationships between the lower trophic levels and hydrography were explored along a latitudinal track extending 165 miles off Newport, Oregon at 44°39.1'N. The three trophic levels tended to be directly correlated. Phytoplankton and herbivorous and carnivorous zooplankton generally peaked in the inshore upwelling zone or in the warm waters along the edges of the plume; the highest catches of nekton were usually taken inside or along the edges of the plume. Median standing stocks of trophic level I remained fairly constant throughout the upwelling season. The biomasses of both trophic levels II and III showed order of magnitude seasonal decreases.

Areal contours of hydrographic parameters, nutrients, and the lower three trophic levels from two summer cruises were compared. Upwelling waters and the Columbia River effluent were both characterized by high standing stocks of phytoplankton and both herbivorous and carnivorous zooplankton. Highest catches of all nektonic groups were generally taken 25-50 miles offshore. Phytoplankton, herbivore, and nutrient areal plots show good overall agreement. Contours of hydrographic parameters do not conform with isopleths of lower trophic level biomass except for a generally longitudinal orientation of the contours. The inadequacy of the sampling regime for elucidating the structure in such a hydrographically and biologically complex system may explain the dearth of well defined relationships observed in both the areal and the Newport line comparisons.

During one cruise, the maxima in chlorophyll a profiles appear to trace the sinking of water upwelled to the surface and its subsequent movement offshore between the seasonal and permanent pycnoclines. These profiles suggest that the seasonal pycnocline may act as a barrier to upwelled water.

Direct correlations between predator groups and prey groups were generally observed. This trend was strikingly demonstrated by comparing copepod and chaetognath median dry biomasses. Several hypotheses are offered to explain this distributional pattern.

Relationships between Lower Trophic Levels and
Hydrography during an Upwelling Season
off Oregon

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INTRODUCTION

This thesis attempts to relate the temporal and spatial distributions of phytoplankton, herbivores, and primary carnivores to both coastal upwelling and the Columbia River plume. Specifically, the study considers (1) whether these two hydrographical phenomena are associated with biomass increases in all three trophic levels, (2) whether westerly advection of upwelled water and plume water cause peaks in successive trophic levels to be sequentially displaced off-shore, (3) how the observed seasonal variations in biomass are related to upwelling and the discharge of plume water, and (4) how the areal distributions of upwelled and plume water off Oregon compare with the distributions of nutrients and of these three trophic levels.

The hydrographic structure off Oregon is largely characteristic of an Eastern Boundary Current region, as described by Wooster and Reid (1963). While the coastal waters are subject to many local influences, they are basically derived from Subarctic waters. Char-acteristics for the northeastern Pacific Ocean have been described by Fleming (1955) and by Tully and Barber (1960). Oregon's nearshore hydrography has been examined by Pattullo and Denner (1965) and by Bourke, Glenne, and Adams (1971), and others.

The slow mean equatorward drift of the California Current brings Subarctic water to the surface waters off Oregon. Using a regression model to study the relationships between the ocean currents and the wind, Collins and Pattullo (1970) calculated a residual southward current of 16 cm/sec in the absence of winds. Variations in the direction and speed of surface currents appear to be the direct result of local wind stress, superimposed upon the residual geostrophic current. Together they produce the northward flowing Davidson Current from October through March, varying surface currents from both north and south during the April and May, and September, transition periods, and the southward flowing California Current from June through August (Burt and Wyatt, 1964). By contrast, a 10 cm/sec poleward flow exists below the permanent pycnocline during most of the year (Smith, Mooers, and Enfield, 1971).

The prevailing north-northwesterly winds from May through September (Duxbury, Morse, and McGary, 1966) also initiate and maintain a net offshore transport of water in the surface Ekman (wind-induced) layer which is approximately 10 meters thick (Mooers, Smith, and Collins, in preparation). Mass compensation requires a net onshore transport of water below the Ekman layer; thus cold, salty water is upwelled from a depth of 100-200 meters offshore and surfaces in a band between the coastline and 10 km

offshore (Smith, Pattullo, and Lane, 1966; Mooers et al., in preparation). This circulation pattern is called upwelling. From Yoshida's (1955, 1967) theories, it was suggested that the coastal upwelling zone is about 50 km wide in middle latitudes, which was observed by Smith et al. (1966) off Oregon.

Through its vertical and horizontal advective components, the upwelling regime exerts a marked influence upon the hydrography, chemistry, and biology of the region. Smith (1968) documents the impact of this phenomenon upon the hydrography. Upwelling produces large inshore-offshore horizontal gradients and decreases nearshore vertical gradients in all hydrographic parameters. During July and August the water at 10 meters depth at NH-5 is generally 8 C cooler than the water at that depth seaward of the edge of the continental shelf. In winter, the difference is seldom even 1 C. The California Current is the only known Eastern Boundary Current region where the salinity increases monotonically with depth. Thus, upwelling off Oregon increases the surface salinity; the mean salinity at 200 meters is 34.5‰, the same value as the summer maximum found at the surface (Pattullo and Denner, 1965). The combined effect of decreasing temperature and increasing salinity with depth results in a strong pycnocline which intersects the surface as a front during upwelling. This permanent pycnocline is associated with the permanent halocline of the Northeast Pacific. Both are elevated and

intensified with the onset of coastal upwelling off Oregon. The inclined frontal layer--the zone between the 25.5 and 26.0 sigma-t surfaces (Collins, 1964)--rises from a depth of about 150 meters at 200 km offshore to a depth of about 80 meters at the shelf edge (30 km offshore), and continues to rise shoreward, often intersecting the sea surface about 10 km offshore to form a surface front (Mooers et al., in preparation).

As might be expected, upwelling also imparts the chemical characteristics of the 100-200 meter offshore waters to the frontal region. During the upwelling season, biological, chemical, and physical processes tend to severely deplete the nutrient concentrations in the layers above the permanent pycnocline. Since the oxygen content in the 100-200 meter zone is relatively low, intensive coastal upwelling reduces the oxygen surface values off Oregon to 60-70% of saturation (Park, Pattullo, and Wyatt, 1962), while increasing the phosphate-phosphorus concentration from minimal surface values of 0.2-0.3 μg-at/l (Anderson, 1964) to values as high as 2.5 μg-at/l (Laurs, 1967). Perhaps equally important, the shallowness of the mixed layer and the velocity shear associated with upwelling are conducive to the turbulent transport of nutrients into the surface layer from below. Smith (1968) remarks that such mixing, while not upwelling per se, is part of the upwelling dynamics.

Areas of coastal upwelling are biologically the richest part of the ocean, especially with regard to man's interests. During active upwelling, the primary production normally approximates and may greatly exceed $1.0 \text{ gCm}^{-2}\text{day}^{-1}$ (Anderson, 1964; Ryther, 1969; Small, Curl, and Glooschenko, in press). Phytoplankton respond to upwelling by a marked increase in the "microplankton" ($\geq 100 \mu$ dia.)/ "nannoplankton" (5-25μ dia.) ratio (Ryther, 1969; Malone, 1971). The larger microplankton are converted into a harvestable form by food chains shorter than those of non-upwelling regions, enhancing the effect of increased primary production upon fish production. Ryther (1969) has estimated that while upwelling regions cover approximately 0.1% of the world ocean they produce about half of the world's fish supply.

Quantitative correlations between upwelling and standing stocks at various trophic levels are difficult to ascertain. As Barber, Dugdale, MacIsaac, and Smith (1971) have pointed out, chemical conditions may temporarily limit photosynthesis immediately following upwelling. There are substantial lag times required for phytoplankton to be converted into biomass at the successive trophic levels (Blackburn, 1965). Simultaneously, the biota involved may be transported away from the site of upwelling and initial high primary productivity.

Qualitatively, the relation between the lower trophic levels and upwelling has received considerable attention. Zooplankton

biomass is generally high in the coastal regions of Eastern Boundary

Currents (Wooster and Reid, 1963). In studies by King (1953) and

Vinogradov and Voronina (1962) in the Central Pacific and Indian

Equatorial regions, respectively, phytoplankton, herbivore, and

carnivore peaks were found at successively greater distances "down-

stream" from the area of upwelling. Smayda (1966) found a positive

correlation among winds, coastal upwelling, phytoplankton, zooplankton,

and anchovies in the Gulf of Panama. After examining data from the

Eastern Tropical Pacific where upwelling is weak but relatively

persistent, Blackburn (1966) suggested that this biologically rich area

may be in a steady state in contrast to the "unbalanced" regions of

seasonal upwelling at higher latitudes. Laurs (1967) related the

biomass distribution of the first three trophic levels to upwelling

off the southern coast of Oregon. He found phytoplankton biomass

was highest inshore during active upwelling, while herbivore and

primary carnivore biomass peaked in the fall, after upwelling had

begun to subside, and in the region where the front had intersected

the surface. He also observed that the highest standing stocks of

trophic level III tended to be found successively seaward as the

upwelling season progressed.

The prevailing north-northwesterly winds from May through

September and the surface currents they induce further affect the

hydrography off Oregon by diverting the effluent of the Columbia

River, the largest river draining the West Coast of the United States. Generally, when the Columbia floods in late May or early June (Budinger, Coachman, and Barnes, 1964) the upwelling regime is already established, and the massive flux is driven to the south and offshore in the form of a well defined plume. Using the 32.5‰ isohaline to mark its boundary, the plume reaches its maximum development in early autumn, when it has been found to extend south into northern Californian waters and offshore to a distance of about 650 km (Budinger et al., 1964). By late autumn, the prevailing southerly winds direct the effluent from the Columbia northward along the Washington coast (Duxbury et al., 1966). Wind-mixing, precipitation, and river runoff simultaneously eradicate the plume structure off Oregon.

As for upwelling, the plume affects the hydrography, chemistry, and biology off the Oregon coast. Being relatively warm and fresh, the plume water is separated from underlying oceanic water by a strong and shallow seasonal pycnocline, coinciding with the seasonal thermocline and plume halocline (Mooers et al., in preparation). This pycnocline tends to inhibit the transfer of properties such as heat and salt. Due to its insulation from subsurface waters, the plume probably also functions as a heat sink for incoming solar radiation (Owen, 1968; Evans, 1972). This surface mixed layer gradually increases in depth as the season progresses, except near

the mouth of the Columbia where it remains very shallow (Evans, 1972). Anderson (1964) reported mixed layer depths of 5-10 meters in May and 30-40 meters by early autumn. The pycnocline at the base of this layer averages 20 meters in depth during the summer and is nearly level except inshore where it tends to merge with the permanent pycnocline to form a surface front (Mooers et al., in preparation). Although a seasonal pycnocline is characteristic of the entire northeastern Pacific off Oregon, Anderson (1964) found the mixed layer depth was generally 5-10 meters greater in waters offshore from the plume. Similarly, Evans (1972) noted that where semi-diurnal tides interrupted the river discharge, and caused "cells" of plume water to be intermingled with shelf water, these cells were surrounded by troughs of deeper mixed layer.

The isolation of the shallow mixed layer affects the distribution of nutrients above the summer pycnocline. Photosynthesis, grazing, vertical migration, and passive sinking of organic matter deplete the nutrients in the surface layer. Although the Columbia is a nutrient source for the coastal photic zone (Anderson, 1964; Ball, 1970) the effect of this nutrient enrichment is spent in high primary productivity in the vicinity of the river mouth rather than contributing greatly to the major portion of the plume (Anderson, 1964).

While surface waters in the nearshore area covered by the Columbia effluent generally contain more phytoplankton and have a

higher rate of photosynthesis than ambient coastal waters, Anderson

(1964) claimed the major influence of Columbia River water on phyto-

plankton production is in the timing of the seasonal cycle (i.e. advanc-

ing the spring bloom). He also found that annual production both inside

and outside the plume was similar (60 $gCm^{-2}yr^{-1}$), except for the high-

production areas immediately off the river mouth. Small and Curl

(in press) found the concentration of chlorophyll a was an inverse

power function of distance from shore between approximately 10 and

165 nautical miles offshore, in the Columbia discharge as well as in

oceanic water.

Published studies relating consumer biomass and the

Columbia plume are conspicuously lacking. Cross (1954) believed

two unusually dense samples of copepods collected during a July

cruise may be associated with the Columbia's discharge. Albacore

may migrate into Oregon waters along the warm waters associated

with the plume (Pearcy and Mueller, 1969).

METHODS AND MATERIALS

Zooplankton and micronekton were quantitatively sampled during six cruises between May and October 1969. (See Table 2 for cruise dates.) The standing stock of chlorophyll a was measured during the first five of these cruises. On four cruises (Coastal Oceanography or COOC's 3, 8, 9, and 10) observations were largely confined to the Newport hydrographic line, a latitudinal track off the Oregon coast at 44°39.1'N. Generally, chlorophyll a and zooplankton were sampled at three nautical miles offshore (NH-3), at ten nautical mile intervals from NH-5 to NH-45, and thereafter at twenty nautical mile intervals out to NH-165. Coinciding nekton samples were obtained from NH-15 to NH-165. At every station, hydrocasts were taken to determine the vertical distribution of temperature, salinity, reactive silicate, and nitrate + nitrite. Secchi disk readings were recorded for many stations occupied during daylight. Besides similarly sampling the Newport line, the other two cruises occupied a well-dispersed array of stations bounded by 46°30'N, 128°W, 42°N, and the Oregon coast (COOC-4), and 46°30'N, 128°W, 44°N, and the Oregon coast (COOC-6).

Temperature readings were obtained from the two reversing thermometers attached to each NIO water bottle. Salinity was analyzed using a Hytech® inductive salinometer (Model 6220) as described by

Brown and Hamon (1961). All nutrient determinations employed a Technicon AutoAnalyzer® using the methods of Hager, Gordon, and Park (1968) for reactive silicate and nitrate + nitrite. All processed data and an explanation of the computational techniques are given in Wyatt, Gilbert, Gordon, and Barstow (1969).

The hydrographic data from the first five cruises were compared with surface wind data recorded at 12-hour intervals at 45.621N, 125.000W (National Marine Fisheries Service/Fleet Numerical Weather Center, 1969). NMFS/FNWC wind data was unavailable for October, 1969. Therefore, hydrographic observations for the October cruise (COOC-10) were compared with the daily wind averages obtained from the South Jetty gauge at Newport (U. S. Environmental Science Services Administration, 1969).

Water samples for chlorophyll a determinations were collected in two-liter Van Dorn bottles from 0, 10, 15, 25, and 50 meters, depth permitting. The pigment concentrations were determined by the method of Strickland and Parsons (1965), with the following exception: filters were dissolved in 6 ml of 90% acetone and then ground for one minute at maximum rpm in an ice bath using a Servall Omni-Mixer® to ensure complete pigment extraction. Linear interpolation between sample data points provided a profile of chlorophyll a vs depth which estimates, somewhat imperfectly, the standing crop of plant material on which animals could feed.

Connecting the data points with the most plausible smooth curve led to essentially the same biomass estimates as those obtained by linear interpolation (Appendix I). On the other hand, there was an appreciable and systematic discrepancy between the chlorophyll values integrated to 50 meters and those integrated to the commonly accepted compensation depth (i.e. the depth of 1% of surface illumination). Integrating to 50 m yielded considerably higher pigment values inshore and slightly lower values offshore (Appendix II). The choice of the former procedure will be explained later.

Most zooplankton hauls were taken with a five-meter-long vertical meter net (VMN) constructed of "O" mesh Nitex® netting (0.571 mm aperture). This net was lowered at about 10 m/min to 200 m, depth permitting, then raised vertically to the surface at 30 m/min. Micronekton was collected with a six-foot Isaacs-Kidd midwater trawl (IKMT) of five millimeter (bar measurement) netting with a one-half-meter net of 0.571 millimeter Nitex® mesh for a cod end. During four cruises (COOC's 4, 6, 9, and 10) a 0.7 meter diameter Bongo net of 0.571 millimeter Nitex® mesh was clamped to the towing wire three meters above the bridle of the IKMT to provide an estimate of zooplankton independent of the VMN. Both nets were towed obliquely between the surface and 200 meters, depth permitting, at a tow speed of five knots. The nets were lowered until 800 meters of wire were paid out and retrieved at 30 m/min.

A calibrated flowmeter was situated inside the mouth of each net. The IKMT was also equipped with a distance-depth recorder. To minimize catch variations due to vertical migration and net avoidance all net hauls were taken between dawn and dusk. Net collections were preserved at sea in 10% formalin in seawater buffered with sodium borate.

The samples were analyzed ashore. Nekton and other large forms were first removed from all net hauls. The VMN and Bongo collections were then subdivided into two approximately equal parts with a Folsom plankton splitter. One half of each original sample was sorted into major taxonomic groups, the other half retained for future reference. Dense half-samples were successively split to facilitate sorting the more abundant taxa. The nektonic components of the IKMT hauls were sorted without splitting. Samples were dried at 60°C to uniform weight in an oven to obtain dry biomass estimates for all groups per $10^3 m^3$ water filtered.

HYDROGRAPHY

Sections of temperature, salinity, and sigma-t were constructed to illustrate the hydrography along the Newport line during the six COOC cruises (Figures 1-6). Surface contours of these same parameters, as well as mixed layer depth, were plotted for COOC's 4 and 6 (Figures 7-10, 14-17). Average concentrations of nitrate + nitrite and silicate in the upper 50 meters for COOC-6 are contoured in Figures 18 and 19. The scale of the areal plots often required omitting fine detail within five miles of the coast. Interpretations of these data are largely based upon the following considerations: the zone between the 25.5 and 26.0 sigma-t surfaces delineates the permanent pycnocline or frontal layer, while the inshore slopes of these isopycnals serve to characterize the intensity of upwelling (Collins, 1964). Surface salinities of ≤ 32.0 and ≥ 32.8 are conservative indicators of plume water and upwelled water, respectively (Wyatt, personal communication). Similarly, temperatures less than 10°C are indicative of coastal upwelling (Smith et al., 1971).

The earliest cruise, COOC-3 (12-21 May), was characterized by intense upwelling (Figure 1). NMFS/FNWC recorded a strong north-westerly wind component (5-12 m/sec) from 10-14 May; the inshore stations were sampled during the latter half of this period. Due to the warm, fresh Columbia River water abutted to the colder, saltier

ocean water, the inshore portion of the frontal layer is intensely

upcurved, intersecting the surface 5-10 miles offshore. Neglecting

"noise" and possibly some low-amplitude internal waves (Collins,

1964), the permanent pycnocline is horizontal west of NH-25, and

ranges from 80-110 meters in depth. The plume extends from NH-20

to NH-45. A comparison with the generalized salinity distribution of

Duxbury et al. (1966) suggests the plume's cross sectional area along

the Newport line was atypically large for May; this is expected con-

comitant with strong upwelling so early in the season. Stefansson

and Richards (1964) noted that the characteristically large overall

differences between coastal ($\leq$ 45 miles offshore) and oceanic ($>$45

miles offshore) regions are obscured by the presence of the plume

inshore early in the upwelling season. However, the plume clearly

accentuated the latitudinal coastal gradients (Figure 1). All sections

showed little stratification; the stability of the water column was

relatively weak, compared to subsequent cruises.

The combined effects of several factors are thought to cause

pronounced irregularities in the vertical distribution of the 8°C iso-

therm, which is generally located in the bottom half of the frontal

layer. Most significantly, a water mass forms near the surface

front, presumably by wave and wind-induced mixing of recently

upwelled water and surface water. During its brief exposure near

the surface, this water is warmed, but its salinity is not appreciably

modified. This water mass sinks and flows seaward at the base of the inclined permanent pycnocline, causing a temperature inversion (Mooers et al., in preparation). Collins, Mooers, Stevenson, Smith, and Pattullo (1968) noted that the pycnocline is a zone of high variability due to the relatively large vertical shear. Nearly isothermal conditions in the ambient waters, internal waves, and "noisy" data can all help to account for the fluctuations in the depth distribution of the 8°C isotherm.

During COOC-4 (18 June-3 July), a weak northerly wind component (1-5 m/sec) which had prevailed for several days became negative for a short period while several inshore stations along the Newport line were being occupied. Upwelling temporarily subsided (Figure 2) due to the winds shifting from northerly to southerly. Such reversals are most common early and late in the season and cause the upwelling season to be divided into upwelling and non-upwelling periods. Offshore, the pycnocline was slightly inclined, shoaling to 70-95 meters at NH-25. Only the inshore portions of the isopleths become level or downwarped during the temporary lapses in upwelling (Pillsbury, 1972; Mooers et al., in preparation).

The sections for this cruise (Figure 2) demonstrate the previously mentioned correspondences between the permanent pycnocline and permanent halocline, both centered around 100 meters, and the newly-formed seasonal pycno-, halo-, and thermoclines, which were all

most pronounced from 0-10 meters depth inshore of NH-45. The

sharp near-surface gradients in all of the seasonal hydrographic

clines agree well with the extremely shallow mixed layer depth for

the entire area (Figure 10) which ranges from less than 2.5-5 meters

out to NH-100, and thereafter remains less than 25 meters. A

shallow lens of plume water covered the Newport line shoreward of

NH-100; the axis of the plume was located at NH-45. The plume

extended south and, to a lesser extent, offshore (Figure 8). Iso-

therms suggest active, incipient, or recently-subsided upwelling

south of Cape Blanco (Figure 7). (Lack of hydrographical data

inside the 12°C isotherm precludes a more definitive statement.)

Sigma-t surface isopycnals (Figure 9) are consistent with the tempera-

ture, salinity, and mixed layer depth contours.

During COOC-6 (31 July-12 August) and the week preceding the

cruise, the observed winds were variable but had a consistently

northerly component of 1-11 m/sec. Moderate upwelling occurred in

a narrow band inshore of NH-5 (Figure 3). The more steeply sloped

frontal layer shoaled to 50-80 meters at NH-25. The seasonal

pycno-, halo-, and thermoclines averaged 15-30 meters depth; this

correlates nicely with mixed layer depths (Figure 17) which range

less than 5 meters along the coast and from 5-20 meters beyond

NH-15, away from the influence of upwelled waters. Plume

waters covered the Newport line seaward of

NH-15 with a bilobed core between 50-85 and 120-155 miles offshore. Surface temperatures offshore and all surface salinities had increased markedly (Figures 14 and 15). Westward extension of the plume (Figures 15 and 16) was also apparent. Isopleths of nitrate + nitrite and silicate integrated to 50 meters (Figures 18 and 19) showed that upwelling and perhaps the Columbia River are important sources of these two nutrients. Both nitrate + nitrite and silicate decreased rapidly moving offshore, although the nitrate + nitrite gradient was more pronounced. An isolated parcel of silicate-rich water was centered around 127°W on the Newport line. Vertical sections and contour plots suggest this patch to be plume water.

The hydrographic data from COOC-8 (18-28 August) showed essentially the same characteristics as those from COOC-6, except for a sharp hump in the frontal layer which was, at first glance, most plausibly attributed to "noise" and/or internal waves (Figure 4). However, the very variable although predominantly northerly winds (+9 to -5 m/sec) may have caused substantial fluctuations in the inshore frontal layer as the inshore stations were being sampled. The previously observed trends continued: the slope of the frontal layer had steepened slightly, rising to 45-75 meters depth at NH-25. The seasonal pycnocline descended to 40 meters, increasing the average mixed layer depth. Plume waters along the Newport line ranged from 15-80, 100-160, and 180 to beyond 185 miles offshore,

the most distant station occupied.

Northerly winds of 1-12 m/sec blew consistently at every 12-hour observation during the first half of September. The strongest winds (7-12 m/sec) were recorded during COOC-9 (9-18 September). This cruise was also characterized by moderate upwelling, but the frontal layer had migrated offshore, surfacing between 4-12 miles off Newport (Figure 5). Of the six COOC cruises, the frontal layer was most steeply inclined during COOC-9; it was located between 18-43 meters at NH-25. The lower limit of the seasonal pycnocline remained close to 40 meters offshore. The plume was weakening and was confined to NH-25 to NH-100. Between the shore and NH-100, there was a difference of 8 C in the surface temperature.

Upwelling had subsided during COOC-10 (22-31 October) (Figure 6). Northerly winds were replaced by southerly winds, and the permanent pycnocline was in the process of being restored to its pre-upwelling level. The frontal layer was downwarped inshore and had descended to 35-55 meters at NH-25. Inshore of NH-85 the seasonal pycnocline had been virtually destroyed; beyond NH-85 it was weak and had deepened to about 55 meters. The 26.5 isopycnal was sharply down-warped inshore. As Smith (1968) noted, this descent of isopycnals toward the coast at depths below 100 meters is a manifestation of the poleward undercurrent which extends to shoaler depths during the Davidson Current regime. The permanent pycnocline was still relatively

steeply inclined compared to the ten-year average for the depth

distribution of the frontal layer during October (Wyatt, unpublished

data), implying that the 1969 upwelling season had lingered longer

than usual. The temperatures in the upper layers were warm, both

inshore and offshore. The plume had regressed to the north of the

Newport line.

All six frontal layer sections agree moderately well with Wyatt's

ten-year averages for the depth distribution of the 25.5 and 26.0

sigma-t isopleths along the Newport line. However, inshore of

NH-25, there are marked discrepancies between Wyatt's generalized

averages and the 1969 plots. These inshore variations are due to

fluctuations in upwelling and are consistent with observations by

Fisher (1970) and Lane (1965) which suggest a 0-3 1/2 day response

time coupling northerly winds and the recurrence of upwelling.

The hydrographical data from these six cruises suggest that winds

also markedly influence the structure and distribution of the plume,

the mixed layer depth, and the stratification of the water column.

Thus, while the long-term seasonal average of the winds and the

induced hydrography behave smoothly, the short-term fluctuations

around the average are appreciable.

TROPHIC LEVEL I

The standing stock of trophic level I (Λ_1) is the biomass of all plant material (living or dead) available for foraging. A relative index of this quantity is generally obtained from chlorophyll a measurements. Unfortunately, chlorophyll a biomass is not always a good estimator of phytoplankton standing stock (Strickland, 1960) since the ratio of chlorophyll a/cell weight varies with species composition, light intensity, nutrient concentrations, and physiological condition. This ratio is even subject to diel variation (Yentsch and Ryther, 1957; Glooschenko, Curl, and Small, in press). However, chlorophyll a content of the photic zone estimates phytoplankton biomass within an order of magnitude (Strickland, 1960), and this correspondence has been utilized in this study.

While the median standing stock of Λ_1 along the Newport line remained fairly constant throughout the upwelling season, the biomass in the coastal ($\leq$ 45 miles from shore) and oceanic (> 45 miles from shore) regions appeared to increase and decrease, respectively, as the season progressed (Figure 23, Table 1); these trends were not statistically significant ($P > .10$, Corner Test; Tate and Clelland, 1957). Throughout the season, coastal standing stocks were consistently higher than oceanic ones ($P \ll .01$, Concordance Test; Tate and Clelland, 1957). The average biomass and standard deviation of Λ_1 were both highest inshore and decreased sharply offshore. Inshore-offshore gradients in biomass and spatial variability were both more marked than temporal gradients.

The standing stock of chlorophyll a at coastal stations appears

to be largely determined by short-term upwelling effects. During

COOC-3, NH-3 and NH-5 were situated shoreward of the frontal

layer (Figure 1). The low standing stocks at these stations may be

attributed to several causes: (1) the vertical velocity component in

this region of intense upwelling may not allow the development of a

bloom during the brief vertical ascent of any given parcel of water

(Cushing, 1971), (2) low temperatures may temporarily limit the

growth rate (Small, personal communication), (3) seed stock may be

scant during the vertical ascent, (4) recently upwelled water may lack

the necessary chelators which biologically condition the water, or may

contain inorganic trace metals which in their unchelated form might

inhibit phytoplankton growth (Barber et al., 1971).

The cessation of upwelling during COOC-4, coupled with the

increased temperature and strong stratification in the surface layers

at NH-3 and NH-5 (Figure 2), may have allowed for enhanced inshore

production. During COOC's 6 and 8, phytoplankton maxima apparently

occurred close to 10 and 5 miles offshore, respectively. Upwelling is

slightly more intense and the surface front is displaced farther offshore

during COOC-6 than COOC-8 (compare Figures 3 and 4). Fluctuations

in upwelling and offshore advection probably determine the location of

the chlorophyll maximum. COOC-9 data suggest that the surface

front (Figure 5) may contain an abundance of phytoplankton near NH-10.

Unfortunately no chlorophyll data are available for this station. The relative maximum around 35-45 miles off Newport may be the remnants of a rich crop that was produced in more northerly coastal waters and translocated to the southwest without incurring heavy grazing. Alternatively, the high standing stock might be the result of the mechanical aggregation of local growth at the convergence front in this region (Figure 5).

The standing stocks of Λ_1 at the oceanic stations (as determined by integrating chlorophyll $\underline{a}$ from 0-50 m) exhibit a slight seasonal trend. As nutrients above the seasonal pycnocline are depleted and daily insolation decreases, the phytoplankton biomass shows a general decline (Figure 23). No explanation is offered for the anomalous oceanic biomass observed during COOC-8 which interrupts the general seasonal decline.

The areal distribution of chlorophyll $\underline{a}$ off the Oregon coast during COOC-4 is shown in Figure 11. The highest concentration of phytoplankton occurred in a 25 mile wide longitudinal strip bounded by the coast. Near the mouth of the Columbia River, this zone of abundance extends to 45 miles offshore. The biomass of phytoplankton in the immediate vicinity of the river mouth is comparable to the oceanic values observed on this cruise; typical coastal values are first observed 15 miles beyond the river mouth. The oceanic Northeast Pacific is characterized by low standing stocks compared

to upwelling regions (Anderson, 1964; Malone, 1971).

The areal distribution of Λ_1 abundance does not show a close correlation with the surface contours of temperature, salinity, or sigma-t (compare Figures 7-9 with Figure 11). No such association should be expected since upwelled waters and the Columbia River effluent (which are often intermixed) are both characterized by high standing stocks. Each of these water sources is associated with extreme, but opposite, values of these hydrographic parameters. Since mixed layer depths are shallow in both upwelling areas and near the mouth of the Columbia, an overall agreement between shallow mixed layer depths and high phytoplankton biomass is expected. This rough correlation is observed (compare Figures 10 and 11).

While the same general longitudinal orientation of chlorophyll $\underline{a}$ contours is evident during COOC-6 (Figure 20), many features are markedly different. Standing stocks are higher in the inshore waters and lower in the oceanic waters; the coastal gradients are much steeper. A band of maximal phytoplankton biomass parallels the coast; its axis varies from several miles offshore at Tillamook Head to about 15 miles offshore in the extremely rich waters off the mouth of the Columbia.

Again, chlorophyll $\underline{a}$ contours do not conform well with those of surface temperature, salinity, and sigma-t (compare Figures 14-16

with Figure 20). Mixed layer depth and chlorophyll a biomass again show a crude but negative correlation (compare Figures 17 and 20).

Nutrient and chlorophyll a contours generally show the best mutual agreement (compare Figures 18 and 19 with Figure 20), especially nitrate + nitrite and chlorophyll a. However, both nitrate + nitrite and silicate concentrations decrease in a seaward direction. The sharper rate of decrease in nitrate + nitrite can be explained in three ways: (1) Nitrate and nitrite are used by more organisms and in greater amounts than silicate. Isolated areas notwithstanding, nitrate is the limiting nutrient in the world ocean (Redfield, Ketchum, and Richards, 1963). (2) While phytoplankton are thought to have no storage capacity for silicate (Curl, personal communication), and extract this nutrient only when needed, they extract nitrate and nitrite whenever these nutrients are available, irrespective of need (Caperon, 1968). (3) Diatom frustules account for virtually all the silicate removed from the water. Since appreciable numbers of diatoms in the Northeast Pacific are generally found only in the nearshore divergence zones due to nutrient limitation at relatively high levels (Malone, 1971), any silicate in the photic layer which "leaks through" the near-shore waters without being utilized will likely remain largely untapped. This may explain the isolated parcel of silicate-rich water centered around 127°W on the Newport line.

TROPHIC LEVEL II

Filter-feeding herbivores comprise trophic level II (Λ_2).
Euphausiids, copepods, salps, doliolids, thecosomatous pteropods,
and crab zoea were all included in Λ_2, although the relative abun-
dances of the latter two groups were insignificant.

Along the Newport line, Λ_2 biomass decreased significantly
($P < .05$, Corner Test; Tate and Clelland, 1957) by an order of
magnitude during the upwelling season (Figure 24, Table 2). The
overall decline was interrupted by a peak during September which
was most pronounced in the coastal region. The seaward decline in
the standing stock was even sharper than the seasonal decrease,
and was also statistically significant ($P < .05$, Corner Test; Tate and
Clelland, 1957). Standing stocks decreased by an order of magnitude
between NH-3 and NH-15. An irregular and more gradual decline
occurred seaward of NH-15. Considerable temporal and spatial
fluctuations in the standard deviations are evident, but no distinct
trends emerge.

Copepods generally comprised a dominant portion of the biomass
of Λ_2 (compare Tables 2 and 6), except early in the season when huge
concentrations of euphausiids were caught at NH-25 (compare Tables
2 and 7). Coastal standing stocks were relatively low during the May
and June cruises and peaked in midseason. Otherwise, the temporal

and spatial distributional features for copepods resemble those described for Λ_2 (compare Tables 2 and 6). Only the decrease in copepod biomass with increasing distance from shore was statistically significant ($P < .05$, Corner Test; Tate and Clelland, 1957). The decline was highly significant ($P \ll .01$) in the coastal region.

Standing stocks of euphausiids declined as the season progressed (Table 7). In coastal waters, euphausiids were the most abundant constituent of Λ_2 in May. The inshore biomass declined precipitously to near-zero values by October. Oceanic stations showed a gradual decline in euphausiid abundance, always maintaining moderate standing stocks.

After decreasing from NH-3 to NH-15, euphausiid biomass increased to a pronounced maximum 25 miles offshore, and then declined seaward. Casual inspection of the net collections suggests the diminutive inshore peak and the absolute maximum at NH-25 were dominated by Thysanoessa spinifera and Euphausia pacifica, respectively. Hebard (1966) reported highest abundances of Euphausia pacifica at NH-25 with maximal concentrations of Thysanoessa spinifera occurring farther inshore. Brinton (1962) considered T. spinifera to be an indicator of upwelling. NH-15 probably represented a transition zone between the centers of distribution of these two species.

The closely related salps and doliolids were considered collectively. These groups were either absent or rare inshore of NH-25 at all times (Table 8). While their distribution was extremely patchy throughout the upwelling season, maximal concentrations occurred during summer between NH-45 and NH-65. They were scarce in late October. The extreme variability in their spatial and temporal distributions is shown in Table 8.

Although the limited and very variable net collections preclude any definitive generalizations regarding the relationships between Λ_2 and hydrography, several tenuous conclusions seem justifiable.

Copepods appear to peak at, or inshore of, NH-3 throughout the upwelling regime (Table 6). During an upwelling season, Pak, Beardsley, and Smith (1970) have observed the previously-mentioned temperature inversion submerging 3 km offshore and then gradually descending below the permanent pycnocline. Thus, NH-3 may be slightly seaward of a one-sided convergence zone between the permanent pycnocline and water upwelled from the inshore cell of Smith et al.'s (1971) two-cell upwelling model. The high standing stocks of copepods found in this convergence zone might be a consequence of enhanced primary production and/or mechanical aggregation. This interpretation suggests copepod biomass should be highest in this region during periods of active upwelling. This may be the case (compare Figures 1, 3-6 and Table 6), but sampling closer to shore

is essential before drawing any definitive conclusions.

Without exception, euphausiid biomass peaks inside or along the inner edge of the Columbia River plume (compare Figures 1-5 and Table 7), perhaps as a consequence of the gradual offshore displacement of the plume during the first half of the season.

Salps and doliolids were also associated with plume water (compare Figures 1-5 and Table 8); maximal abundances occurred at NH-45 and NH-65. The high biomass at these intermediate stations may be related to the pronounced heating of offshore surface waters during the season (Pattullo et al., 1969). Hubbard and Pearcy (1971) recorded a similar distribution of salps off the Oregon coast.

Composite medians of phytoplankton and herbivore standing stocks showed an overall seasonal inverse relationship (compare Figures 23 and 24). Unfortunately, no phytoplankton data are available for COOC-10, at which time the herbivore biomass had declined precipitously. If coastal and oceanic regions are considered separately, the standing stocks of the two trophic levels varied directly early in the season; thereafter they varied irregularly at coastal stations, inversely at oceanic stations. Although more closely coupled seasonal relationships between Λ_1 and individual groups of Λ_2 can be cited

(e.g., the inverse relationship between coastal chlorophyll $\underline{a}$ biomass and coastal euphausiid biomass (compare Tables 1 and 7), it should be noted that seasonal variations in median Λ_2 biomass and its constituents were in terms of orders of magnitude. Inshore and offshore medians in chlorophyll $\underline{a}$ biomass each varied seasonally by no more than a factor of two; the seasonal variation in the composite chlorophyll $\underline{a}$ median is $<20\%$. Relative constancy of chlorophyll $\underline{a}$ in the offshore waters of the Northeast Pacific has been documented by Steemann Nielsen (1962), Parsons (1965), and others. Perhaps, as McAllister (1959) and Parsons (1965) have observed, the life cycles of herbivores are closely tuned to the seasonal fluctuation in primary production which may vary by a factor of 40 (Parsons, 1965).

Figure 12 shows the areal distribution of Λ_2 during COOC-4. High standing stocks of herbivores were found in upwelling regions, off the mouth of the Columbia, and, to a lesser extent, in the nearshore portion of the oceanic region. Thus, surface contours of temperature, salinity, and sigma-t (Figures 7-8) show little conformity with those of Λ_2 biomass. Mixed layer depth (Figure 10) and Λ_2 isopleths are also basically uncorrelated. A general positive correlation between Λ_1 and Λ_2 is observed in coastal waters (Figures 11 and 12); sparse data points suggest the oceanic region is characterized by relatively low values of both Λ_1 and Λ_2.

During COOC-6, Λ_2 biomass contours (Figure 21) parallel the coast. The axis of the band of maximal standing stock of Λ_2 varies from about 7 miles offshore at Cape Lookout to about 20 miles offshore at the mouth of the Columbia. Although Λ_2 contours lack the detail and the tightly-packed configuration of the chlorophyll a contours just off the mouth of the Columbia (compare Figures 21 and 20), this difference may be related to sample density. In any case, the biomass trends of both Λ_1 and Λ_2 are strikingly similar. Thus, the previously-mentioned comparisons between chlorophyll a and nutrient isopleths (compare Figures 18 and 19 with 20) obtain between Λ_2 and nutrient isopleths (compare Figures 18 and 19 with 21). Nutrient concentrations decline monotonically with increasing distance from the shore; Λ_1 and Λ_2 both peak several miles off the coast, the seaward decline being much greater than the shoreward decrease. Surface contours of temperature, salinity, and sigma-t (Figures 14-16) show little correlation with contours of Λ_2, other than a general inverse correlation between Λ_2 and temperature in the coastal region. The excessive nearshore variations in mixed layer depth isopleths (Figure 17) obscure any overall correlation that may exist between this parameter and Λ_2 biomass.

TROPHIC LEVEL III

Trophic level III (Λ_3) includes all primary carnivores. While the composition of Λ_3 is not completely known (Cushing, 1971), fish, shrimp, cephalopods, chaetognaths, medusae, siphonophores, ctenophores, amphipods, annelids, and gymnosomatous pteropods were included in this trophic level. The first three groups are nektonic vertically migrating organisms that were sampled with the IKMT. The remaining groups (i.e., the zooplankton) were sampled with Bongo nets for the areal surveys during COOC's 4 and 6.

A comparison of Figures 24 and 25 shows Λ_3 biomass is distributed very similarly to that of Λ_2, the only differences being less drastic decreases in standing stock, both as the season progressed and with increasing distance offshore. While no trends are statistically significant for total Λ_3, VMN Λ_3 and IKMT Λ_3 decreased and increased, respectively, going seaward ($P < .01$ for both trends, Corner Test). Total Λ_3 biomass is unavailable for NH-3 and NH-5 (Table 5) since IKMT hauls were not taken at these stations. However, the VMN component of Λ_3 (Table 3) is sufficient to produce an upward inflection in Figure 25 (dashed line) were the curve extended shoreward. Had IKMT hauls been taken at NH-3 and NH-5, Table 4 and Figure 26 imply their contributions to Λ_3 biomass would have been insignificant. In general, only zooplankton contributed significantly to biomass at NH-15 (compare Tables 3 and 4)

At distances ≥ 25 miles offshore, zooplankton and nekton biomasses were almost equally important.

The low catches of nekton inshore of NH-25 (i.e., the region where zooplankters of Λ_3 peak) indicate that depth may limit the horizontal distribution of vertical migrants (Pearcy, 1964). Since euphausiids are the preferred food of the most abundant species of mesopelagic fishes caught off Newport (Tyler, 1970), maximal fish biomass at NH-45 (Table 9) may reflect a compromise between (1) abundant euphausiid forage, and (2) sufficient depth of water column for reaching preferred light intensity during the day (Pearcy, 1964).

All nektonic groups behaved similarly (Tables 9-11 and Figure 26) and are therefore examined collectively. An overall decline in the standing stock throughout the season was interrupted by a slight midsummer peak for fishes and shrimps. Coastal and oceanic stations show this same seasonal response, although coastal biomass is generally two to three times lower. Catches of fishes and shrimps were very low at NH-15, peaked at NH-45, and then fluctuated irregularly. Cephalopods were similarly distributed along the Newport line, except for their modest peak occurring at NH-25.

Medusae, siphonophores, and ctenophores were considered as a single group. Standing stocks tended to decrease as the season progressed, but a relative maximum in late summer interrupted the decline (Table 12). The corner test indicated no trends are

statistically significant. The highest catches were associated with coastal stations; offshore values were irregular but noticeably lower.

Chaetognaths were abundant both in May and late summer (Table 13); the separate peaks were due to high standing stocks in the oceanic and coastal regions, respectively. Standing stocks declined dramatically from peak abundances at NH-3 to minimal ones at NH-15. Seaward of NH-15, the biomass fluctuated between intermediate levels. The marked inshore decline caused the corner test to indicate a highly significant ($P < .01$) biomass decrease, even though there were no overall latitudinal biomass gradients at the offshore stations.

Scanty amphipod data suggest a significant decline in biomass throughout the season ($P < .05$), although inshore stations showed a sharp peak in late August (Table 14). Quantifiable biomasses were most consistently obtained in offshore waters.

Trace amounts of annelids characterized all stations ≤ 25 miles offshore (Table 15). Highest standing stocks were observed at NH-45 and NH-65; seaward stations had intermediate and variable values.

Again, extreme caution is necessary when generalizing from such a meager collection of net hauls, so widely dispersed in both time and space. However, several relationships between Λ_3 and hydrography are apparent.

Although maximal standing stocks were taken between NH-125 and NH-165 during May, the highest catches of all individual nektonic groups were generally inside or along the edges of the plume (compare Figures 1-5 with Tables 4 and 9-11). Data from COOC-9 agree especially well with this trend. Despite sketchy data, medusae + siphonophores + ctenophores appear to peak either in the inshore up-welling zone shoreward of the inclined permanent pycnocline or inside and along the edges of the plume (compare Figures 1-5 with Table 12). Maximal abundances of chaetognaths were found offshore during COOC-3, and at the inshore upwelling zone later in the season (compare Figures 1-5 with Table 13).

Except for the offshore peaks associated with unseasonably early upwelling in mid-May, standing stocks of Λ_3 were thus largely confined to two major regions: (1) the inshore upwelling zone described above, and (2) the warm waters in and along the edges of the plume, abutting against the recently-upwelled waters in the Ekman layer. Both of these areas are fronts--boundaries between surface waters of different densities, recognizable by strong horizontal gradients of temperature and/or salinity, and accompanied by some sinking of one or both types of water involved (Blackburn, 1965). Griffiths (1965) and Laurs (1967) have documented the utility of fronts in determining the spatial and temporal distributions of lower trophic level biota. Convergent fronts are thought to mechanically

aggregate plankton while divergent fronts may cause conditions specifically favorable to the growth of a large standing stock of plankton. Nekton are thought to move into a front to feed on the abundance of plankton. A comparison of Figures 1-5 with Tables 1, 2, and 5 shows that peak biomasses often occur near the frontal regions associated with the inshore upwelling zone and the edges of the plume.

Since Λ_2 was most abundant in these same two regions, a direct correlation should obtain between these two trophic levels. Figures 24 and 25 show this to be the case; paired inshore, offshore, and composite median curves for seasonal trends and the median latitudinal curves all have the same general shapes. Λ_3 values are generally lower and variations are somewhat damped.

The areal distribution of Λ_3 off the Oregon coast during COOC-4 is shown in Figure 13. Contours run longitudinally with virtually no noticeable correlation with the very well defined plume (compare Figures 15 and 16 with Figure 13), although the axis of maximal standing stock does shift from about 50 miles off Newport to about 35 miles off the Columbia. A similar maximum at intermediate distances offshore was noted by Day (1971) in the waters off Vancouver, Canada. Although a positive correlation between the standing stocks of Λ_3 and Λ_2 (Figures 13 and 12) is seen off Newport and, to a lesser extent, off Tillamook Head, no such relationship is evident at the intermediate

latitudes. No significant relationships between Λ_3 biomass and temperature, salinity, and sigma-t isopleths are apparent (compare Figures 7-9 with Figure 13), for the reasons stated earlier. Chlorophyll a (Figure 11) and, more surprisingly, mixed layer depth (Figure 10), also poorly match the configuration of Λ_3. However, the generally parallel orientation of isopleths of the above parameters should be noted.

During COOC-6, the variability of the very limited number of data points revealed no large-scale structure in the distributional features of Λ_3 (Figure 22). Extremely low standing stocks of Λ_3 were associated with both the intense upwelling region surrounding Newport and the waters off the mouth of the Columbia. Since these areas were rich in nitrate + nitrite and silicate (Figures 18 and 19) and had high standing stocks of chlorophyll (Figure 20), quasi-inverse relationships exist between Λ_3 contours and isopleths of these three parameters.

DISCUSSION

The trophic level approach is a useful simplification for studying how ecosystems work. In a rough way, it enables the quantification and prediction of the energy flux through the system. The shortcomings of this approach are well documented. Parsons and LeBrasseur (1971) demonstrated that the energy flow through populations of grazing zooplankton or feeding juvenile fish is strongly dependent on the sizes and distributions of the food organisms. Keast (1971) showed that behavioral, physiological, and anatomical specialization underlie particular food selections. Moreover, the past history of the individual and the ability of organisms to operate on more than one trophic level depending upon environmental conditions have been reported by Lasker (1966) for Euphausia pacifica. Thus, determining the abundance of potential food energy in particular pathways of an ecosystem requires a knowledge of the intrinsic morphometric, physiological and behavioral properties of the component animals. Merely knowing the total biomass, ideally in units of ash free dry weight which represent tissues of comparable metabolic activity from plankter to plankter (Raymont, 1963) is not of paramount importance since it is not possible to use the total biomass of any trophic level to express its impact on the preceding or succeeding trophic level. Nevertheless,

this study has suggested the conclusions already mentioned as well as some intriguing speculations.

As was previously mentioned, there is an appreciable and systematic discrepancy between chlorophyll $\underline{a}$ values integrated to 50 m and those integrated to the commonly accepted compensation depth (i. e. the lower limit of the photic zone). The former procedure yields considerably higher pigment values inshore and slightly lower values offshore (Appendix II). Lack of samples from below 50 m on most Van Dorn casts precludes integrating to the compensation depth for several oceanic stations. Therefore, chlorophyll $\underline{a}$ profiles were consistently integrated to 50 m. Since phytoplankton biomass available to herbivores is a primary consideration, this method seems acceptable. However, advection and sinking of chlorophyll below the compensation depth may still be an important source of food for grazers. Also, near-surface pycnoclines may restrict vertical migrations to depths below the photic zone (Farran, 1947).

Chlorophyll $\underline{a}$ profiles from COOC-8 (Figure 27) and COOC-9 (Figure 28) suggest the possible importance to herbivores of chlorophyll $\underline{a}$ situated below the compensation depth, which generally ranges from 10-25 m at coastal stations and 25-60 m at oceanic stations. (Appendix II lists compensation depths for stations occupied during COOC-4.)

Figure 27 also demonstrates that in nearshore regions chlorophyll a may behave in a manner consistent with Smith et al.'s (1971) two-cell upwelling model and the previously mentioned optical studies by Pak et al., 1971. These studies indicated a cross-sectional flow which was seaward near the surface, shoreward at the top of the inclined permanent pycnocline, seaward at the bottom of the inclined frontal layer, and shoreward below that. The seasonal pycnocline (delimited by the 24.0 and 24.6 isopycnals; Mooers, 1970) may act as a barrier to upwelled water, causing the sinking of this surfaced water along with the entrained chlorophyll, and its subsequent movement offshore between the two pycnoclines. This pattern is evident in Figure 27. Previous studies have led Small (personal communication) to consider the feasibility of using chlorophyll a, as well as other biological parameters, as a quasi-conservative Lagrangian tracer of upwelled water. Often, weakened gradients in or above the seasonal pycnocline allow upwelled water to continue offshore at the surface instead of sinking between the two pycnoclines. Under these circumstances, a chlorophyll a maximum has also been observed to extend seaward at the sea surface (Small and Ramberg, 1971; Schonzeit, unpublished data).

Figure 28 shows the gradual descent of the subsurface chlorophyll maximum in offshore waters which Anderson (1969) believes to be characteristic of the Northeastern Pacific. Anderson has

demonstrated that this layer is photosynthetically active despite light

intensities approximating 0.1% of surface illumination. Data from

four oceanic stations spaced about 30' longitude apart (Table 16) show

a continual accretion of chlorophyll in the 50-75 m depth zone with

increasing distance offshore while the chlorophyll content in the 0-

50 m layer remains virtually unchanged. (Constant chlorophyll

content from 0-50 m was not observed at oceanic stations along the

Newport line during COOC-9, as shown in Figure 28.) Assuming (1)

grazing and all other factors remain constant, (2) the chlorophyll $\underline{a}$

in the 50-75 m zone is productive, and (3) the chlorophyll maximum

is at constant depth, these data suggest that the effect of increased

illumination is quantitatively more important than increased proximity

to the permanent pycnocline (and, hence, to a source of nutrients).

Another plausible hypothesis is based on the belief that healthy dia-

toms maintain neutral buoyancy by means of an "ion pump" (Beklem-

ishev, Petrikova, and Semina, 1961). Nutrient-deficient diatoms may

sink to a level where increased nutrients enable the diatoms to stabi-

lize themselves. These diatoms might subsist at marginal light and

nutrient requirements while being advected offshore. The chlorophyll

concentration in this layer increases as cells continue to sink from

above. This "conveyor belt" mechanism may operate until decreasing

illumination causes these cells to lose their ability to photosynthesize

and, eventually, to osmoregulate, after which they sink out of the

water column. Muehlberg and Kulm (in preparation) propose a model to explain the transport of diatoms and the sedimentation of their frustules based on the two-cell upwelling model and the buoyancy considerations mentioned above.

The previously mentioned similarity between the seasonal and temporal distributions of Λ_2 and Λ_3 (Figures 24 and 25) merits closer scrutiny. While Λ_2 is entirely planktonic, Λ_3 includes both plankton and nekton. When copepods and chaetognaths, representative plankters of Λ_2 and Λ_3, respectively, are plotted on the same set of axes (Figure 29), the direct correlation between the medians is remarkable. (It must be borne in mind, however, that any differences between the shapes of the curves are suppressed by plotting the biomass on a logarithmic scale.) LeBrasseur (1965) also noted a similar trend in the temporal distribution of copepods and chaetognaths at Weather Station "P" (45.621°N, 125.000°W). The direct correlation between this predator-prey pair despite the strong oscillations in biomass may be explained by many hypotheses, none of which are mutually exclusive.

The two groups may exhibit the same kind of patchiness because their spatial distributions are a function of the physics of the ocean--with all plankters being distributed into the same types or patches of water. Such multi-species distributions may result from the "search time" for locating suitable patches being small compared

with the "utilization time" during which conditions in a typical patch remain favorable. Physiological and behavioral mechanisms may foster group coherence; in the present case, for example, copepods and chaetognaths may be transported together as a result of similar patterns of vertical migration. Very precise timing of annual life cycles may also be a significant factor.

Patchiness appears to be an important factor in the ecology of many organisms of the lower trophic levels. Lasker (1966) believed Euphausia pacifica exploits aggregations of copepods rather than depending on its marginal ability to filter enough carbon from a dilute suspension. Ivlev (1961) showed that animals convert, and grow more effectively, on food which is distributed in a patchy way, than on food which is distributed evenly. Clearly, aggregations could control the position of nekton and larger plankton. In such cases, the utility of the median in characterizing biomass distributions would require careful reevaluation.

Comparing Λ_2 and Λ_3 biomasses (Figures 24 and 25) suggests another shortcoming of attempting to elucidate ecosystem structure solely from standing stock data. The biomasses of both trophic levels are generally of the same order of magnitude. At the two farthest offshore stations, Λ_3 biomass is even higher than that of Λ_2. More strikingly, an inverse biomass pyramid is generally observed at Weather Station "P" between Λ_1 and Λ_2, a high herbivore biomass

being sustained on a small phytoplankton base (Strickland, 1965). As

Curl (1962) has noted, "the standing crop of plankton at any given time

is a result of gross production minus attrition due to mortality and

katabolism over a preceding interval." Thus, its magnitude can give no

precise picture of production rates, especially in the oceanic Northeast

Pacific, where there is such close coupling between Λ_1 and Λ_2. In

this region herbivores "anticipate" the spring burst in primary produc-

tion; their grazing pressure at Weather Station "P" is sufficient to

maintain chlorophyll $\underline{a}$ biomass at near-constant concentrations, while

primary production varies annually by a factor of 40 (Strickland, 1965).

Thus, sharp increases in Λ_1 are never observed; the bursts in primary

production manifest themselves only as increases in the standing stocks

of the successive trophic levels. Chlorophyll $\underline{a}$ measurements alone

would fail to distinguish such an area from a truly unproductive one in

which the phytoplankton and herbivore peaks were out of phase.

It should be noted that while Λ_2 and Λ_3 curves are basically

similar, the median trace of the latter is a suppressed version of the

former. Although the variance associated with increasing abundance

is generally multiplicative and tends to "explode" at high population

densities, the increased variance of Λ_2 cannot likely be attributed to

the variance being directly related to the mean since the log scale tends

to maintain the variability within the same linear distance from all

central tendencies. Perhaps this consideration justifies the use of

semi-log plots for studying such distributions. At any rate, the decreased variability in Λ_3 appears to be real.

Perhaps the muted response of Λ_3 to varying concentrations results from increasing resilience of the higher trophic levels which generally have longer lives and can better integrate and "average out" fluctuations in environmental parameters (e.g. food fluctuations). LeBrasseur's (1965) data from Weather Station "P" agree with this concept. He found copepods and chaetognaths both exhibited a seasonal cycle, but the fluctuations of copepod biomass were more pronounced.

The lag time between eating and incorporating food energy into either growth or reproductive output is also a factor which could tend to increase, as well as decrease variability. Blackburn (1965) demonstrated that three months was a reasonable estimate of the average time for phytoplankton material to be converted into tissue of small primary carnivores in the Eastern Tropical Pacific. During the entire time, the biota involved may be transported away from the site of upwelling.

The complexity of the circulation in the Northeast Pacific is well documented (Laurs, 1967; Mooers et al., in preparation, and others). The waters covering separate parts of the Newport line are likely to have surfaced in different latitudes at different times and from different depths; they may have been transporting dissimilar biotas for varying amounts of time. Thus, the dearth of statistically significant relationships between the lower trophic levels and

hydrography may be partially attributed to the complexity of the system. As Steele (1961) has noted, apparent randomness and poor correlations between different biological variables may result from well defined and interrelated processes if the scale of the study is too large and the sampling regime too diffuse.
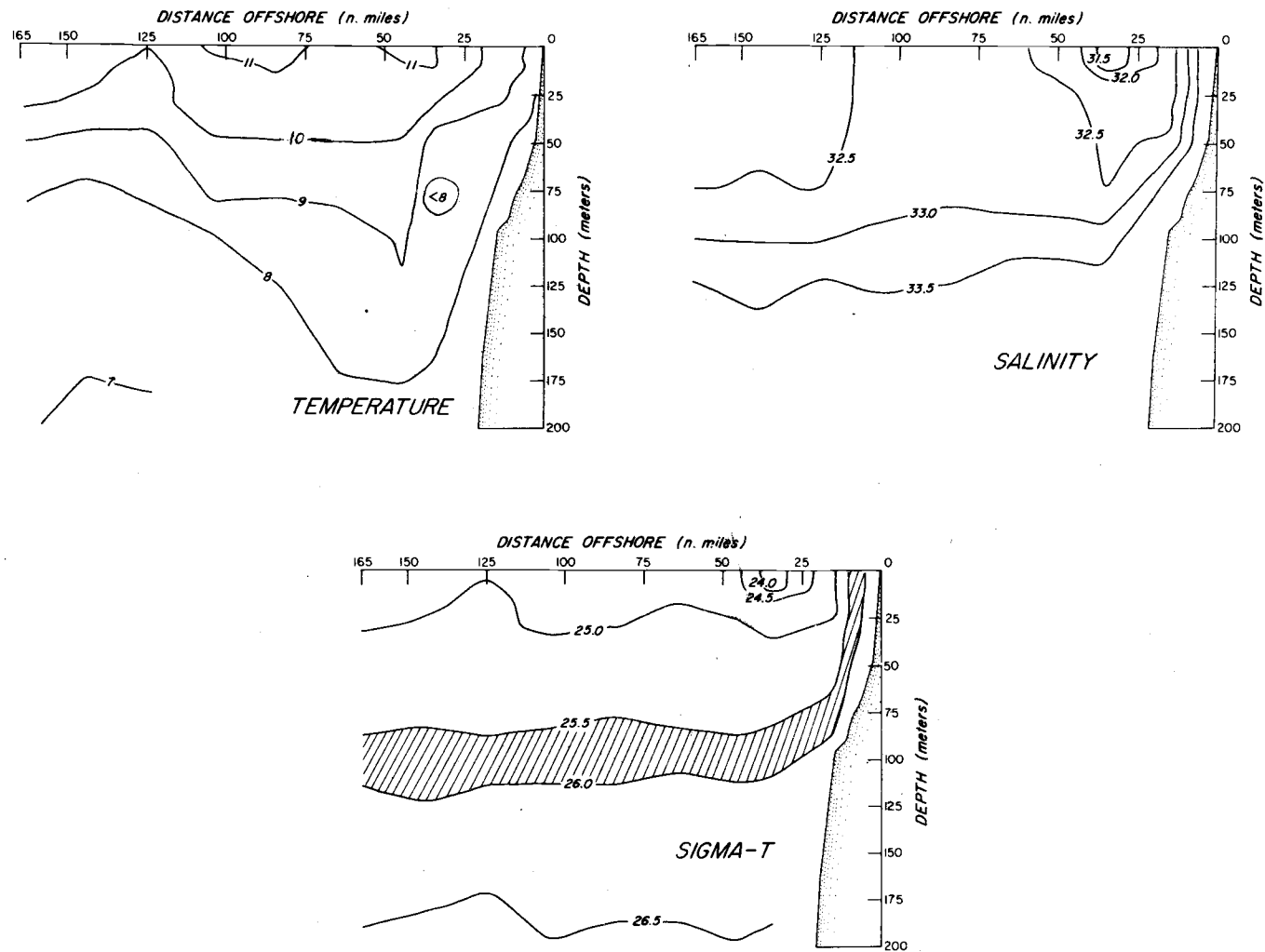
Figure 1.   Temperature (°C), salinity (‰), and sigma-t sections along the Newport line for COOC-3, 12-15 May 1969.
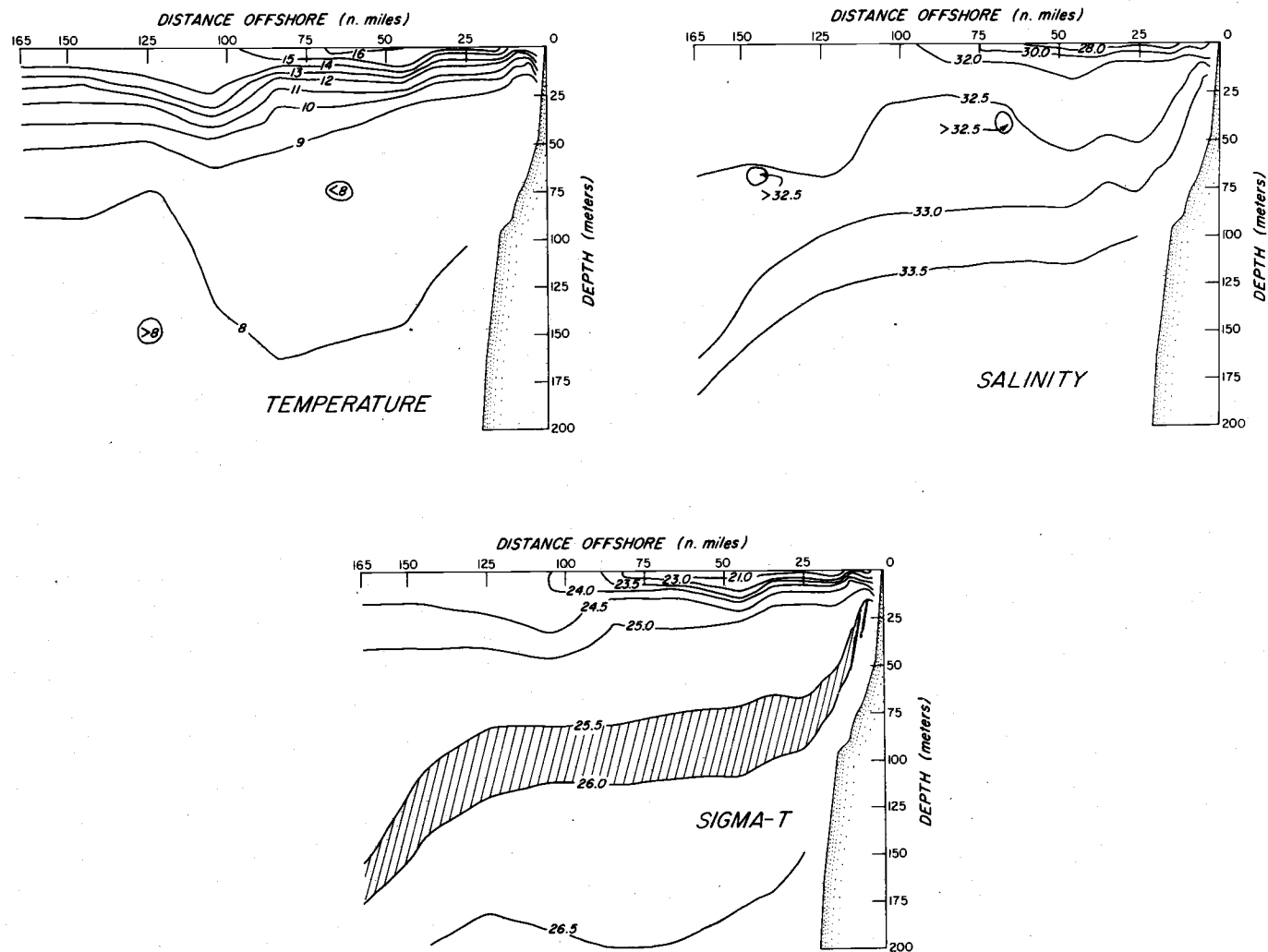
Figure 2.   Temperature (°C), salinity (‰), and sigma-t sections along the Newport line for COOC-4, 27 June-1 July 1969.
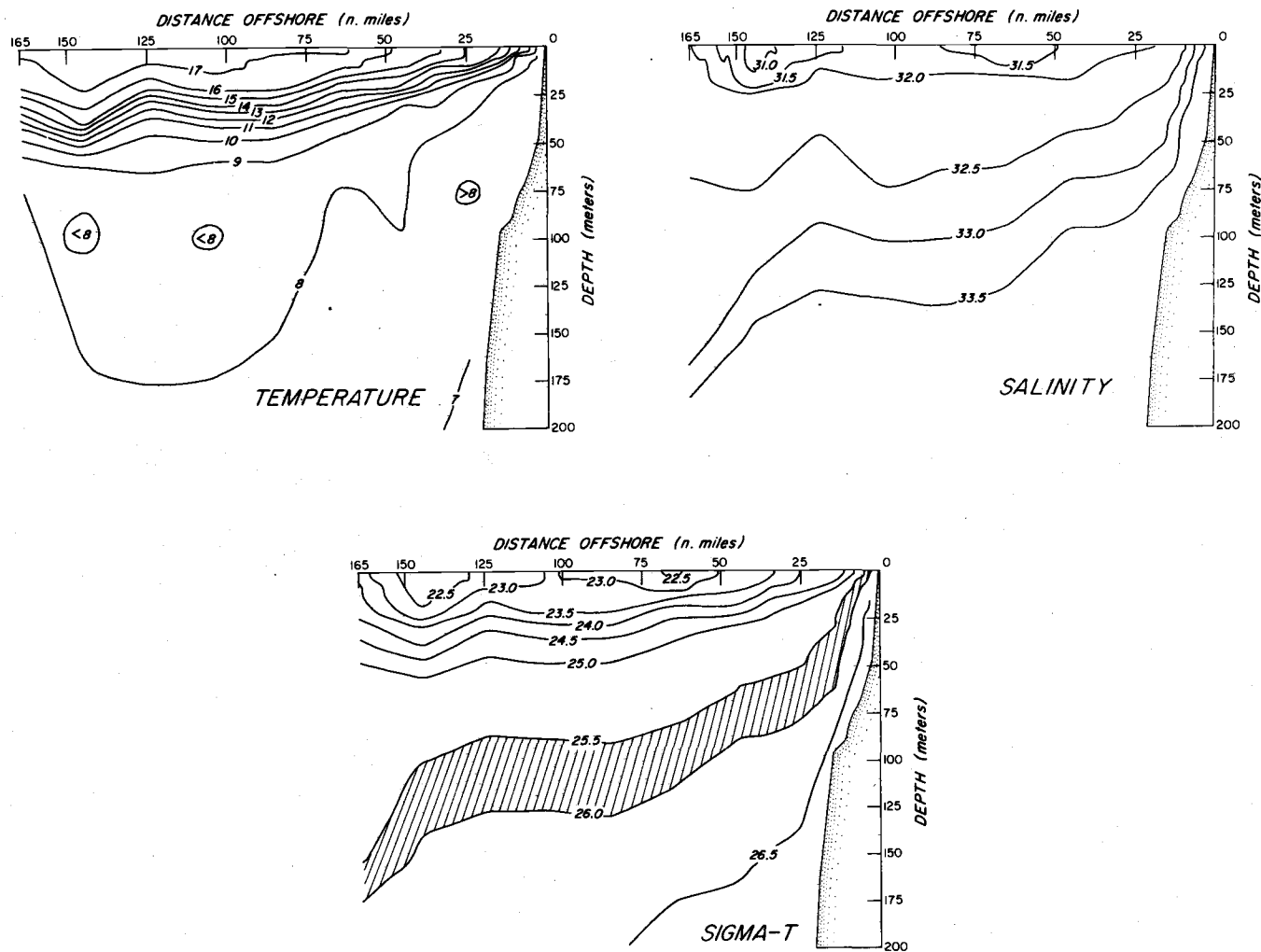
Figure 3.   Temperature (°C), salinity (‰), and sigma-t sections along the Newport line for COOC-6, 5-12 August 1969.
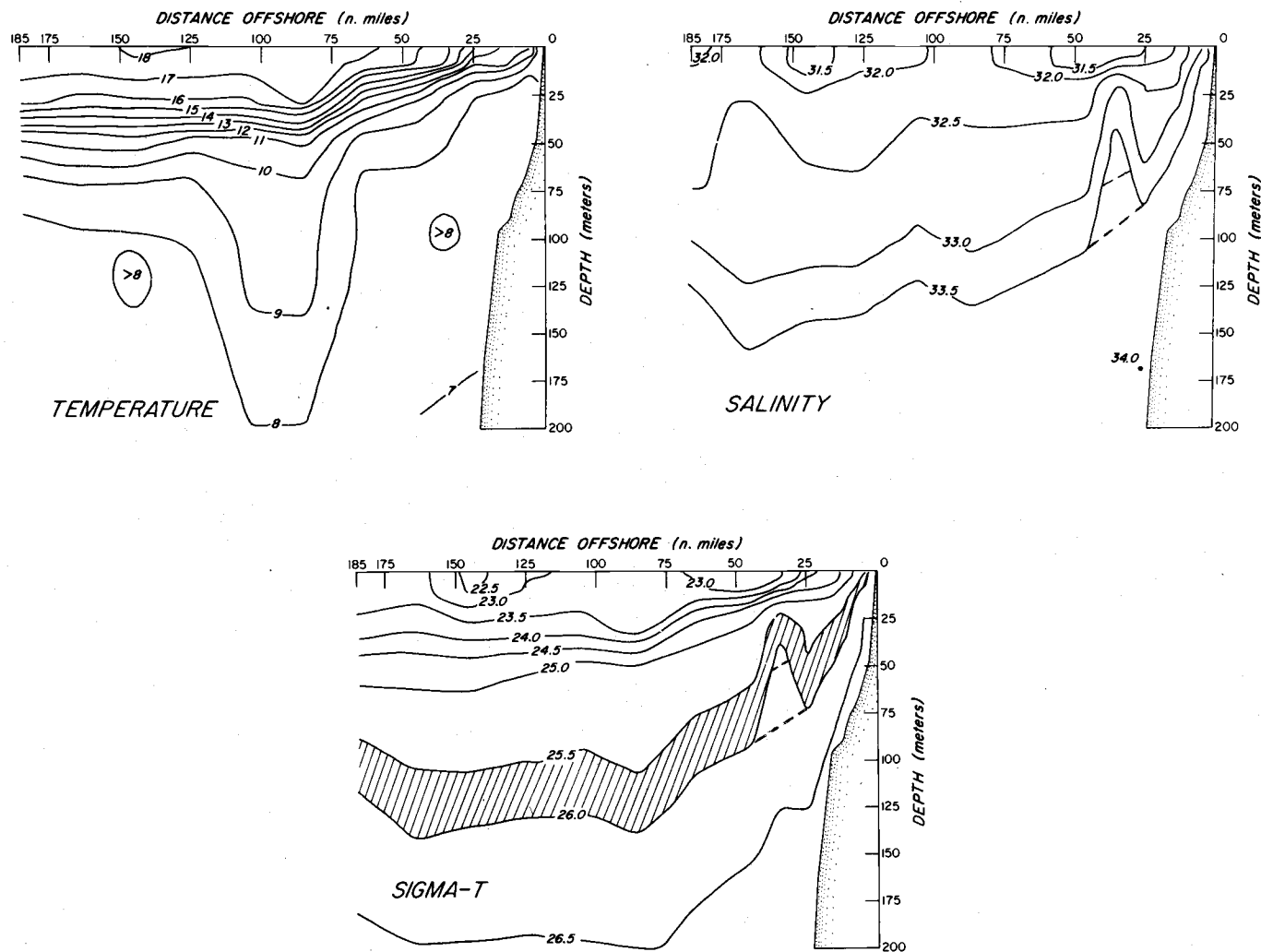
Figure 4. Temperature (°C), salinity(‰), and sigma-t sections along the Newport line for COOC-8, 18-21 August 1969.
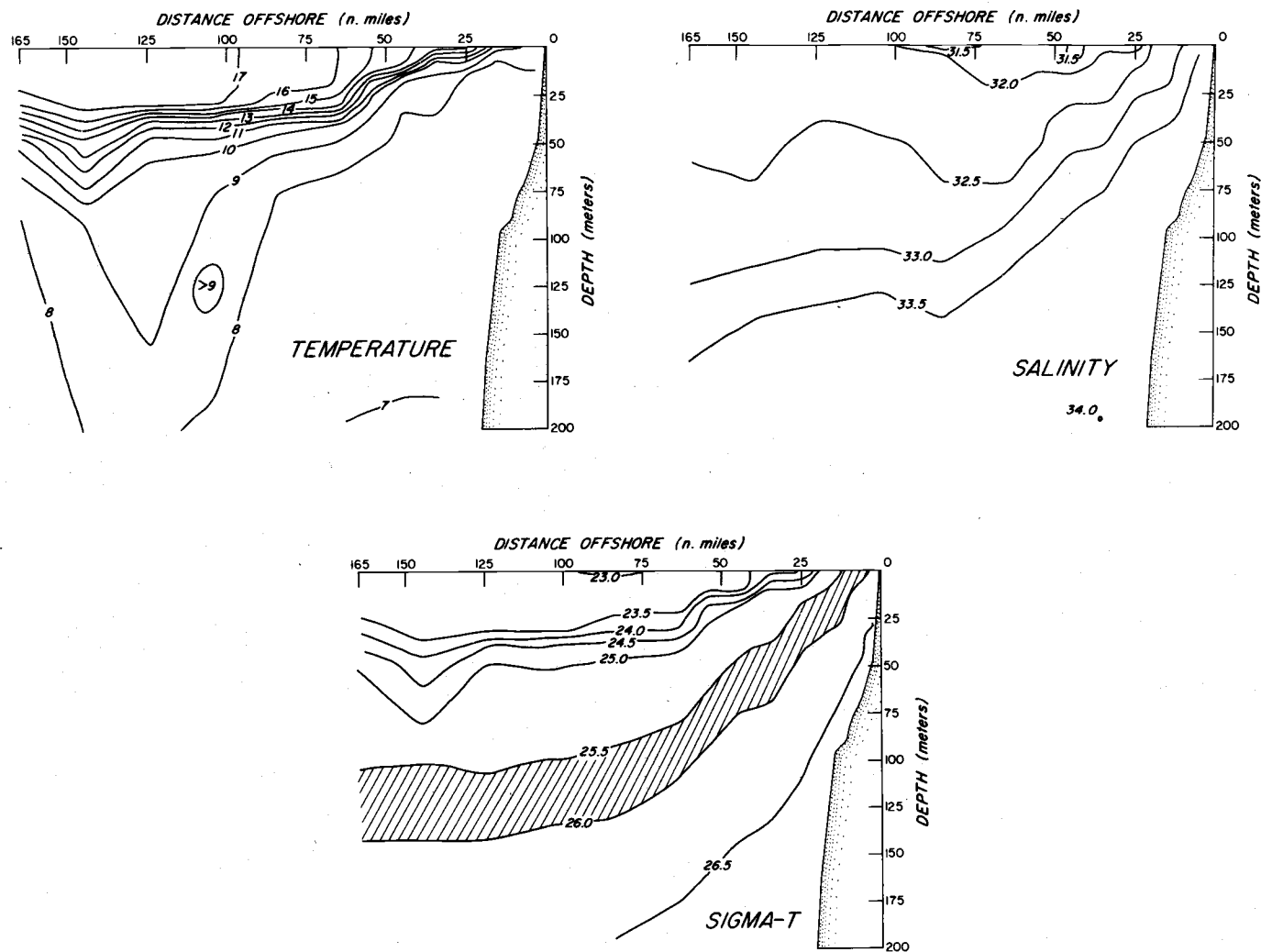
Figure 5. Temperature (°C), salinity (‰), and sigma-t sections along the Newport line for COOC-9, 9-14 September 1969.
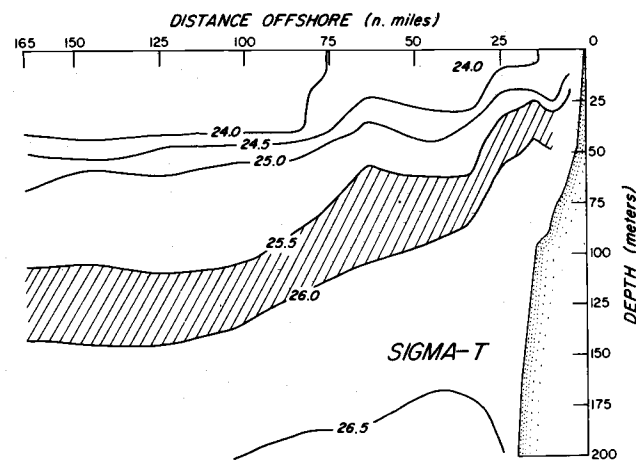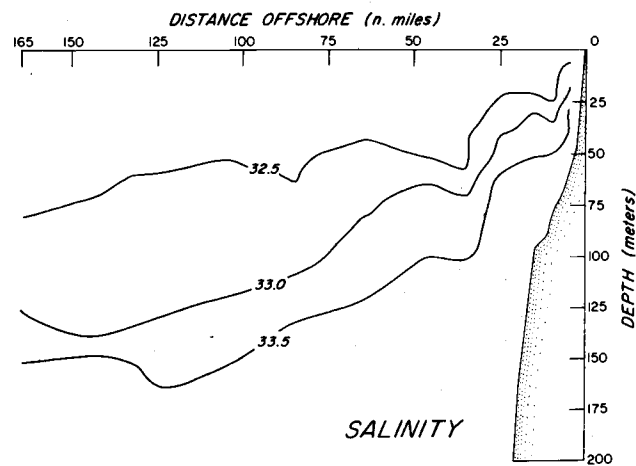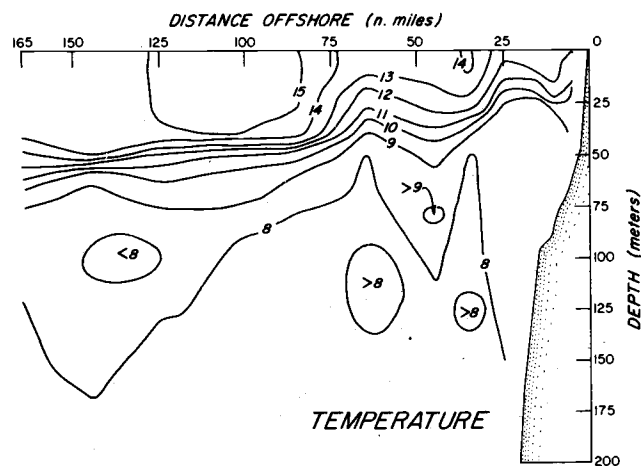
Figure 6. Temperature (°C), salinity (‰), and sigma-t sections along the Newport line for COOC-10, 22-27 October 1969.

DESTRUCTION ISLAND TO PT. ST. GEORGE
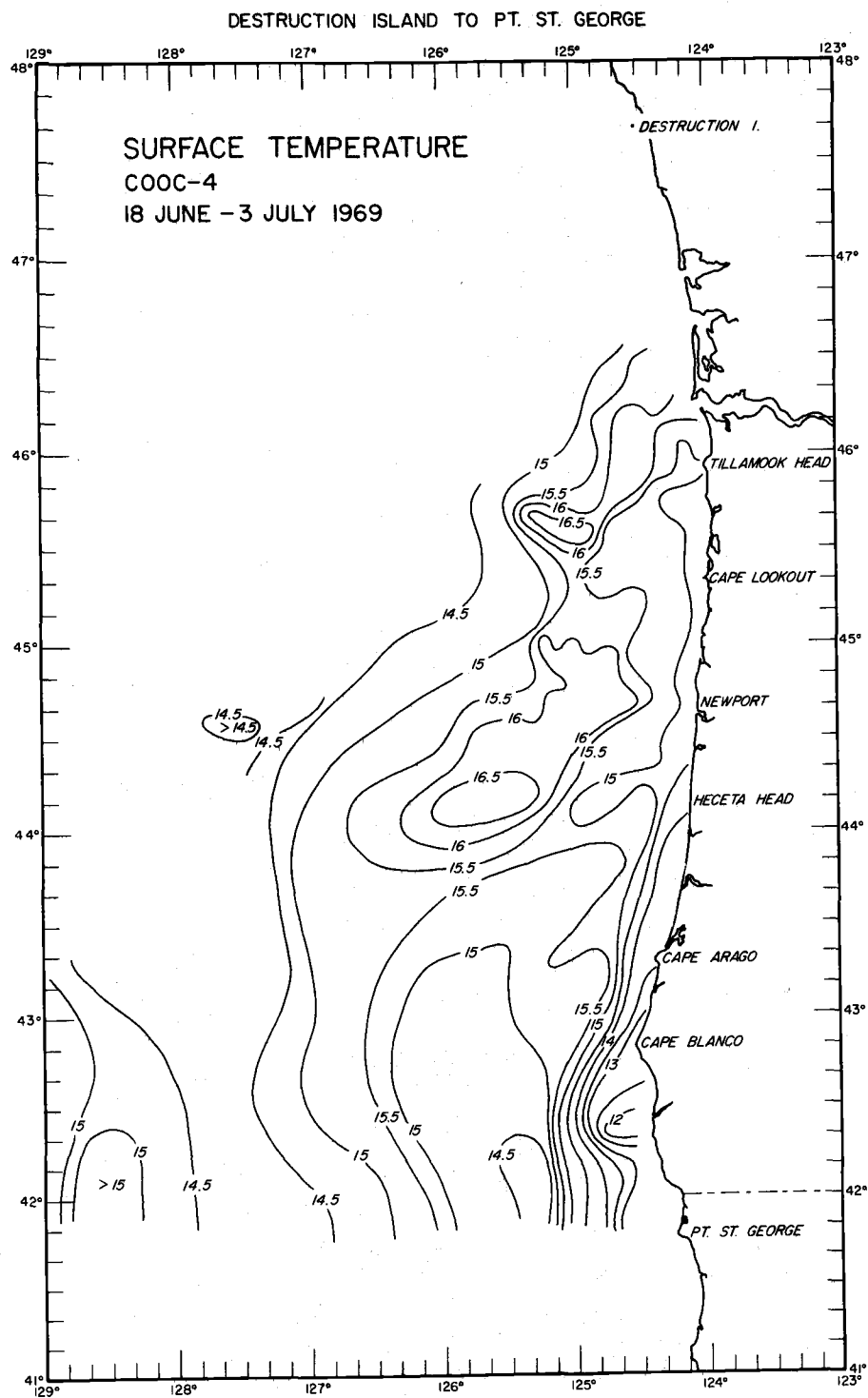
Figure 7. Surface temperature (°C) contours for COOC-4, 18 June-
3 July 1969.
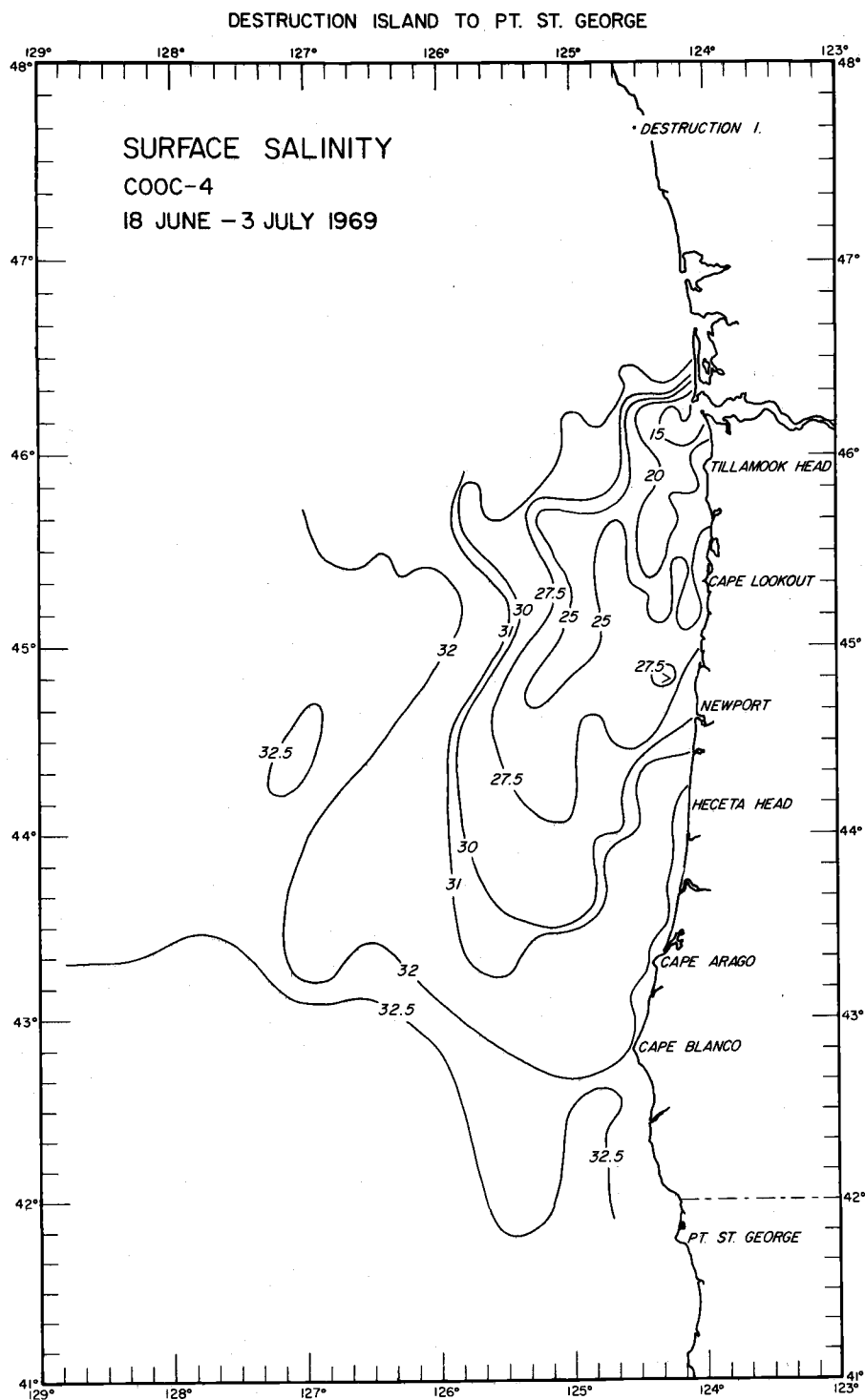
Figure 8. Surface salinity (‰) contours for COOC-4, 8 June-3 July 1969.
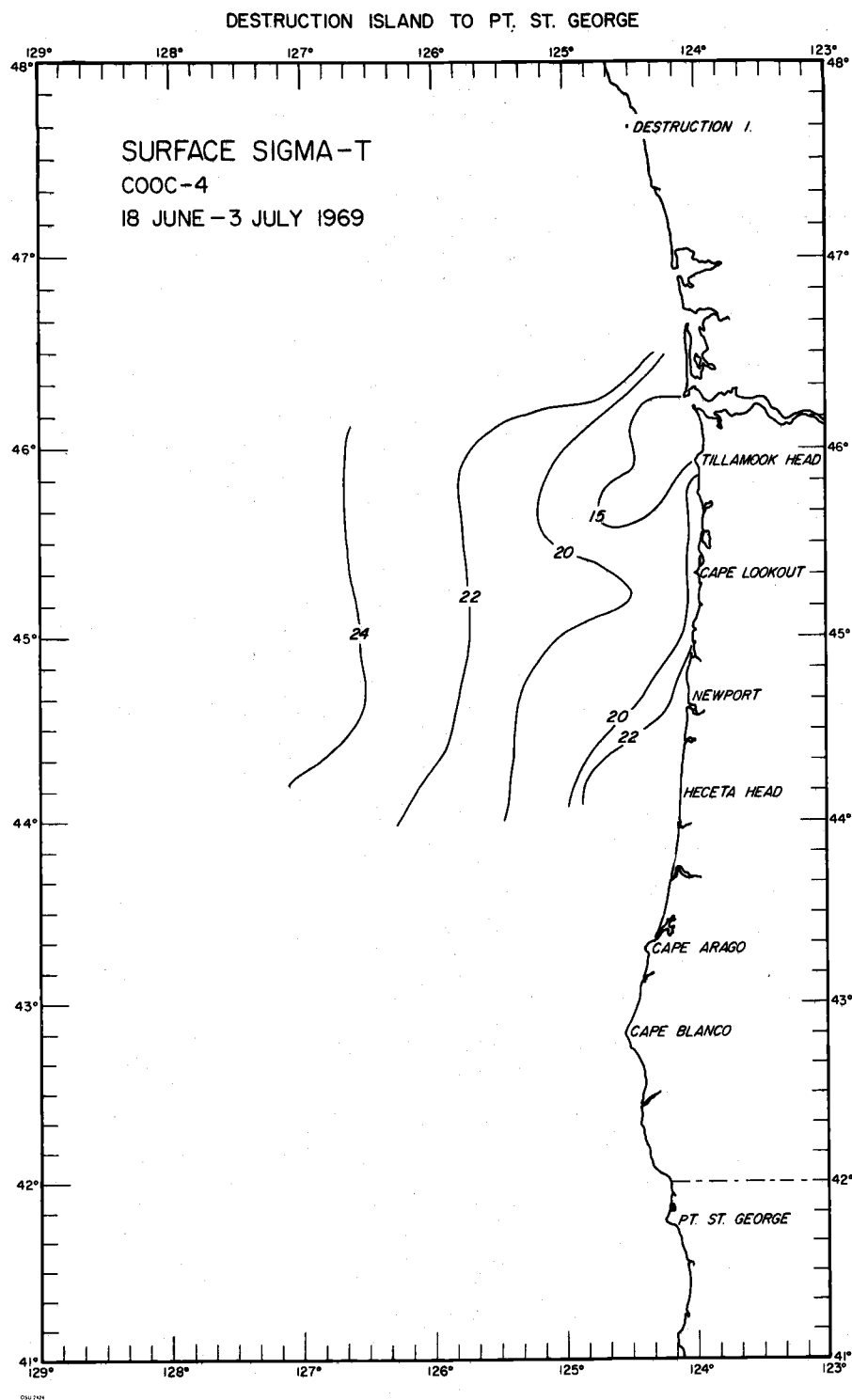
Figure 9. Surface sigma-t contours for COOC-4, 18 June-3 July 1969.

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DESTRUCTION ISLAND TO PT. ST. GEORGE
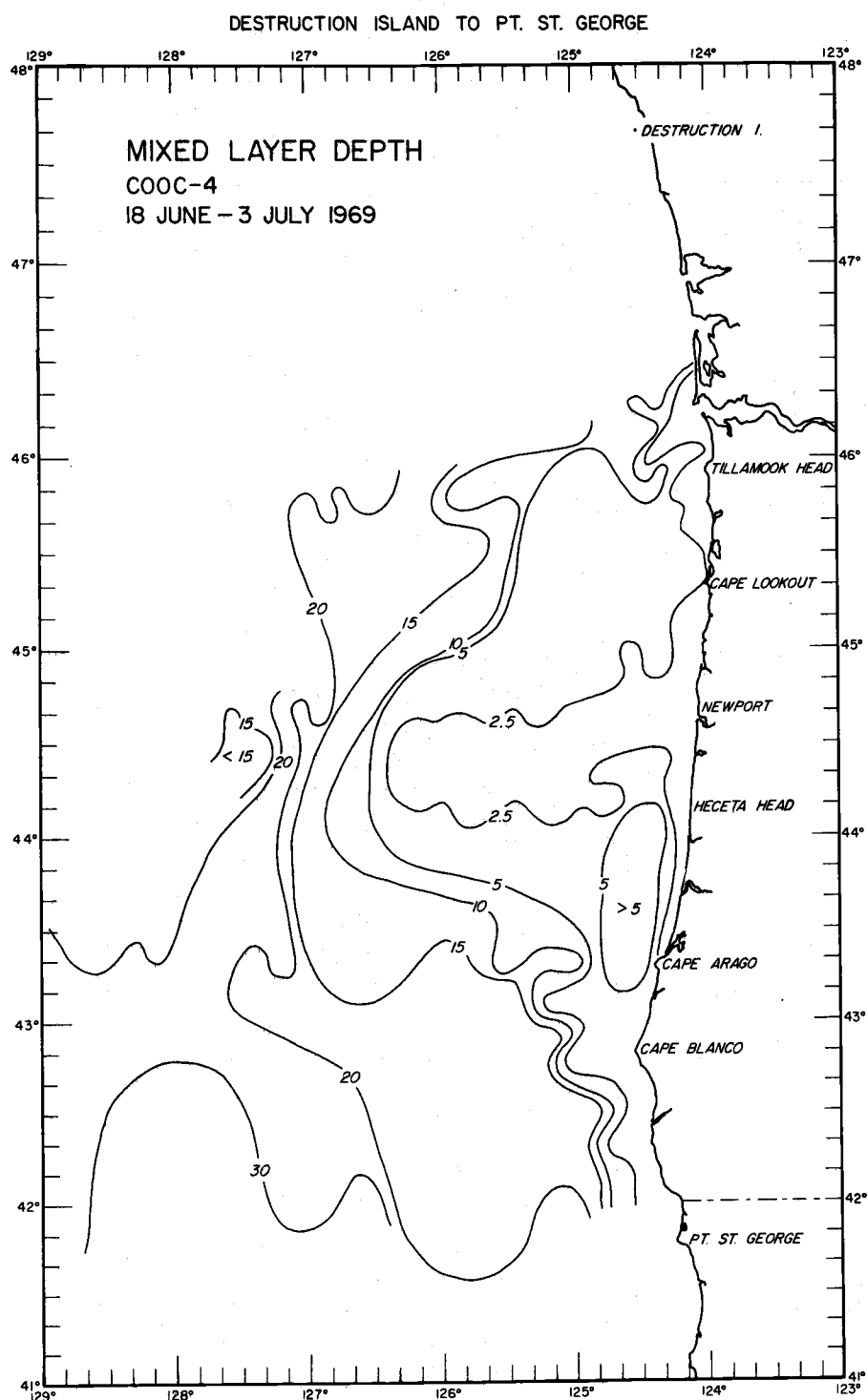
Figure 10. Mixed layer depth (m) contours for COOC-4, 18 June-
3 July 1969.
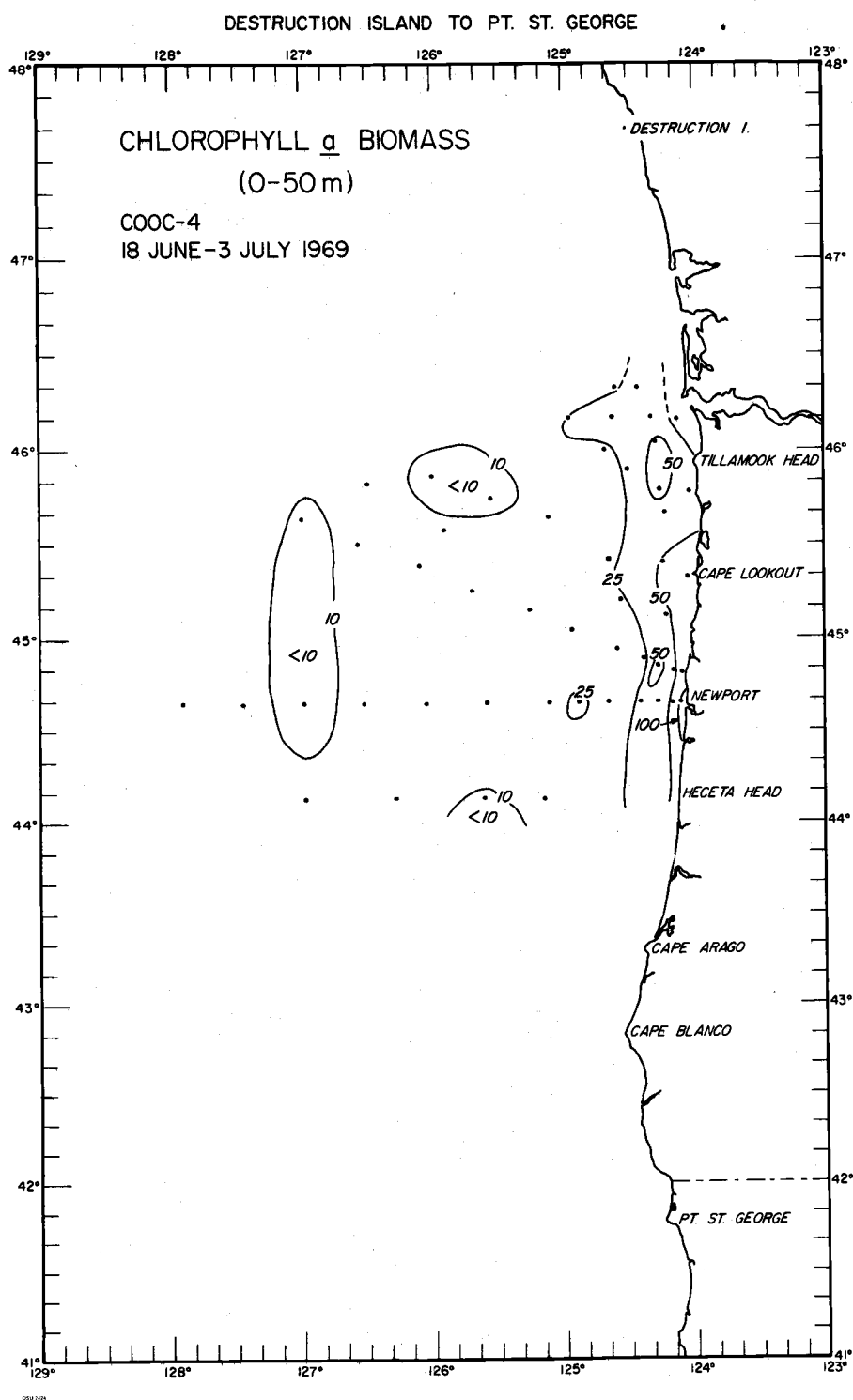
Figure 11.   Chlorophyll a biomass (mg/m^2 from 0-50 m)
contours for COOC-4, 18 June-3 July 1969.

DESTRUCTION ISLAND TO PT. ST. GEORGE

Λ_2 BIOMASS
COOC-4
18 JUNE-3 JULY 1969

DESTRUCTION I.

TILLAMOOK HEAD

CAPE LOOKOUT

100

10

10

10

<10

HECETA HEAD

CAPE ARAGO

CAPE BLANCO

PT. ST. GEORGE

Figure 12. Λ_2 dry biomass (g/10^3m^3 from 0-200 m) contours for COOC-4, 18 June-3 July 1969.

DESTRUCTION ISLAND TO PT. ST. GEORGE

Λ_3 BIOMASS
COOC-4
18 JUNE-3 JULY 1969

DESTRUCTION I.

TILLAMOOK HEAD
0.2

CAPE LOOKOUT
4   4   2   0.2

2   0.2

HECETA HEAD

CAPE ARAGO

CAPE BLANCO

PT. ST. GEORGE

OSU 2424
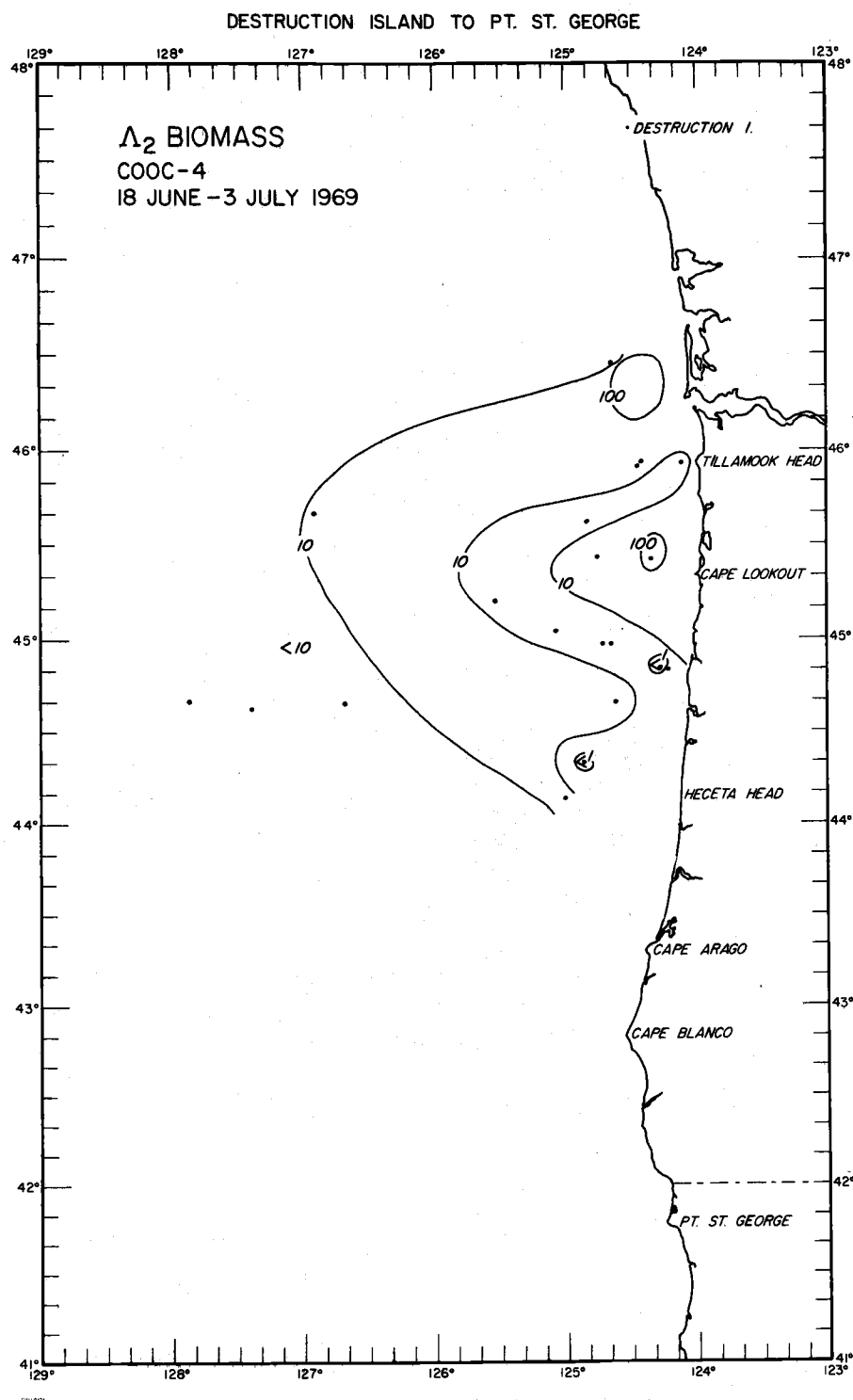
Figure 13. Λ_3 dry biomass (g/10^3m^3 from 0-200 m)
contours for COOC-4, 18 June-3 July 1969.
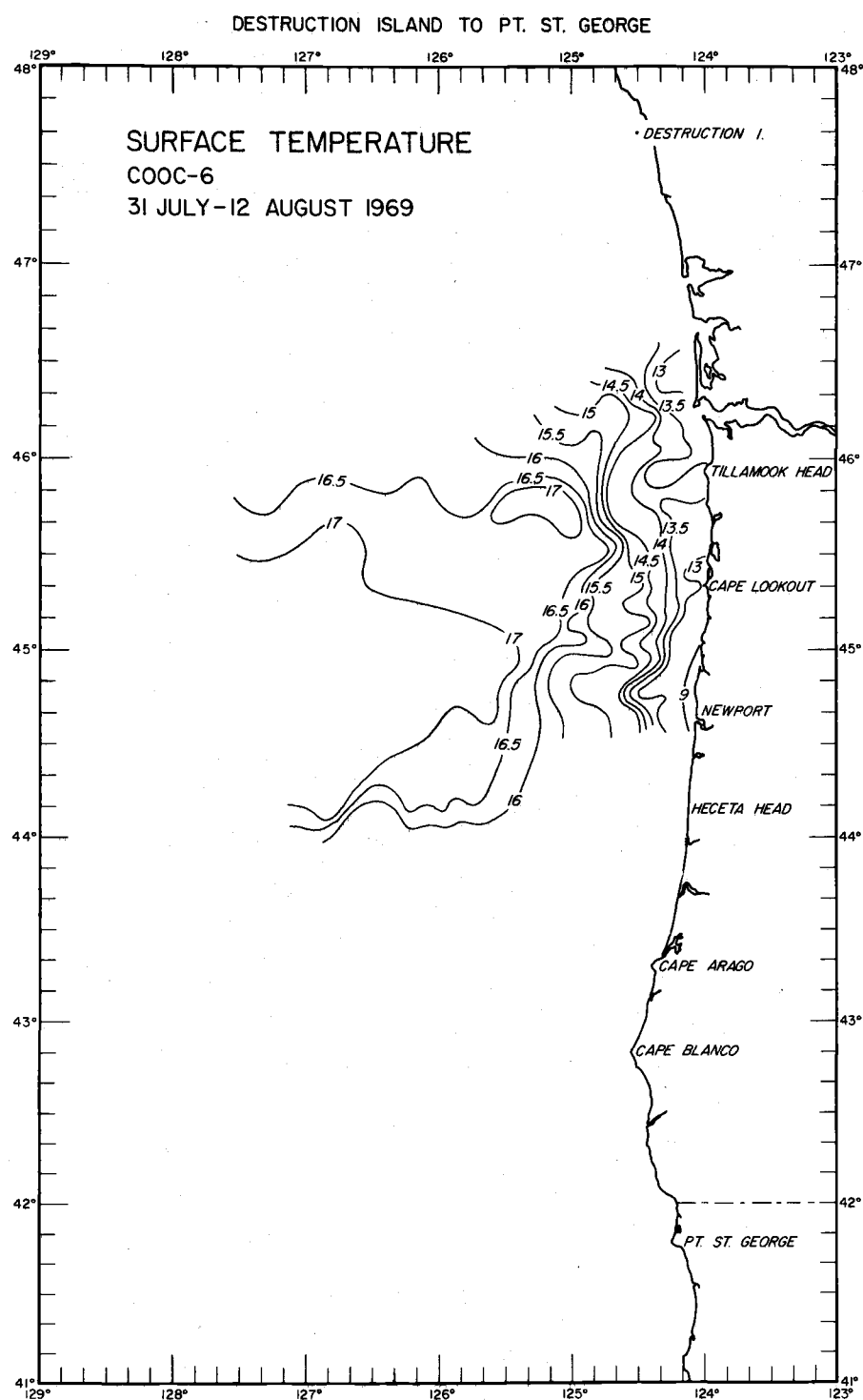
Figure 14. Surface temperature (°C) contours for COOC-6, 31 July-
12 August 1969.

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Figure 15. Surface salinity (‰) contours for COOC-6, 31 July-
12 August 1969.
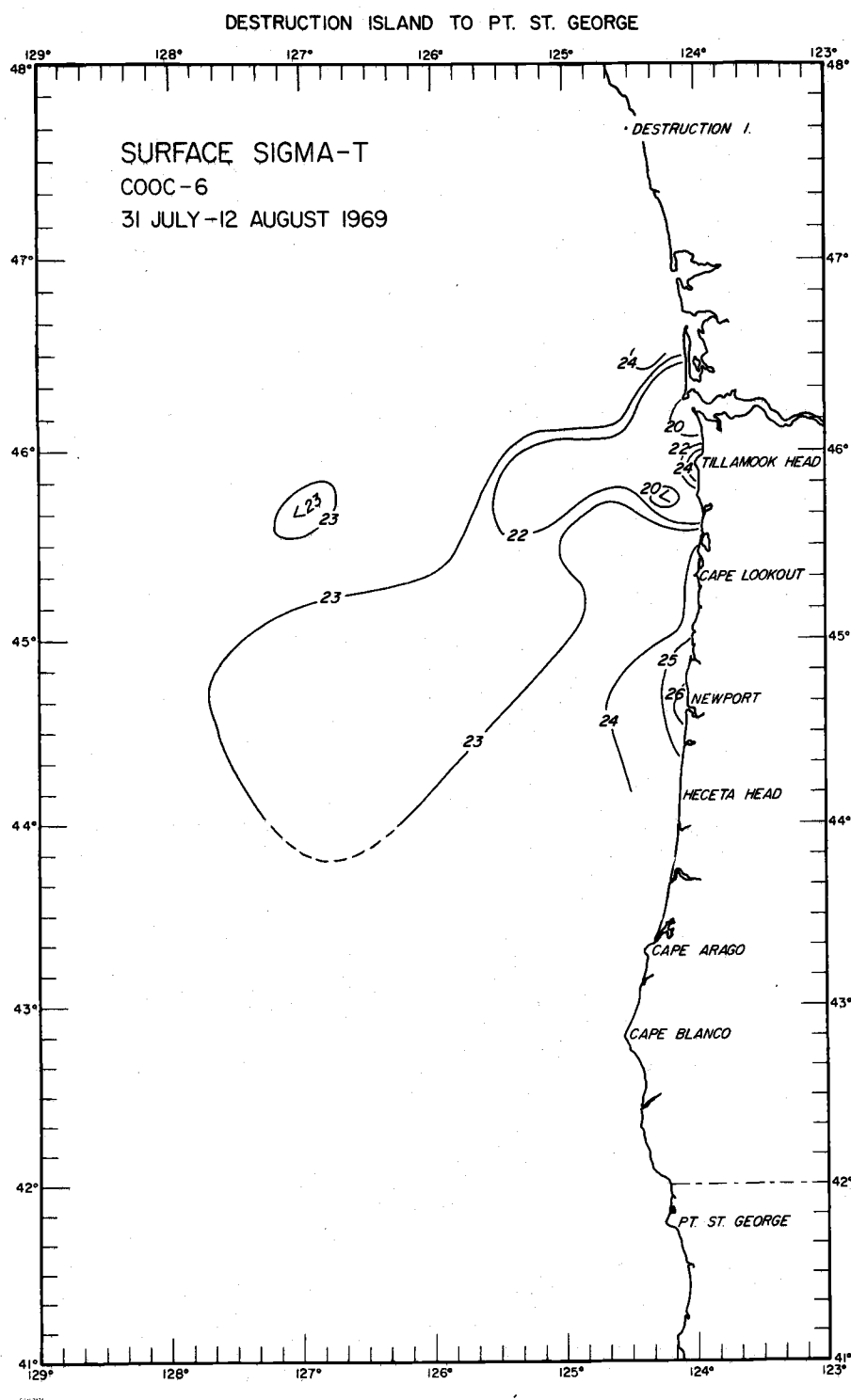
Figure 16. Surface sigma-t contours for COOC-6, 31 July-12 August 1969.
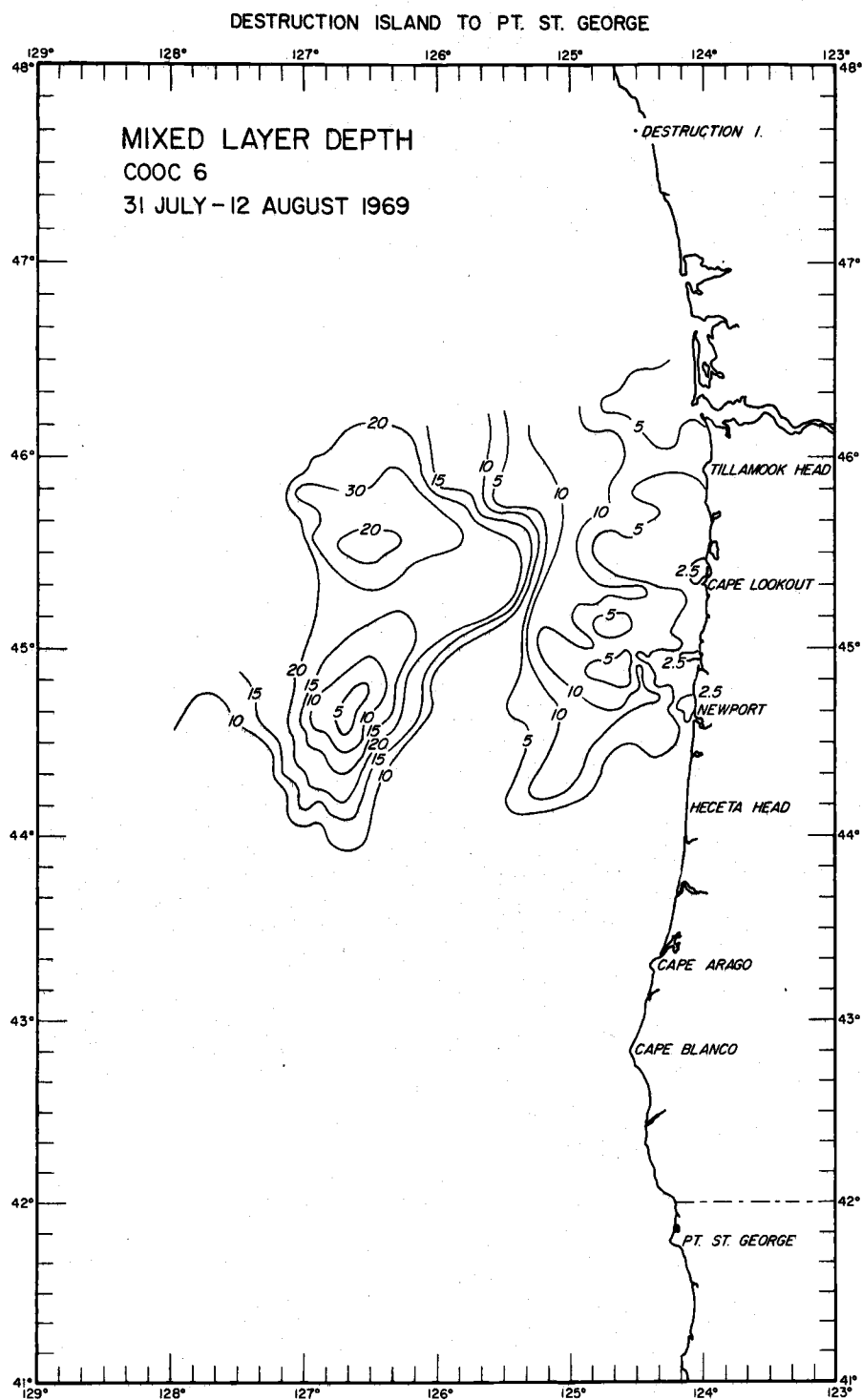
Figure 17. Mixed layer depth (m) contours for COOC-6, 31 July-
12 August 1969.

DESTRUCTION ISLAND TO PT. ST. GEORGE

AVERAGE NITRATE + NITRITE
CONCENTRATION
(0-50 m)
COOC-6
31 JULY-12 AUGUST 1969
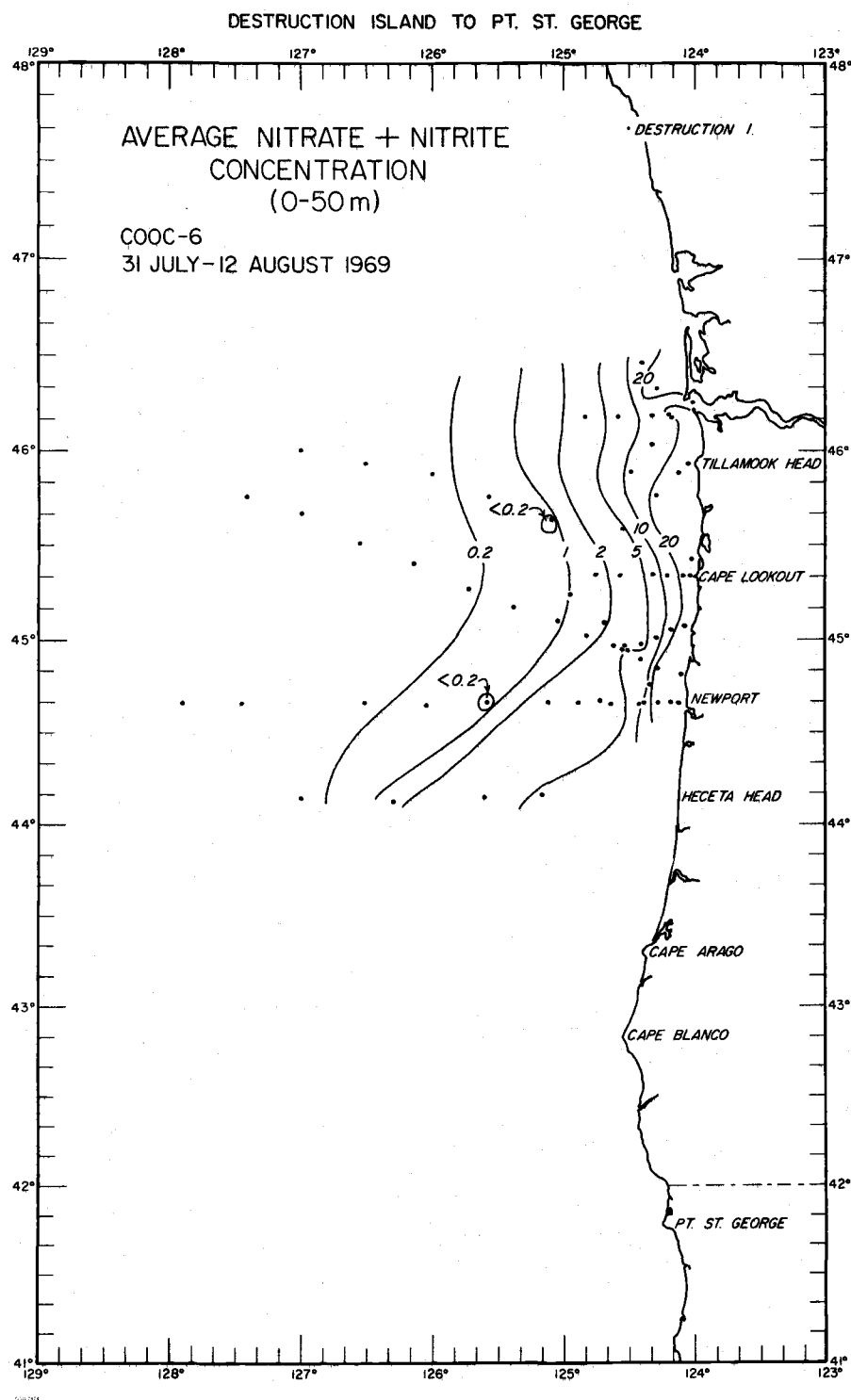
Figure 18. Average concentration of nitrate + nitrite (μg-at/l from 0-50 m) contours for COOC-6, 31 July-12 August 1969.

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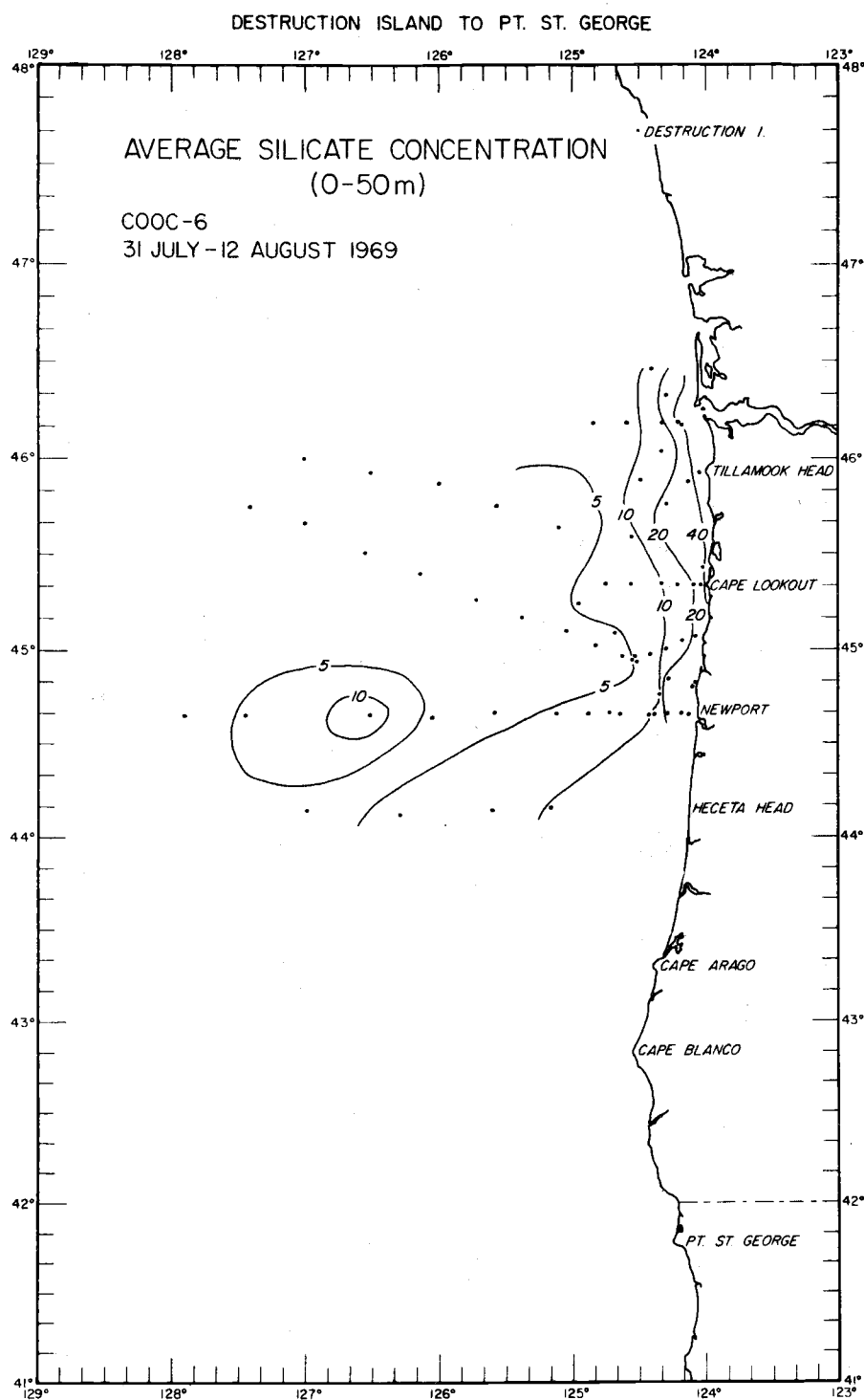
Figure 19. Average concentration of silicate (μg-at/l from 0-50 m) contours for COOC-6, 31 July-12 August 1969.
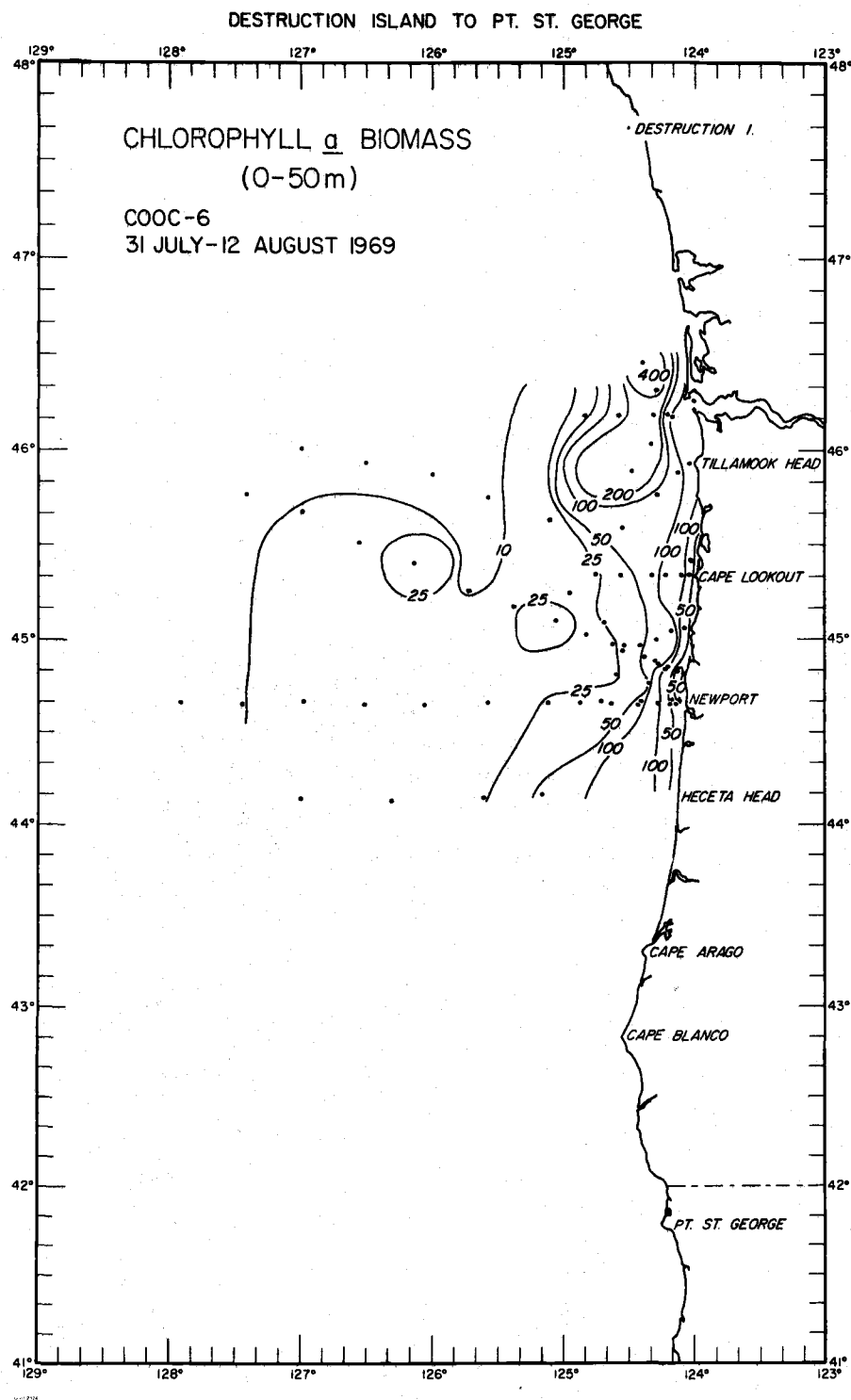
Figure 20. Chlorophyll a biomass (mg/m^2 from 0-50 m) contours for COOC-6, 31 July-12 August 1969.
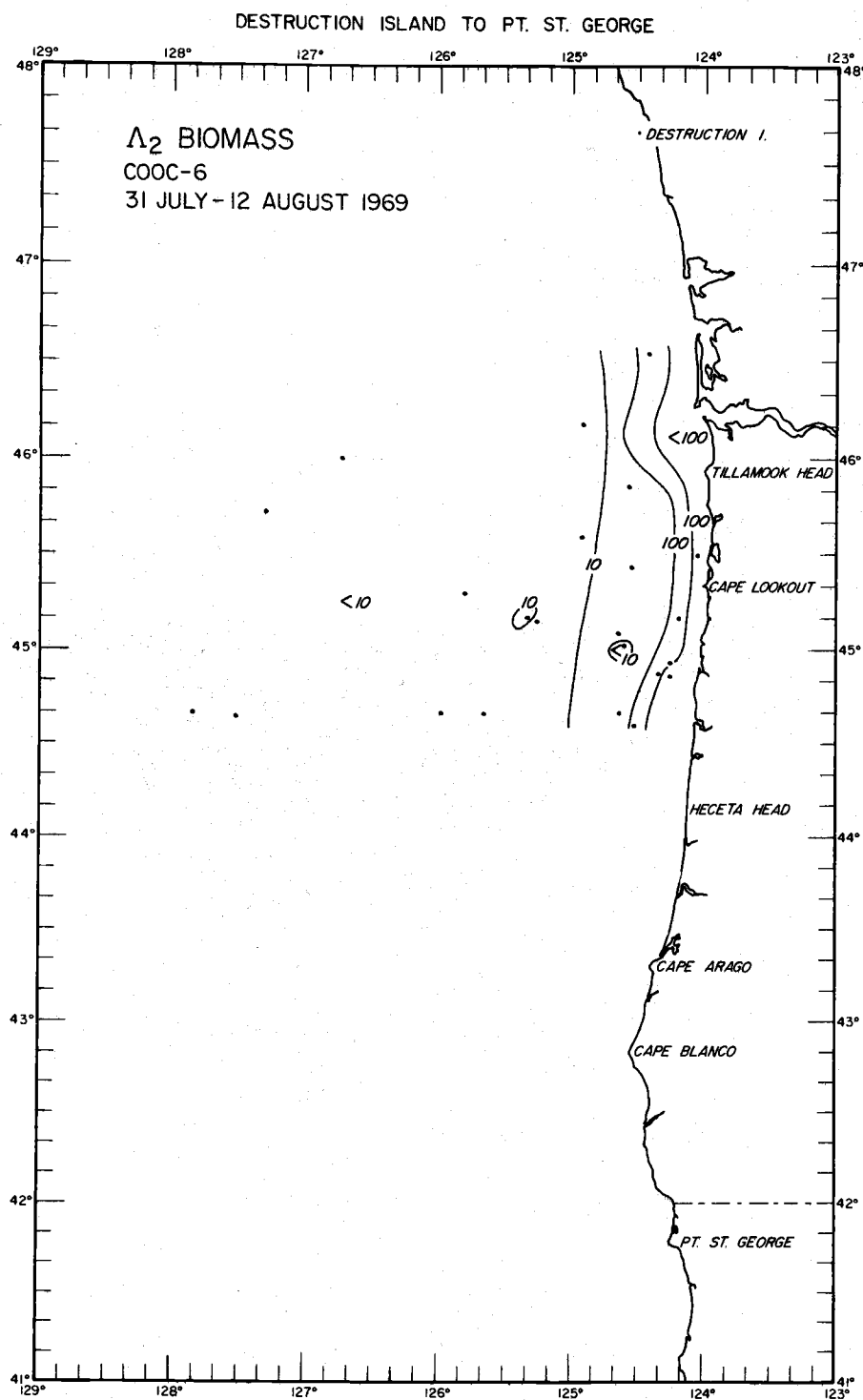
Figure 21. A_2 dry biomass (g/10^{3}m^3 from 0-200 m) contours for COOC-6, 31 July-12 August 1969.

DESTRUCTION ISLAND TO PT. ST. GEORGE
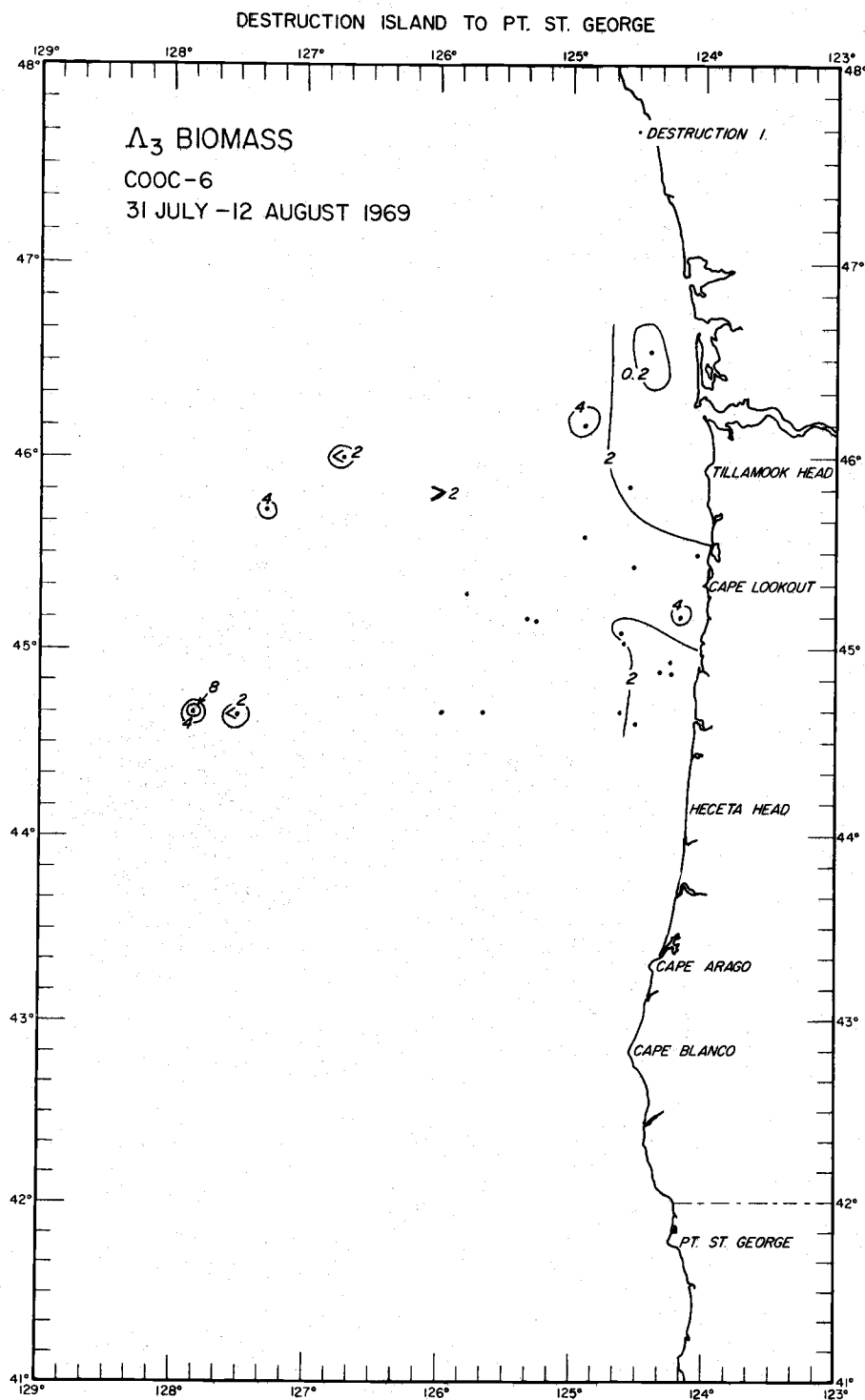
Figure 22. A_3 dry biomass (g/10^3m^3 from 0-200 m) contours for COOC-6, 31 July-12 August 1969.
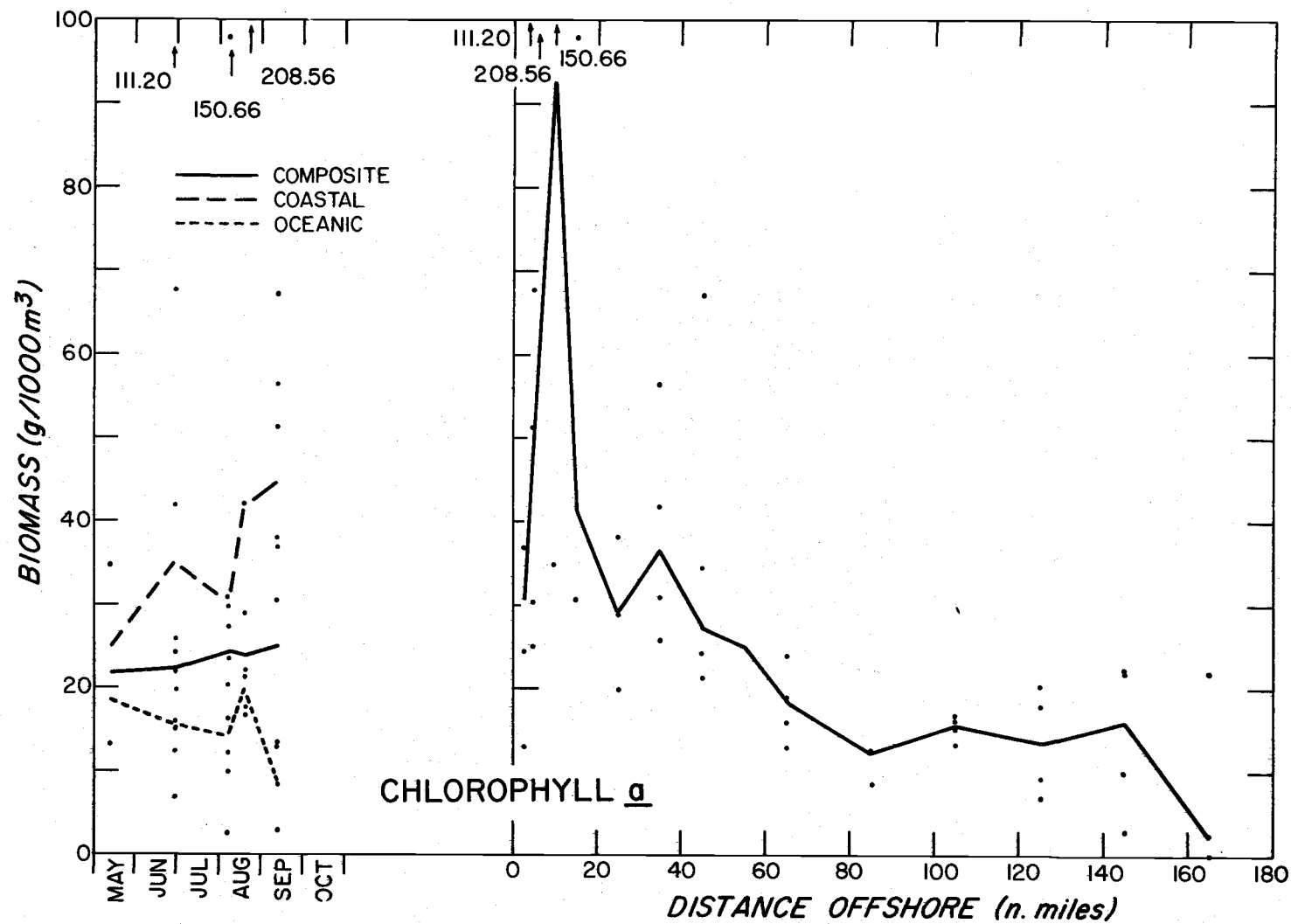
Figure 23. Chlorophyll _a_ biomass (mg/m^2 from 0-50 m): spatial and temporal variations along the Newport line during the 1969 COOC cruises.
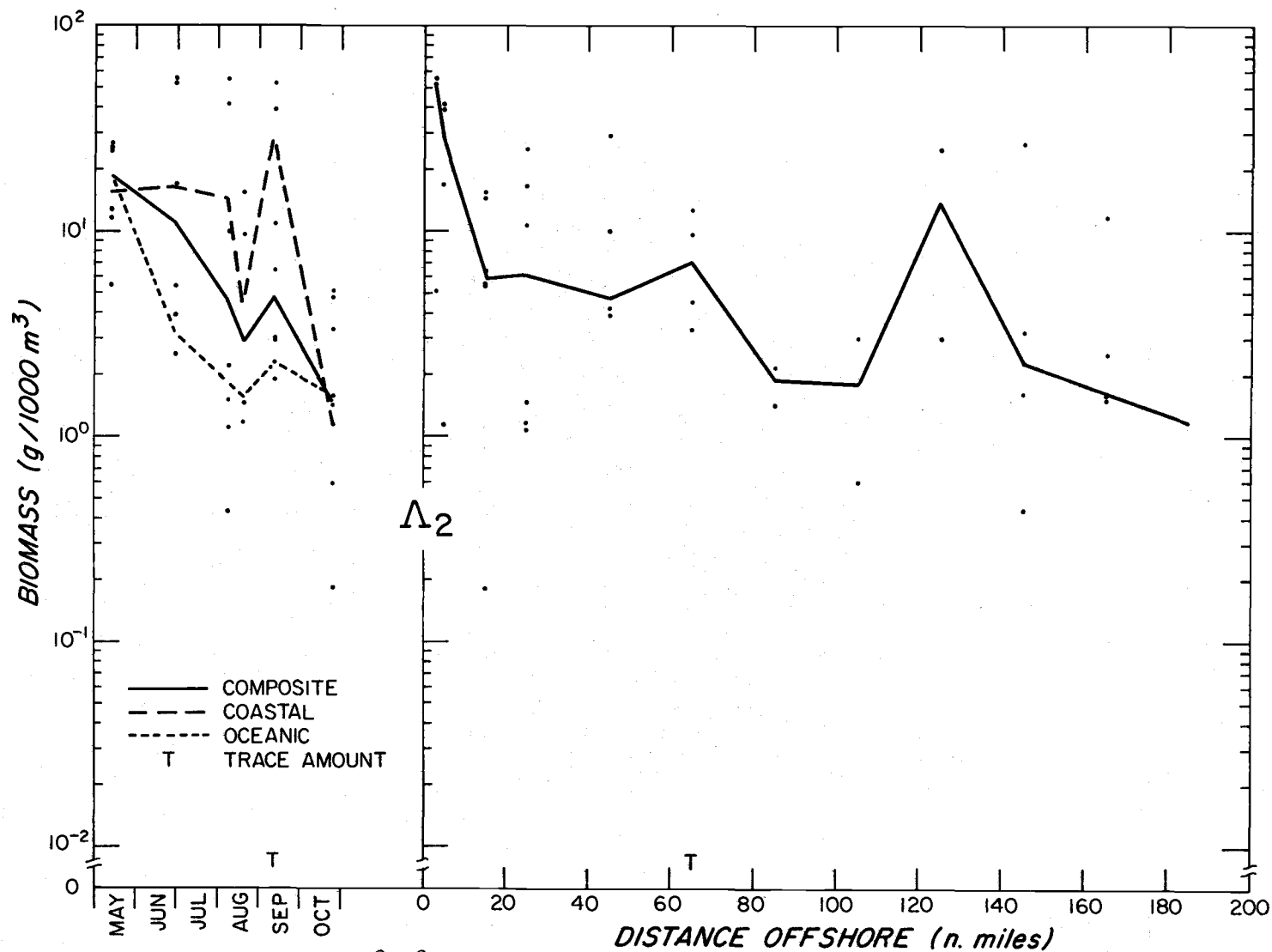
Figure 24. Λ_2 dry biomass ($g/10^3 m^3$ from 0-200 m): spatial and temporal variations along the Newport line during the 1969 COOC cruises.
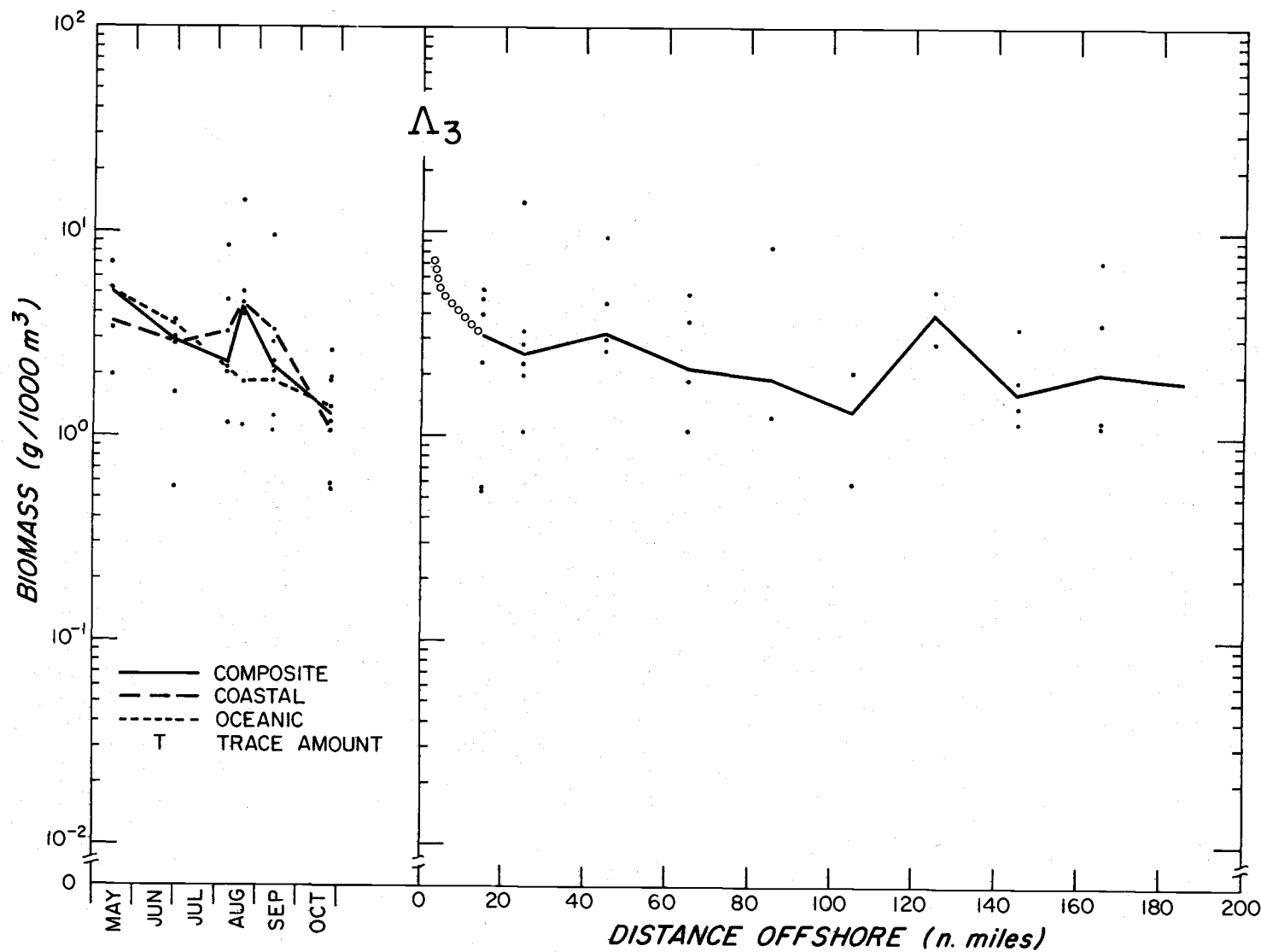
Figure 25. Λ_3 dry biomass ($g/10^3 m^3$ from 0-200 m): spatial and temporal variations along the Newport line during the 1969 COOC cruises. Circles inshore of NH-15 indicate VMN components of Λ_3.
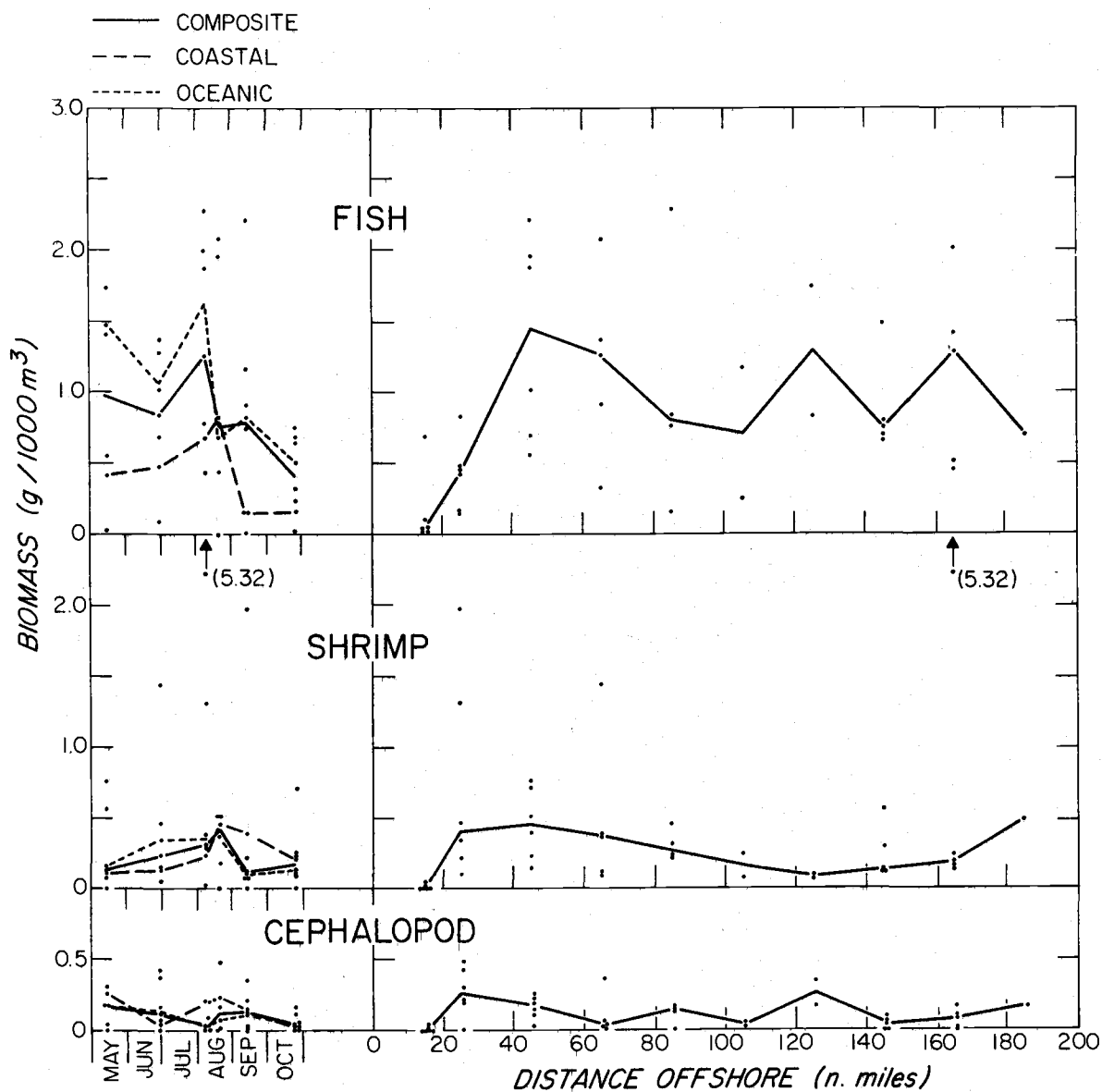
Figure 26. Nekton dry biomass (g/10³ m³ from 0-200 m): spatial and temporal variations along Newport Line during the 1969 COOC cruises.
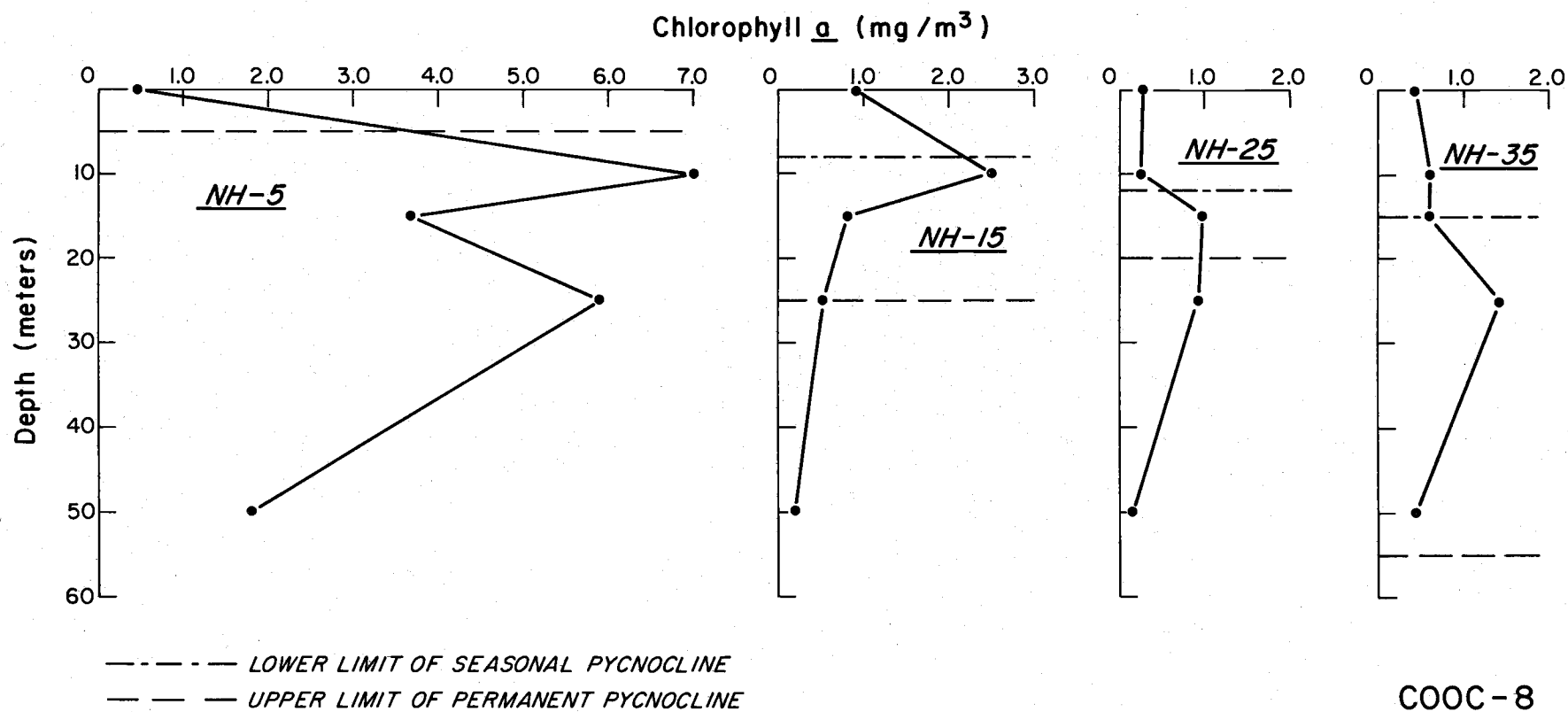
Figure 27. Chlorophyll <u>a</u> (mg/m³ from 0-50 m) profiles at NH-5, NH-15, NH-25, and NH-35. Data from COOC-8, 18-21 August 1969.
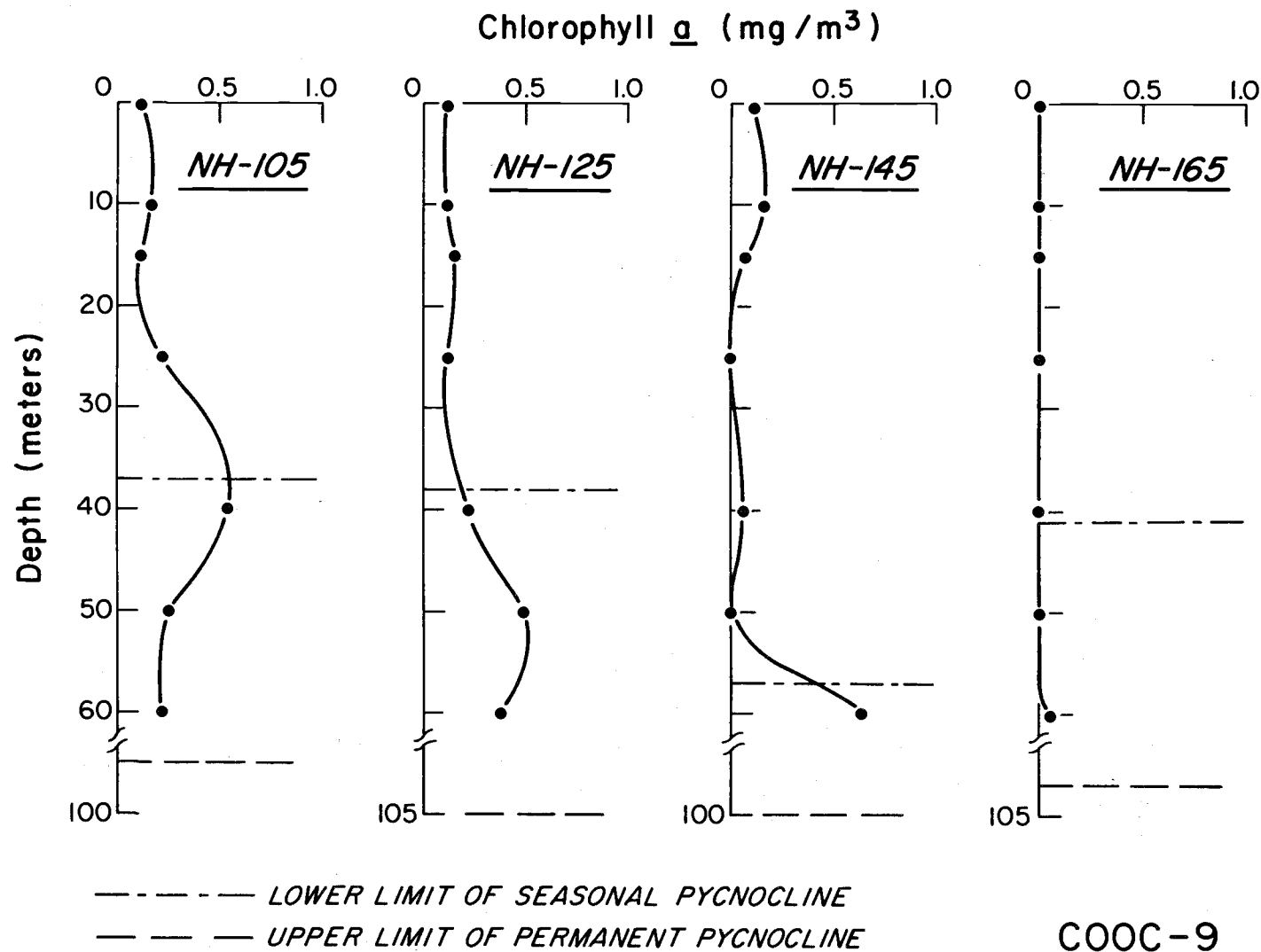
Figure 28. Chlorophyll a (mg/m³ from 0-60 m) profiles at NH-105, NH-125, NH-145, and NH-165. Data from COOC-9, 9-14 September 1969.
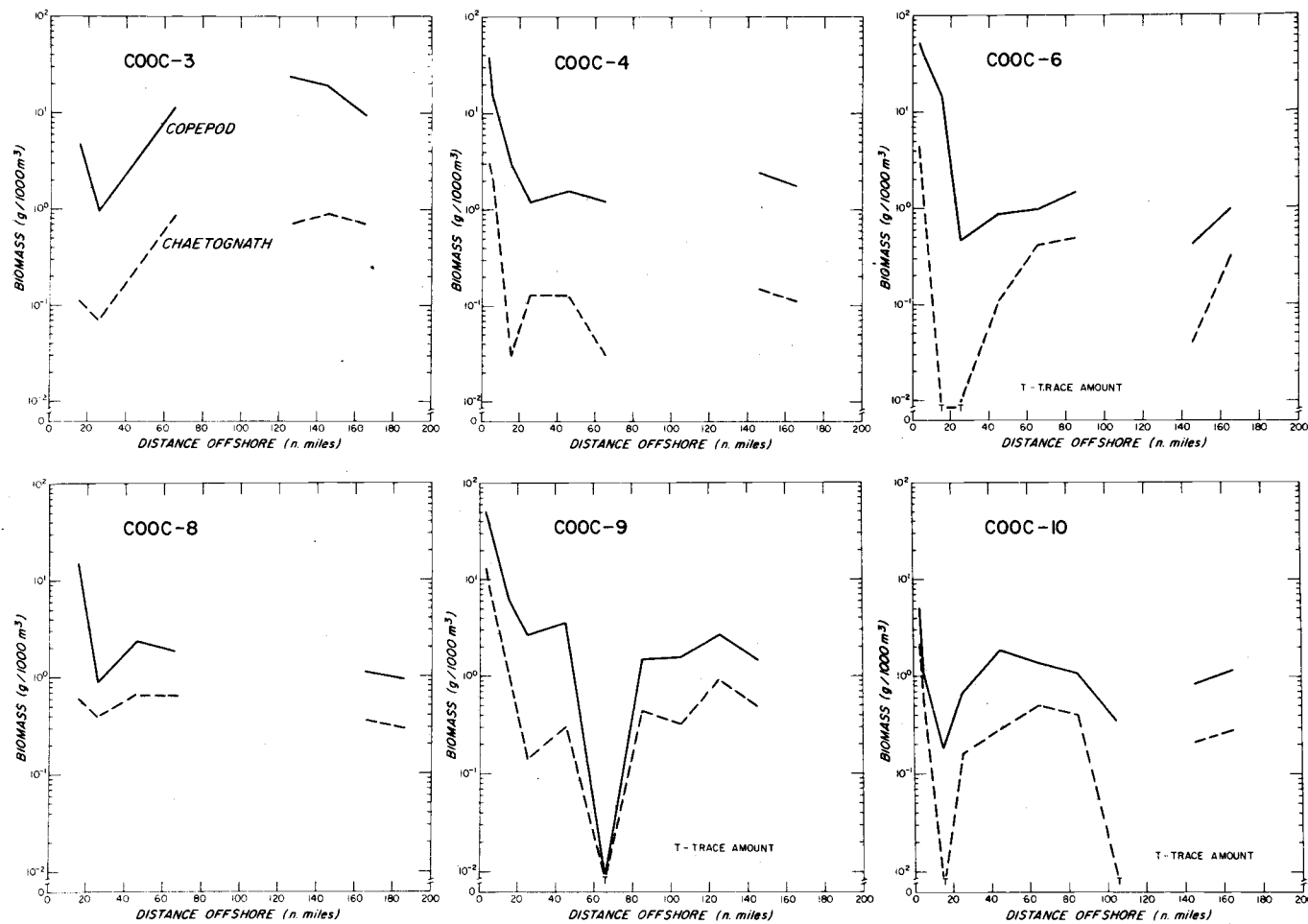
Figure 29.   A comparison of copepod and chaetognath dry biomasses ($g/10^3 m^3$ from 0-200 m) along the Newport line during the 1969 COOC cruises.

Table 1. Chlorophyll a Biomass (mg/m²) Integrated from 0-50 m: Spatial and Temporal Variations Along the Newport Line (Chlorophyll a at NH-3 integrated from 0-25 m).

Cruise	Miles Offshore Along Newport Line														Mean	Median	Coastal* Median	Oceanic** Median	S
	3	5	10	15	25	35	45	55	65	85	105	125	145	165					
COOC-3 5/12-5/15/69	13.10	24.93					34.55		18.46						22.76	21.70	24.93	18.46	9.23
COOC-4 6/27-7/1/69	111.20	67.78	34.84	41.93	19.72	25.81	24.23		15.89	12.23	15.10	6.81	22.23	21.88	32.28	22.23	34.84	15.50	28.40
COOC-6 8/5-8/12/69	24.33	30.23	150.66	97.81	29.21	30.93	27.20		18.65	12.16	16.15	20.23	9.93	2.63	36.16	24.33	30.23	14.16	41.42
COOC-8 8/19-8/21/69		208.56		41.73	28.93	41.93	21.25		23.93		16.76	17.76	22.06		46.99	23.93	41.73	19.91	61.31
COOC-9 9/9-9/14/69	36.95	51.38		30.48	38.01	56.53	67.16	25.01	12.98	8.41	13.33	9.08	2.95	0.00	27.10	25.01	44.70	9.08	21.74
Mean	46.40	76.58	92.75	52.99	28.97	38.80	34.88	25.01	17.98	10.93	15.34	13.47	14.29	8.17					
Median	30.64	51.38	92.75	41.83	29.07	36.43	27.20	25.01	18.46	12.16	15.63	13.42	16.00	2.63					
S	44.29	75.74	81.90	30.36	7.47	13.60	18.71		4.05	2.19	1.50	6.53	9.50	11.95					

*Coastal region, ≤ 45 miles from shore.

**Oceanic region, > 45 miles from shore.

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Table 2. VMN Λ_2 Dry Biomass $(g/10^3m^3)$: Spatial and Temporal Variations Along the Newport Line.

Cruise	Miles Offshore Along Newport Line					
	3	5	15	25	45	65	85	105	125	145	165	185	Mean	Median	Coastal* Median	Oceanic** Median	S
COOC-3 5/12-5/15/69			5.48	25.25		12.75			24.74	26.54	11.59		17.73	18.75	15.37	18.75	8.90
COOC-4 6/27-7/1/69	55.25	16.96	5.39	16.48	3.89	52.25				3.18	2.49		19.49	10.94	16.48	3.18	21.92
COOC-6 8/5-8/12/69	54.36	41.40	14.34	1.08	9.90	4.50	2.17			.43	1.47		14.41	4.50	14.34	1.82	19.79
COOC-8 8/19-8/21/69			15.15	1.44	4.20	9.56					1.54	1.14	5.51	2.87	4.20	1.54	5.70
COOC-9 9/9-9/14/69	51.54	39.07	6.37	10.84	29.17	T	1.88	3.00	2.96	2.29			14.71	4.69	29.17	2.29	18.42
COOC-10 10/22-10/27/69	5.12	1.12	.18	1.17	4.73	3.31	1.40	.59		1.60	1.58		2.08	1.49	1.17	1.58	1.71
Mean	41.57	24.64	7.82	9.38	10.38	13.73	1.82	1.80	13.85	6.81	3.73	1.14					
Median	52.95	28.02	5.93	6.14	4.73	7.03	1.88	1.80	13.85	2.29	1.58	1.14					
S	21.35	19.16	5.80	10.04	10.79	19.41	0.39	1.70	15.40	11.08	4.41						

*Coastal region, ≤ 45 miles from shore.

**Oceanic region, > 45 miles from shore.

T = Trace amount

Table 3. VMN Λ_3 Dry Biomass $(g/10^3 m^3)$:   Spatial and Temporal Variations Along the Newport Line.

| Cruise | | | | | Miles Offshore Along Newport Line | | | | | | | | | | Coastal* | Oceanic** | |
	3	5	15	25	45	65	85	105	125	145	165	185	Mean	Median	Median	Median	S
COOC-3 5/12-5/15/69			5.20	1.16		3.78			3.09	1.28	5.34		3.31	3.44	3.18	3.44	1.83
COOC-4 6/27-7/1/69	7.72	5.29	.42	1.58	1.82	.47				.73	1.91		2.49	1.70	1.82	.73	2.63
COOC-6 8/5-8/12/69	7.56	1.73	3.93	.32	.90	.50	5.88			.08	.63		2.39	.90	1.73	.57	2.74
COOC-8 8/19-8/21/69			3.93	12.27	1.79	2.50					.49	.46	3.57	2.15	3.93	.49	4.46
COOC-9 9/9-9/14/69	13.11	8.21	2.27	.95	6.72	T	.72	.79	1.58	.88			3.52	1.27	6.72	.79	4.36
COOC-10 10/22-10/27/69	3.14	4.75	.51	.67	1.11	1.40	.76	.05		.63	.51		1.35	.72	1.11	.63	1.46
Mean	7.88	5.00	2.71	2.83	2.47	1.44	2.45	.42	2.34	.72	1.78	.46					
Median	7.64	5.02	3.10	1.06	1.79	.95	.76	.42	2.34	.73	.63	.46					
S	4.08	2.65	1.97	4.65	1.08	1.45	2.97	.52	1.07	.44	2.08						

*Coastal region, $\leq$ 45 miles from shore.   T = Trace amount

**Oceanic region, > 45 miles from shore.

Table 4. IKMT Λ_3 Dry Biomass $(g/10^3m^3)$: Spatial and Temporal Variations Along the Newport Line.

Cruise	\ 15	\ 25	Miles Offshore Along Newport Line 45	\ 65	\ 85	\ 105	\ 125	\ 145	\ 165	\ 185	Mean	Median	Coastal* Median	Oceanic** Median	S
COOC-3 5/12-5/15/69	.04	.84	1.58				1.99	2.08	1.74		1.38	1.66	.84	1.99	.79
COOC-4 6/27-7/1/69	.14	1.25	1.19	3.18	1.46			.89	1.62		1.39	1.25	1.19	1.54	.93
COOC-6 8/5-8/12/69	.74	1.96	2.31	1.67	2.60			1.08	7.41		2.54	1.96	1.96	2.14	2.24
COOC-8 8/19-8/21/69	.01	1.77	2.70	2.52					.63	1.37	1.50	1.57	1.77	1.37	1.05
COOC-9 9/9-9/14/69	.02	2.36	2.76	1.05	.52	1.27	1.26	.96			1.28	1.16	2.36	1.05	.90
COOC-10 10/22-10/27/69	.03	.39	1.51	.46	1.16	.53		.76	.66		.69	.60	.39	.66	.46
Mean	.16	1.43	2.01	1.78	1.44	.90	1.63	1.15	2.41	1.37					
Median	.04	1.51	1.95	1.67	1.31	.90	1.63	.96	1.62	1.37					
S	.29	.74	.67	1.09	.87	.52	.52	.53	2.84						

*Coastal region, $\leq$ 45 miles from shore.

**Oceanic region, > 45 miles from shore.

Table 5. VMN Λ_3 + IKMT Λ_3 Dry Biomass (g/10³m³): Spatial and Temporal Variations Along the Newport Line.

Cruise	3	5	15	25	45	65	85	105	125	145	165	185	Mean	Median	Coastal* Median	Oceanic** Median	S
						Miles Offshore Along Newport Line											
COOC-3 5/12-5/15/69			5.24	2.00					5.08	3.36	7.08		4.55	5.08	3.62	5.08	1.94
COOC-4 6/27-7/1/69			.56	2.83	3.01	3.65			1.62	3.53			2.53	2.92	2.83	3.53	1.21
COOC-6 8/5-8/12/69			4.67	2.28	3.21	2.17	8.48		1.16	2.04			3.43	2.28	3.21	2.11	2.49
COOC-8 8/19-8/21/69			3.94	14.04	4.49	5.02				1.12	1.83		5.07	4.22	4.49	1.83	4.65
COOC-9 9/9-9/14/69			2.29	3.31	9.48	1.05	1.24	2.06	2.84	1.84			3.01	2.18	3.31	1.84	2.72
COOC-10 10/22-10/27/69			.54	1.06	2.62	1.86	1.92	.58		1.39	1.17		1.39	1.28	1.06	1.39	0.71
Mean			2.87	4.25	4.56	2.75	3.88	1.32	3.96	1.87	2.99	1.83					
Median			3.12	2.56	3.21	2.17	1.92	1.32	3.96	1.62	2.04	1.83					
S			2.05	4.86	2.84	1.58	4.00	1.05	1.58	0.87	2.49						

*Coastal region, ≤ 45 miles from shore.

**Oceanic region, > 45 miles from shore.

Table 6. Copepod Dry Biomass $(g/10^3m^3)$:   Spatial and Temporal Variations Along the Newport Line.

Cruise	3	5	15	25	45	65	85	105	125	145	165	185	Mean	Median	Coastal* Median	Oceanic** Median	S
COOC-3 5/12-5/15/69			4.85	.96		11.43			24.07	19.19	9.50		11.67	10.47	2.91	15.31	8.68
COOC-4 6/27-7/1/69	38.61	15.25	2.98	1.21	1.57	1.20				2.45	1.77		8.13	2.11	2.98	1.77	13.19
COOC-6 8/5-8/12/69	53.44	41.40	14.34	.46	.87	.97	1.48			.42	.98		12.71	.98	14.34	.98	20.39
COOC-8 8/19-8/21/69			15.15	.89	2.35	1.82					1.10	.92	3.71	1.46	2.35	1.10	5.64
COOC-9 9/9-9/14/69	51.06	38.55	6.37	2.68	3.55	T	1.48	1.58	2.69	1.45			10.94	2.69	6.37	1.48	18.17
COOC-10 10/22-10/27/69	5.12	1.12	.18	.67	1.85	1.38	1.07	.35		.83	1.16		1.37	1.10	1.12	1.07	1.40
Mean	37.06	24.08	7.31	1.15	2.04	2.80	1.34	.97	13.38	4.87	2.90	.92					
Median	44.84	26.90	5.61	.93	1.85	1.29	1.48	.97	13.38	1.45	1.16	.92					
S	22.26	19.27	6.12	.79	1.00	4.27	.24	.87	15.12	8.04	3.70						

*Coastal region, ≤ 45 miles from shore.

**Oceanic region, > 45 miles from shore.

T = Trace amount

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Table 7. Euphausiid Dry Biomass $(g/10^3 m^3)$: Spatial and Temporal Variations Along the Newport Line.

| Cruise | Miles Offshore Along Newport Line | | | | | |
	3	5	15	25	45	65	85	105	125	145	165	185	Mean	Median	Coastal* Median	Oceanic** Median	S
COOC-3 5/12-5/15/69			.51	24.29		.53			.52	7.08	2.09		5.84	1.31	12.40	1.31	9.39
COOC-4 6/27-7/1/69	.15	1.59	2.41	15.27	.37	.82				.73	.69		2.75	.78	1.59	.73	5.11
COOC-6 8/5-8/12/69	.92	T	T	.62	.67	3.12	.63			T	.49		.72	.62	.62	.56	.96
COOC-8 8/19-8/21/69			T	.55	.62	.50					.15	.16	.33	.33	.55	.16	.26
COOC-9 9/9-9/14/69	.48	.51	T	6.54	4.02	T	.40	.48	.15	.64			1.32	.48	.51	.40	2.18
COOC-10 10/22-10/27/69	T	.00	T	.50	2.88	1.93	.24	.24		.72	.42		.69	.33	T	.42	.96
Mean	.39	.53	.49	7.96	1.71	1.15	.42	.36	.34	1.83	.77	.16					
Median	.32	.26	T	3.58	.67	.68	.40	.36	.34	.72	.49	.16					
S	.41	.75	.96	9.85	1.64	1.16	.20	.17	.26	2.95	.76						

*Coastal region, ≤ 45 miles from shore.   T = Trace amount

**Oceanic region, > 45 miles from shore.

Table 8.   Salp + Doliolid Dry Biomass $(g/10^3m^3)$:   Spatial and Temporal Variations Along the Newport Line.

Cruise	Miles Offshore Along Newport Line												Mean	Median	Coastal* Median	Oceanic** Median	S
	3	5	15	25	45	65	85	105	125	145	165	185					
COOC-3 5/12-5/15/69			.00	.00		.52			.11	.27	T		.15	.06	.00	.19	.21
COOC-4 6/27-7/1/69	.00	.00	.00	.00	1.95	50.23			T	.02			6.53	T	.00	.02	17.67
COOC-6 8/5-8/12/69	.00	T	.00	T	8.37	.41	.05		T	T			.98	T	T	.03	2.77
COOC-8 8/19-8/21/69			T	T	1.24	7.23					.29	.07	1.47	.18	T	.29	2.86
COOC-9 9/9-9/14/69	.00	.00	.00	1.61	21.61	T	T	.94	.12	.19			2.45	.06	.00	.12	6.75
COOC-10 10/22-10/27/69	T	T	.00	.00	T	T	.09	T		.05	T		.01	T	T	T	.03
Mean	T	T	T	.27	6.63	9.73	.05	.47	.12	.10	.06	.07					
Median	.00	T	.00	T	1.95	.47	.05	.47	.12	.05	T	.07					
S	.00	.00	.00	.66	8.98	20.04	.04	.66	.01	.12	.13						

*Coastal region, $\leq$ 45 miles from shore.   T = Trace amount

**Oceanic region, > 45 miles from shore.

Table 9. Fish Dry Biomass ($g/10^3m^3$): Spatial and Temporal Variations Along the Newport Line.

Cruise	Miles Offshore Along Newport Line										Mean	Median	Coastal* Median	Oceanic** Median	S
	15	25	45	65	85	105	125	145	165	185					
COOC-3 5/12-5/15/69	.04	.43	.56				1.74	1.48	1.42		.95	.99	.43	1.48	.69
COOC-4 6/27-7/1/69	.10	.48	1.02	1.37	.84			.69	1.28		.83	.84	.48	1.06	.45
COOC-6 8/5-8/12/69	.69	.45	1.88	1.26	2.29			.79	2.01		1.34	1.26	.69	1.64	.73
COOC-8 8/19-8/21/69	T	.83	1.96	2.08					.45	.69	1.00	.76	.83	.69	.84
COOC-9 9/9-9/14/69	.02	.16	2.22	.92	.16	1.17	.83	.75			.78	.79	.16	.83	.72
COOC-10 10/22-10/27/69	.03	.17	.69	.33	.76	.24		.66	.51		.42	.42	.17	.51	.27
Mean	.15	.42	1.39	1.19	1.01	.71	1.29	.87	1.13	.69					
Median	.04	.44	1.45	1.26	.80	.71	1.29	.75	1.28	.69					
S	.27	.25	.72	.64	.90	.66	.64	.34	.66						

*Coastal region, ≤ 45 miles from shore.

**Oceanic region, > 45 miles from shore.

T = Trace amount

Table 10. Shrimp Dry Biomass $(g/10^3m^3)$: Spatial and Temporal Variations Along the Newport Line.

Cruise	15	25	45	65	85	105	125	145	165	185	Mean	Median	Coastal* Median	Oceanic** Median	S
COOC-3 5/12-5/15/69	.00	.10	.76				.08	.56	.15		.28	.13	.10	.15	.31
COOC-4 6/27-7/1/69	.04	.34	.14	1.44	.46			.13	.23		.40	.23	.14	.35	.48
COOC-6 8/5-8/12/69	.02	1.31	.23	.38	.31			.29	5.32		1.12	.31	.23	.35	1.90
COOC-8 8/19-8/21/69	.00	.46	.51	.37					.18	.51	.34	.42	.46	.37	.21
COOC-9 9/9-9/14/69	.00	1.98	.39	.12	.22	.07	.07	.10			.37	.11	.39	.10	.66
COOC-10 10/22-10/27/69	.00	.21	.71	.09	.23	.24		.10	.13		.21	.17	.21	.13	.22
Mean	.01	.73	.46	.48	.31	.16	.08	.24	1.20	.51					
Median	.00	.40	.45	.37	.27	.16	.08	.13	.18	.51					
S	.02	.75	.25	.55	.11	.12	.01	.20	2.30						

(Miles Offshore Along Newport Line)

*Coastal region, $\leq$ 45 miles from shore.

**Oceanic region, > 45 miles from shore.

Table 11. Cephalopod Dry Biomass $(g/10^3m^3)$: Spatial and Temporal Variations Along the Newport Line.

Cruise	Miles Offshore Along Newport Line										Mean	Median	Coastal* Median	Oceanic** Median	S
	15	25	45	65	85	105	125	145	165	185					
COOC-3 5/12-5/15/69	.00	.31	.26				.17	.04	.17		.16	.17	.26	.17	.12
COOC-4 6/27-7/1/69	.00	.43	.03	.37	.16			.07	.11		.17	.11	.03	.14	.17
COOC-6 8/5-8/12/69	.03	.20	.20	.03	T			T	.08		.08	.03	.20	.02	.09
COOC-8 8/19-8/21/69	.01	.48	.23	.07					T	.17	.16	.12	.23	.07	.18
COOC-9 9/9-9/14/69	.00	.22	.15	.01	.14	.03	.36	.11			.13	.13	.15	.11	.12
COOC-10 10/22-10/27/69	.00	.01	.11	.04	.17	.05		T	.02		.05	.03	.01	.04	.06
Mean	.01	.28	.16	.10	.12	.04	.27	.04	.08	.17					
Median	.00	.27	.18	.04	.15	.04	.27	.04	.08	.17					
S	.01	.17	.08	.15	.08	.01	.13	.05	.07						

*Coastal region, $\leq$ 45 miles from shore.

**Oceanic region, > 45 miles from shore.

T = Trace amount

Table 12. Medusa + Siphonophore + Ctenophore Dry Biomass $(g/10^3m^3)$:   Spatial and Temporal Variations Along the Newport Line.

Cruise	3	5	15	25	45	65	85	105	125	145	165	185	Mean	Median	Coastal* Median	Oceanic** Median	S
COOC-3 5/12-5/15/69			4.92	1.02		2.25			2.02	.19	.46		1.81	1.52	2.97	1.24	1.73
COOC-4 6/27-7/1/69	4.42	3.22	.40	1.45	1.52	.20				.49	1.67		1.67	1.49	1.52	.49	1.47
COOC-6 8/5-8/12/69	2.92	T	3.93	.32	.57	.09	5.18			.04	.31		1.48	.32	.57	.20	1.98
COOC-8 8/19-8/21/69			3.18	11.70	.84	1.76					.14	.17	2.97	1.30	3.18	.17	4.43
COOC-9 9/9-9/14/69	T	T	1.17	.80	6.30	T	.28	.13	.65	.36			.97	.32	.80	.28	1.91
COOC-10 10/22-10/27/69	.93	4.14	.51	.51	.74	.65	.27	.02		.17	.08		.80	.51	.74	.17	1.21
Mean	2.07	1.84	2.35	2.63	1.99	.83	1.91	.08	1.34	.25	.53	.17					
Median	1.93	1.61	2.18	.91	.84	.43	.28	.08	1.34	.19	.31	.17					
S	1.99	2.16	1.92	4.46	2.43	.95	2.83	.08	.97	.18	.65						

*Coastal region, $\leq$ 45 miles from shore.

**Oceanic region, > 45 miles from shore.

T = Trace amount

Table 13. Chaetognath Dry Biomass $(g/10^3m^3)$: Spatial and Temporal Variations Along the Newport Line.

Cruise	\multicolumn{12}{c}{Miles Offshore Along Newport Line}			Coastal*	Oceanic**	
	3	5	15	25	45	65	85	105	125	145	165	185	Mean	Median	Median	Median	S
COOC-3 5/12-5/15/69			.11	.07		.86			.70	.91	.70		.56	.70	.09	.78	.37
COOC-4 6/27-7/1/69	3.18	2.07	.03	.13	.13	.03				.15	.11		.73	.13	.13	.11	1.21
COOC-6 8/5-8/12/69	4.47	1.73	T	T	.11	.41	.49			.04	.32		.84	.32	.11	.37	1.46
COOC-8 8/19-8/21/69			.61	.39	.66	.63					.35	.29	.49	.50	.61	.35	.16
COOC-9 9/9-9/14/69	13.11	8.10	1.09	.14	.30	T	.44	.32	.92	.48			2.49	.46	1.09	.44	4.45
COOC-10 10/22-10/27/69	2.17	.61	T	.16	.29	.50	.40	T		.21	.28		.46	.29	.29	.28	.63
Mean	5.73	3.13	.31	.15	.30	.41	.44	.16	.81	.36	.35	.29					
Median	3.83	1.90	.07	.14	.29	.46	.44	.16	.81	.21	.32	.29					
S	5.01	3.37	.45	.13	.22	.34	.04	.23	.16	.35	.22						

*Coastal region, ≤ 45 miles from shore.

**Oceanic region, > 45 miles from shore.

T = Trace amount

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Table 14. Amphipod Dry Biomass $(g/10^3 m^3)$: Spatial and Temporal Variations Along the Newport Line.

Cruise	\multicolumn{12}{c}{Miles Offshore Along Newport Line}						Mean	Median	Coastal* Median	Oceanic** Median	S
	3	5	15	25	45	65	85	105	125	145	165	185					
COOC-3 5/12-5/15/69			.17	.07		.11			.32	.10	.22		.17	.14	.12	.17	.09
COOC-4 6/27-7/1/69	T	T	T	T	.09	.21				.05	.12		.06	.03	T	.12	.08
COOC-6 8/5-8/12/69	.17	T	T	T	.08	T	.04			T	T		.03	T	T	T	.06
COOC-8 8/19-8/21/69			.15	.18	.15	.01				T	T		.08	.08	.15	T	.09
COOC-9 9/9-9/14/69	T	.12	T	T	T	T	T	.15	T	.04			.03	T	T	T	.06
COOC-10 10/22-10/27/69	.04	T	T	T	.07	.06	.05	.03		.09	.03		.04	.04	T	.05	.03
Mean	.05	.03	.05	.04	.08	.07	.03	.09	.16	.06	.07	T					
Median	.02	T	T	T	.08	.04	.04	.09	.16	.05	.03	T					
S	.08	.06	.08	.07	.05	.08	.03	.08	.23	.04	.10						

*Coastal region, $\leq$ 45 miles from shore.
**Oceanic region, > 45 miles from shore.

T = Trace amount

Table 15. Annelid Dry Biomass $(g/10^3m^3)$: Spatial and Temporal Variations Along the Newport Line.

Cruise	Miles Offshore Along Newport Line												Mean	Median	Coastal* Median	Oceanic** Median	S
	3	5	15	25	45	65	85	105	125	145	165	185					
COOC-3 5/12-5/15/69			.00	T		.09			.06	T	.03		.03	.02	T	.05	.04
COOC-4 6/27-7/1/69	.00	T	.00	.01	.09	.03				.05	.02		.03	.02	T	.03	.03
COOC-6 8/5-8/12/69	.00	.00	.00	.00	.14	T	.02			.00	T		.02	.00	.00	T	.05
COOC-8 8/19-8/21/69			.00	.00	.15	.10					T	T	.04	T	.00	T	.07
COOC-9 9/9-9/14/69	.00	.00	T	T	.13	.00	T	.14	T	T			.03	T	T	T	.06
COOC-10 10/22-10/27/69	T	.00	.00	T	T	.19	.05	T		.16	.05		.05	T	T	.05	.07
Mean	T	T	T	T	.10	.07	.02	.07	.03	.04	.02	T					
Median	.00	.00	.00	T	.13	.06	.02	.07	.03	T	.02	T					
S	.00	.00	.00	.00	.06	.07	.02	.10	.04	.07	.02						

*Coastal region, $\leq$ 45 miles from shore.

**Oceanic region, > 45 miles from shore.

T = Trace amount

Table 16. A Comparison of Chlorophyll a from 0-50 m and
50-75 m at Four Oceanic Stations off Tillamook Head.

Station	Position	Integrated chlor a (mg/m^2) 0-50 m	Integrated chlor a (mg/m^2) 50-75 m
C54	45°52.8' 126°00.0'	5.43	5.35
C50	45°56.4' 126°30.4'	5.60	7.20
A46	46°00.0' 127°00.0'	5.15	8.75
A39	45°45.3' 127°25.9'	5.55	11.50

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APPENDICES

APPENDIX I

Smooth Curve <u>vs</u> Linear Interpolation Estimates of Chlorophyll <u>a</u>
Integrated to 50 m.   (Data from COOC-9)

Station	A Chlorophyll <u>a</u> (mg/m^2) integrated to 50 m using curves	B Chlorophyll <u>a</u> (mg/m^2) integrated to 50 m using straight line approximation	$\frac{B}{A}$ x 100
NH-3*	37.88	36.95	97.54
NH-5	46.58	51.38	110.30
NH-15	30.09	30.48	101.29
NH-25	35.98	38.01	105.64
NH-35	56.46	56.53	100.12
NH-45	63.21	67.16	106.24
NH-55	25.07	25.01	99.76
NH-65	13.87	12.98	93.58
NH-85	8.38	8.41	100.35
NH-105	14.16	13.33	94.13
NH-125	8.69	9.08	104.48
NH-145	3.07	2.95	96.09
NH-165	(~0)	(~0)	---

$$\frac{B}{A} \text{ x 100: } \quad \text{Mean} = 100.79$$
$$s = 5.12$$

*Chlorophyll <u>a</u> integrated to 25 m at this station.

APPENDIX II

Chlorophyll a Values Integrated to 50 m vs Those Integrated to
Compensation Depth ($Z_{1\%}$). (Data from COOC-4)

NH-Station	Secchi Disc (d) Reading	Extinction Coefficient (k=1.7/d)	Comp. Depth ($Z_{1\%}$=4.61/k)	A Chlor a mg/m^2 to $Z_{1\%}$	B Chlor a mg/m^2 to 50 m	$\frac{B}{A}$ x 100
3*	3.75	.453	10.2	56.8	111.2	195.8
5	7.00	.243	19.0	46.1	67.8	147.2
10	9.50	.179	25.8	25.4	34.8	137.3
15	9.00	.189	24.4	32.4	41.9	129.5
25	9.00	.189	24.4	9.2	19.7	214.1
35	10.5	.162	28.5	13.6	25.8	190.1
45	10.74	.158	29.2	13.1	24.2	185.1
65	9.50	.179	25.8	7.8	15.9	208.7
105	23.0	.074	62.4	20.9	15.1	72.2
125	19.5	.087	52.9	8.4	6.8	80.8
145	17.0	.100	46.1	19.2	22.3	115.6
165	18.5	.092	50.2	22.0	21.9	99.7

$$\frac{B}{A} \times 100: \quad \text{Mean} = 149.99$$
$$s = 50.09$$

*Chlorophyll a integrated to 25 m at this station.

APPENDIX III

SAMPLING DIFFERENCES BETWEEN VERTICAL METER

NETS AND BONGO NETS

Comparisons of VMN and Bongo hauls suggest that these two nets sample the plankton differently, despite their being of identical mesh size and sampling the same depth range. Table III-1 lists the biomasses $(g/10^3 m^3)$ for all paired tows during the COOC series. When data from all three cruises are pooled, the signed-rank test (Tate and Clelland, 1957) indicates that the greater efficiencies of the Bongo in catching plankton and euphausiids is highly significant ($P<.01$ and $P\ll.01$, respectively), while neither net caught significantly more copepods nor chaetognaths ($P>.20$). The Bongo also caught significantly more euphausiids during COOC's 6 and 10 and more copepods during COOC-6 ($P \leq.05$). (There were insufficient data for testing the COOC-4 tows.) Only euphausiids were consistently caught in higher numbers in the Bongo. Perhaps these strong swimmers can sense the vibrations in the bridle of the VMN as it ascends and generally avoid being caught. The Bongo was fished on oblique tows, traveling at more than 5 times the speed of the VMN, and had no obstructions blocking the mouth. Thus, it gives little warning to trigger an avoidance reaction.

Table III-1. Bongo <u>vs</u> Vertical Meter Net Dry Biomass (g/10^{3}m^3) for Paired Hauls Located Along the Newport Line.

Σ Plankton		Euphausiid		Copepod		Chaetognath	
Bongo	VMN	Bongo	VMN	Bongo	VMN	Bongo	VMN
(COOC-4)							
33.99	18.06	32.83	15.27	1.01	1.21	0.15	0.13
6.36	3.92	2.68	0.73	2.51	2.45	0.31	0.15
3.09	4.40	1.72	0.69	1.05	1.77	T	0.11
(COOC-6)							
14.87	1.40	10.39	0.62	4.29	0.46	0.19	T
7.23	5.00	4.22	3.12	1.94	0.97	0.18	0.41
3.76	8.04	1.27	0.63	1.74	1.48	0.40	0.49
3.78	0.51	2.31	T	0.74	0.42	0.64	0.04
6.37	2.10	2.65	0.49	2.47	0.98	0.77	0.32
159.38	2.65	153.40	T	5.50	T	T	T
(COOC-10)							
3.44	0.69	0.85	T	2.12	0.18	0.06	T
11.32	3.57	10.70	0.50	0.40	0.67	0.03	0.16
15.58	5.84	13.59	2.88	1.08	1.85	0.24	0.29
13.67	4.71	8.42	1.93	1.24	1.38	0.20	0.50
2.76	2.15	0.90	0.24	0.75	1.07	0.25	0.40
1.22	0.79	0.35	0.24	0.33	0.35	0.12	T
3.19	2.32	1.83	0.72	0.61	0.83	0.21	0.21
0.75	2.14	0.19	0.42	0.26	1.16	0.05	0.28