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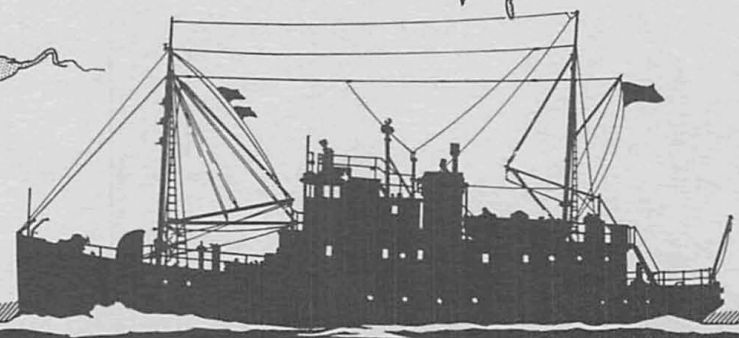
COLUMBIA RIVER EFFLUENT IN THE NORTHEAST PACIFIC OCEAN, 1961, 1962: SELECTED ASPECTS OF PHYTOPLANKTON DISTRIBUTION AND PRODUCTION

By

George C. Anderson

U.S. Atomic Energy Commission
Contract AT(45-1)-1725
and
Office of Naval Research
Contract Nonr-477(10)
Project NR 083-012

Reference M63-50
December 1963



SEATTLE, WASHINGTON 98105

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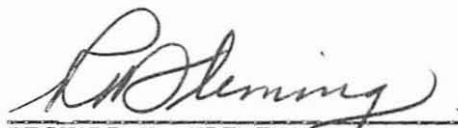
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ABSTRACT

The distribution of chlorophyll a and phytoplankton productivity off the Washington and Oregon coasts has been observed during 14 cruises of the R. V. Brown Bear from January, 1961 to June, 1962.

Surface waters in the area covered by the Columbia River effluent generally contained more phytoplankton and had a higher rate of photosynthesis than ambient waters. The densest and most variable populations were found during summer in coastal upwelling areas and directly off the river mouth. Although there was little seasonal change in standing stock, production was quite variable with minima in winter and summer and a large spring bloom and lesser autumn pulse.

The major influence of Columbia River water on phytoplankton production appeared to be in the timing of events in the seasonal cycle. Phytoplankton development was noticeably affected by differences in the depth of the mixed layer and the sharp pycnocline during summer. However, total annual production both inside and outside of the plume was similar ($60 \text{ g C/m}^2/\text{year}$). The effect of nutrients introduced by river water appeared to be spent in high production areas immediately off the mouth of the river.

The seasonal variation of C^{14} - chlorophyll a uptake ratios was marked. Low values occurred during winter with a maximum during the spring bloom. "Dead" or inactive chlorophyll appeared to be negligible at all times, judging from regressions of these relationships.

INTRODUCTION

Since January, 1961, the Department of Oceanography has been carrying on intensive studies of certain aspects of physical, chemical, geological, and biological oceanography in the Columbia River effluent area of the northeast Pacific Ocean. Bimonthly cruises of three weeks duration have been made to the area to determine seasonal variations in various properties. The frequency of cruises has been somewhat greater in summer than in winter months. An oceanographic data report for the first five cruises was recently issued (University of Washington, Department of Oceanography, 1963) and other reports for subsequent cruises will appear at intervals. The present report will deal with some features of the biology of the area from January, 1961 through June, 1962.

The biological emphasis is on the seasonal study of the phytoplankton and those zooplankton organisms retained by fine-mesh nets. Attempts are made to demonstrate the relationship of plankton distribution and activity with hydrographic and chemical conditions in and adjacent to the effluent area. Phytoplankton studies include assessments of the standing crop, rates of production, and size fractions of the population. An areal and vertical distribution study has been made of the taxonomic composition of the phytoplankton population during January, 1961 (Hobson, 1963). Seasonal studies of the taxonomic composition and species abundance of zooplankton in the upper one hundred meters are in progress. Because little is known concerning the biology of this region of the northeast Pacific Ocean, seasonal and distributional studies of organisms and populations are necessary. It is hoped that this investigation will provide a solid foundation for future biological work in the area.

The primary objective of this paper is to relate the standing crop and production of the plankton to seasonal variations in the distribution of Columbia River effluent. In pursuing this objective, new information is being obtained concerning seasonal and annual variations of populations in a rather extensive geographic area. The few seasonal phytoplankton productivity studies conducted in other oceanic areas have, for the most part, been limited to variations measured at a single station (e.g. Menzel and Ryther 1960, McAllister 1962). Noteworthy exceptions are the seasonal studies conducted on the continental shelf off New York (Ryther and Yentsch 1958) and the Fladen Ground (Steele 1956). In addition to the study of those waters influenced by freshwater discharge, observations are also being made in coastal upwelled regions and in areas offshore from Columbia River influence. Thus, the data afford comparisons of areas with widely differing hydrographic conditions. It has been possible to establish the annual rate of primary production and the seasonal cycles; and, since the study is being continued for several years, some idea of annual variation will be obtained. Greater emphasis is now being given to specialized projects of phytoplankton population growth which include measurements of short-term variations, both day-to-day and diurnal, experimental effects of nutrient enrichment in different hydrographic areas, seasonal response of populations to varying light conditions and some observations on zooplankton - phytoplankton relationships.

There is little information of the effects on plankton of large freshwater discharges into oceanic areas. However, it may be expected that the effect of the Columbia River discharge on the distribution and activity of planktonic organisms will be marked and will vary seasonally with the amount and quality of discharge and its subsequent distribution. In studies of the Mississippi discharge, Riley (1937) found high chlorophyll and phosphorous concentrations near the mouth of the river during high runoff, indicating an increase in standing stock of phytoplankton brought about by high nutrient content. In a later study, Thomas and Simmons (1960) found no over-all statistical differences in productivity between river, plume, and Gulf areas at any given season although it was admitted that the studies may not have been carried out far enough into the Gulf. However, the species of phytoplankton were separated into a river association of freshwater forms and a Gulf association of marine forms, while both associations were found in the mixing zone of freshwater with seawater (Simmons and Thomas 1962). In the Mediterranean Sea, Liebman (1935) found a marked increase in zooplankton volumes during the flood stage of the Nile. The discharge of nutrient-rich Nile waters during the flood is followed immediately by a massive outburst of diatoms composed mainly of Skeletonema costatum and several species of Chaetoceros (Halim 1960). The composition of the plankton as a whole was typically neritic (Oren and Komarovsky 1961). Certain organisms, such as the cladoceran Podon polyphemoides have been used as possible indicators for the presence of the Nile flood (Komarovsky 1953).

The scope of this paper is limited to a seasonal and local description of phytoplankton population distribution and production. Certain relationships between phytoplankton production and hydrography will be noted. The effect of nutrient distribution on phytoplankton population development is discussed; but, due to the preliminary nature of the report, only selected features are given at this time. The annual production in four sub areas of widely varying conditions is presented. Also included are some features of C^{14} uptake - chlorophyll a relationships, an analysis of which is in progress. A treatment of the zooplankton and special studies of phytoplankton are deferred until later reports.

METHODS

Biological sampling was carried out on all cruises of the R. V. Brown Bear pertaining to the Columbia River Study (Table 1). In most cases, stations coincided with those planned for physical and chemical measurements. Standard techniques were used whenever possible. Emphasis was placed on collecting large numbers of samples for statistical evaluation. However, because only one or two people were aboard for biological work, some of the stations were not sampled during each cruise.

TABLE I

Summary of cruises off the Washington and Oregon coasts
by R. V. Brown Bear, January 1961-June 1962

Cruise No.	Date
275	10-27 January, 1961
280	7-24 March, 1961
282	3- 7 April, 1961
287	8-24 May, 1961
288	9-19 June, 1961
290	6-25 July, 1961
291	28 July - 13 August, 1961
292	14-20 August, 1961
293	14 September - 20 October, 1961
297	28 November - 18 December, 1961
299	23 January - 7 February, 1962
304	27 March - 12 April, 1962
308	7-19 June, 1962
309	20 June - 9 July, 1962

Phytoplankton

At each station, samples were routinely taken with modified Van Dorn plastic samplers (6-liter capacity) at four depths within the euphotic zone which corresponded to 100, 50, 10 and 1 percent of surface light intensity. These depths were computed from extinction coefficients derived from Secchi disc measurements using the formula $K = \frac{1.7}{\text{Secchi measurement}}$ (Poole and Atkins

1929). Continuous recording of incident solar radiation was made with a Kipp Zonen solarimeter equipped with a Speedomax circular chart recorder. Beginning with cruise 297, a standard depth of 100 m was added to the sampling schedule and, in some cases, samples were taken to 200 m for additional estimates of chlorophyll.

Generally, 3 liters of water was filtered through HA Millipore[®] 1 filters (pore size $0.45 \mu + 0.02$) with the addition of a small amount of MgCO_3 . Filters were trimmed and stored in a desiccator in the dark for future quantitative analysis of plant pigments. Duplicate small samples (50-100 ml) from selected stations were preserved in formalin and in Lugol's acetic acid solution for future quantitative estimates of species abundance.

Rates of production were measured with the C^{14} isotope method (Steemann Nielsen 1952) using 125-ml pyrex light and dark bottles. Carbon¹⁴, as Na_2CO_3 was stored in 2-ml ampoules and had a strength of about $2.5 \mu\text{c/ml}$. After inoculation with C^{14} , the samples were incubated for a period of three to six hours in a constant temperature and illumination incubator. The incubator is similar to that described by Steemann Nielsen (1952), with a rotating wheel holding the samples and a water bath with running seawater for temperature control. Illumination was provided by a bank of 20 watt

1 Registered trademark, Millipore Filter Corporation, Bedford, Massachusetts.

"Cool-white" fluorescent bars which produce approximately 850 foot-candles (9150 lux) at the sample site. After incubation, the samples were filtered on 25 mm diameter Millipore PH filters (pore size $0.3 \mu \pm 0.02$) with a vacuum of 375-500 mm Hg. After a rinse with 5 ml filtered seawater, the filters were placed in individual plastic containers and stored in desiccators with silica gel. The results obtained with the incubator technique are herein-after referred to as "incubator productivity".

Simulated in situ measurements of production were made daily at a "noon" station, according to recommendations made by the International Council for the Exploration of the Sea (Ryther *et al.* 1958). Each day, regardless of ship's position, a station was taken about 45 minutes before noon. In addition to the procedure described above, a duplicate set of light and dark bottles was prepared and incubated in a deck-mounted incubator exposed to full natural illumination and temperature controlled by running surface seawater. Optical conditions from which the samples were taken were simulated with neutral density filters. The incubation period was from noon to sunset. At sunrise, a surface sample was taken and incubated in both the routine manner and in the deck incubator until noon. The contribution of different size groups of phytoplankton in surface water at each noon station was estimated by filtration of aliquots of C^{14} -tagged surface water samples. Six filters, ranging in pore size from 35 to 0.22 microns, were used (net-35.0 μ ; SM-5.0 μ ; AA-0.8 μ ; HA-0.45 μ ; PH-0.3 μ ; GS-0.22 μ). Water samples from each depth were frozen for future analysis of nitrate, silicate and phosphate.

In the laboratory, the C^{14} -treated filters were exposed to fuming HCl for 10-15 minutes to remove traces of inorganic C^{14} . Geiger counting was done with a Nuclear-Chicago D-47 gas flow counter with micromil window, 161-A scaler, C-110 automatic sample changer and C-111 B printing timer. Each sample was counted to a minimum number of 1280 disintegrations so that the reliable error of counting (probability of 90%) is less than 5%. After counting, calculations were made with IBM processing which involved corrections for dark bottle uptake, background, C^{14} strength, variations in inorganic carbon content of seawater, coincidence loss and isotope effect (5%).

Plant pigment samples were processed according to the method of Richards with Thompson (1952) as modified by Creitz and Richards (1955). Corrections for turbidity were made by subtracting the reading at 750 m μ from all wavelengths. Calculations were done by IBM processing.

Zooplankton

Throughout the first year of these studies, zooplankton samples were taken twice daily - near noon and midnight. Standard-size Clarke-Bumpus samplers equipped with No. 12 mesh nylon nets (110 μ mesh aperture) were towed horizontally at four equally spaced depths within the upper 100 m. Samples were preserved in weak formalin buffered with borax. Series of surface plankton pump samples were taken during some cruises to study vertical migration.

Methods of examination and enumeration of zooplankton organisms are in the process of being developed for the Columbia River Study. Special series of replicate samples are being examined and analyzed to determine

requirements for aliquot size, number of aliquots necessary, number of organisms necessary to count, etc. so that the results can be expressed within desired statistical limits.

HYDROGRAPHY

Hydrographic conditions in the Columbia River effluent area will be described in detail by others in later reports (Budinger, Coachman and Barnes 1963). Briefly, the vertical distribution of salinity in the off-shore area is characterized by a halocline 75 to 150 m thick, situated 75 to 100 m beneath the surface. In winter, the surface layer is well mixed, but during summer, thermal stratification develops and the surface temperatures increase (about 8°C over that in winter).

The seasonal distribution of Columbia River effluent as defined by the salinity distribution during 1961 - 1962 is illustrated in Figs. 1 to 11. The 32.5 ‰ isopleth has been selected as a convenient feature to mark the boundary of the river plume. During winter months, the low salinity water lies close along the Washington coast, north of the mouth of the river. During summer it lies south of the river mouth, a shift accompanying the change in wind pattern from southwesterly in winter to northerly in summer. The plume reached its maximum development in early autumn when it was found to extend south into northern California waters and offshore to a distance of about 350 miles. The identity of the plume to the south of the river mouth was lost during autumn and early winter storms and the low salinity water formed a narrow band along the coast north of the river. Upwelled water at the surface along the Oregon coast was evident during summer but varied in intensity with wind speed and direction and was covered in part by the plume of freshwater.

The Columbia River water was confined to a relatively thin surface layer during the development of the summer plume. The lower limit was marked by a well developed pycnocline. In May, the surface layer ranged in thickness from 5 to 10 m and gradually increased in depth as the season progressed. By early autumn, the depth of the pycnocline was 30 to 40 m. In waters offshore from Columbia River influence, vertical mixing occurred to a depth of 70 to 80 m during winter and early spring. By June, a thermocline was found at a depth of 10 to 20 m. The summer thermocline increased in depth to a maximum of 30 to 40 m by early autumn. In general, during summer, the depth of the mixed layer was 5 to 10 m greater in waters offshore from the plume.

NUTRIENT CHEMISTRY

The seasonal cycle of plant nutrients off the Washington - Oregon coasts has been treated by Stefánsson and Richards (1963). Concentrations of nutrients in the mixed layer in winter were high in contrast to those in summer. The average concentrations in the upper 10 m during winter reached maxima of about 55 µg-at./liter silicate, 25 µg-at./liter nitrate, and 2 µg-at./liter phosphate along the coast, whereas, farther offshore the values were in the order of 10 µg-at./liter silicate, 5-6 µg-at./liter nitrate, and 1 µg-at./liter phosphate. During spring and summer, nutrients were rapidly utilized by the phytoplankton. Phosphate and silicate appeared to be in great enough quantity that it is doubtful that they became limiting to phytoplankton growth during the annual cycle although they dropped

significantly in concentration. Minimal quantities were 0-2 $\mu\text{g-at./liter}$ silicate and 0.2-0.3 $\mu\text{g-at./liter}$ phosphate. However, nitrate diminished to values as low as 0-4 $\mu\text{g-at./liter}$ in May and by mid-summer it was absent or scarcely detectable in surface offshore waters. Nutrients were more rapidly consumed in plume waters than farther offshore indicating greater phytoplankton activity in the surface layer of the plume. The concentration of nutrients remained high in upwelled waters along the coast during summer.

The seasonal variations in nutrient content are influenced by phytoplankton utilization, the extent of vertical mixing, and by nutrient addition from coastal sources. The hydrographic features of major importance are the relatively shallow depth of the mixed layer and sharp pycnocline during summer which limits vertical exchange. Nutrients are depleted by photosynthesis in the surface layer and tend to accumulate below the pycnocline, where they are not generally available to the euphotic zone until winter mixing begins. Increased vertical mixing during summer storms contributes some nutrients to surface waters. Significant quantities of nutrients are added to the system from the Strait of Juan de Fuca and from coastal upwelling during summer. The Columbia River contributes considerable silicate, some nitrate, and negligible phosphate.

SEASONAL DISTRIBUTION OF CHLOROPHYLL a AND PRIMARY PRODUCTION

Surface Distribution

The seasonal change of solar radiation is shown in Fig. 12. The distributions of chlorophyll a and productivity in surface waters are given in Figs. 13 to 33. Appropriate contour intervals were chosen to show the seasonal and horizontal variations in chlorophyll a and "incubator productivity", but the simulated in situ values were too few to contour.

Chlorophyll a in January, 1961 was in relatively high concentration close to shore from the mouth of the Columbia River north along the Washington coast (Fig. 13). The distribution at this time was quite patchy. Oceanic waters, i.e. those waters beyond Columbia River and other coastal influence, contained less than 0.2 mg/m^3 chlorophyll a while the waters associated with the effluent contained more than 0.5 mg/m^3 . Productivity (Fig. 14) at this time was low, oceanic waters showing less than 0.75 $\text{mg C/m}^3/\text{hour}$ and effluent waters more than 2.0 (2-5) $\text{mg C/m}^3/\text{hour}$. The surface simulated in situ observations showed a preponderance of higher values near the coast.

In March, 1961, the distribution was very similar to January in that higher concentrations of chlorophyll and greater rates of assimilation were recorded nearshore in association with the freshwater effluent (Figs. 15 and 16). "Incubator productivity" had increased somewhat since January in oceanic waters but little change had occurred in effluent waters. The seasonal increase in solar radiation was accompanied by an increase in simulated in situ productivity rates.

The spring bloom of phytoplankton was observed during the May, 1961 cruise. All indices showed a marked increase (Figs. 17 and 18). The peak of the bloom possibly could have occurred between the March and May cruises. However, in 1962, the values obtained during an early spring cruise (March 27 to April 12) were intermediate between the observations made in March and May of 1961. It is, therefore, quite probable that the May, 1961 observations were made close to the time of major phytoplankton population development, but the lack of continuous observation makes the situation uncertain. The distribution of biological properties parallels the horizontal distribution of low salinity water. At this time of decreasing wind velocity, low salinity water formerly lying along the coast, spread offshore in a westerly direction. The amount of chlorophyll was not distinctly higher than in January or March, except close inshore along the Washington coast where the values were 1-2 mg/m³. "Incubator productivity" was markedly higher in all areas: oceanic waters were in the 1-2 mg C/m³/hour range and the effluent water in the 5-50 mg C/m³/hour range. Simulated in situ observations ranged from 5-25 mg C/m³/day in oceanic waters to more than 100-200 mg C/m³/day in the effluent area.

In June, during the development of the plume in a southerly direction, high values of both chlorophyll and productivity were found to be in close association with the effluent (Figs. 19 and 20). Due to the brevity of the cruise, much interpolation was necessary. "Incubator productivity" showed a striking drop in phytoplankton activity, with oceanic waters decreasing to less than 0.3 mg C/m³/hour, and nearshore values to less than 5.0 mg C/m³/hour.

In July, chlorophyll a dropped to less than 0.1 mg/m³ in oceanic waters (Fig. 21). However, the 0.1 mg/m³ isopleth followed very closely the west and south boundaries of the plume indicating a slightly higher standing stock in surface waters of the plume. High values (up to 8.0 mg/m³) were found in upwelling areas along the Oregon coast. The 0.3 mg C/m³/hour isopleth of "incubator productivity" also loosely defined the outer boundaries of the plume (Fig. 22). However, simulated in situ values in and west of the plume showed little variation.

During August, there was a slight increase in both productivity and chlorophyll in the effluent area (Figs. 23 and 24). Stimulation of production by coastal upwelling was especially evident at this time.

Difficulty was encountered with the productivity measurements during the September - October cruise. Many of the data were rejected because of possible bacterial contamination in the light and dark bottles, leaving too few values to contour adequately. Therefore, only chlorophyll values are shown (Fig. 25). Again the 0.1 mg/m³ chlorophyll a contour followed the outer boundary of the plume. The influence of coastal upwelling appeared to advance westward as the summer progressed. The 0.2 mg/m³ chlorophyll contour was found between 125° and 126° W in July, between 126° and 127° W in August, and at 127° W in September - October.

The observations from the following two winter cruises, November - December (Figs. 26 and 27) and January - February (Figs. 28 and 29), compare favorably with the previous winter; i.e. highest values of both chlorophyll and productivity were found along the coast especially north of the river mouth.

However, the January-February data show somewhat higher chlorophyll values (0.2-0.3 mg/m³) in oceanic waters than shown by other winter cruises.

The chlorophyll distribution in April, 1962 (Fig. 30) was somewhat similar to that observed in May, 1961. However, assimilation rates at this time (Fig. 31) were not equal to those recorded during the spring bloom in 1961. Apparently, population development was just entering into a period of rapid increase marking the beginning of the spring bloom. Exceedingly low rates of production were observed directly off and west of the Columbia River mouth during a period of increased freshwater discharge from coastal rains. Surface salinity was considerably reduced, and, although the standing stock of phytoplankton remained high in the area, the vigor of the population was reduced to a low level.

The last cruise in the present series, June, 1962, provided further substantiation of the results obtained in the same time interval during 1961. The spring bloom was obviously over and the beginning of the summer minimum was again observed (Figs. 32 and 33).

Thus, the seasonal cycle of the phytoplankton beyond coastal waters is rather typical of that observed in many other oceanic studies. Although there was very little change in standing stock throughout the season, judging from changes in chlorophyll *a*, the variations in primary productivity showed a typical winter minimum, followed by a large increase during spring, and a summer minimum. Both surface chlorophyll and surface productivity observations were useful in corroborating the distribution of Columbia River effluent and areas of upwelling as delineated by the distribution of salinity and oxygen.

Areal Distribution in the Euphotic Zone

Figs. 34 to 44 show a cruise by cruise summary of the regional variations in chlorophyll *a* and simulated in situ primary productivity in the euphotic zone. Observations are expressed on an areal basis. The depth of the euphotic zone is assumed to occur at the level of one percent of surface illumination.

The seasonal picture derived from the areal presentation is quite similar to that already described from surface values. Briefly, the amount of chlorophyll at all seasons was typically low in offshore waters but was higher in winter than in summer. The area covered by the plume during summer maintained a standing stock slightly higher than was found farther offshore. Highest and most variable standing stocks were found during summer directly off the river mouth and in coastal areas where upwelling occurred. Primary productivity, on the other hand, was closely related to incident radiation during winter and spring, i.e. low in winter with an increase during spring. There were two peaks of production, a major bloom in May and a lesser pulse during autumn. There appeared to be little difference during summer in total production between waters of the plume and oceanic waters.

There was little apparent relationship between chlorophyll distribution and Columbia River effluent during winter months. In January and March, oceanic waters contained less than 10 mg/m^2 chlorophyll a. Intermediate between oceanic waters and the coast, higher values were observed (range $15\text{-}36 \text{ mg/m}^2$). Along the coast, values dropped to $5\text{-}10 \text{ mg/m}^2$. During the spring bloom, chlorophyll concentration showed little increase with the exception of coastal waters where the values increased to $20\text{-}30 \text{ mg/m}^2$ with a maximum of 85 mg/m^2 near Cape Flattery. The relationship between chlorophyll content and plume waters became evident during summer months. For the most part, values ranged between 5 and 10 mg/m^2 in the plume and were less than 5 mg/m^2 offshore from it. Upwelling areas reached maximal values of greater than 100 mg/m^2 while the area directly off the river mouth varied between 20 and 50 mg/m^2 . The following winter again showed a pattern of higher chlorophyll content in an intermediate area between coastal and offshore waters.

The winter distribution of primary productivity (simulated in situ) is similar to that described for chlorophyll. In both winters, values of less than $0.08 \text{ g C/m}^2/\text{day}$ in oceanic waters and less than $0.09 \text{ g C/m}^2/\text{day}$ in coastal waters were separated by a band of more productive waters (range 0.05 to $0.2 \text{ g C/m}^2/\text{day}$). During the spring, productivity increased markedly to $0.3\text{-}0.5 \text{ g C/m}^2/\text{day}$ in offshore areas and $0.4\text{-}0.7 \text{ g C/m}^2/\text{day}$ in the near vicinity of the Columbia River. A summer minimum beginning in June and persisting to August was noted in most regions outside of the upwelling and river mouth areas. Typical values at this time were slightly greater than $0.1 \text{ g C/m}^2/\text{day}$ in the plume and somewhat less beyond it. Areas near the river ranged from $0.14\text{-}0.38 \text{ g C/m}^2/\text{day}$ while a maximum value of $1.21 \text{ g C/m}^2/\text{day}$ was found in upwelled waters. An autumn increase in production was noted in plume waters ($0.08\text{-}0.35 \text{ g C/m}^2/\text{day}$) and in oceanic waters ($0.16\text{-}0.29 \text{ g C/m}^2/\text{day}$). This was followed by a drop in production to less than $0.10 \text{ g C/m}^2/\text{day}$ in all waters by November - December.

Vertical Distribution

Single stations have been selected to show the distribution of chlorophyll a and productivity (simulated in situ) with depth during different seasons of 1961. The stations were chosen from four different areas which are (1) oceanic waters beyond Columbia River influence, (2) a region southwest of the river mouth which is not influenced by the river during winter but which is covered by the plume during summer, (3) directly off the river mouth, and (4) regions of coastal upwelling.

In Area 1, chlorophyll a was quite uniformly distributed throughout the euphotic zone at all seasons (Fig. 45). In March, total photosynthesis was low but there was a suggestion of surface light inhibition if one assumes that the distribution of photosynthesis with depth in a well mixed water column will reflect the distribution of submarine light. Photosynthesis increased markedly in May but dropped to successively lower levels in June and July. In all three months, surface inhibition of photosynthesis occurred. The autumn pulse was marked by maximum photosynthesis at the surface.

The vertical distribution of both chlorophyll and productivity in Area 2 in winter and spring was similar to that described above (Fig. 46). However, as the plume developed over the area in summer, the depth of the euphotic zone decreased, presumably due to a higher concentration of plankton

and possibly to turbidity associated with river water. Productivity remained relatively high on a volumetric basis in contrast to offshore waters. The depth of the euphotic zone increased again after the disappearance of the plume in late autumn.

Area 3, off the river mouth, is characterized by high turbidity along with high productivity and standing crop of phytoplankton (Fig. 47). In view of the instability of the environment - due to variations in volume of freshwater involved, tidal effects, complex stratification, and changes in amount of suspended particulate matter introduced by the river - it is difficult to make generalizations regarding the seasonal cycle. However, some of the highest rates of production and standing crop were found in this area and productivity was sustained at a high rate throughout the summer. Thus, it is probably an area of major importance for the uptake and turnover by phytoplankton of radioisotopes introduced by the river.

Area 4, along the Oregon coast, is a region of intensive upwelling during summer when the wind is from the north (Fig. 48). During winter, the vertical distribution of phytoplankton was similar to that in offshore waters except that the euphotic zone was shallower and productivity was slightly greater which is to be expected. During upwelling, production was greatly stimulated by the nutrient-rich waters and remained high throughout the season (maximum $1.2 \text{ g C/m}^2/\text{day}$). These changes were accompanied by an increase in chlorophyll content with a very uneven vertical distribution and a decrease in the depth of the euphotic zone.

Fig. 49 shows the vertical distribution of chlorophyll *a* for each cruise along a section at $44^{\circ}45' \text{ N}$. The section extends from the coast near Newport, Oregon to as far offshore as $129^{\circ}00' \text{ W}$ in some cruises. Because the cruises did not have common sections, it was necessary to construct the figures by interpolation from horizontal plots at different depths. They are, therefore, somewhat diagrammatic. From Cruise 275 through Cruise 293 (January - October, 1961), samples were restricted to the euphotic zone. After this time, samples were routinely taken to 100 m depth. The location of the section was chosen to compare conditions between coastal and oceanic areas and to show the effect during summer of upwelling and Columbia River effluent.

The sections reflect no change which can be associated with Columbia River discharge from January through May, 1961. A gradual increase in chlorophyll content at all depths occurred as shore was approached during this time and a maximum at intermediate depths occurred in March. The concentration in offshore waters increased to about 0.2 mg/m^3 chlorophyll *a* during the spring bloom. During the summer and autumn (Cruises 288-293) the effect of upwelling was evident in coastal regions. The plume area was characterized by a chlorophyll content in the $0.1\text{-}0.2 \text{ mg/m}^3$ range, at first evenly mixed within the euphotic zone, but later distributed as a thin surface layer. Oceanic waters contained less than 0.1 mg/m^3 . During winter and the remaining cruises of 1962, the chlorophyll content to 100 m depth is shown. For the most part, very low levels were found at this depth.

ANNUAL PRODUCTION

Annual photosynthetic production in the euphotic zone has been calculated for each of the four areas defined in the section on vertical distribution of chlorophyll a and primary production (page 10). Because of limitations in sampling frequency there is some uncertainty in the estimation of annual production. Furthermore, measurements made in any selected area spaced a few days apart or even made on successive days may be quite different due to variations in incident radiation and to changes in the physiological state of the population, especially in periods of rapid growth or decline. It was possible to calculate maximum and minimum values of annual production by selecting the highest and lowest station values for each cruise in areas where multiple measurements were made. The following results were obtained:

TABLE 2

Estimates of annual production
in areas off the Washington and Oregon coasts, 1961

Area	Annual Production g C/m ² /year	Range g C/m ² /year	Mean Daily Production g C/m ² /day
1 (Oceanic)	61	43-78	0.17
2 (Plume)	60	46-73	0.16
3 (River Mouth)	88		0.24
4 (Upwelling)	152		0.42

There was little or no difference between plume and oceanic waters. The striking fact is that annual production is so low in these waters. It is similar to that reported from Station "P" (45° N, 145° W; 70 g C/m²/year, McAllister 1962), the Sargasso Sea (72 g C/m²/year, Menzel & Ryther 1960), the Fladen Ground (57-82 g C/m²/year, Steele 1956), and Danish inshore waters (mean value 74 g C/m²/year, Steemann Nielsen 1958). All of these areas, with the exception of Station "P" are recognized as nutrient impoverished areas. However, nutrients remain abundant throughout the year at Station "P" (McAllister, Parsons and Strickland 1960) while a summer nutrient deficiency exists in the Columbia River area which appears to be effective in keeping production low. Higher levels of annual production have been reported in other areas, such as the continental slope off New York (120 g C/m²/year, Ryther and Yentsch 1957) and in Long Island Sound (180 g C/m²/year, Riley 1956).

C¹⁴ UPTAKE - CHLOROPHYLL a RELATIONSHIPS

A fairly constant relationship between chlorophyll and photosynthesis measurements for different species of algae and over a wide range of chlorophyll content has been noted by various workers (see review by Strickland 1960). However, the ratios reported at optimal light intensities

from several studies varied widely, ranging from 1-2 mg C assimilated/hour/mg chlorophyll in natural populations to as high as 10 in cultures of algae. Ryther and Yentsch (1957) reported a mean ratio of 3.7 obtained from experimental results and from various field studies. The purpose of investigating these ratios was to devise a method whereby primary production could be calculated from the chlorophyll content, the total daily incident radiation and the extinction coefficient of the water column, thus eliminating the necessity for making measurements of photosynthesis. However, the method assumes that the ratio is constant and that all of the chlorophyll is active in photosynthesis.

The present study contributes additional information to ratios encountered in seasonal studies from incubator measurements. The light intensity (850 foot-candles) chosen was believed at the time to be suboptimal, at least for surface waters, in the area investigated.² A regression analysis was used to show the relationship in surface waters for all cruises (Figs. 50 to 59). The ratios calculated from the slope of the regression lines ranged from 1.6 in winter to a maximum of 9.8 during the spring bloom. Typically, the values were low in winter ranging from 1.6-3.7. After the spring bloom, the ratio dropped to a summer minimum (2.2-3.6) but increased to 5.5 during increased phytoplankton production in August. Also, maximum scatter occurred with high ratios during periods of increased phytoplankton activity.

The reason for the very low ratios reported during winter is due in part to excessive light used in incubation. It was found in later investigations that light measuring 850 foot-candles was inhibiting the phytoplankton production in surface waters during January, 1963. However, the correction for this effect applied to the January, 1961 data would raise the ratio less than twofold. Apparently, nutrient deficiency is the cause of the low but variable ratios in summer. Separation of the data into subareas according to differences in salinity gave little indication of significantly different ratios within cruises but this analysis is still in preliminary stages.

The presence of varying amounts of "dead" or inactive chlorophyll throughout the year could lead to serious errors in the relationship described above. Gillbricht (1952), with a regression analysis of chlorophyll, cell counts, and seston from samples taken in Kiel Bay, demonstrated that there was about as much chlorophyll associated with detritus as with living organisms. However, this does not appear to be of concern in the present instance since the data suggest the absence of "dead" chlorophyll throughout the year. A regression line would intercept the origin if one assumes a linear relationship between chlorophyll and photosynthesis and if there was no "dead" chlorophyll. In the present study, the regression line comes very close to the origin at most times, but in some cases intercepts the photosynthesis axis. This is probably a result of being unable to measure small amounts of chlorophyll, yet being able to record low levels of photosynthesis, thus giving the anomaly of positive photosynthesis with zero chlorophyll.

² An analysis of subsurface samples will involve the separation of "shade adapted" populations below the thermocline in summer and will not be treated at the present time.

Similarly, Steele and Baird (1961), found no evidence of "dead" chlorophyll in Aberdeen Bay and the Fladen Ground, from analyses of C^{14} uptake and chlorophyll measurements.

DISCUSSION

It is well recognized that the beginning of the spring bloom in deep temperate waters is brought about by an increase in available light accompanied by a decrease in the depth of the mixed layer (see review by Anderson and Banse, 1963). However, the depth of the mixed layer must be less than the critical depth (the depth of the mixed layer at which respiration and photosynthesis are equal) to produce a bloom (Sverdrup 1953). Nutrients, generally abundant in winter, are rapidly exhausted above the thermocline in summer, during which period there is limited exchange through the pycnocline and the population declines to a summer minimum. Replenishment of nutrients in summer occurs through turbulent exchange with the deeper water and, to a lesser extent, from regeneration in the euphotic zone (Ketchum 1947, Steele 1956). Stability of the water is reduced in autumn by surface cooling and the decrease in stability along with increased wind stress leads to increased vertical mixing. The resulting increase in exchange and upward diffusion of nutrients might effect a fall bloom. The development of the bloom is dependent upon the amount of nutrient addition, the depth of the mixed layer, and the level of incident radiation.

In the Columbia River effluent area, it appears that the depth of the mixed layer is usually shallower than the critical depth. Because of the permanent halocline, the mixed layer depth is never greater than about 75 m. Net production during winter appears to be positive, as evidenced by the increase in standing stock at this time. However, light is not present in sufficient amount to produce a phytoplankton bloom. Periods of temporary thermal stratification, followed by periods of mixing, mark the beginning of the spring bloom. The persistent summer thermocline does not occur until later. After the summer thermocline develops above the permanent halocline, photosynthesis rapidly exhausts the nutrient pool and production falls to low levels. Apart from nutrient sources from vertical mixing and regeneration, additional quantities may be added from coastal upwelling and the Columbia River effluent. The autumn pulse of phytoplankton production is probably due to increased upward advection of nutrients at a time when incident radiation is relatively high in contrast to winter conditions. Because of the permanent halocline and the shallow mixed layer depth during summer, the transport of nutrients into the surface layer from deep water is reduced and thus, annual production is low.

The major influence of Columbia River water on phytoplankton production appears to be in the timing of events rather than in any gross differences in annual production. Because of the somewhat shallower mixed layer and higher temperature of the plume, production in the mixed layer of the plume during early summer proceeds at a greater rate than in oceanic waters. Nutrients are, therefore, utilized at a greater rate and are depleted before the oceanic area. Preliminary results of short-term experiments to show the effect of Columbia River water on ambient water have failed to show a stimulation of production at different times of the year.

It should be expected that autumn production in oceanic waters would be higher, due to less stability of the water column. An examination of a section made through the outer boundary of the plume in October, 1962 supports this idea. Within the plume the pycnocline was still well developed but beyond it the waters generally were less stratified and particularly so in patches. It is possible that by the time stratification breaks down in the plume area, light would be much less favorable for growth.

It has been noted that significant amounts of silicate, and to a lesser extent, nitrate, are introduced by the river (Stefánsson and Richards 1963). However, it appears that the effect of this nutrient enrichment is spent in high production in the vicinity of the river mouth rather than contributing greatly to the major portion of the plume. It is probable also that nutrients from upwelled water, which intermixes with river water, contribute to the high production observed near the river mouth. The effect of nutrient-rich upwelled water is clearly evident south of the river along the Oregon coast. Westerly advection of coastal upwelled water is probably responsible for the progressive increase in width of the band of high production along the coast during summer.

The total annual production was seen to be low (60-61 g C/m²/year) both in the plume and in oceanic waters. The only other estimate of annual production in the general area of the present study is that reported from Station "P" (70 g C/m²/year, McAllister 1962). It is reasonable to expect that production might be higher at Station "P" because of the abundance of nutrients in surface waters throughout the year. Further confirmation for the low productivity of the effluent area is the low surface production off the coast from 35°-45° N (Holmes 1958). Although only two measurements were reported and were a greater distance offshore than estimates from this study, they represented the lowest values in a series of measurements extending from about 5° S to 55° N in offshore waters. Similarly, Koblenz-Mishke (1960) found comparably low values during the visit of the Vityaz to these waters during autumn, 1958.

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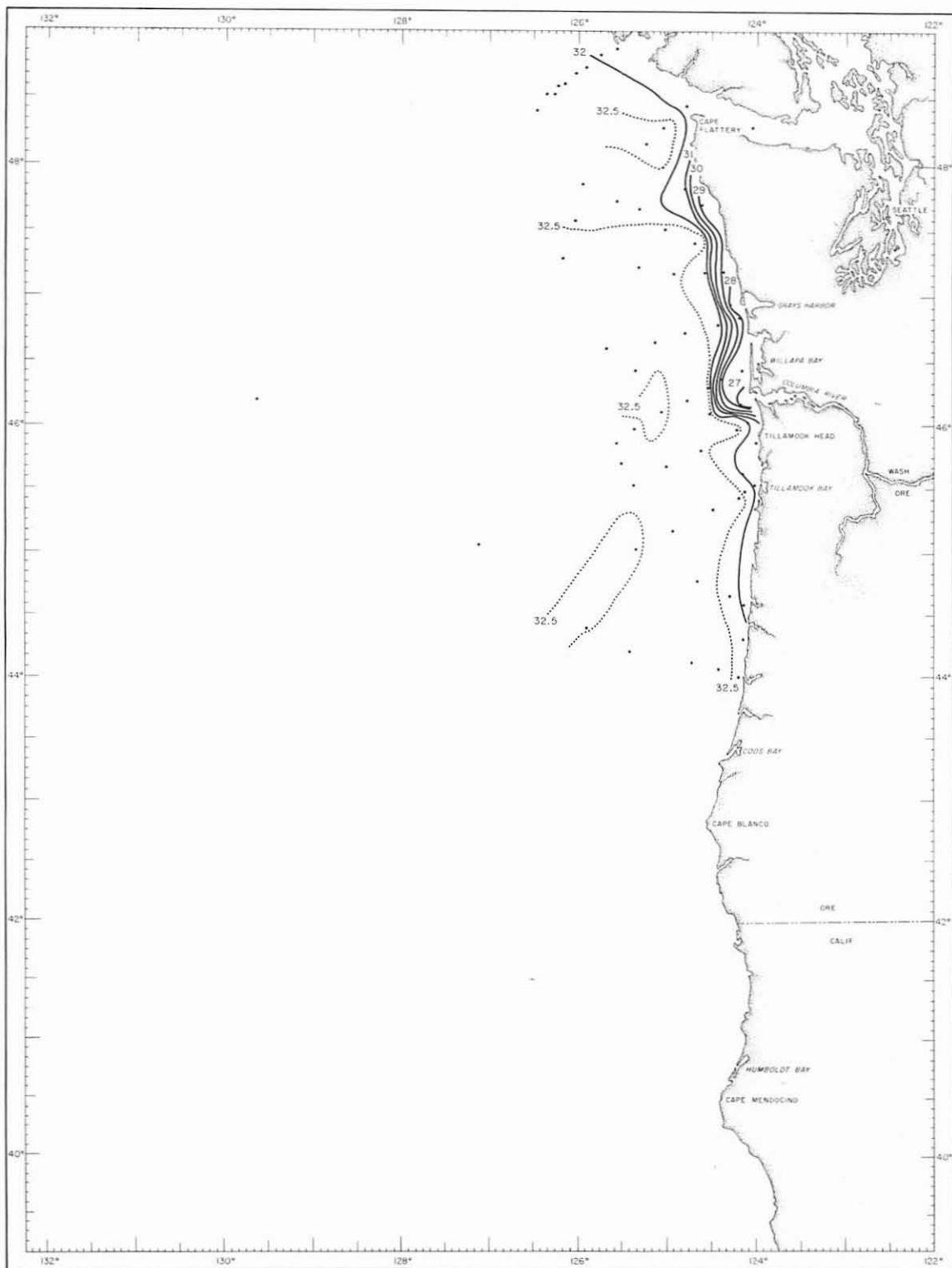


Fig. 1 Distribution of surface salinity off the Washington and Oregon coasts, January, 1961.

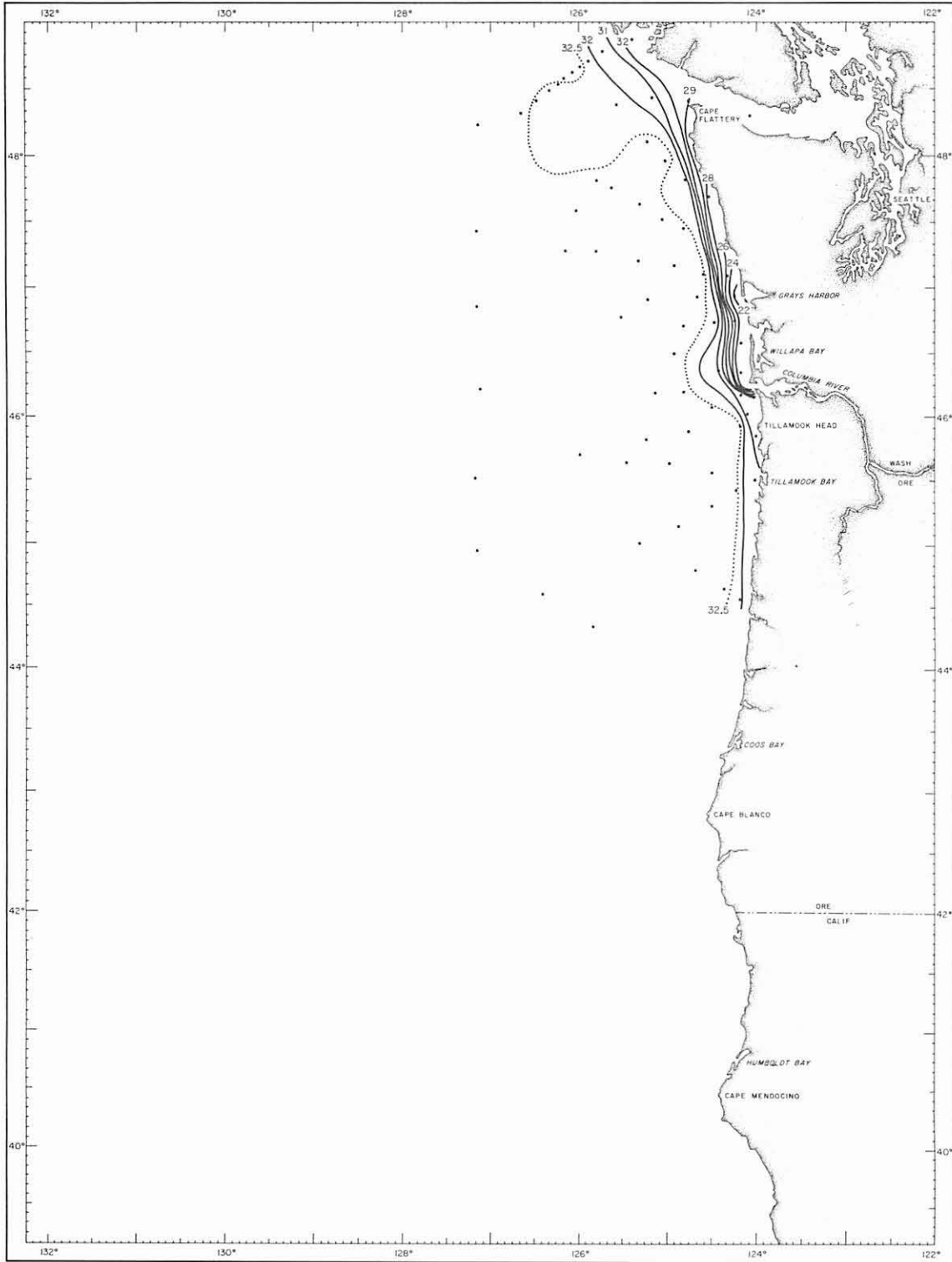


Fig. 2 Distribution of surface salinity off the Washington and Oregon coasts, March, 1961.

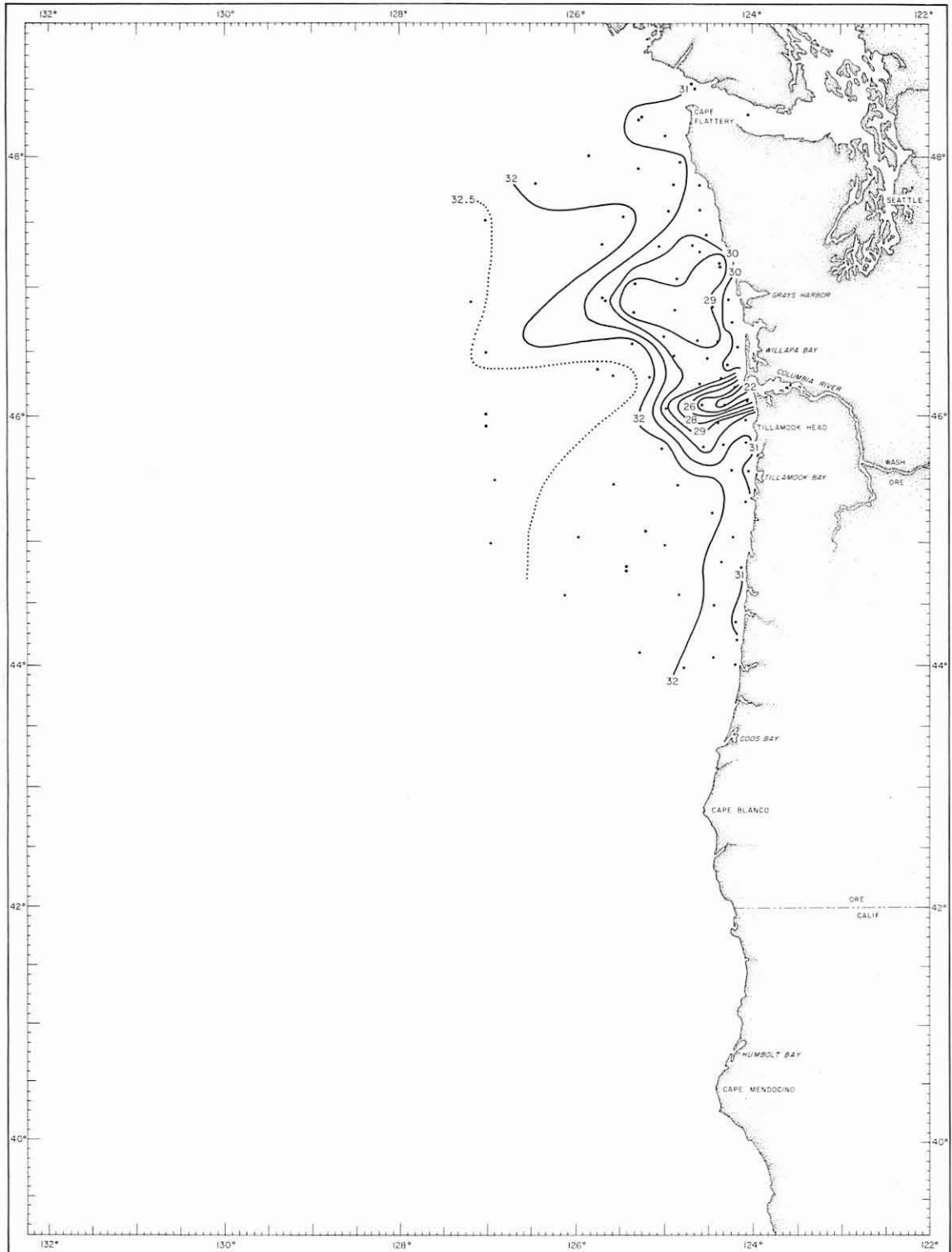


Fig. 3 Distribution of surface salinity off the Washington and Oregon coasts, May, 1961.

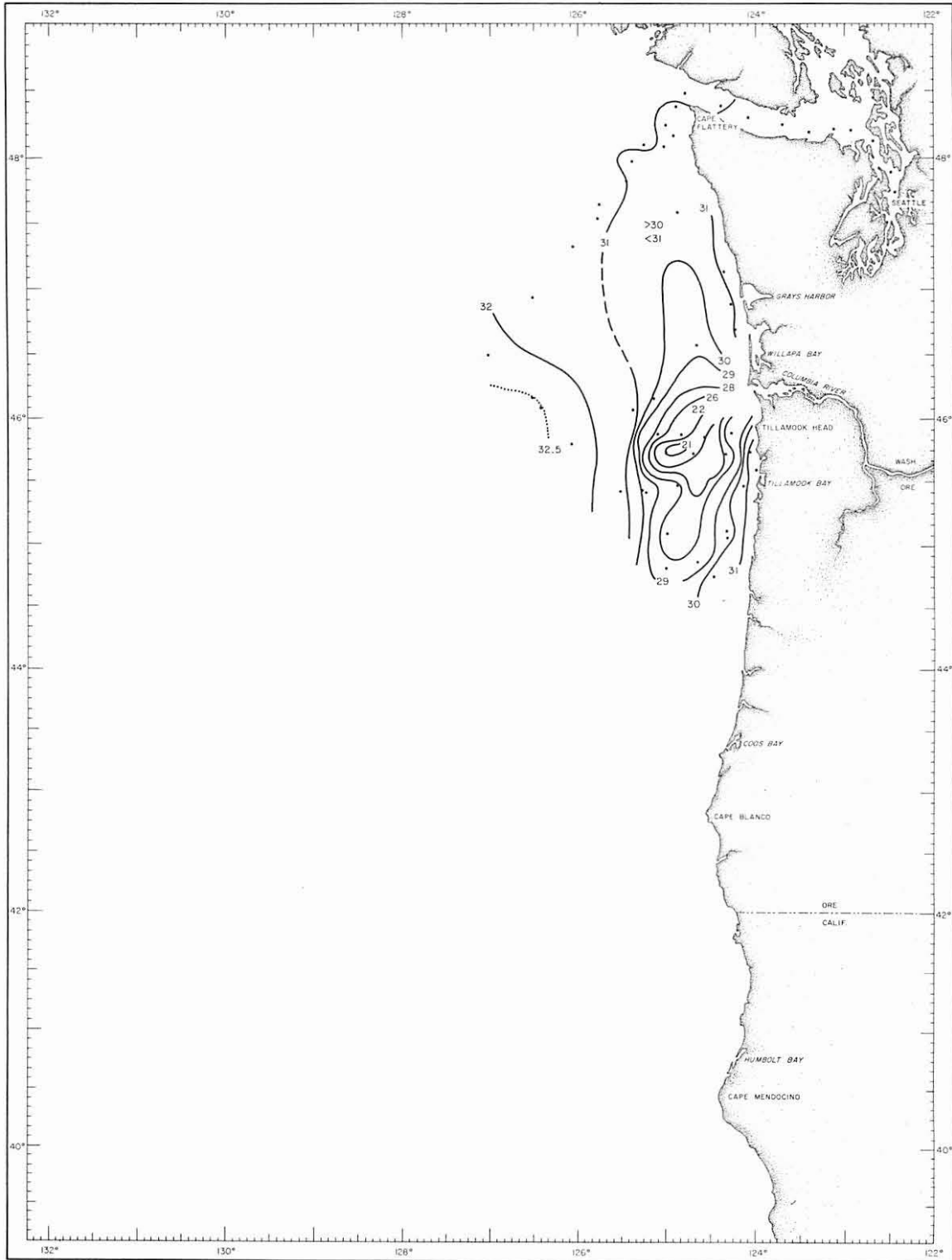


Fig. 4 Distribution of surface salinity off the Washington and Oregon coasts, June, 1961.

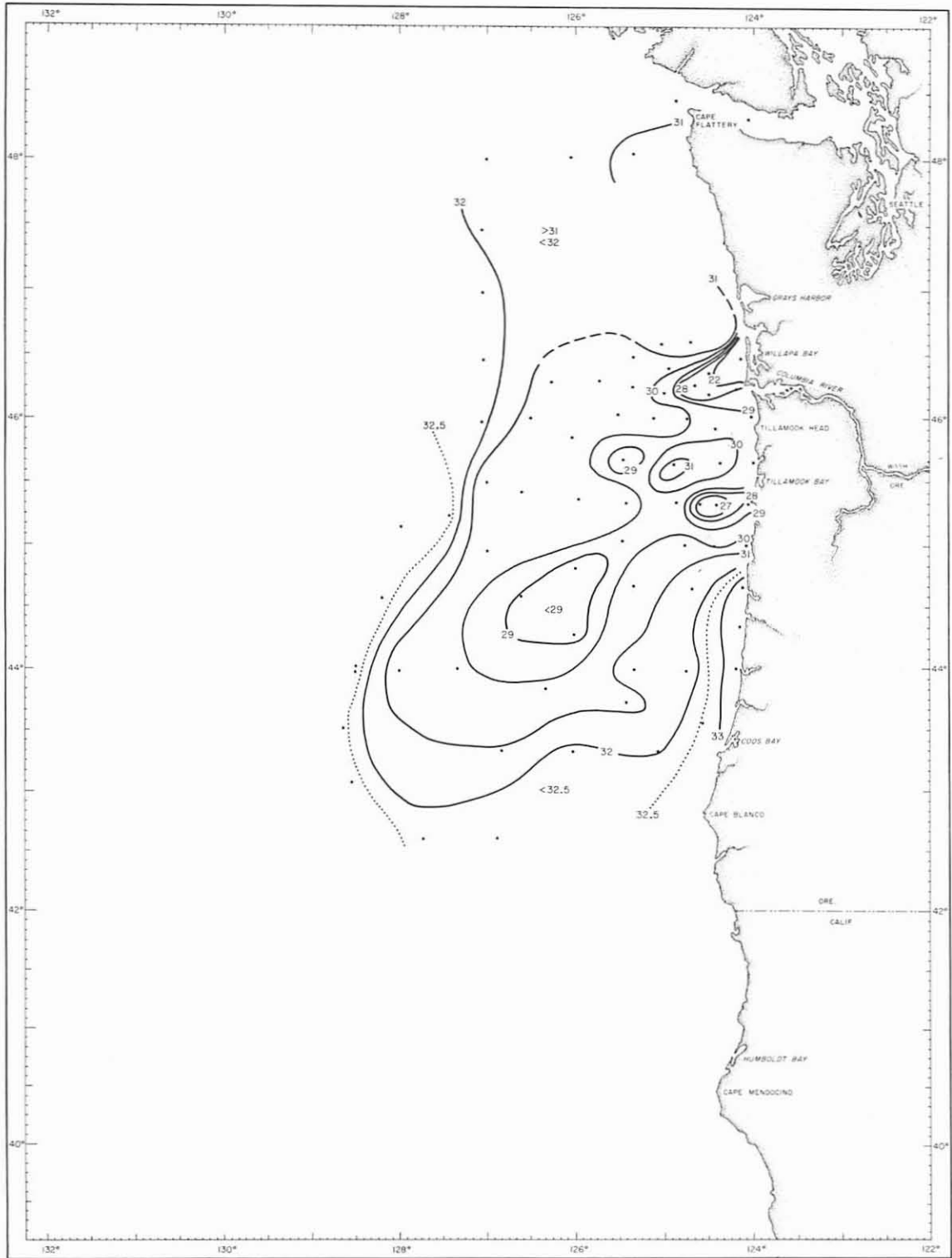


Fig. 5 Distribution of surface salinity off the Washington and Oregon coasts, July, 1961.

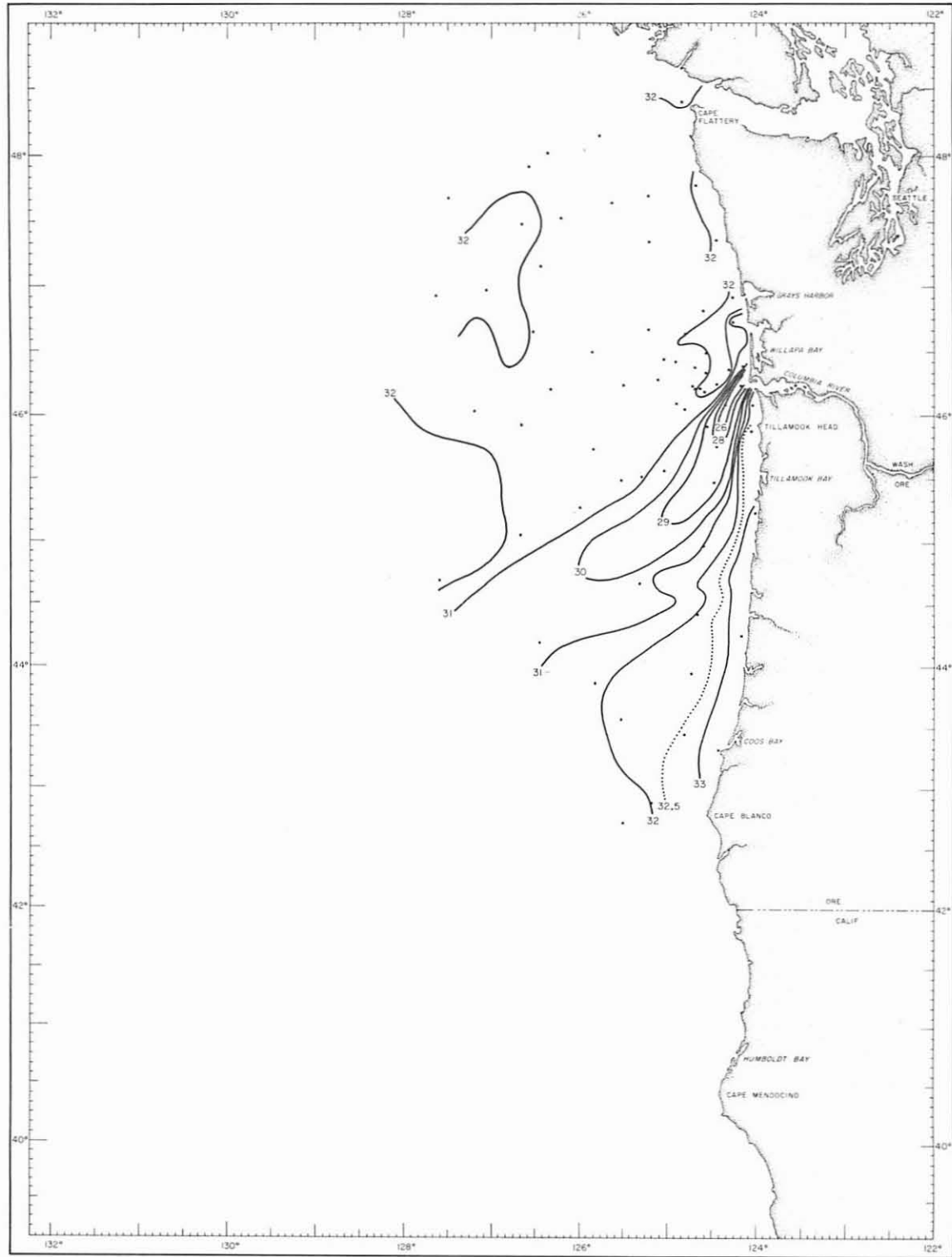


Fig. 6 Distribution of surface salinity off the Washington and Oregon coasts, August, 1961.

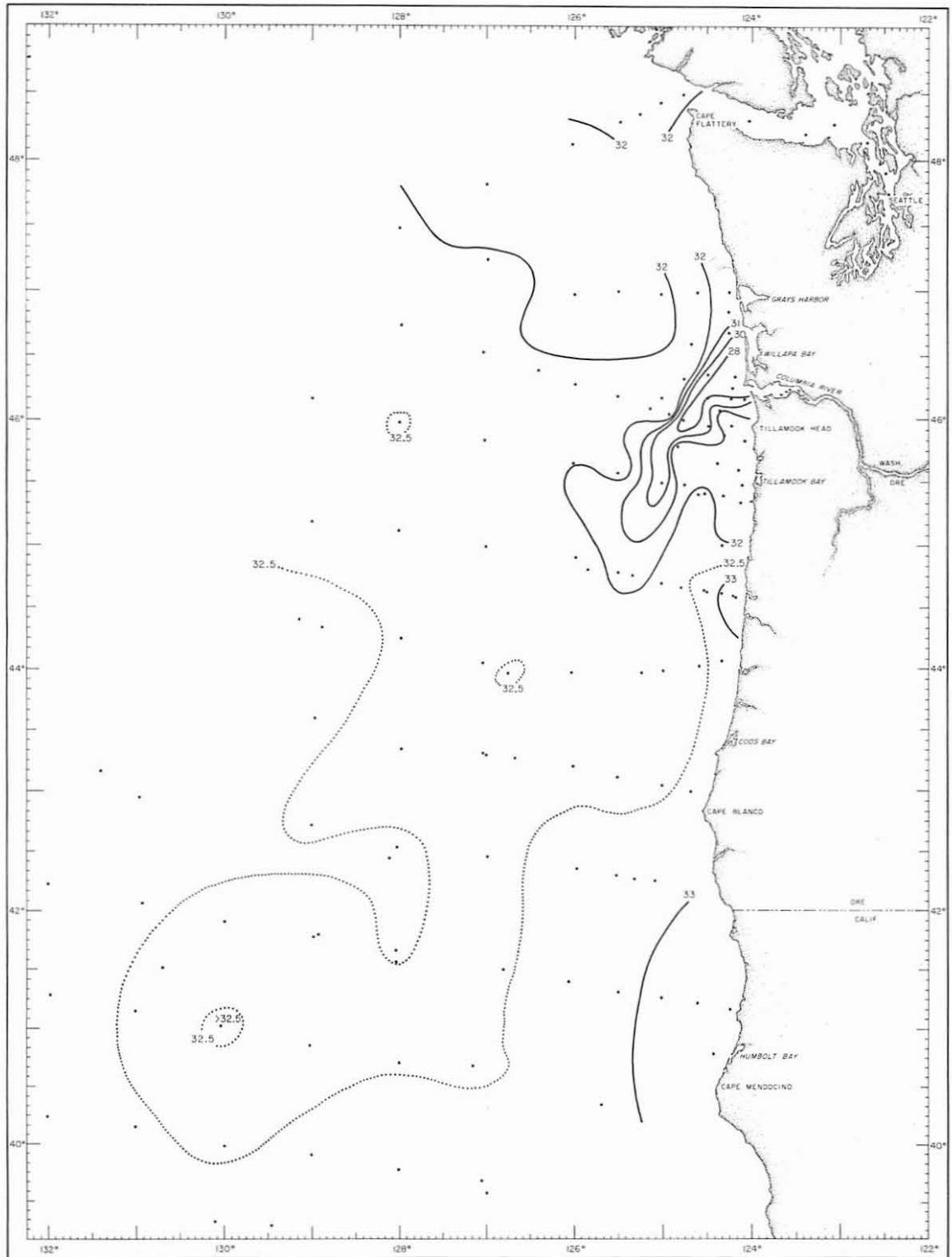


Fig. 7 Distribution of surface salinity off the Washington and Oregon coasts, September-October, 1961.

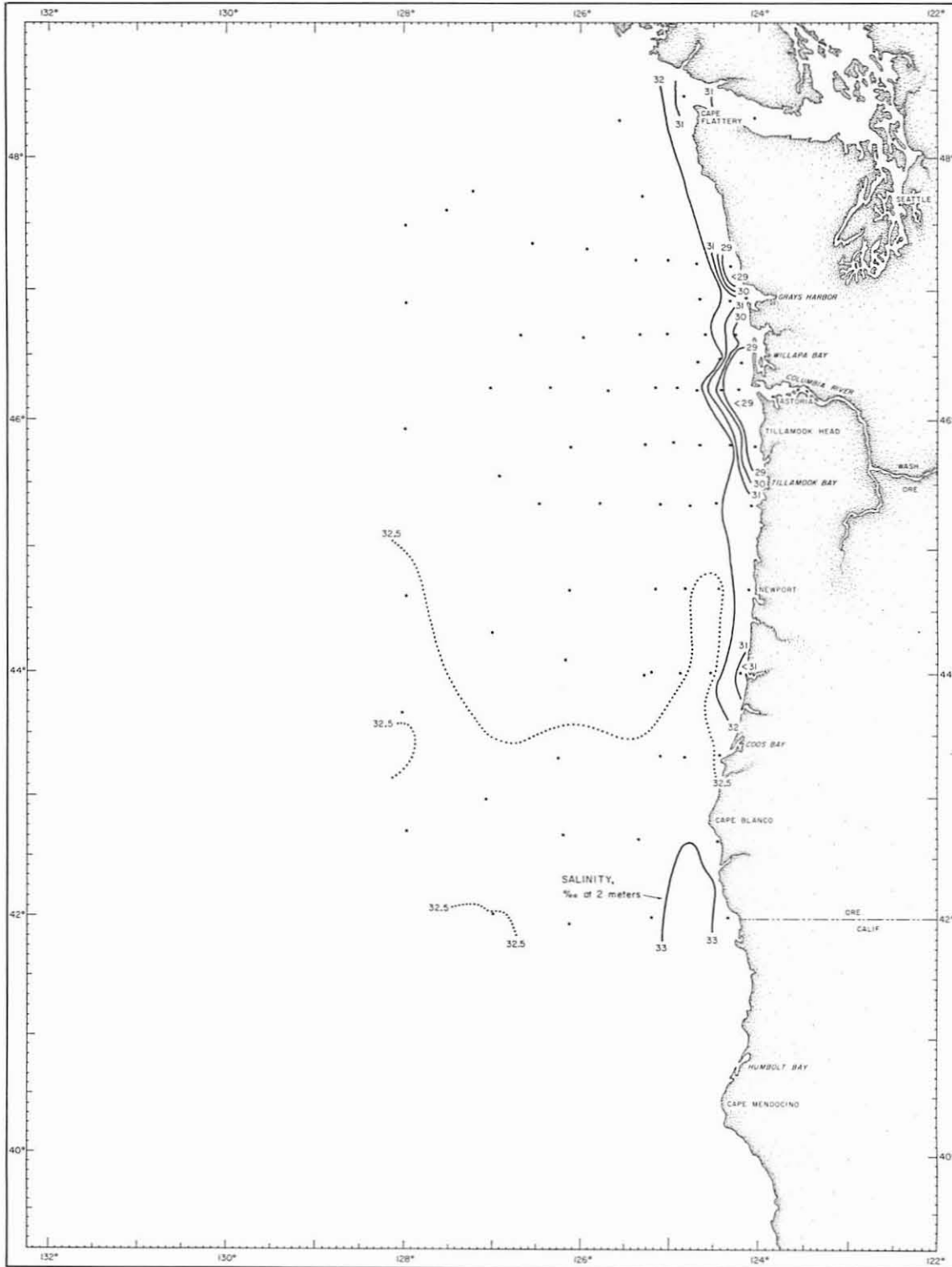


Fig. 8 Distribution of surface salinity off the Washington and Oregon coasts, November-December, 1961.

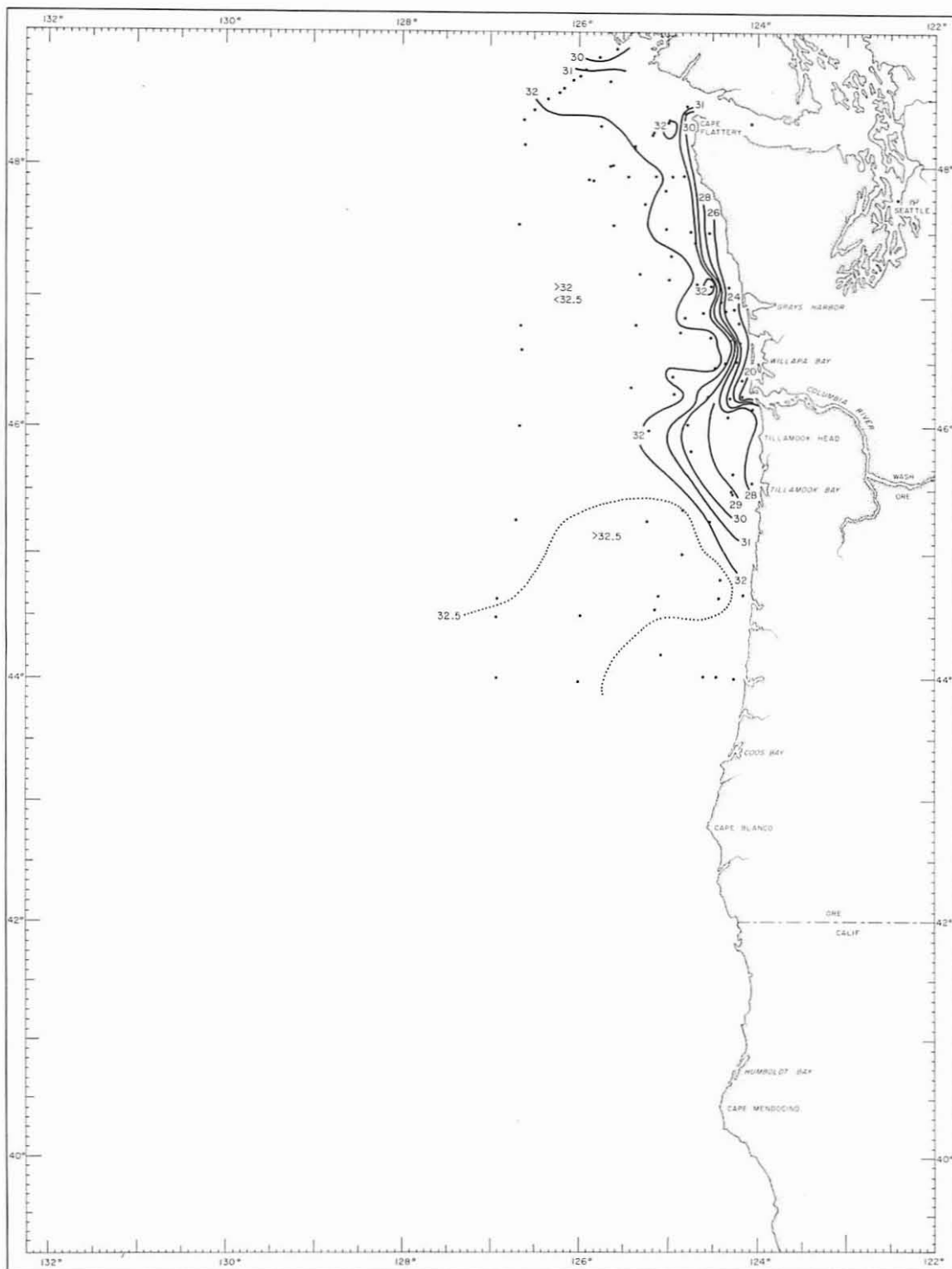


Fig. 9 Distribution of surface salinity off the Washington and Oregon coasts, January-February, 1962.

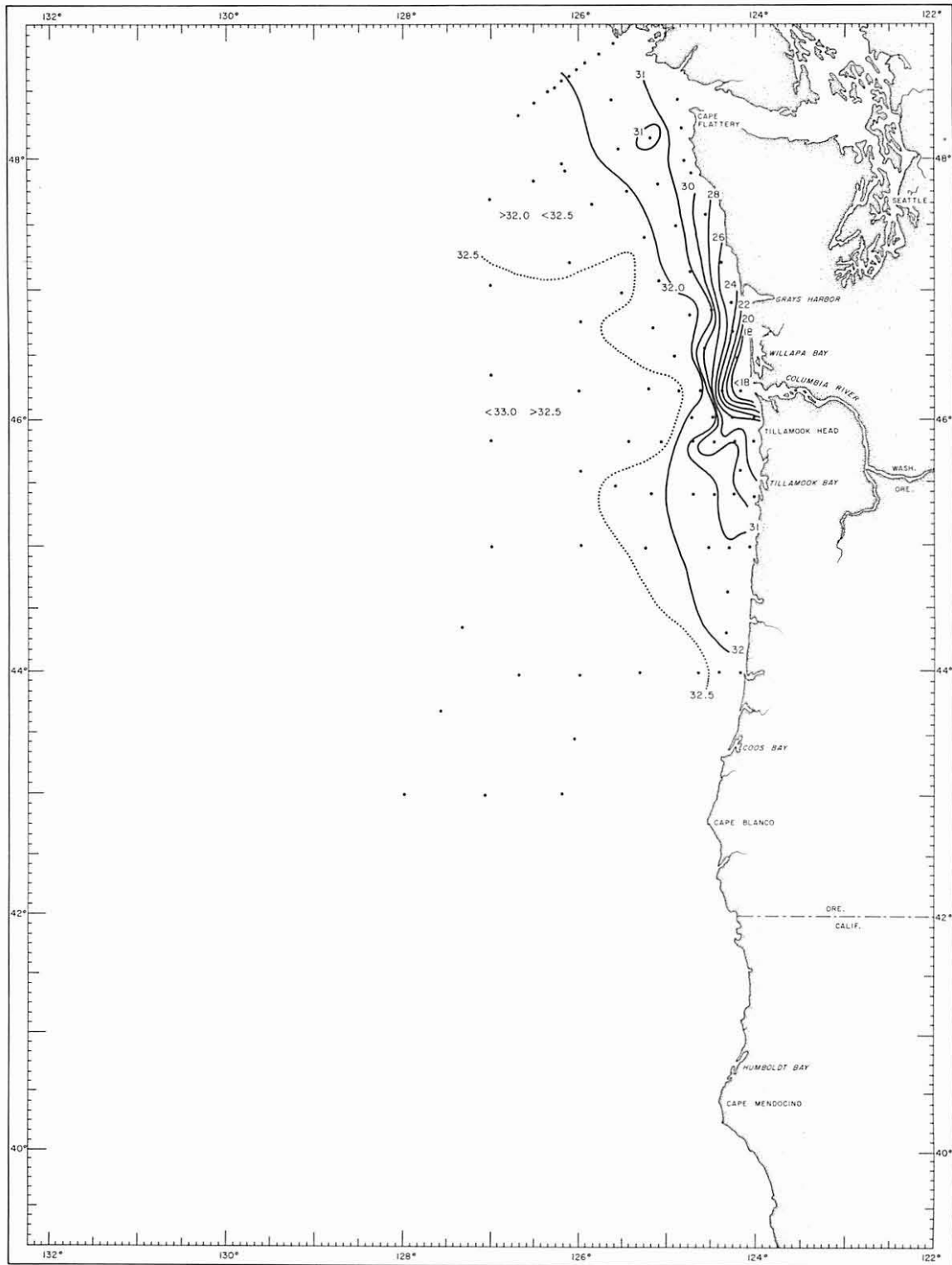


Fig. 10 Distribution of surface salinity off the Washington and Oregon coasts, March-April, 1962.

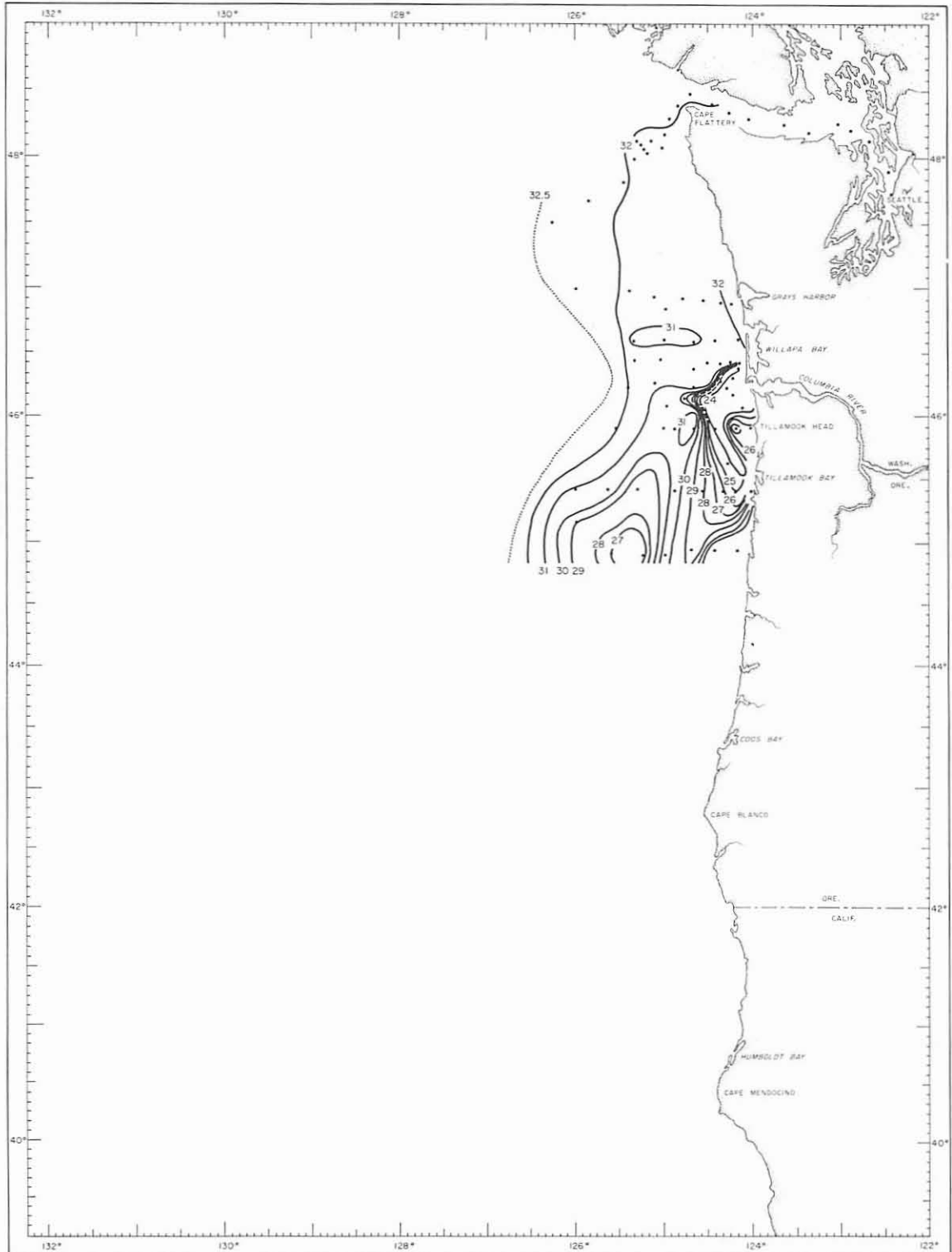


Fig. 11 Distribution of surface salinity off the Washington and Oregon coasts, June, 1962.

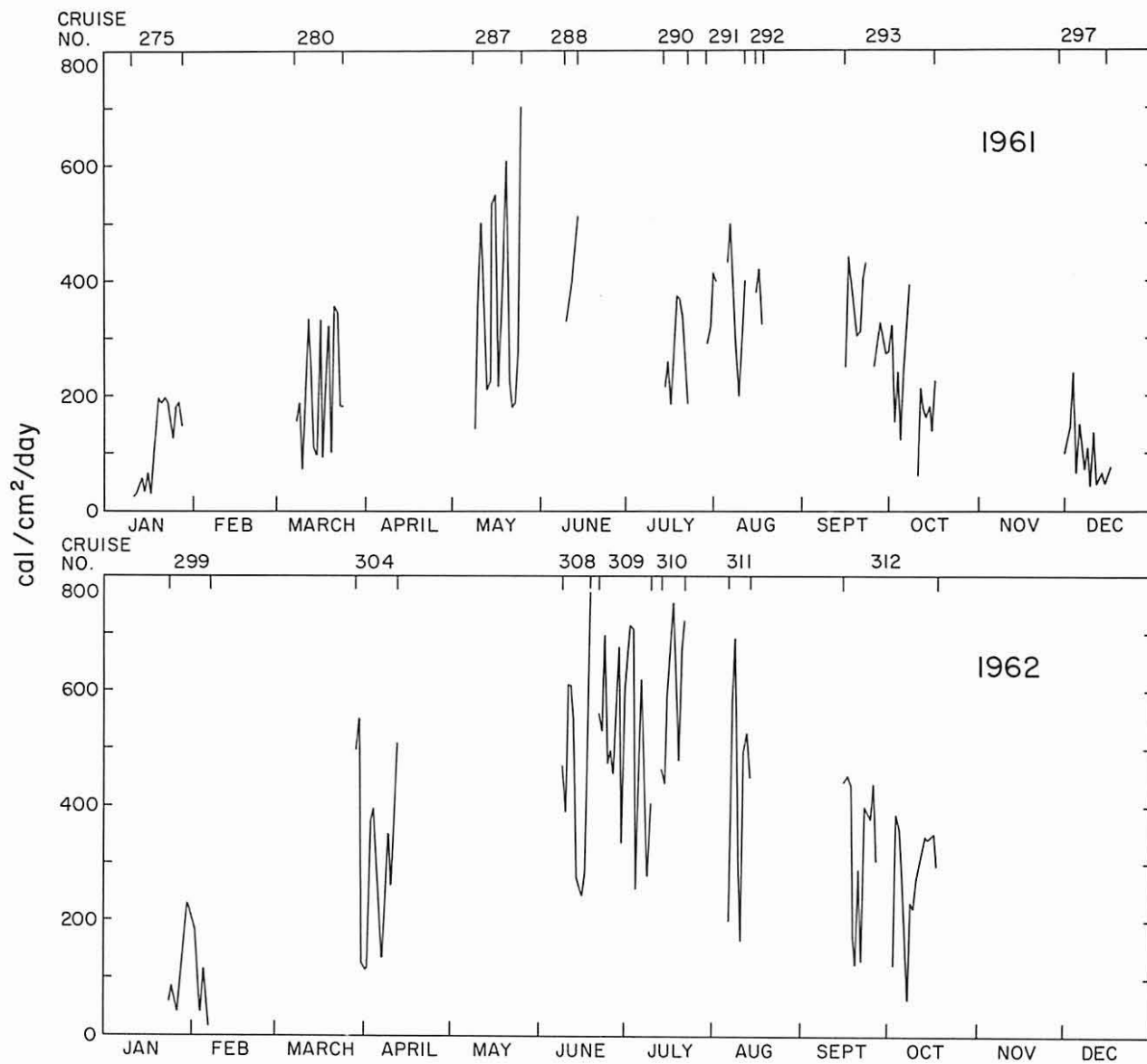


Fig. 12 Seasonal and annual variations of solar radiation during cruises of Brown Bear, 1961-62.

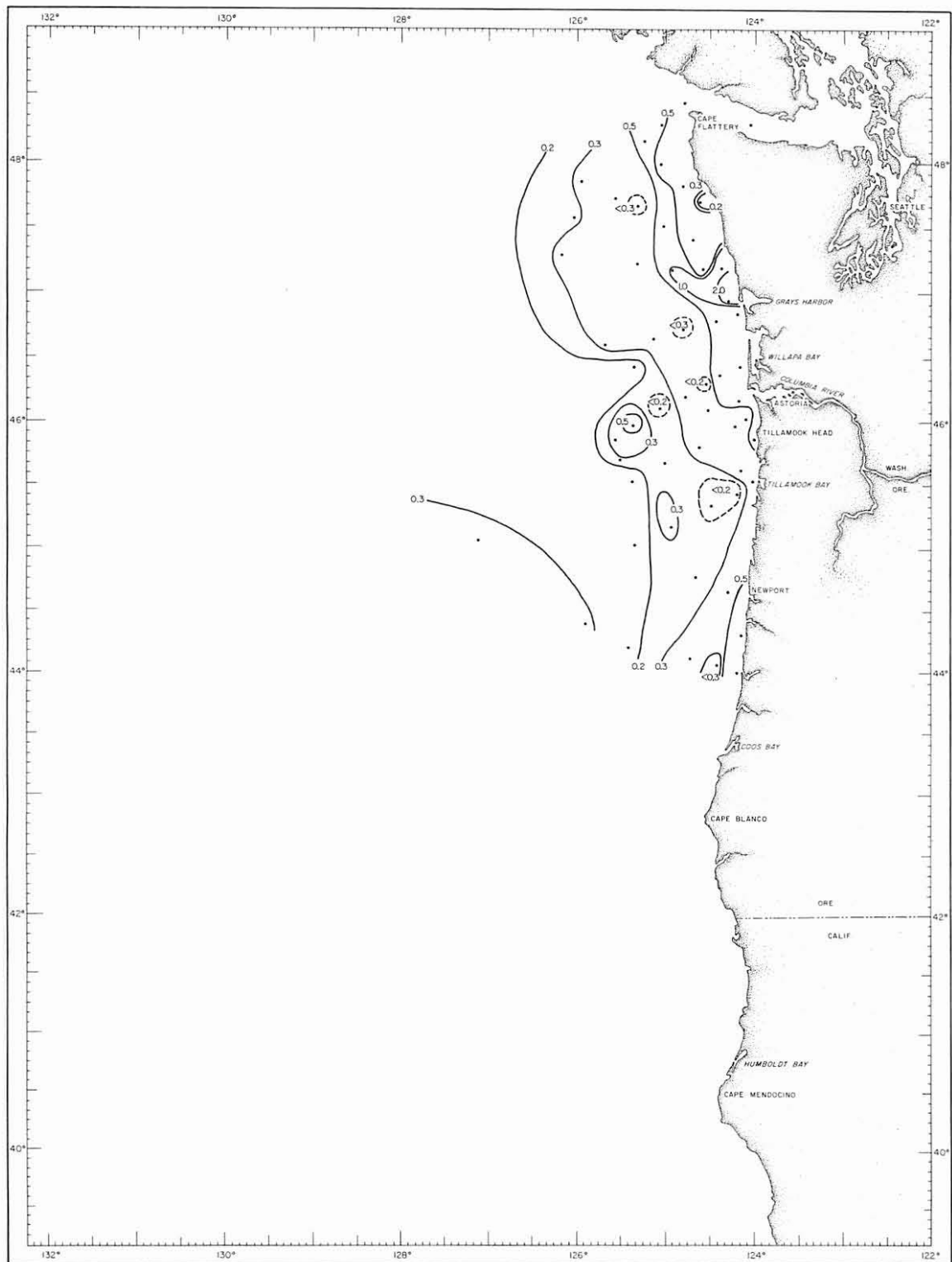


Fig. 13 Distribution of chlorophyll *a* (mg/m^3) in surface waters off the Washington and Oregon coasts, January, 1961.

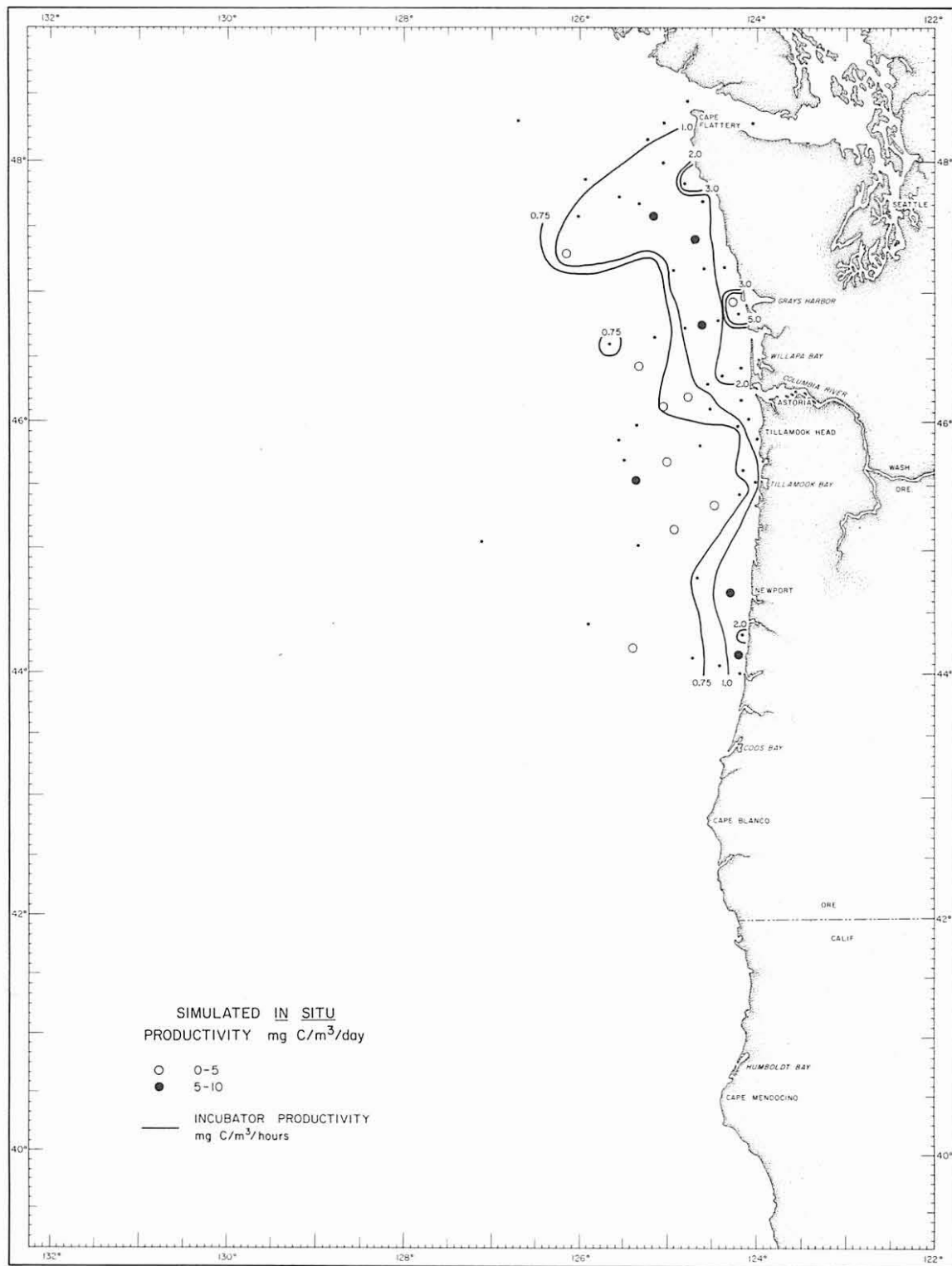


Fig. 14 Distribution of primary productivity in surface waters off the Washington and Oregon coasts, January, 1961.

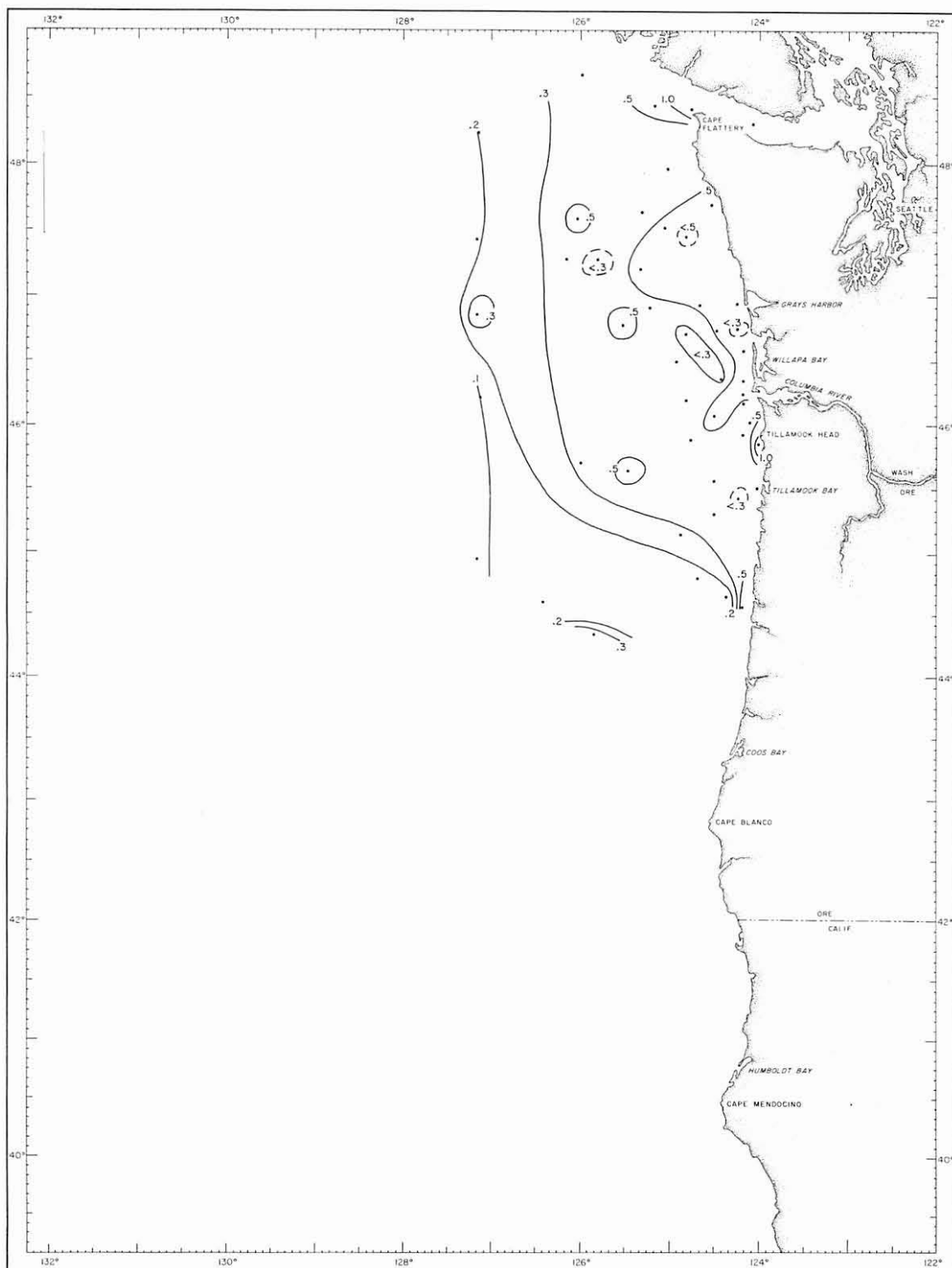


Fig. 15 Distribution of chlorophyll *a* (mg/m^3) in surface waters off the Washington and Oregon coasts, March, 1961.

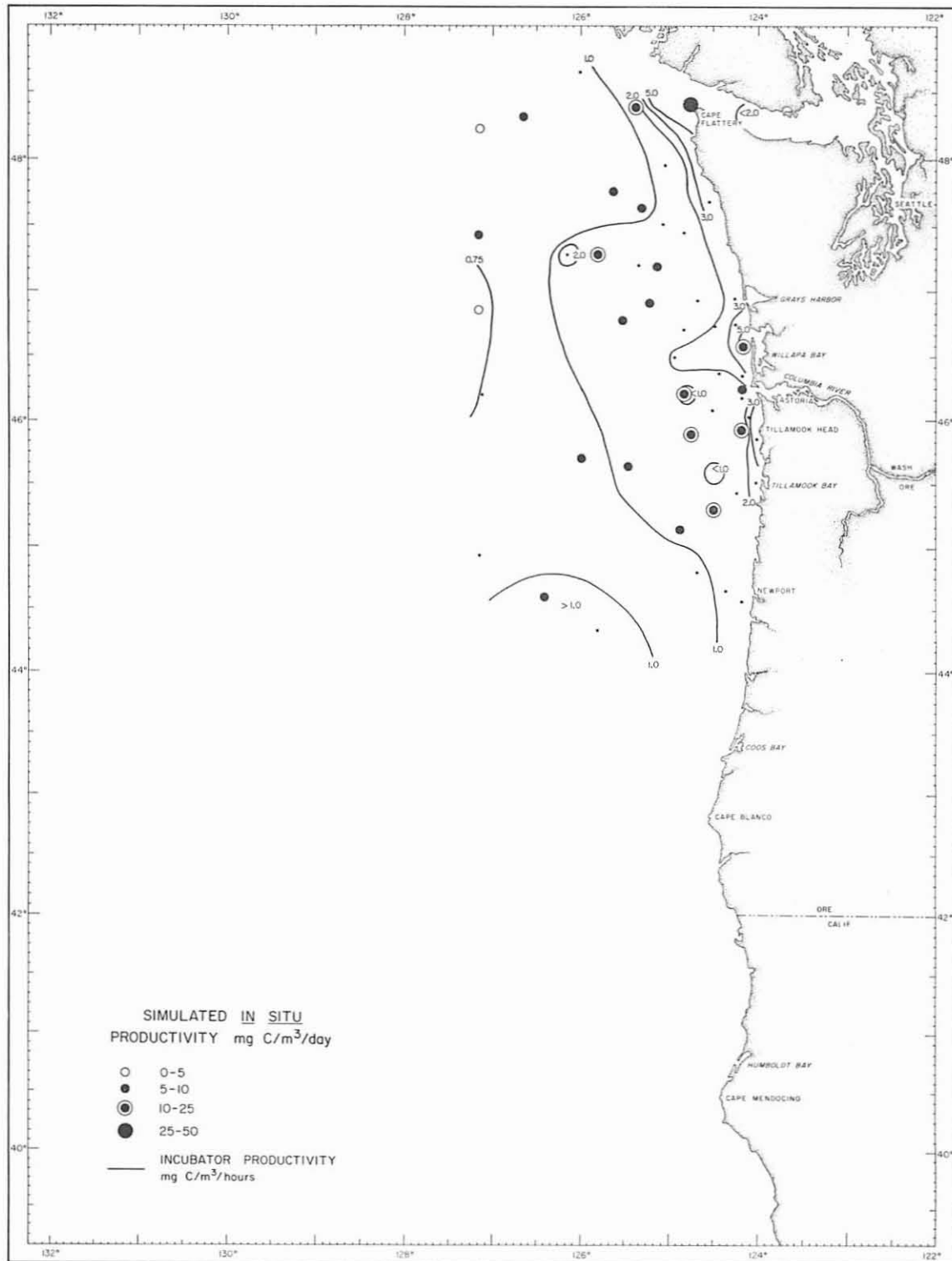


Fig. 16 Distribution of primary productivity in surface waters off the Washington and Oregon coasts, March, 1961.

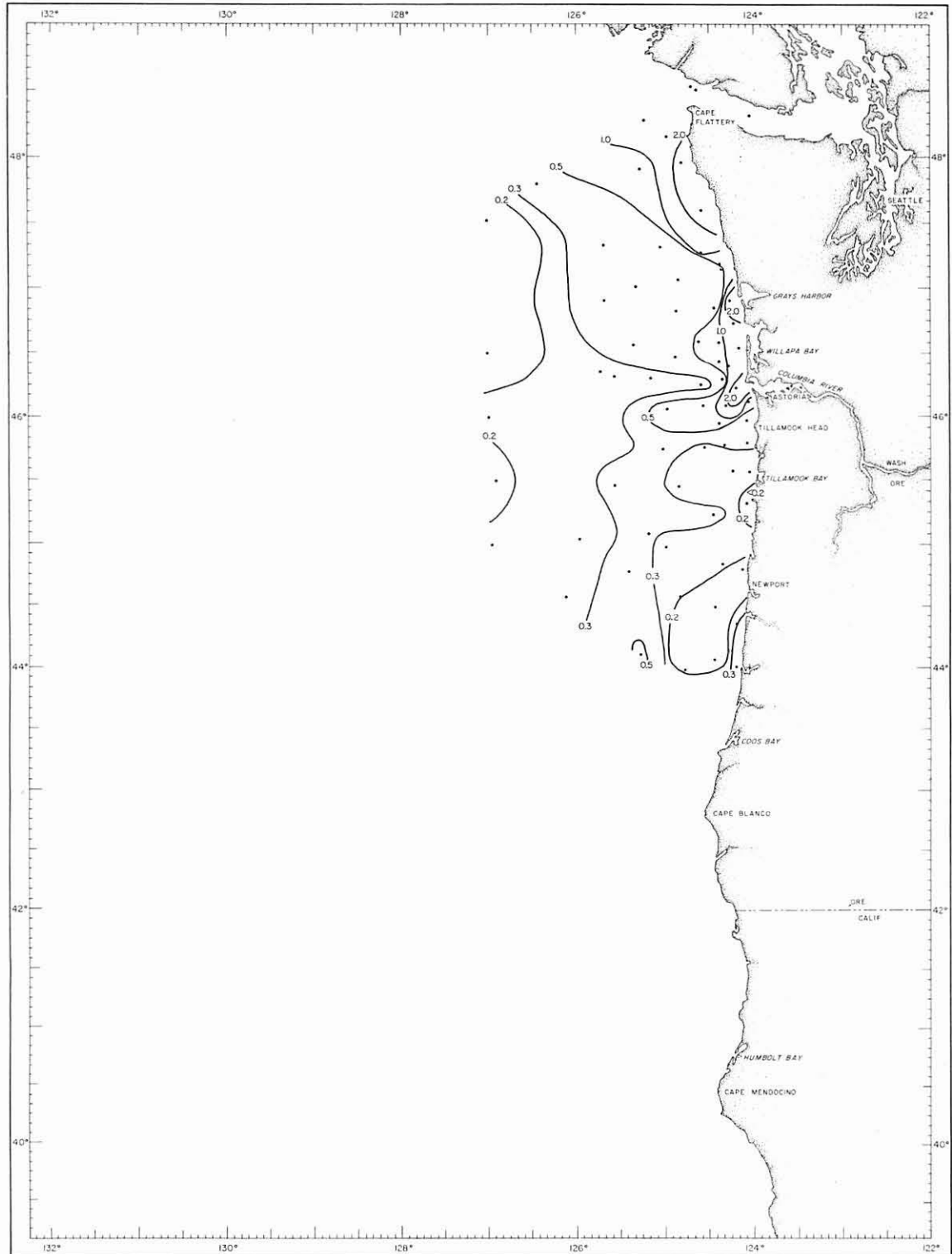


Fig. 17 Distribution of chlorophyll *a* (mg/m^3) in surface waters off the Washington and Oregon coasts, May, 1961.

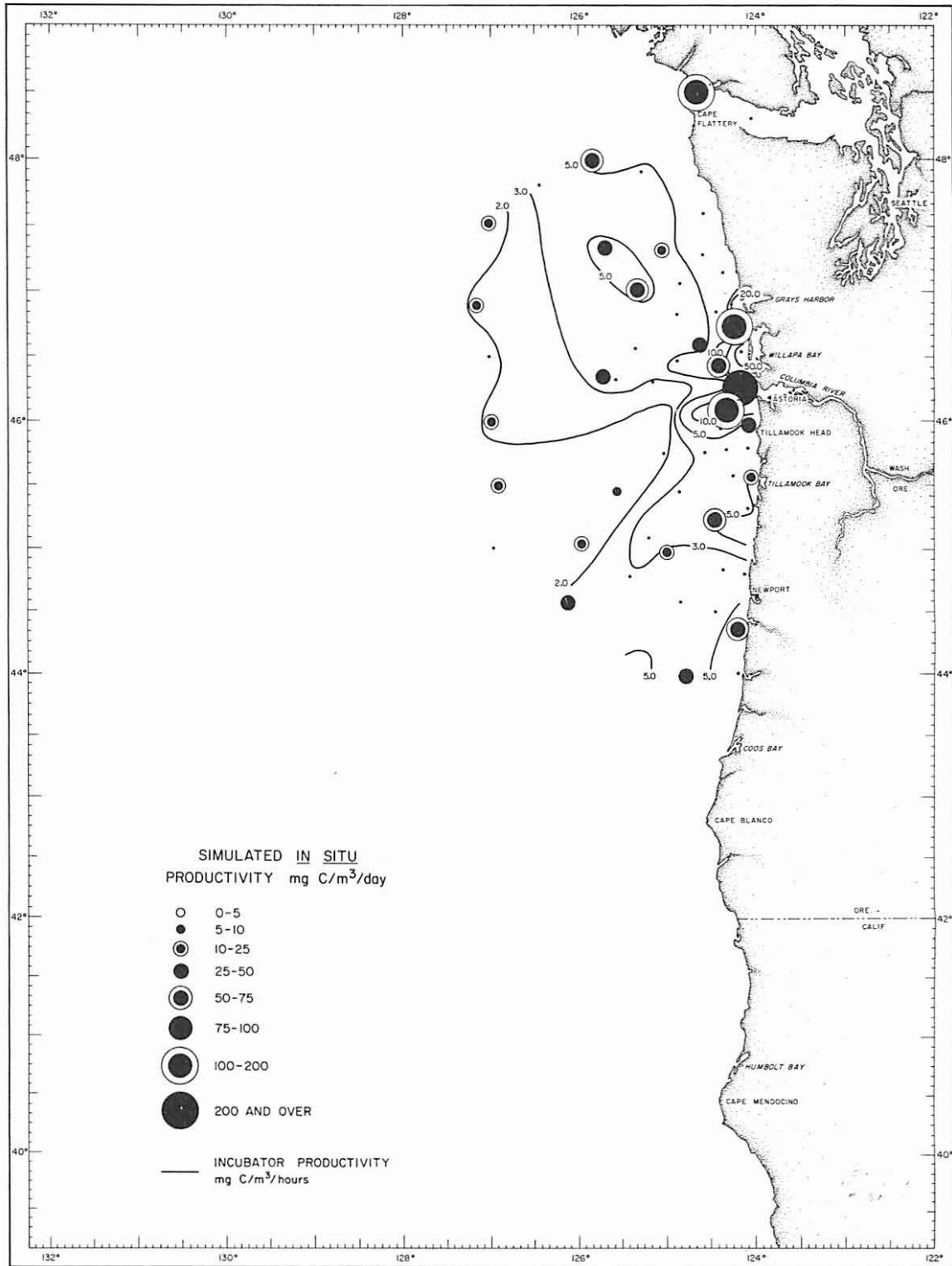


Fig. 18 Distribution of primary productivity in surface waters off the Washington and Oregon coasts, May, 1961.

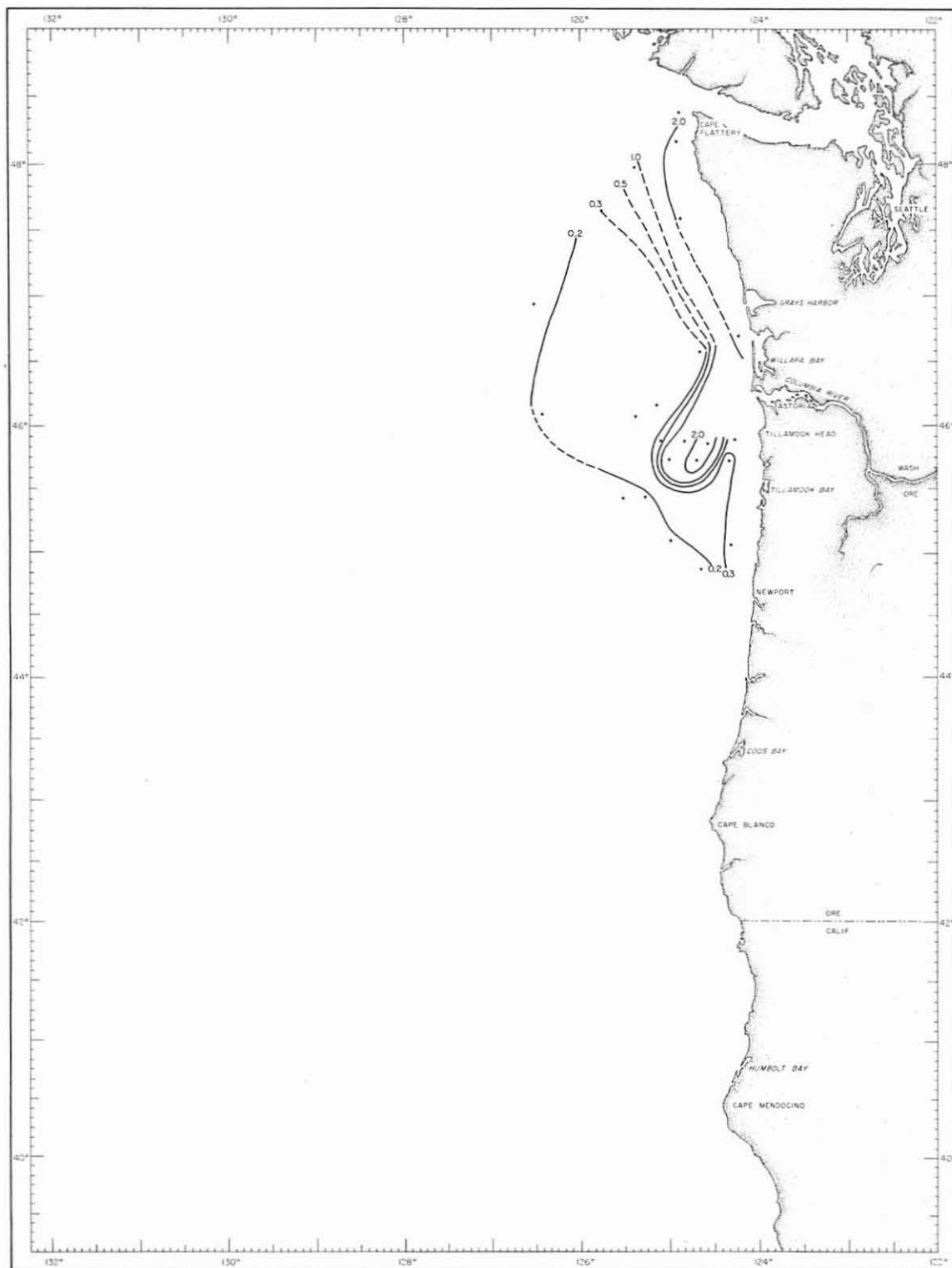


Fig. 19 Distribution of chlorophyll *a* (mg/m^3) in surface waters off the Washington and Oregon coasts, June, 1961.

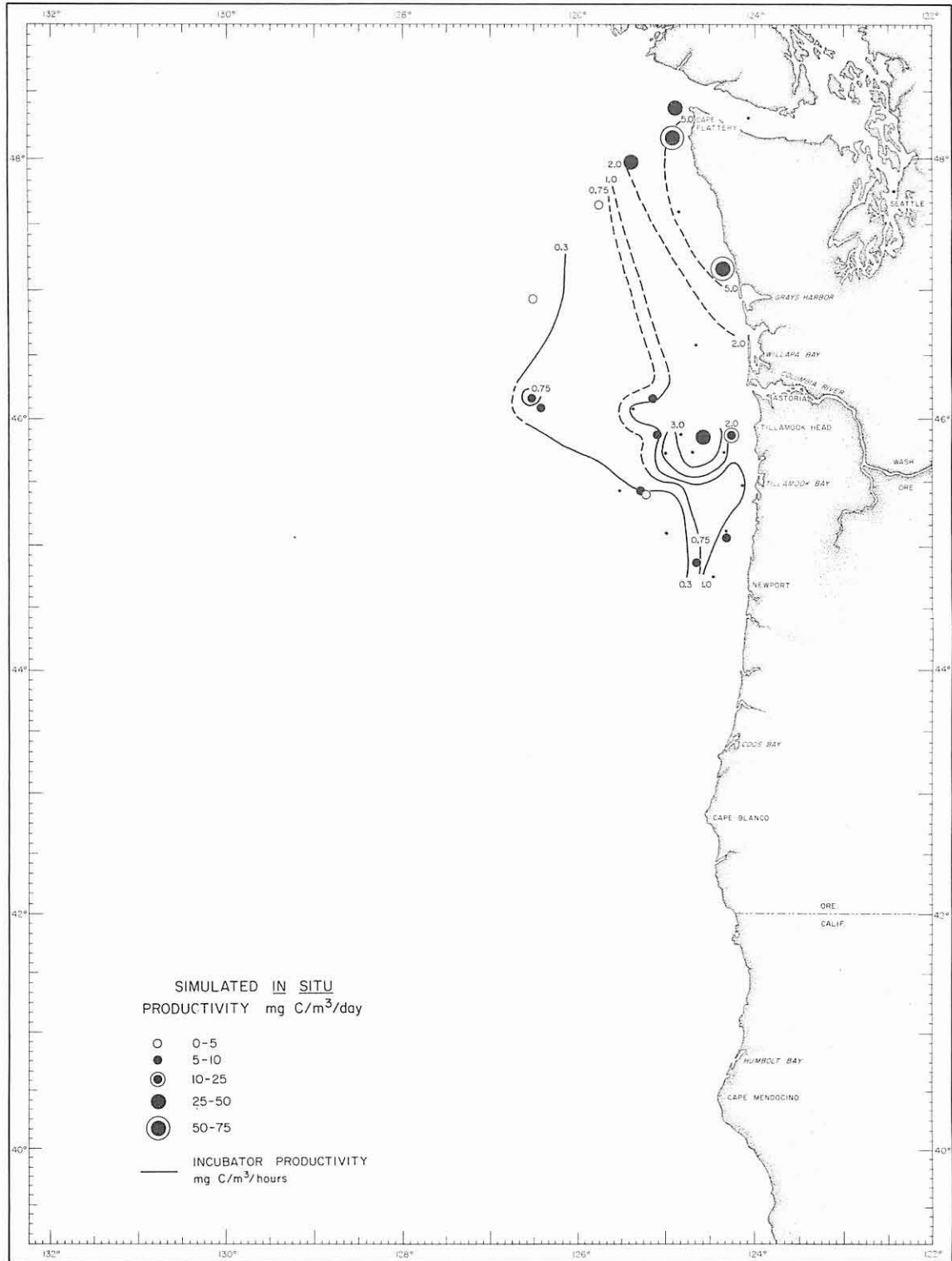


Fig. 20 Distribution of primary productivity in surface waters off the Washington and Oregon coasts, June, 1961.

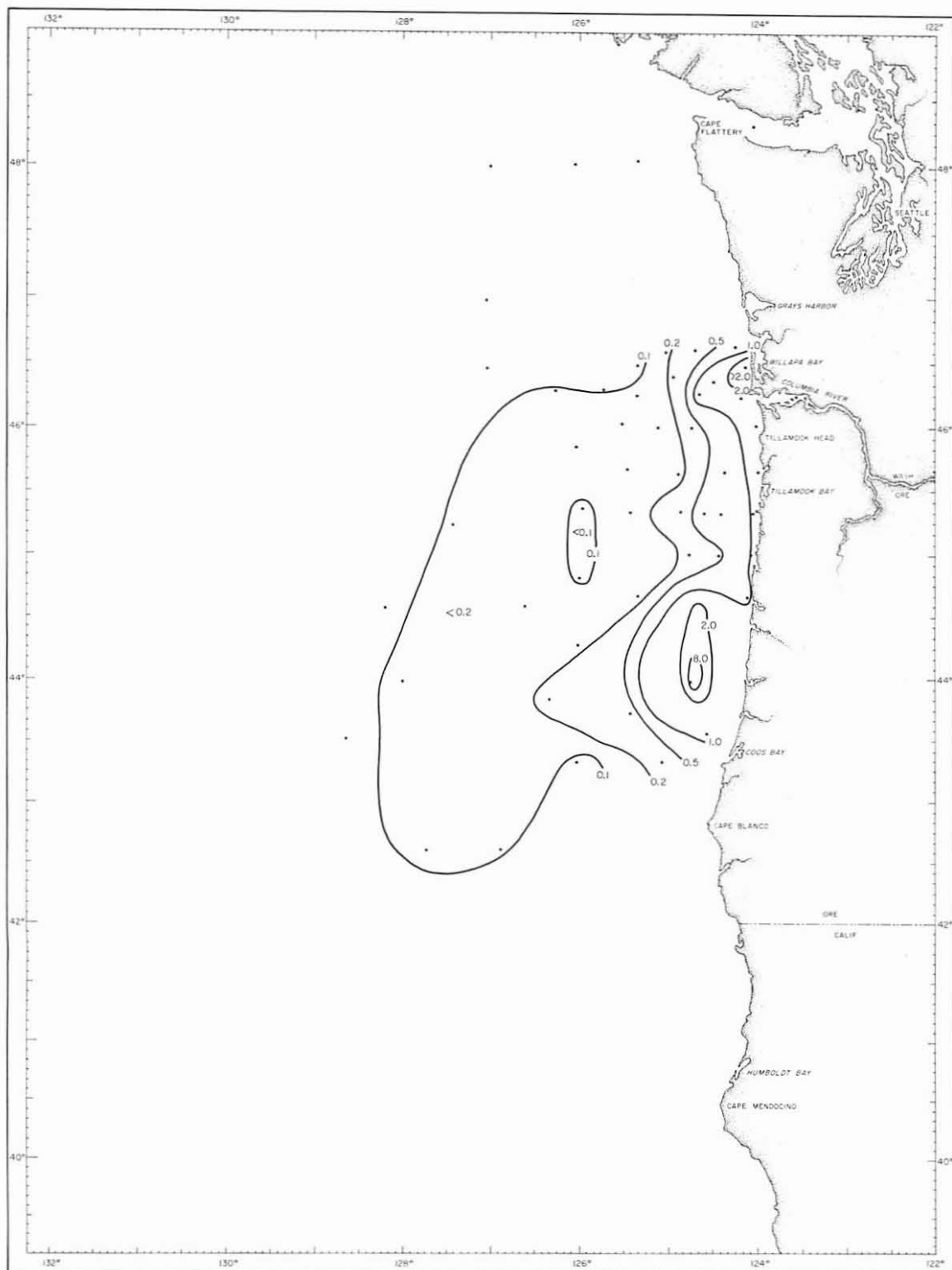


Fig. 21 Distribution of chlorophyll a (mg/m^3) in surface waters off the Washington and Oregon coasts, July, 1961.

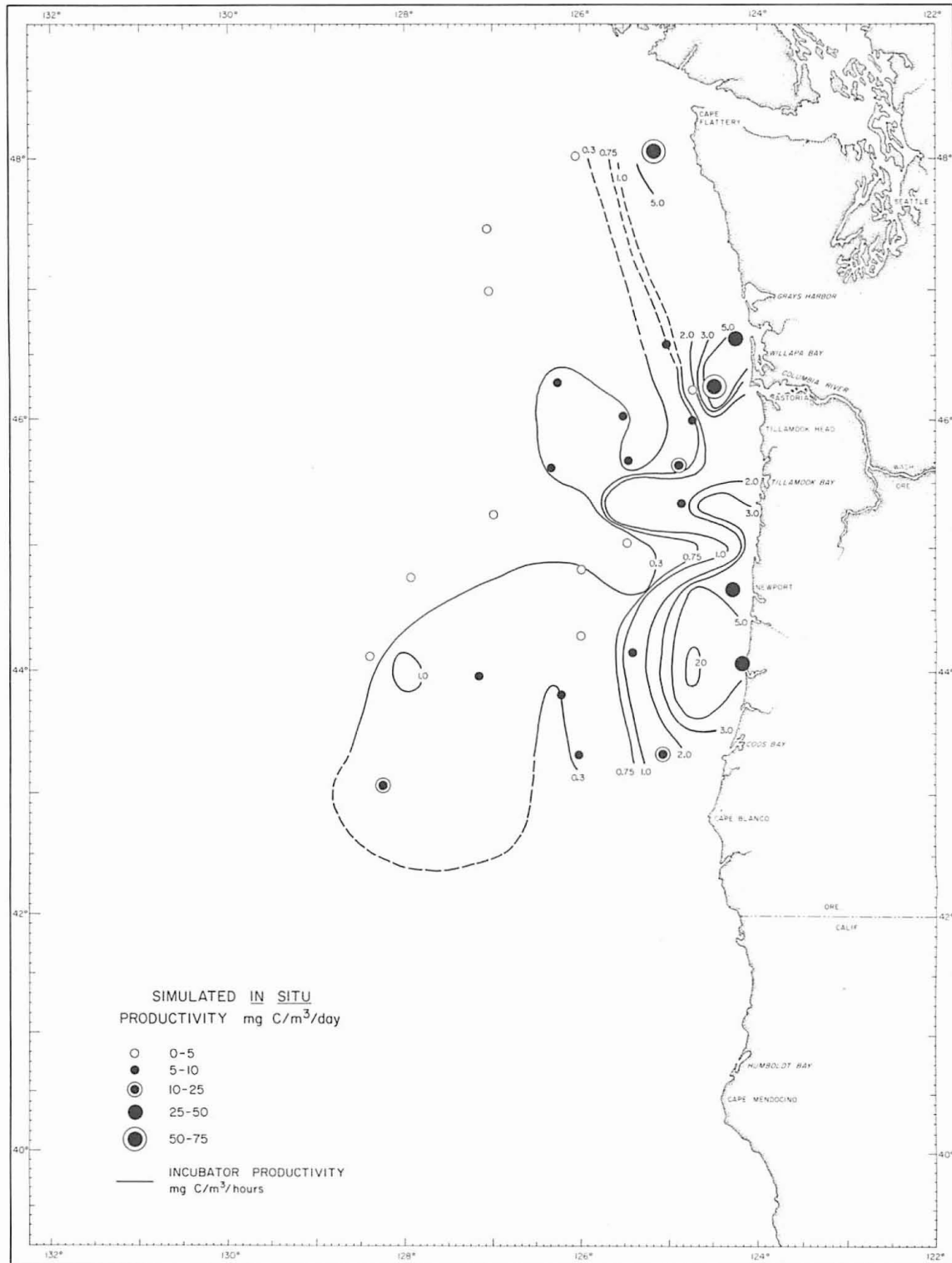


Fig. 22 Distribution of primary productivity in surface waters off the Washington and Oregon coasts, July, 1961.

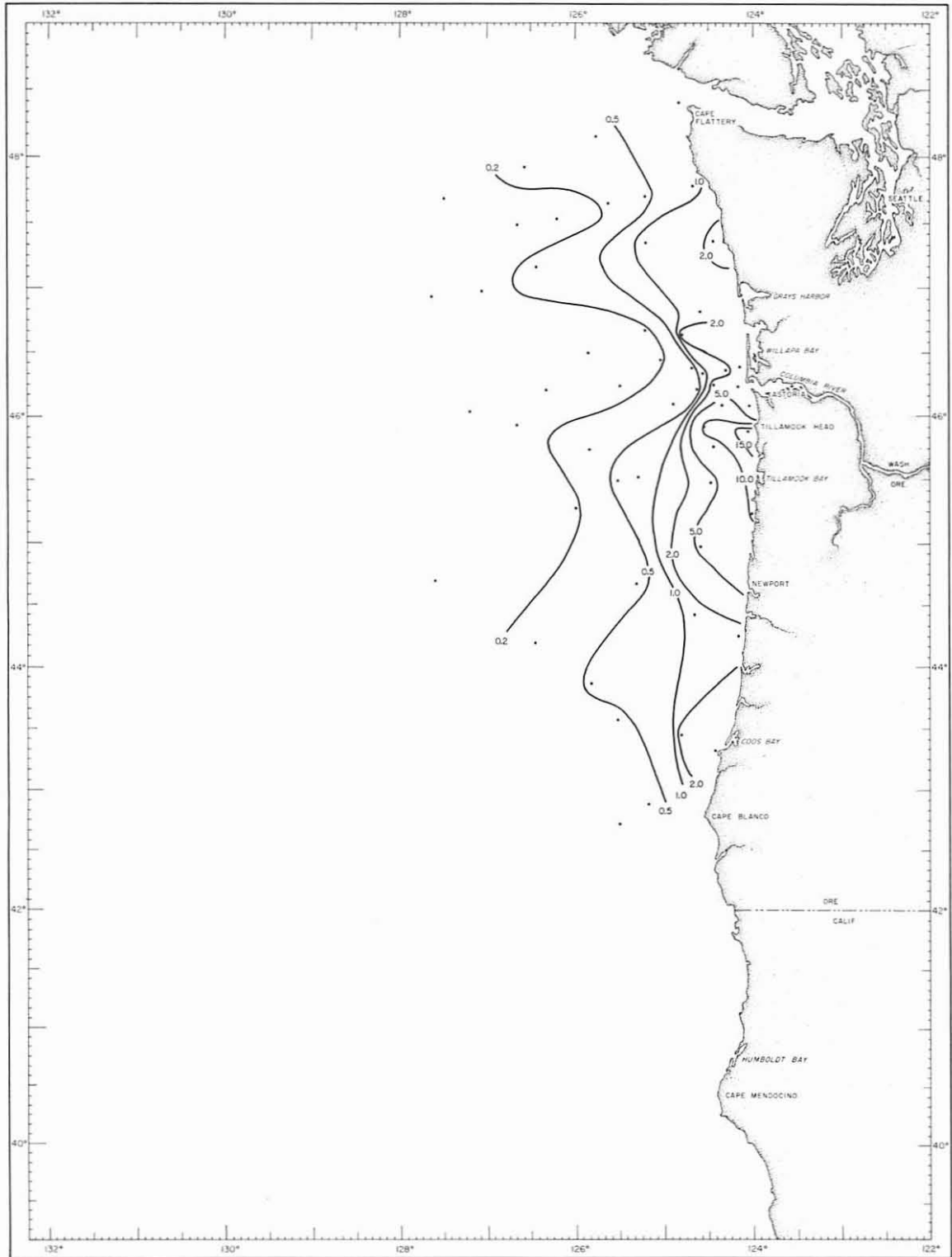


Fig. 23 Distribution of chlorophyll *a* (mg/m^3) in surface waters off the Washington and Oregon coasts, August, 1961.

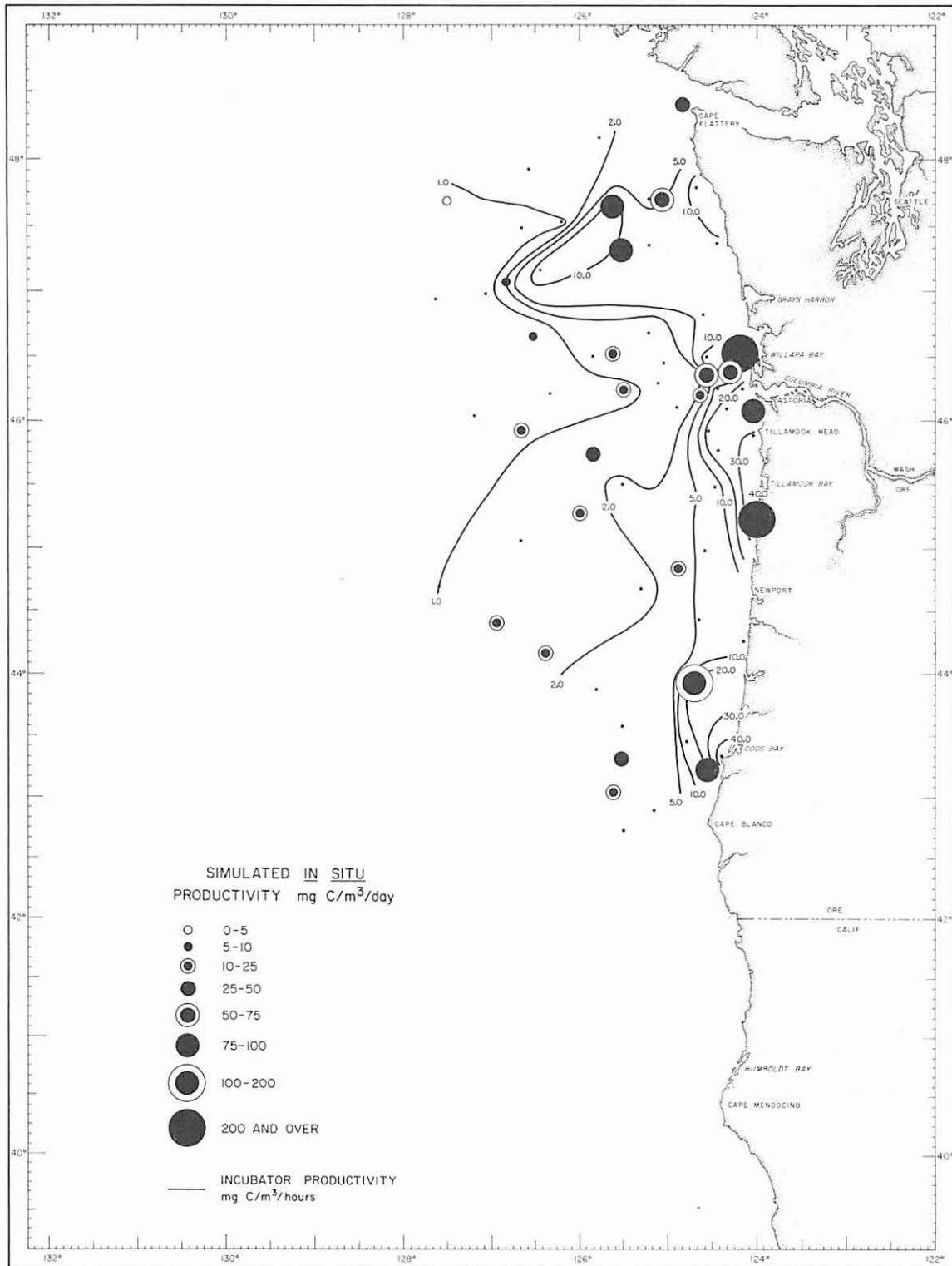


Fig. 24 Distribution of primary productivity in surface waters off the Washington and Oregon coasts, August, 1961.

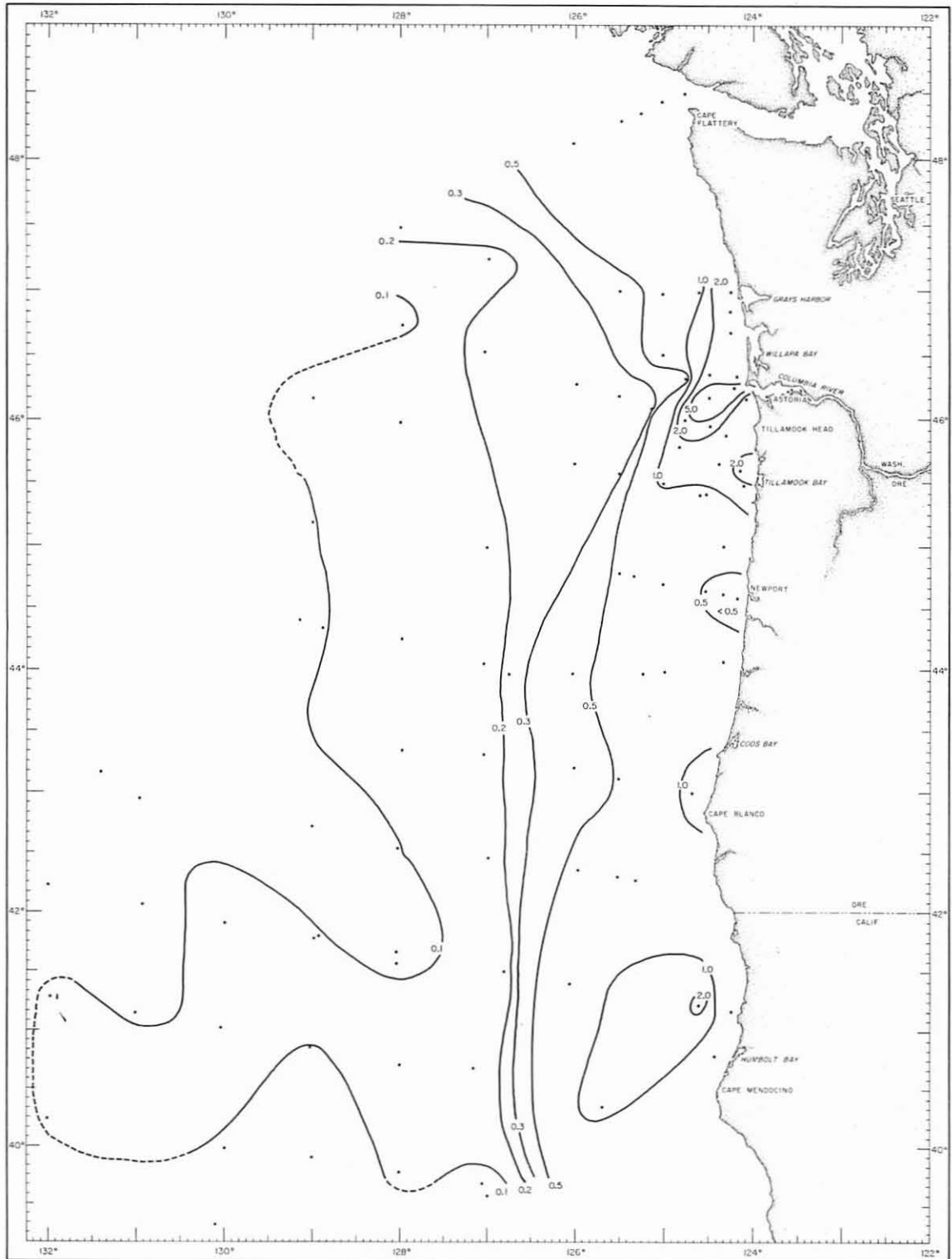


Fig. 25 Distribution of chlorophyll *a* (mg/m^3) in surface waters off the Washington and Oregon coasts, September-October, 1961.

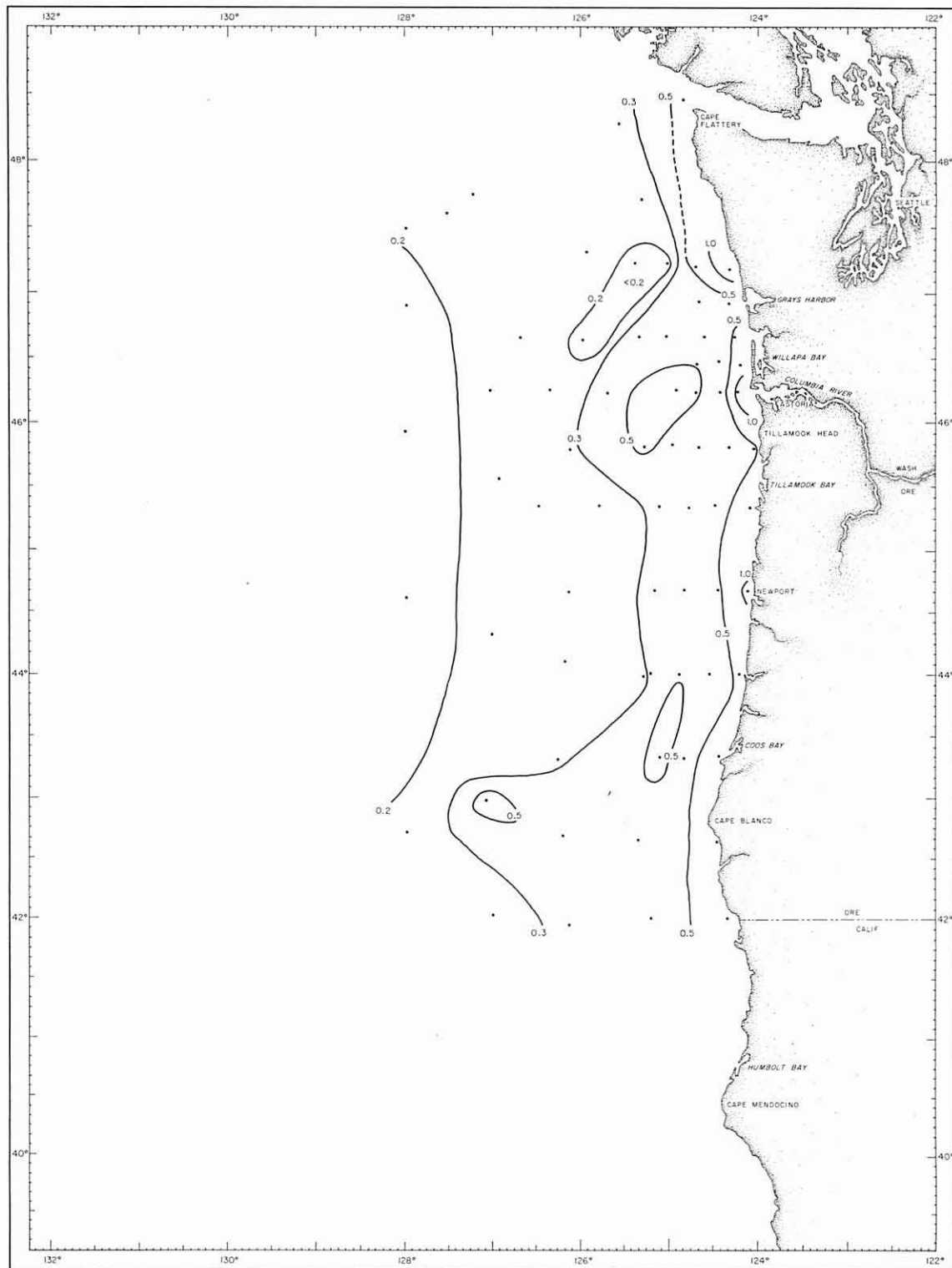


Fig. 26 Distribution of chlorophyll *a* (mg/m^3) in surface waters off the Washington and Oregon coasts, November-December, 1961.

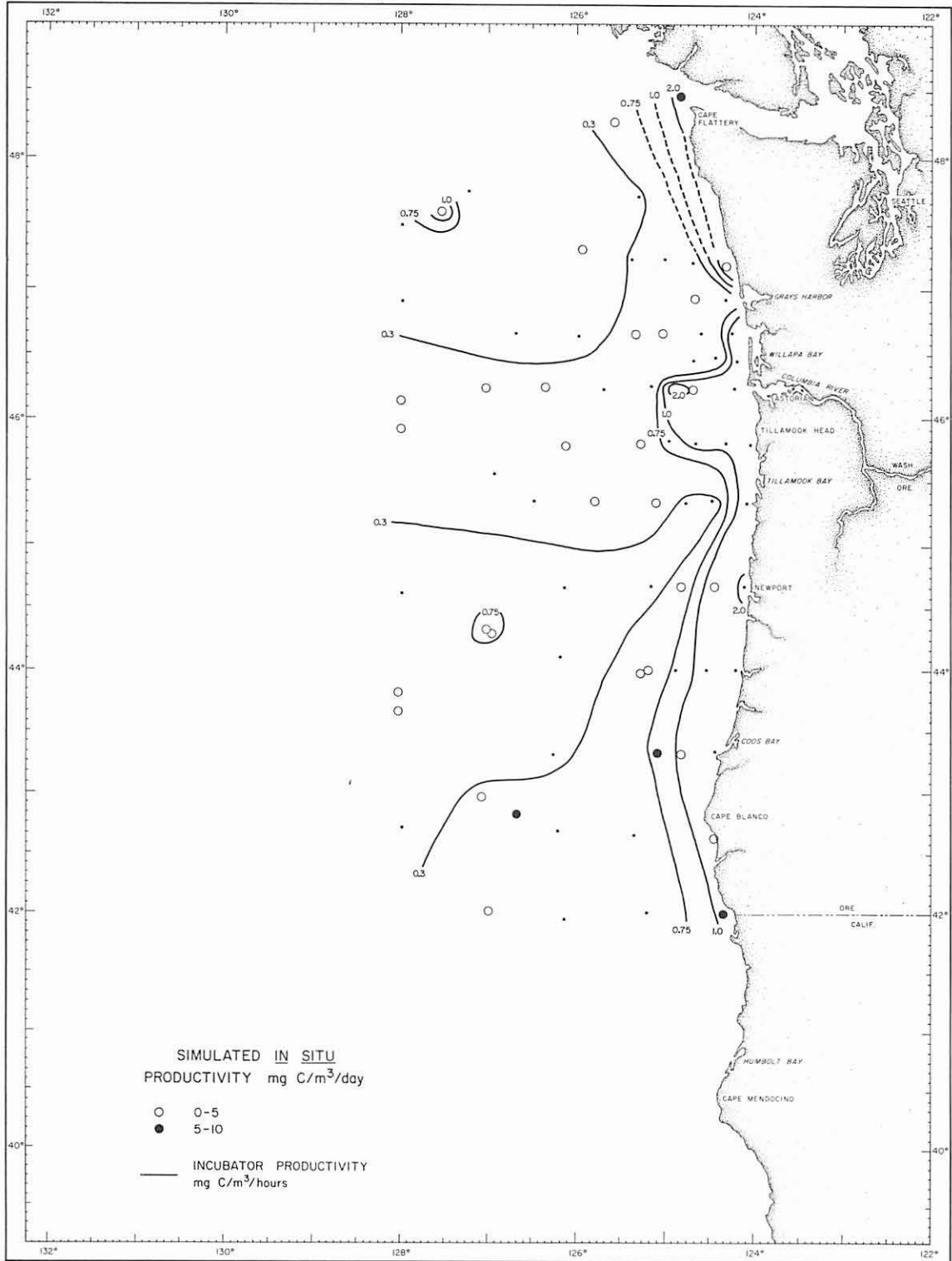


Fig. 27 Distribution of primary productivity in surface waters off the Washington and Oregon coasts, November-December, 1961.

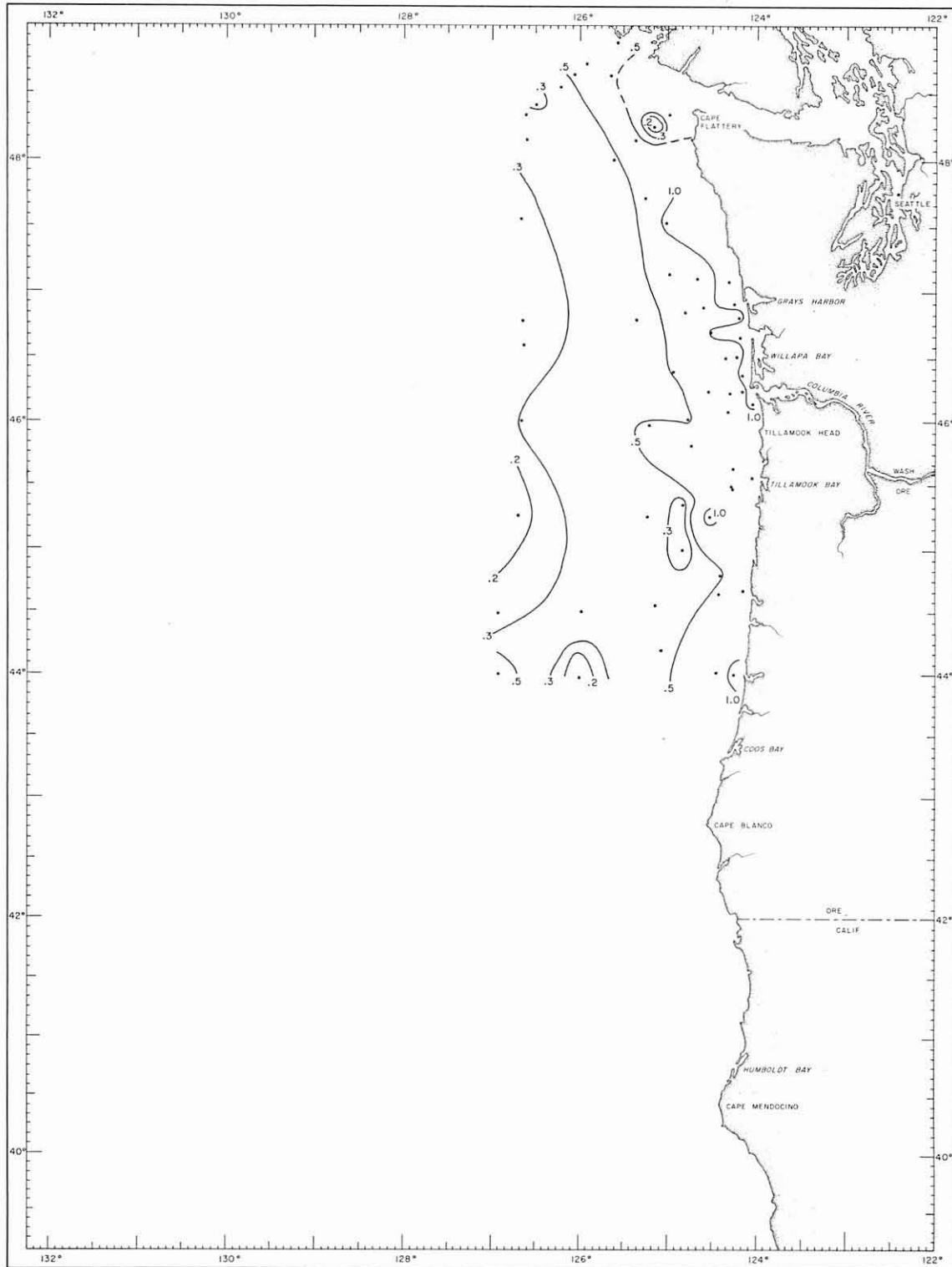


Fig. 28 Distribution of chlorophyll *a* (mg/m^3) in surface waters off the Washington and Oregon coasts, January-February, 1962.

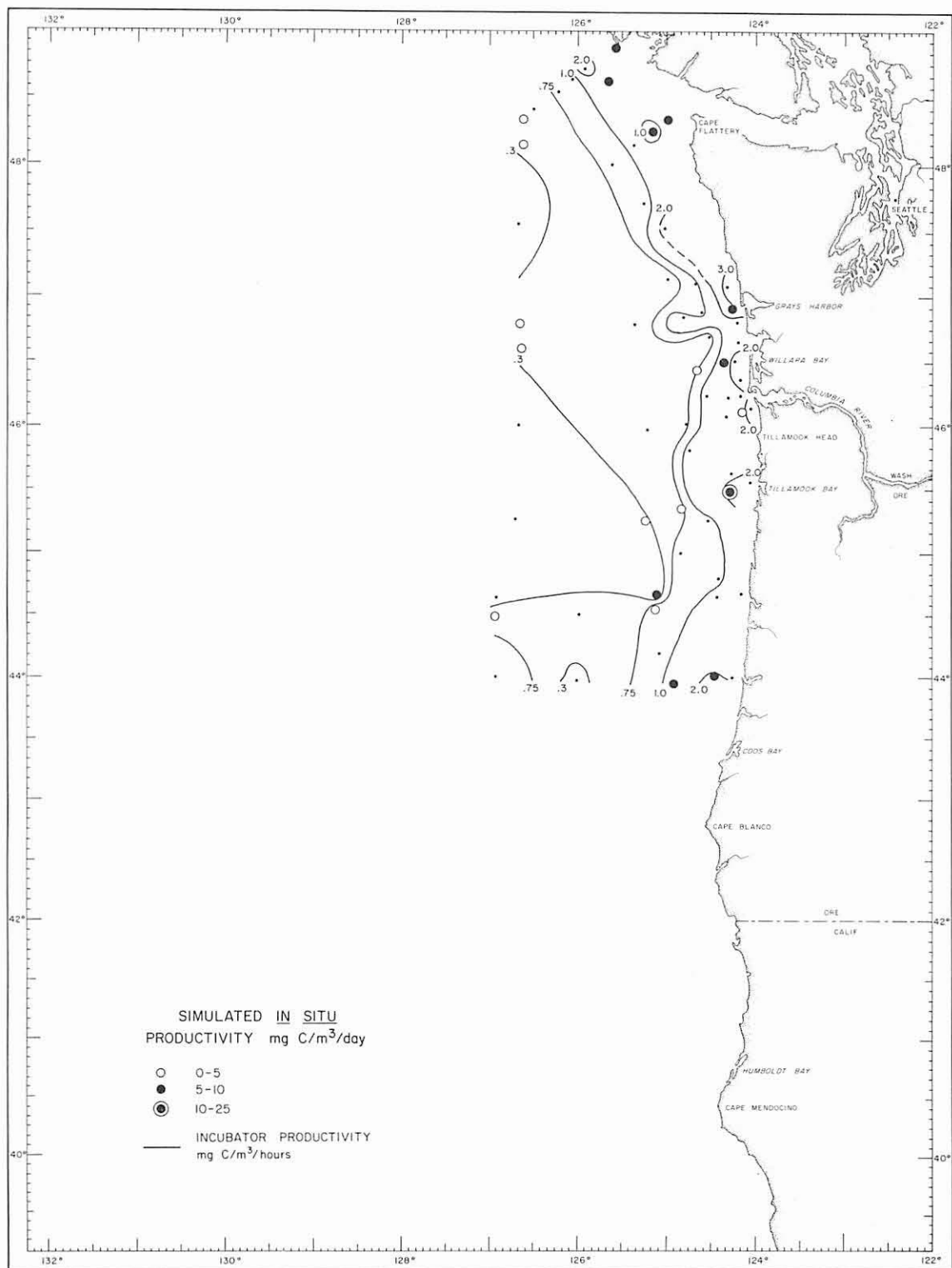


Fig. 29 Distribution of primary productivity in surface waters off the Washington and Oregon coasts, January-February, 1962.

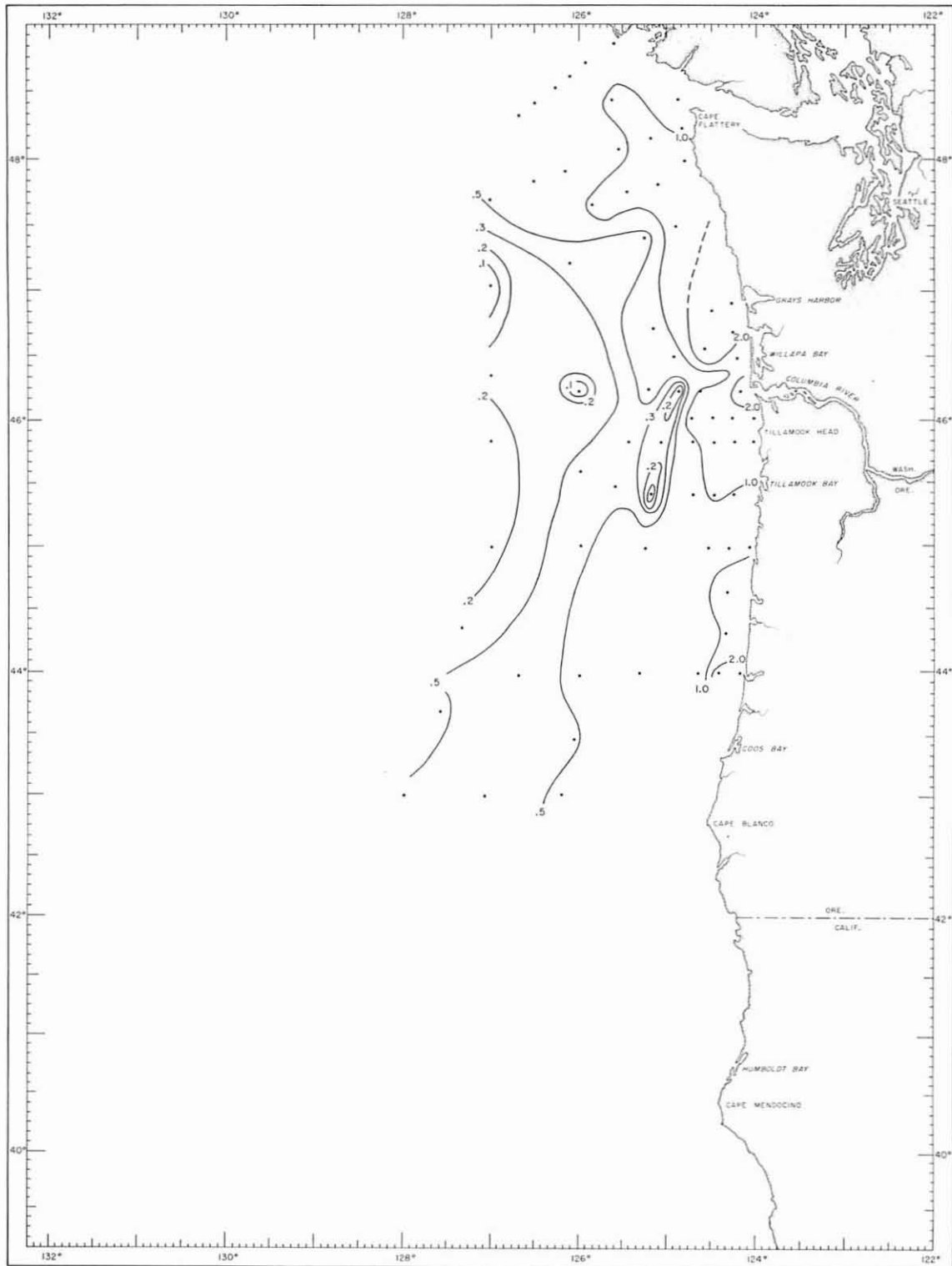


Fig. 30 Distribution of chlorophyll *a* (mg/m^3) in surface waters off the Washington and Oregon coasts, March-April, 1962.

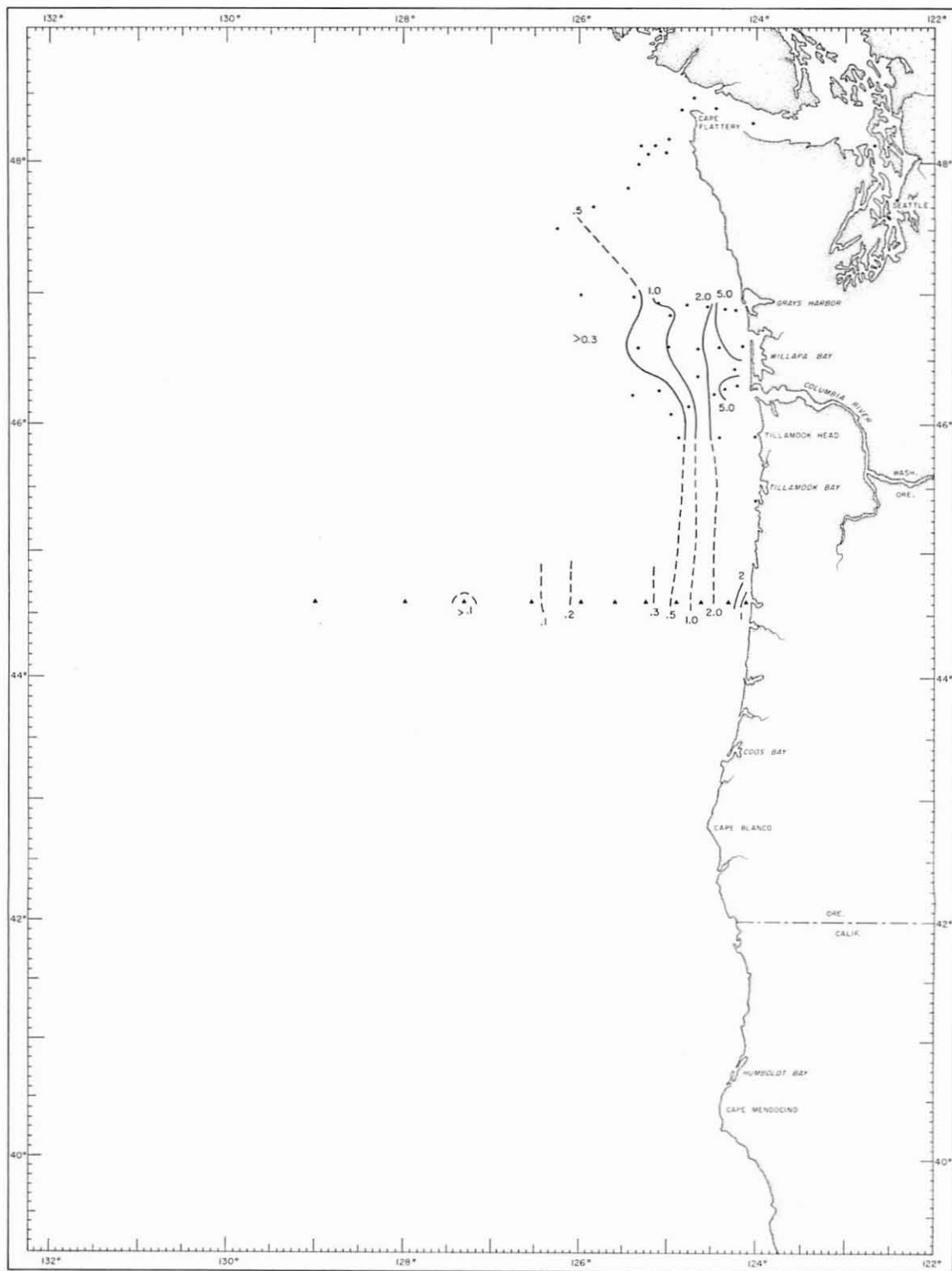


Fig. 32 Distribution of chlorophyll *a* (mg/m^3) in surface waters off the Washington and Oregon coasts, June, 1962.

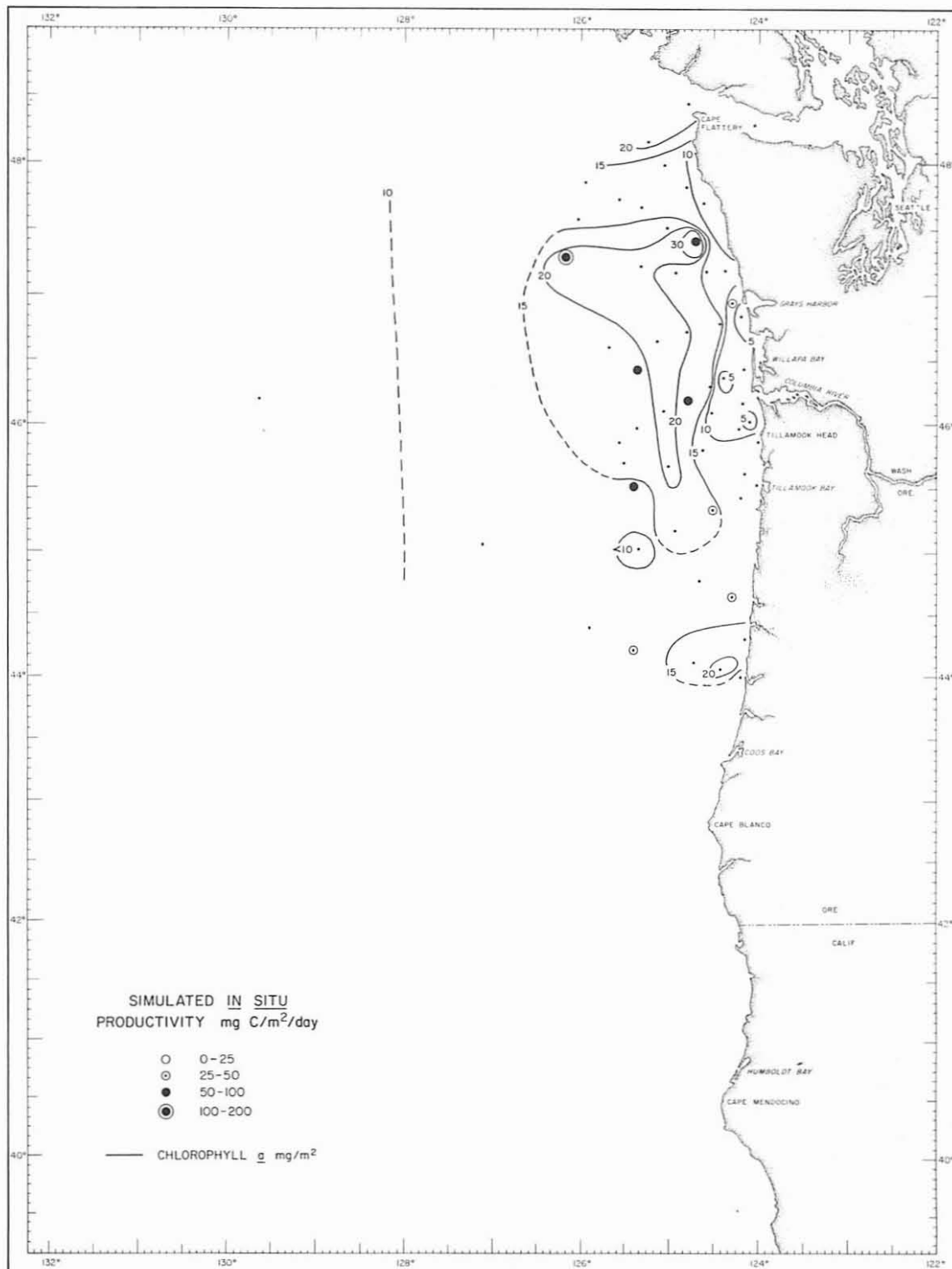


Fig. 34 Distribution of chlorophyll *a* and primary productivity in the euphotic zone off the Washington and Oregon coasts, January, 1961.

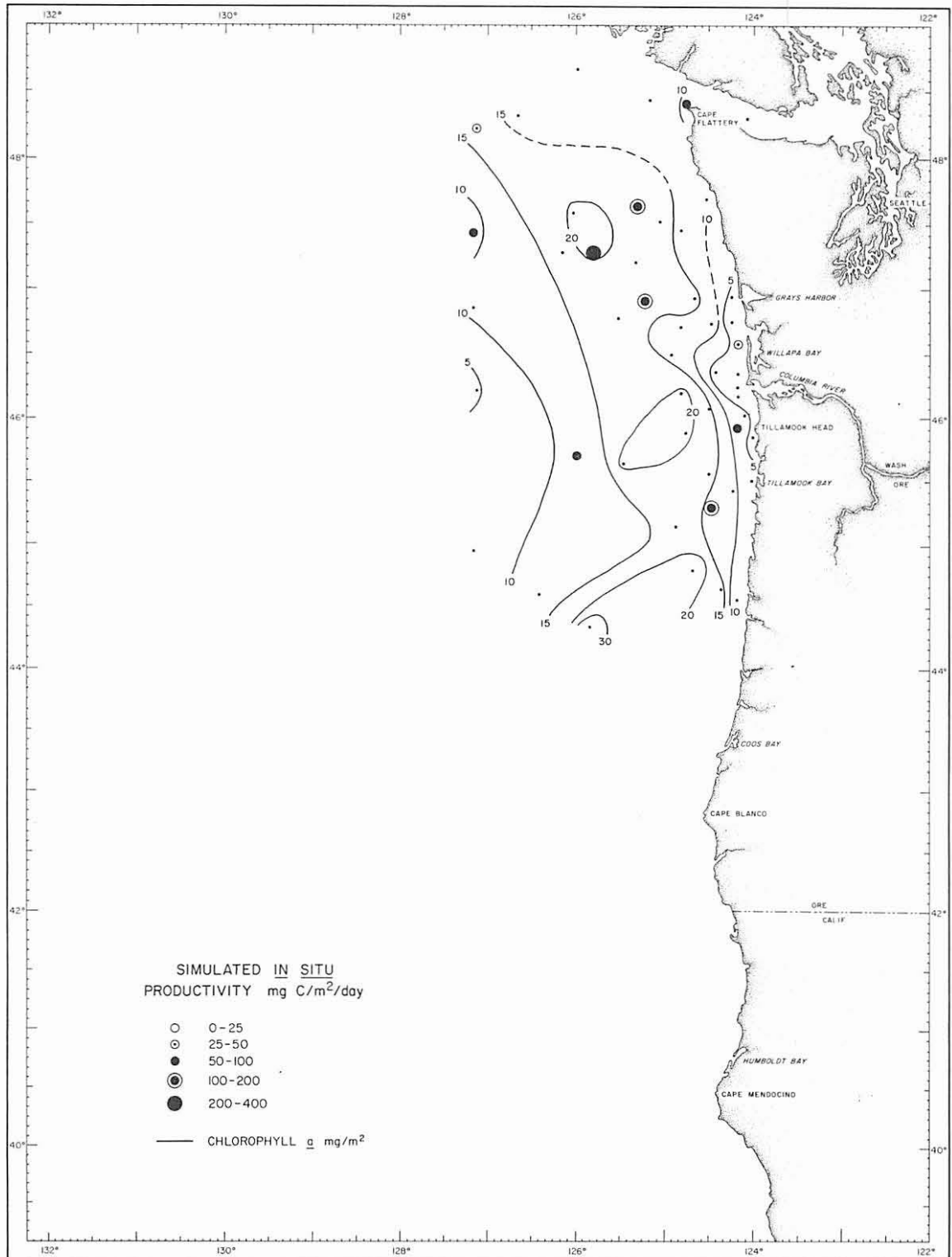


Fig. 35 Distribution of chlorophyll a and primary productivity in the euphotic zone off the Washington and Oregon coasts, March, 1961.

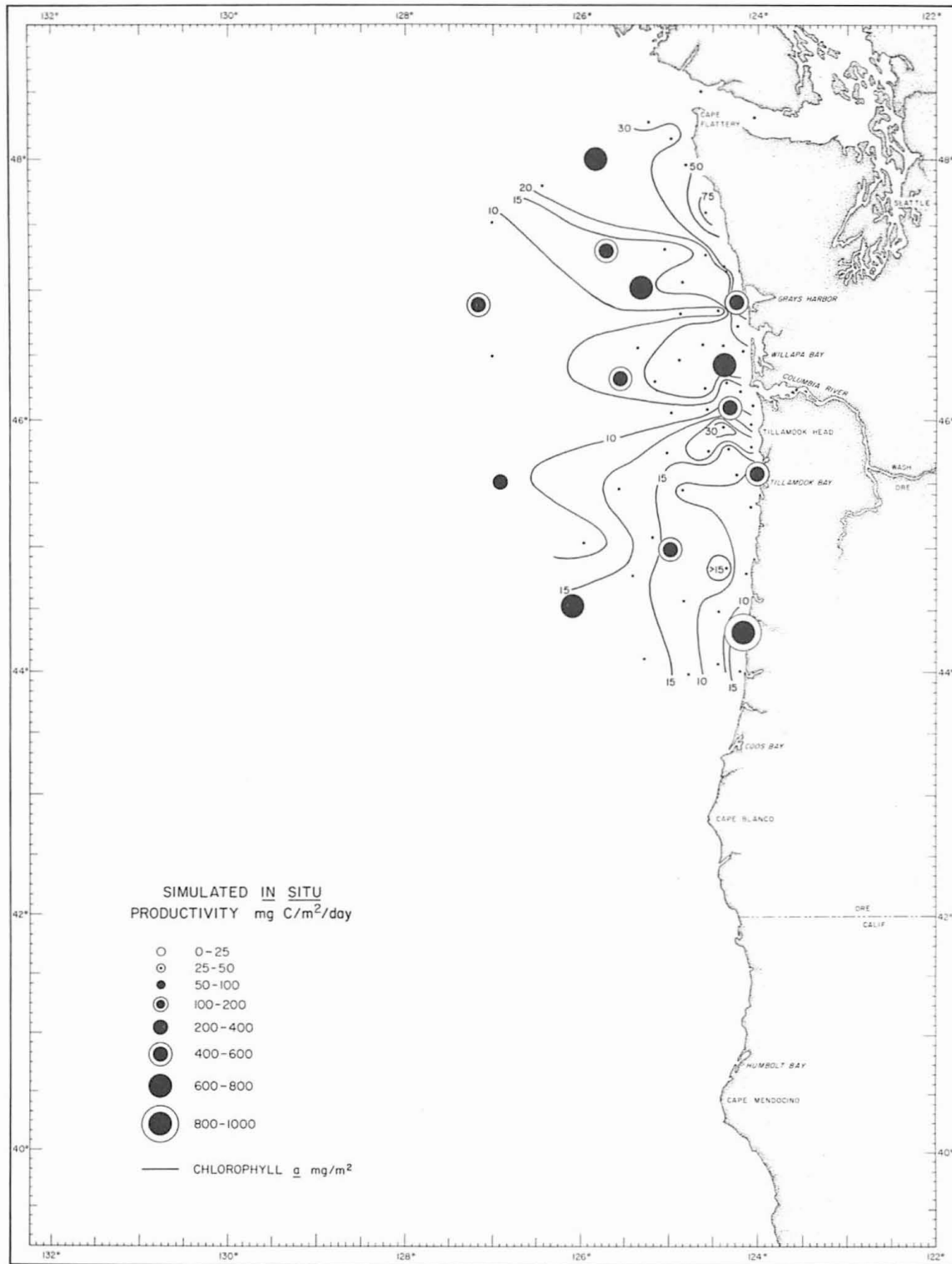


Fig. 36 Distribution of chlorophyll *a* and primary productivity in the euphotic zone off the Washington and Oregon coasts, May, 1961.

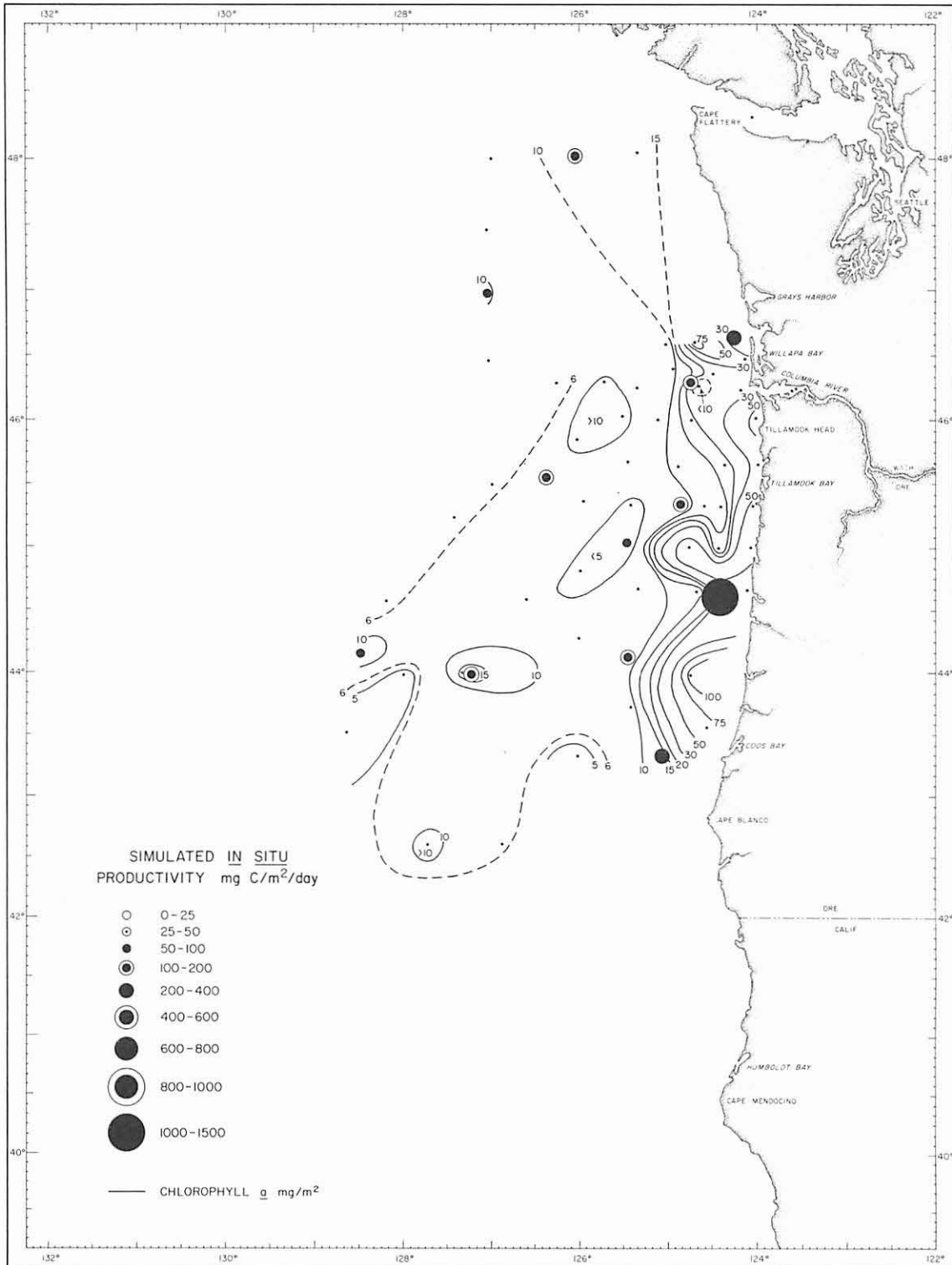


Fig. 38 Distribution of chlorophyll *a* and primary productivity in the euphotic zone off the Washington and Oregon coasts, July, 1961.

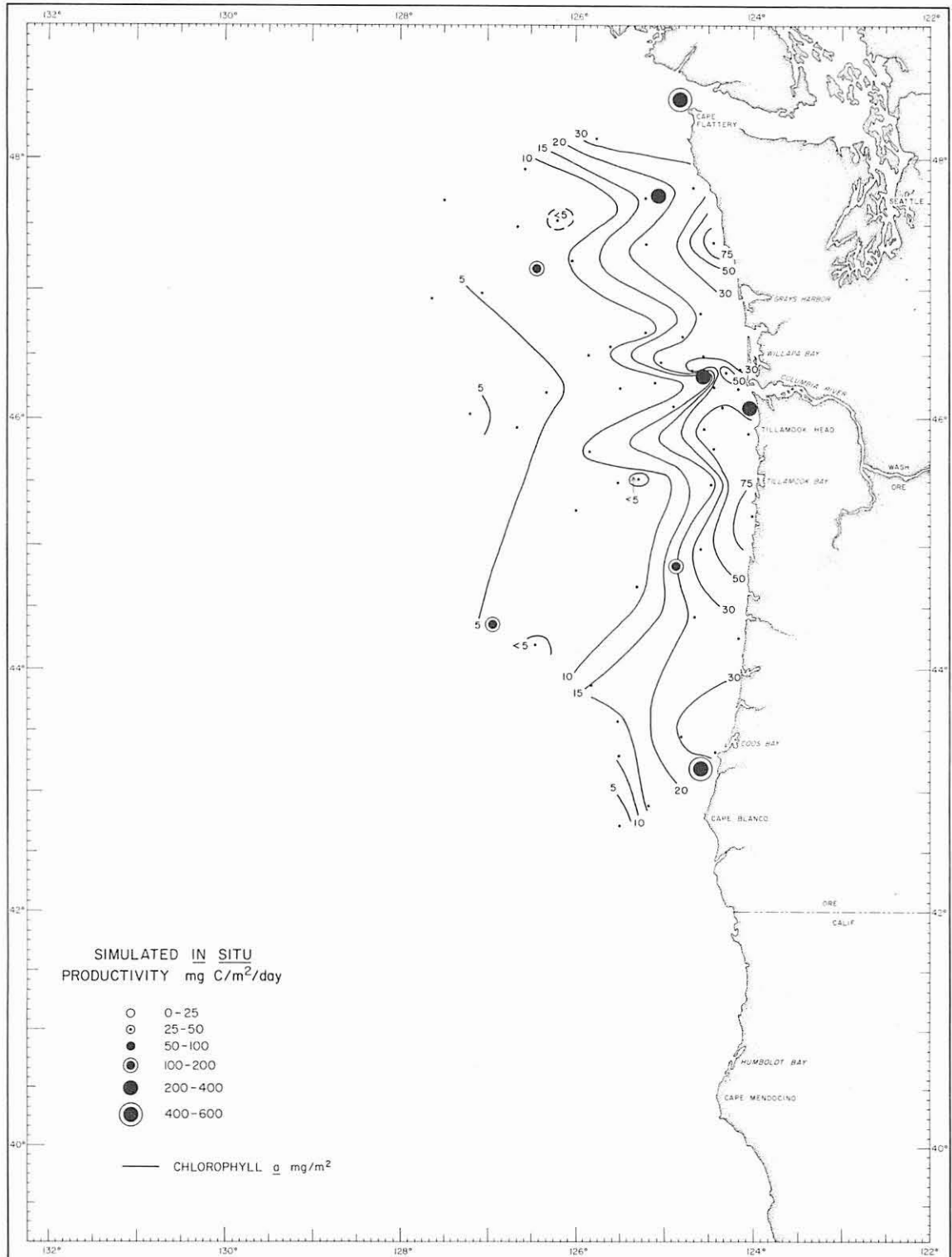


Fig. 39 Distribution of chlorophyll a and primary productivity in the euphotic zone off the Washington and Oregon coasts, August, 1961.

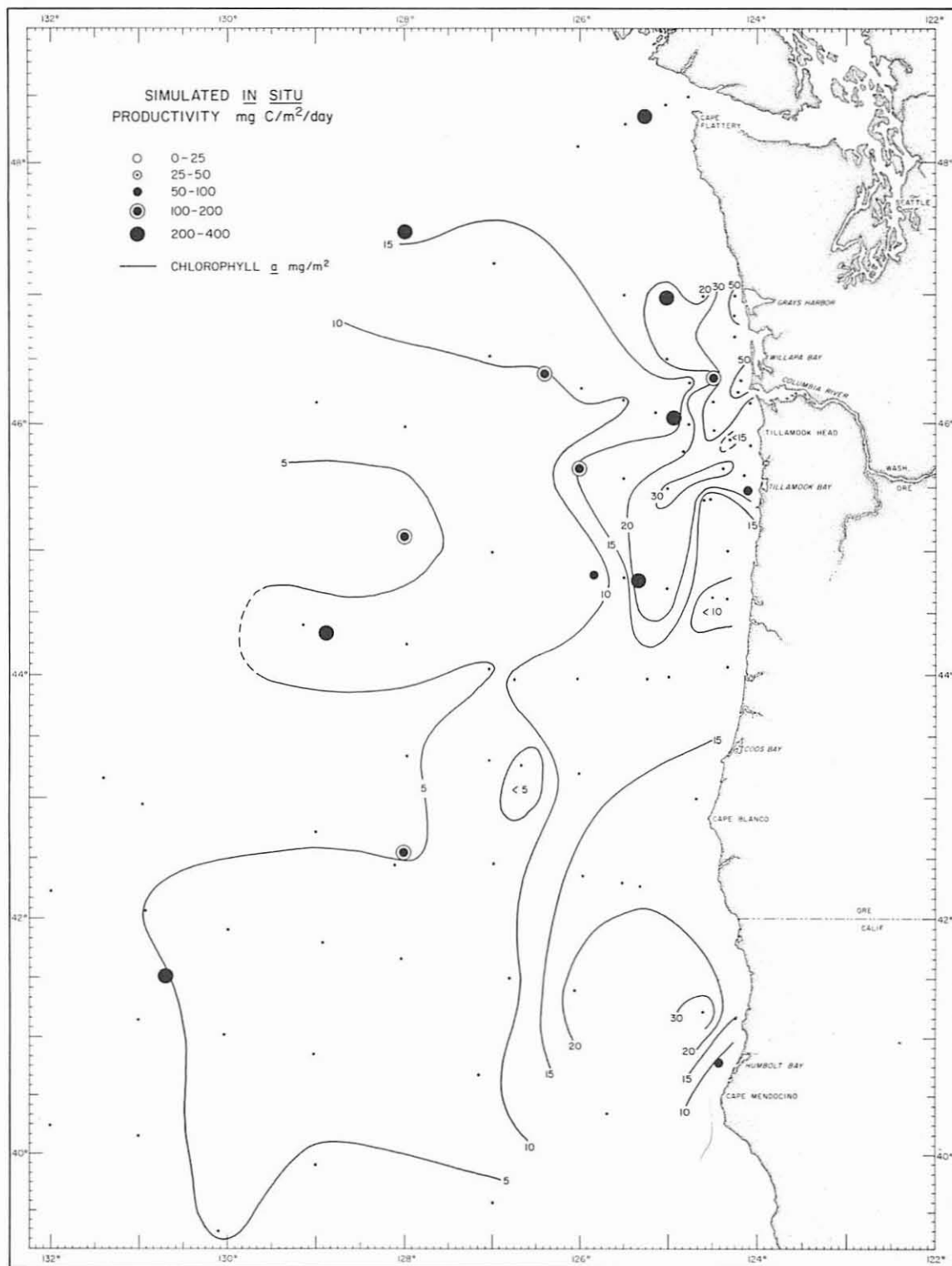


Fig. 40 Distribution of chlorophyll \underline{a} and primary productivity in the euphotic zone off the Washington and Oregon coasts, September-October, 1961.

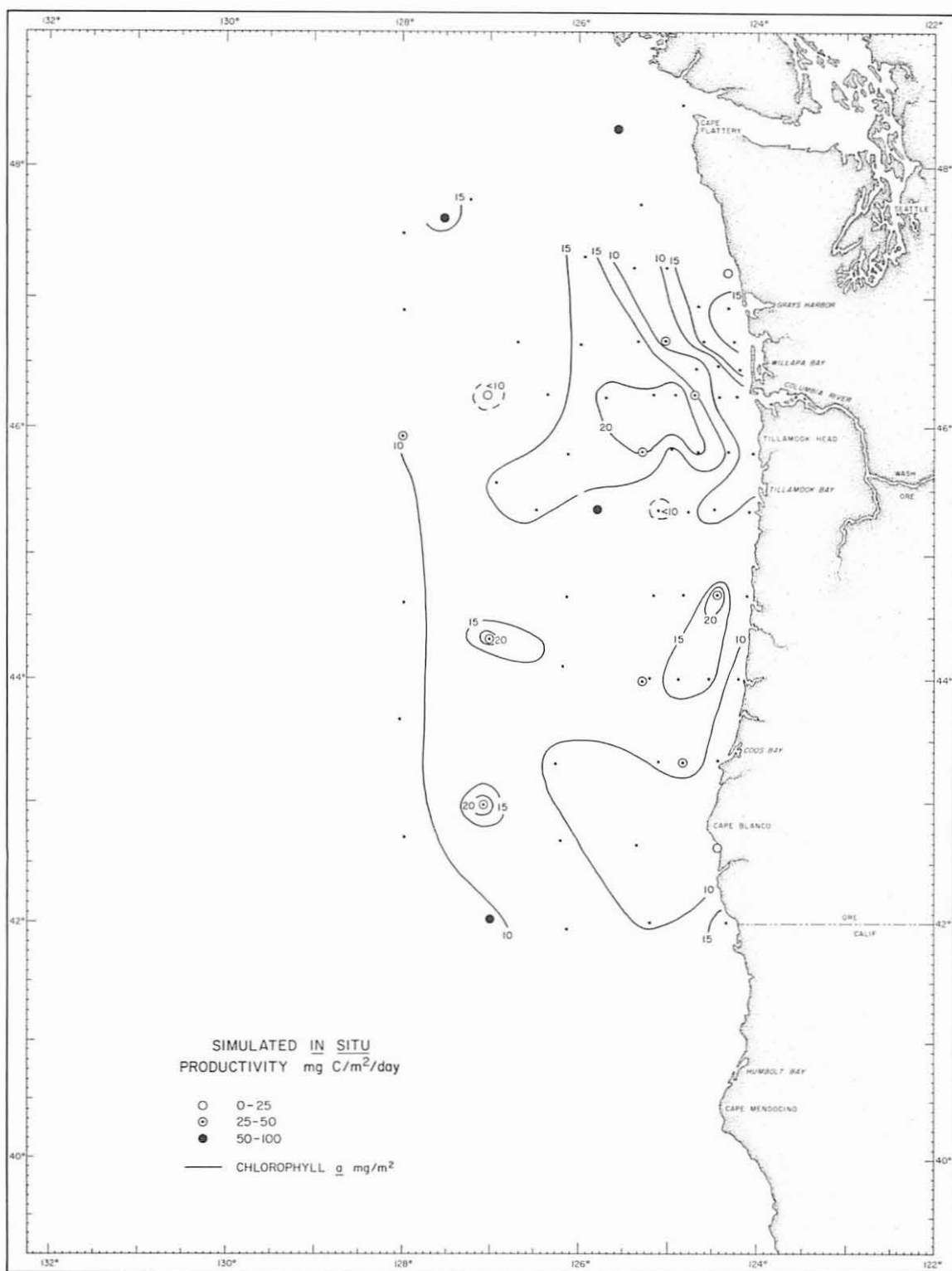


Fig. 41 Distribution of chlorophyll *a* and primary productivity in the euphotic zone off the Washington and Oregon coasts, November-December, 1961.

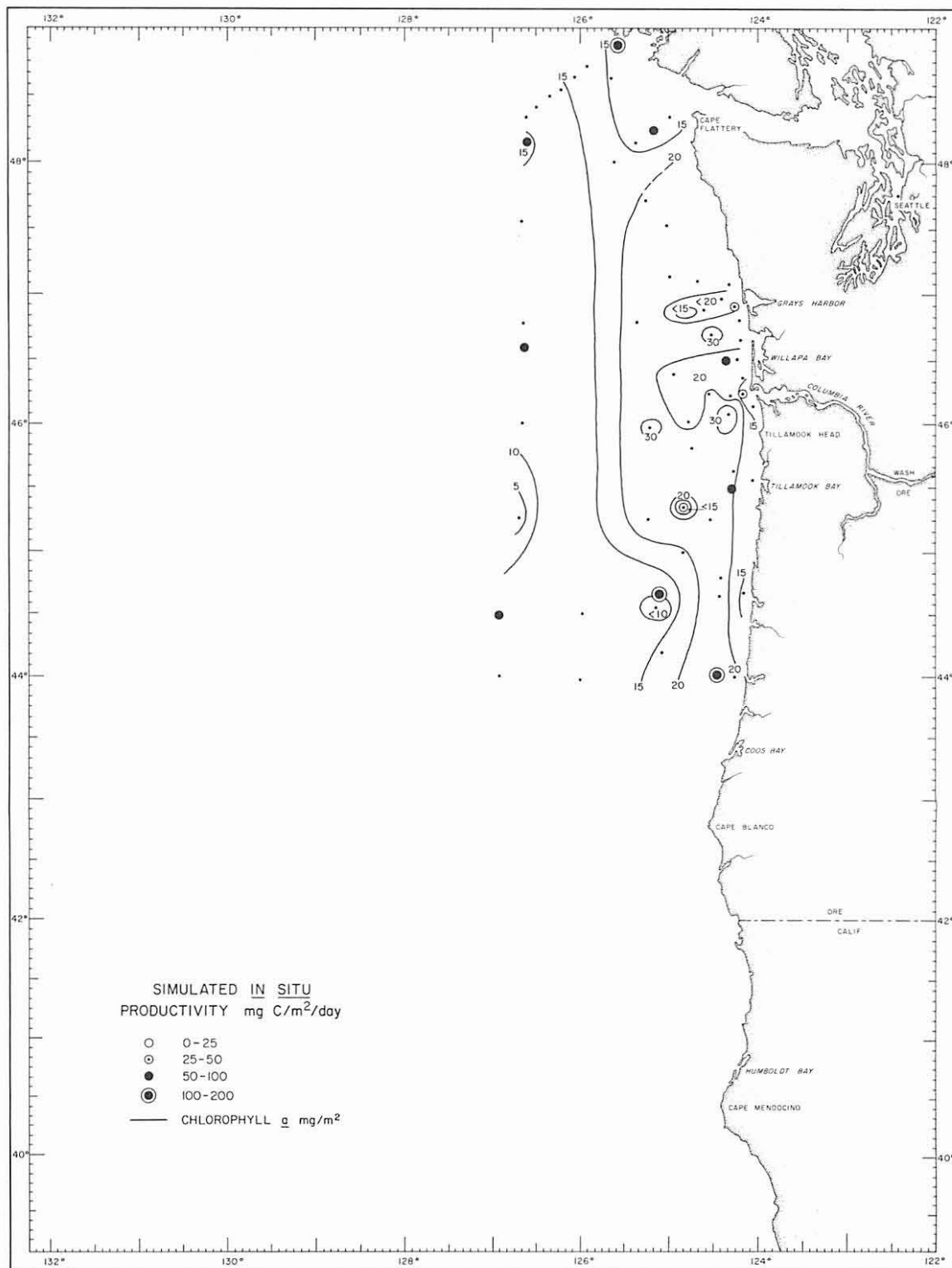


Fig. 42 Distribution of chlorophyll a and primary productivity in the euphotic zone off the Washington and Oregon coasts, January-February, 1962.

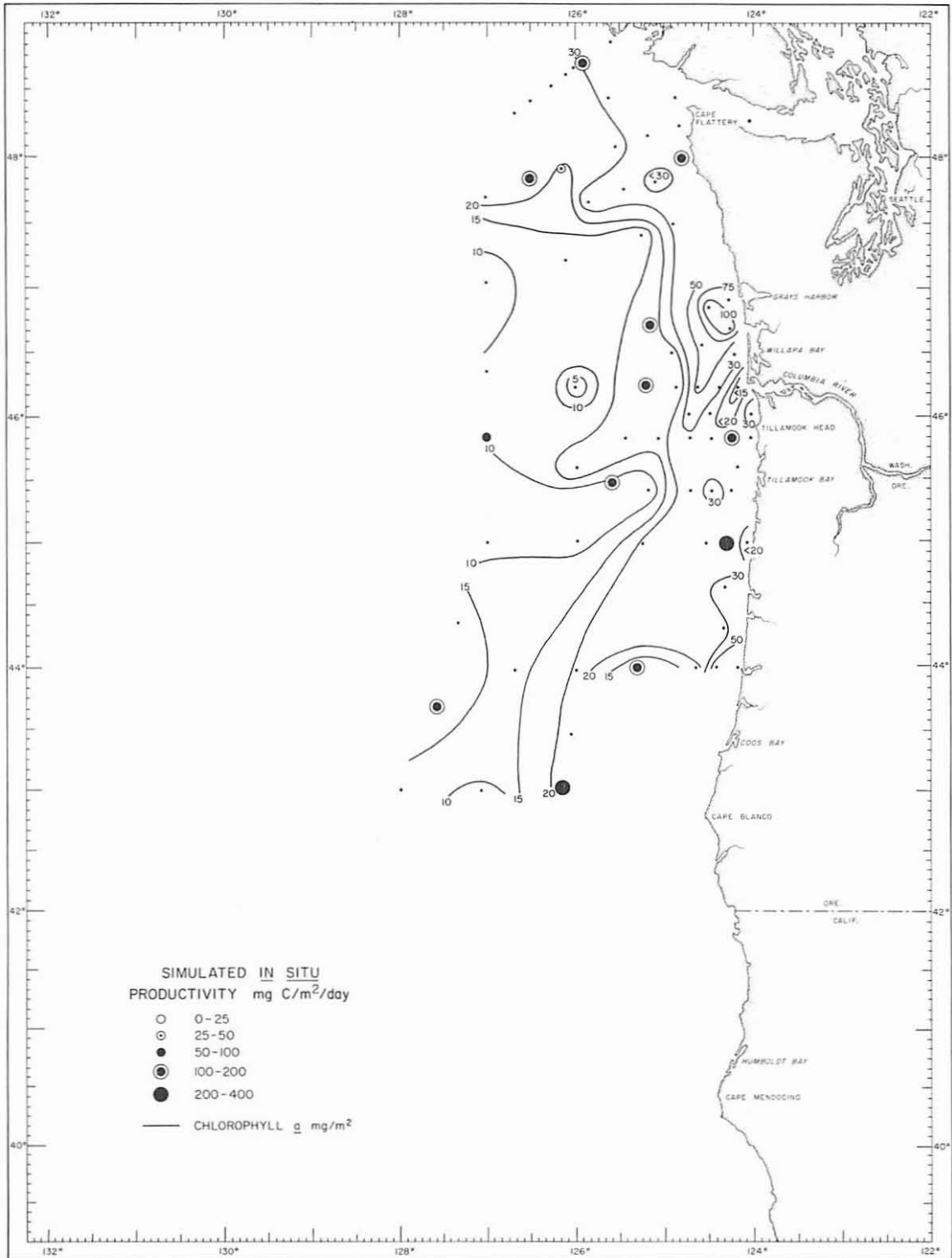


Fig. 43 Distribution of chlorophyll *a* and primary productivity in the euphotic zone off the Washington and Oregon coasts, March-April, 1962.

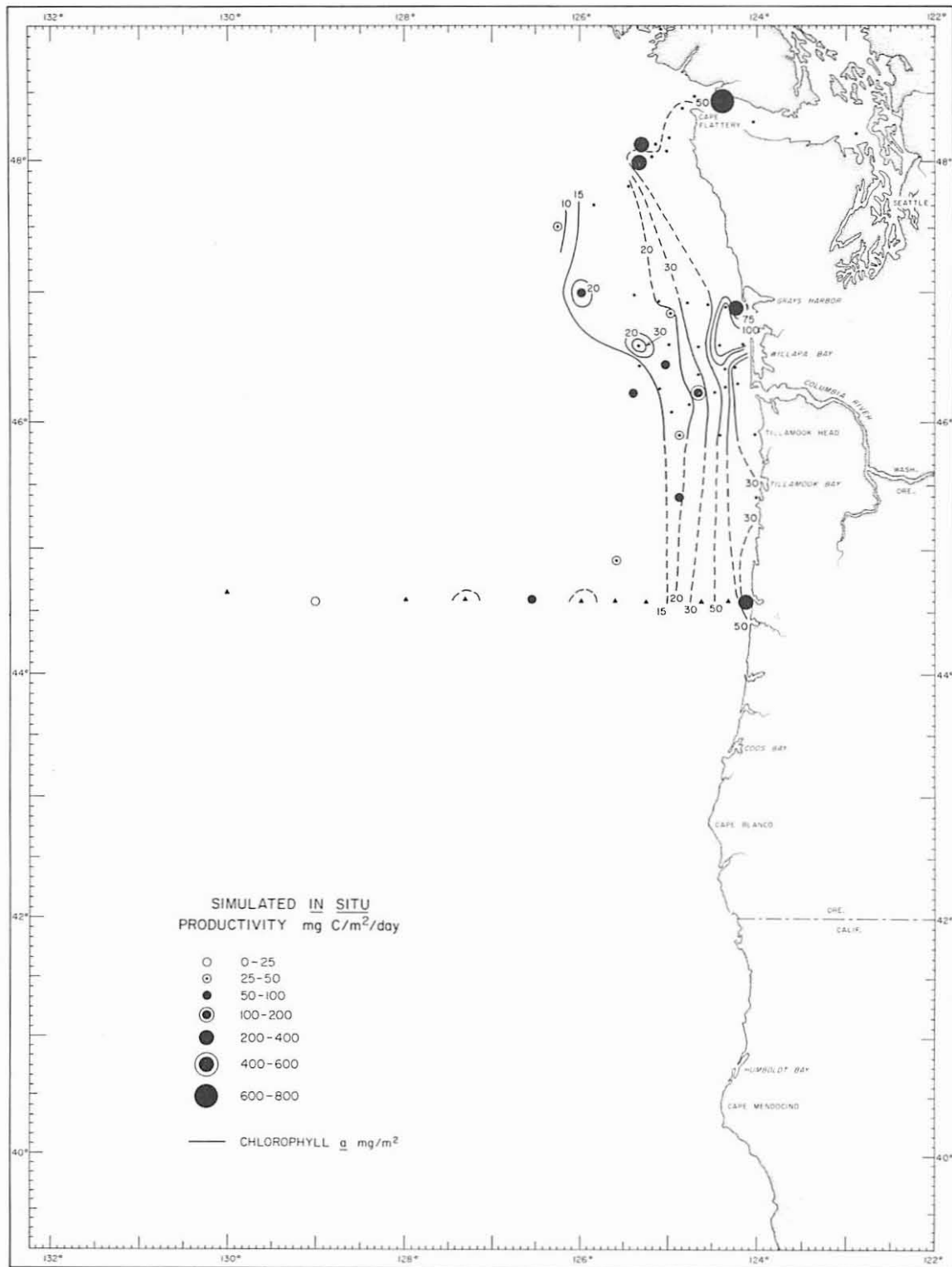


Fig. 44 Distribution of chlorophyll a and primary productivity in the euphotic zone off the Washington and Oregon coasts, June, 1962.

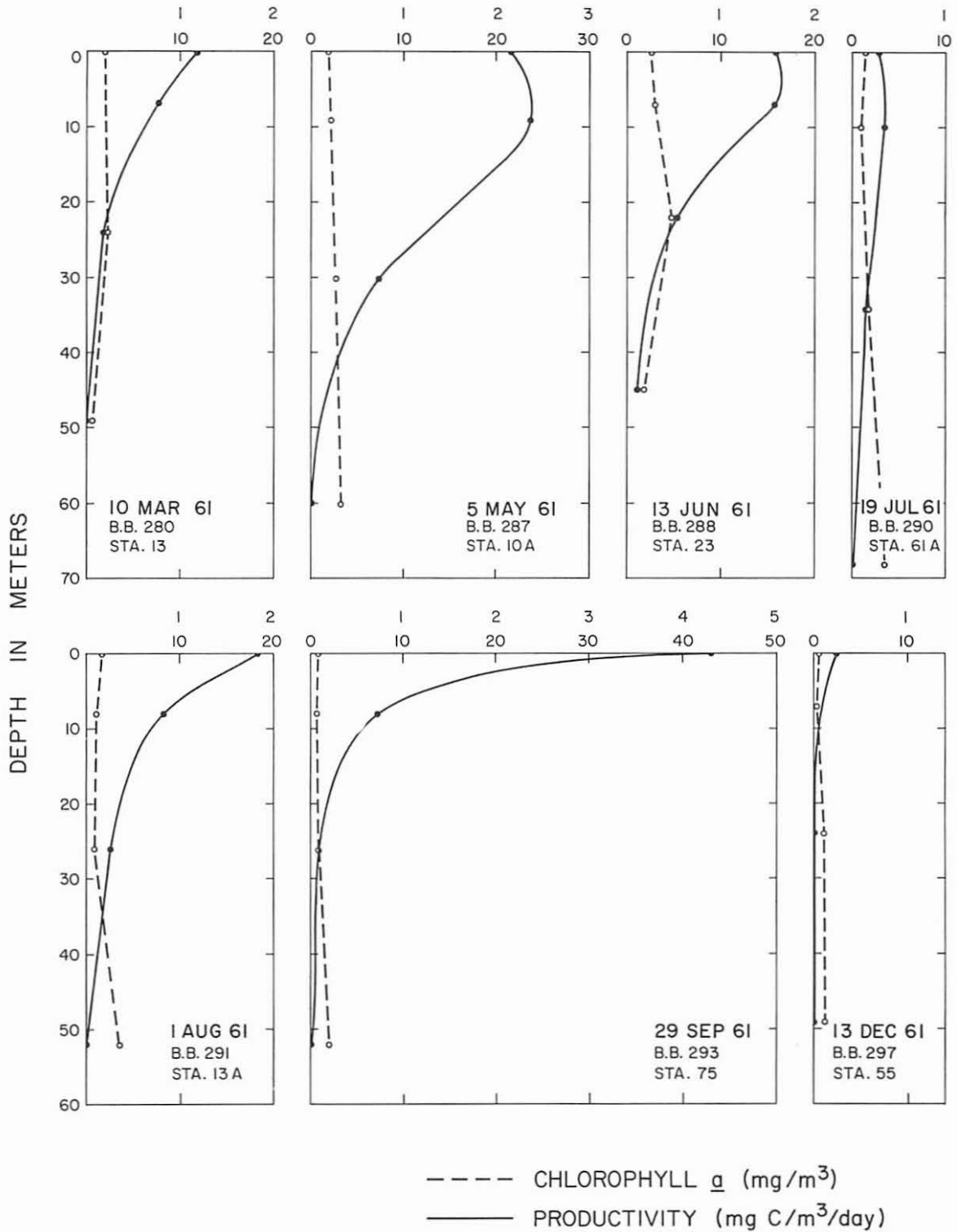


Fig. 45 Vertical and seasonal distributions of chlorophyll *a* and primary productivity at selected stations in Area 1 (see text), 1961-62.

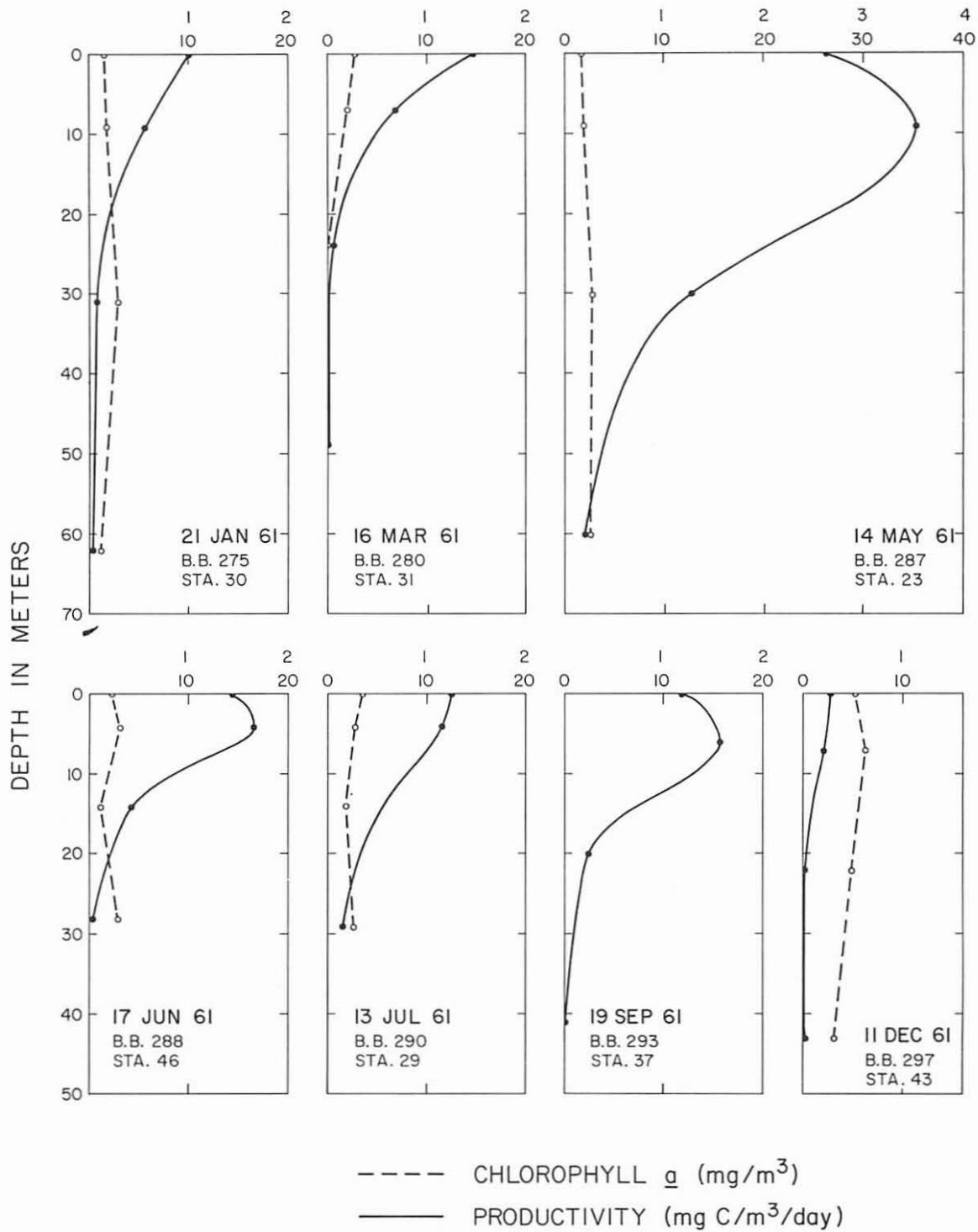


Fig. 46 Vertical and seasonal distributions of chlorophyll *a* and primary productivity at selected stations in Area 2 (see text), 1961-62.

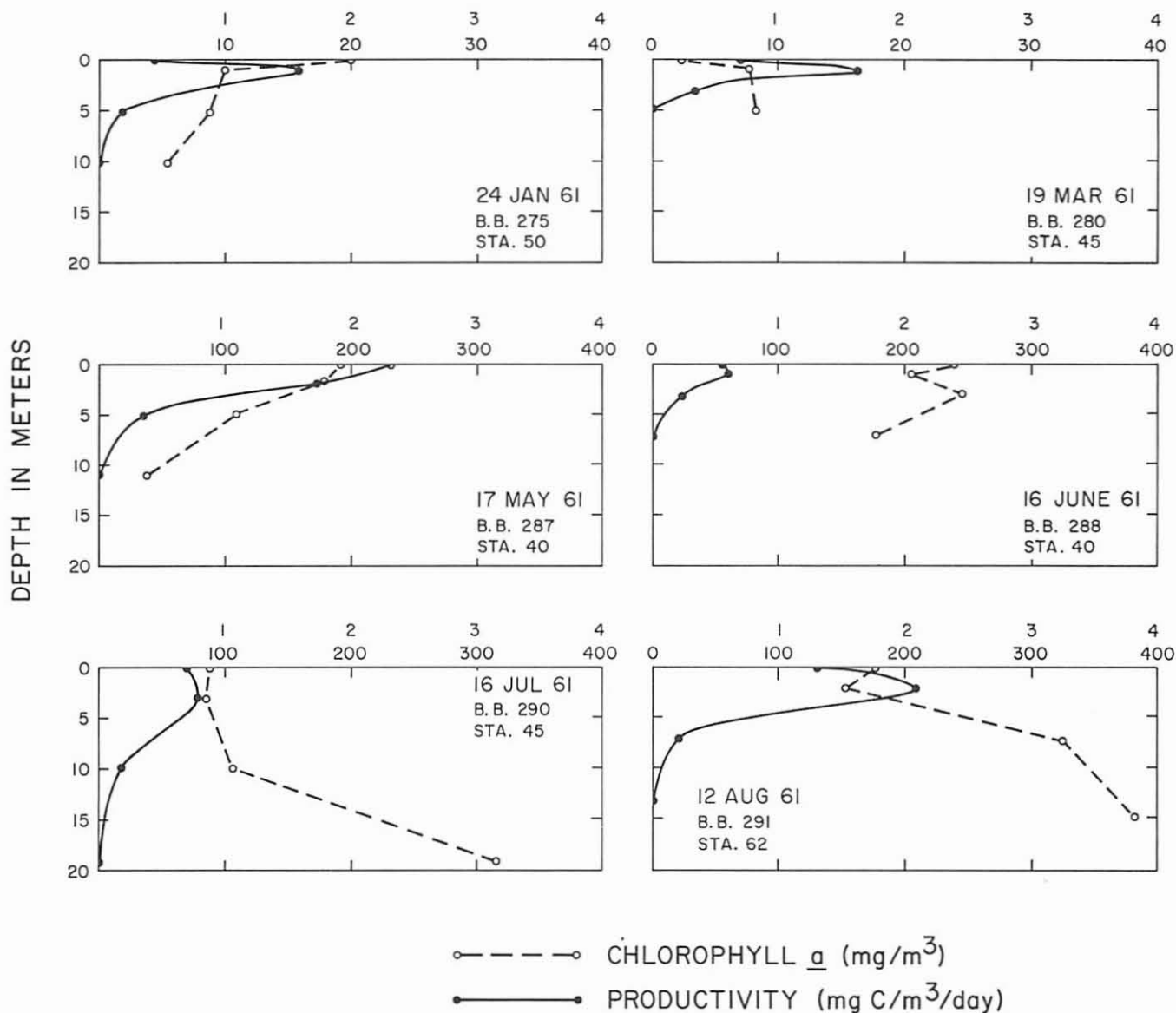


Fig. 47 Vertical and seasonal distributions of chlorophyll *a* and primary productivity at selected stations in Area 3 (see text), 1961-62. Note changes in scale.

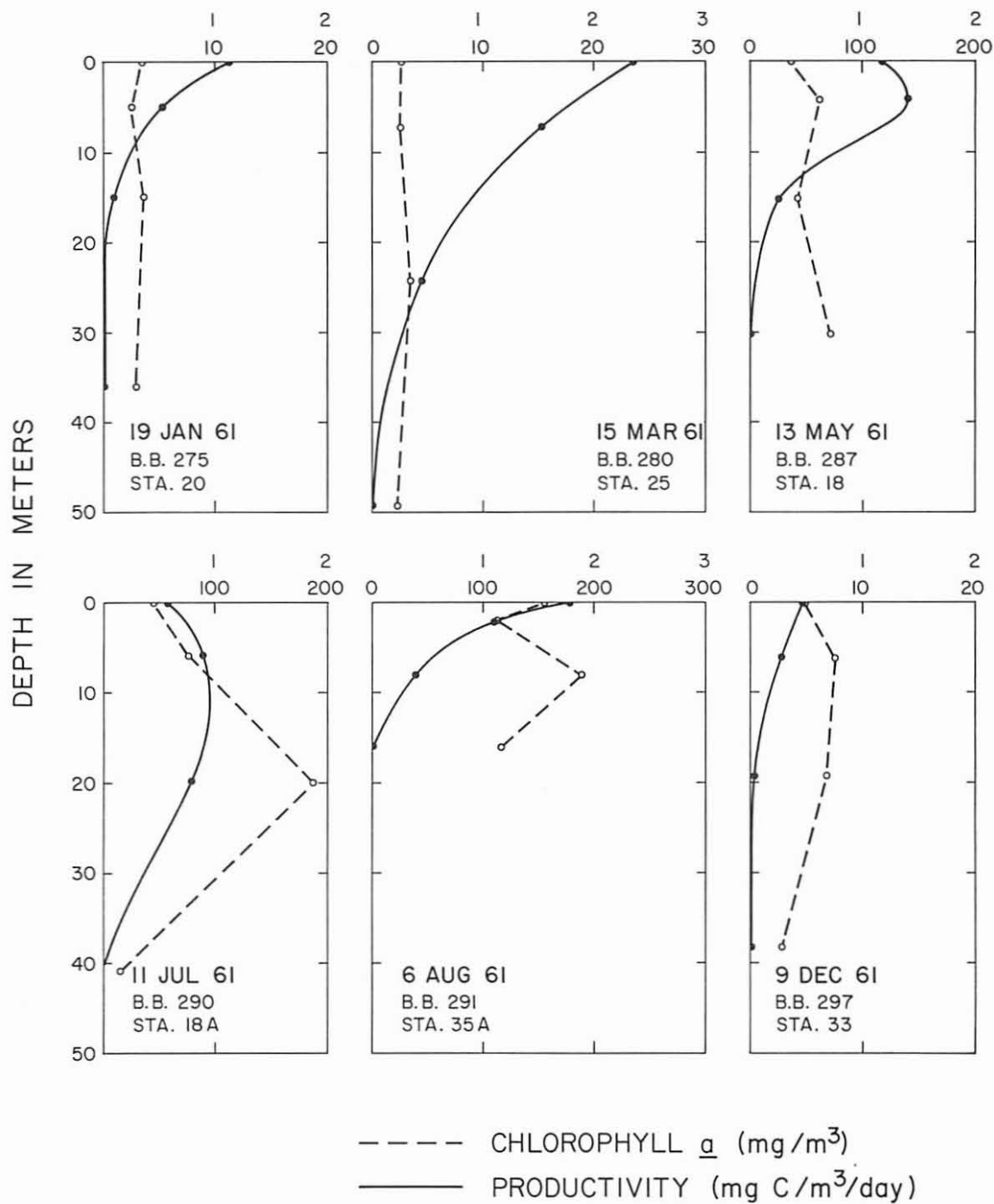


Fig. 48 Vertical and seasonal distributions of chlorophyll a and primary productivity at selected stations in Area 4 (see text), 1961-62. Note changes in scale.

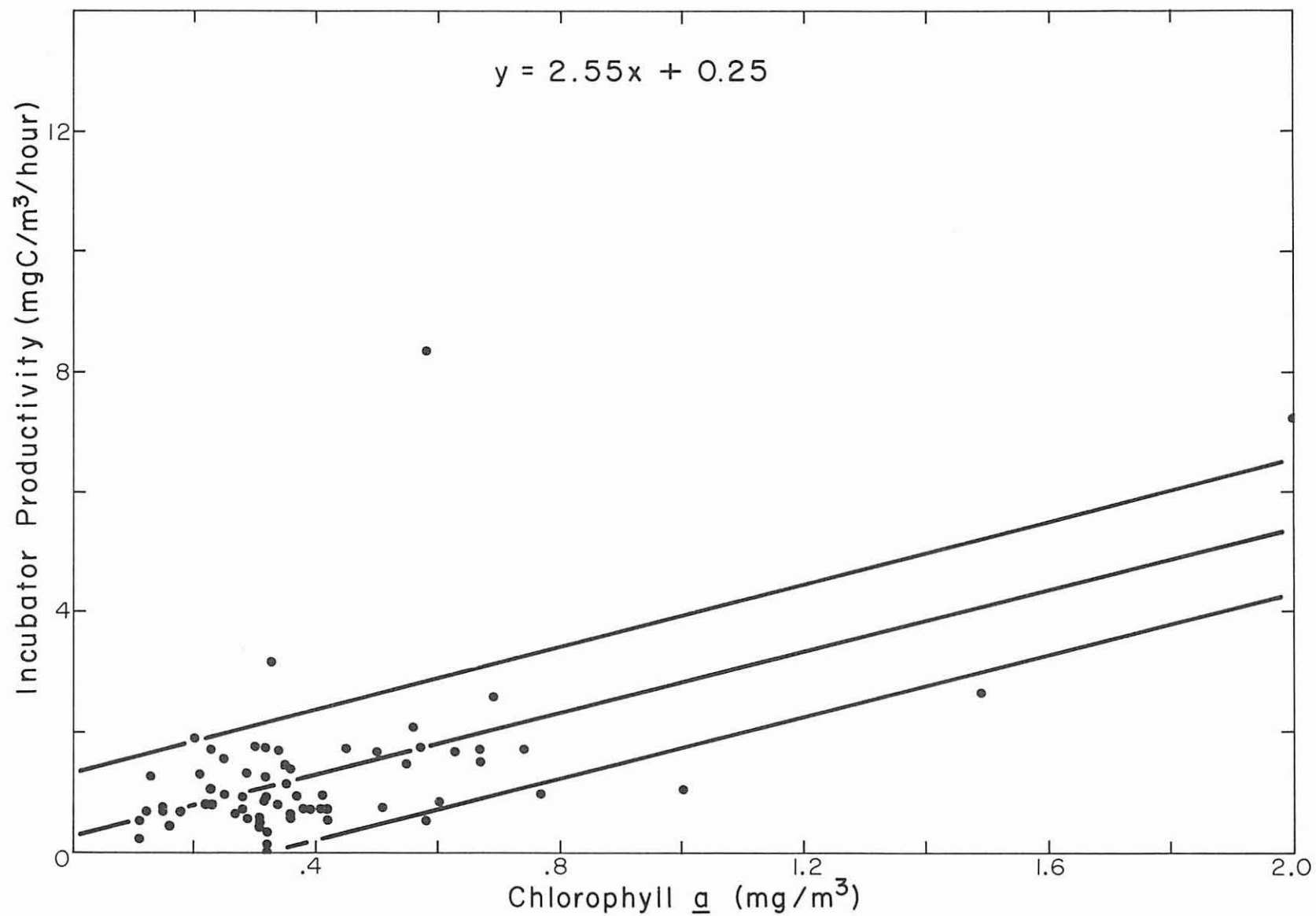


Fig. 50 Primary productivity and chlorophyll a relationships in surface waters off the Washington and Oregon coasts, January, 1961.

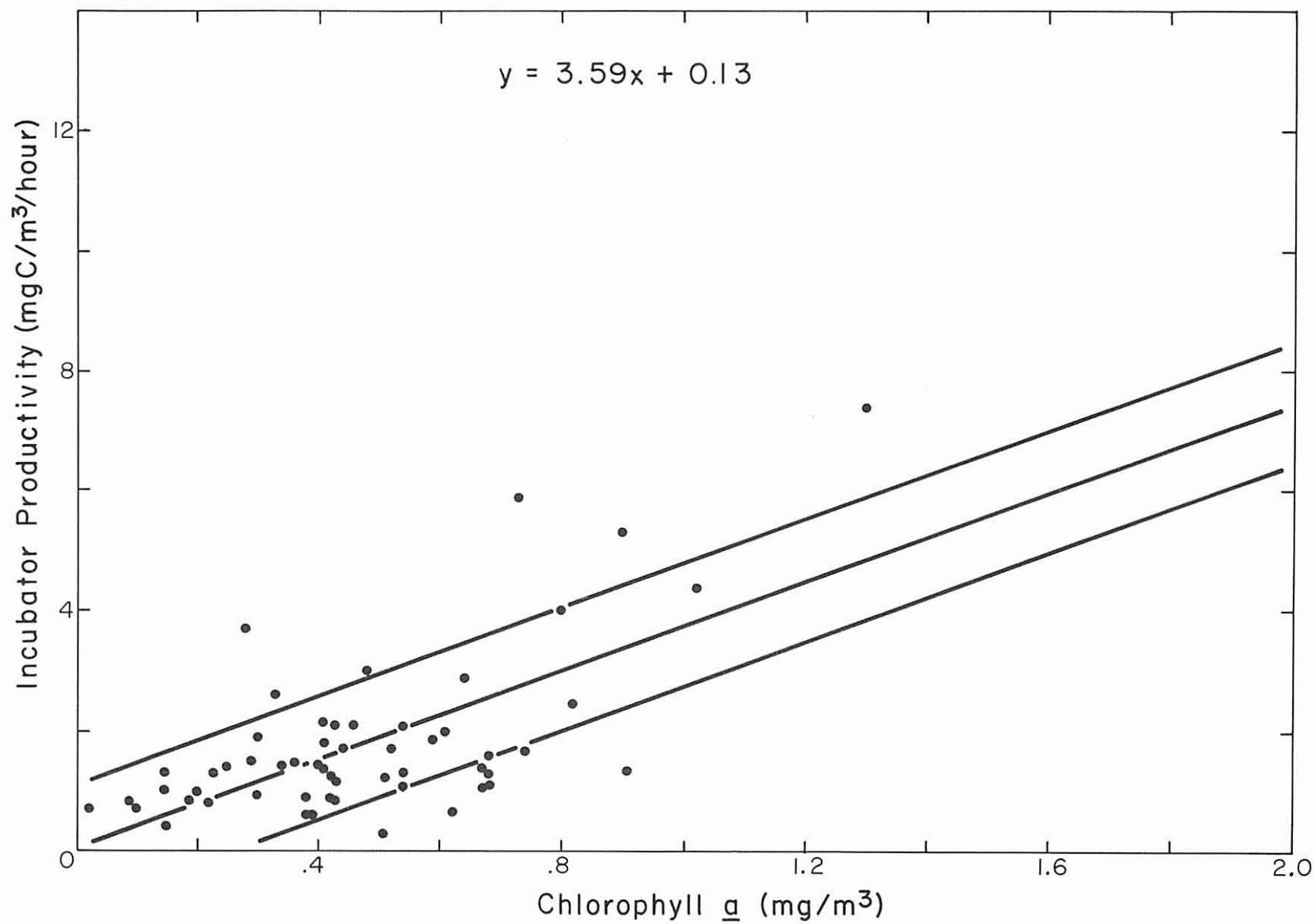


Fig. 51 Primary productivity and chlorophyll a relationships in surface waters off the Washington and Oregon coasts, March, 1961.

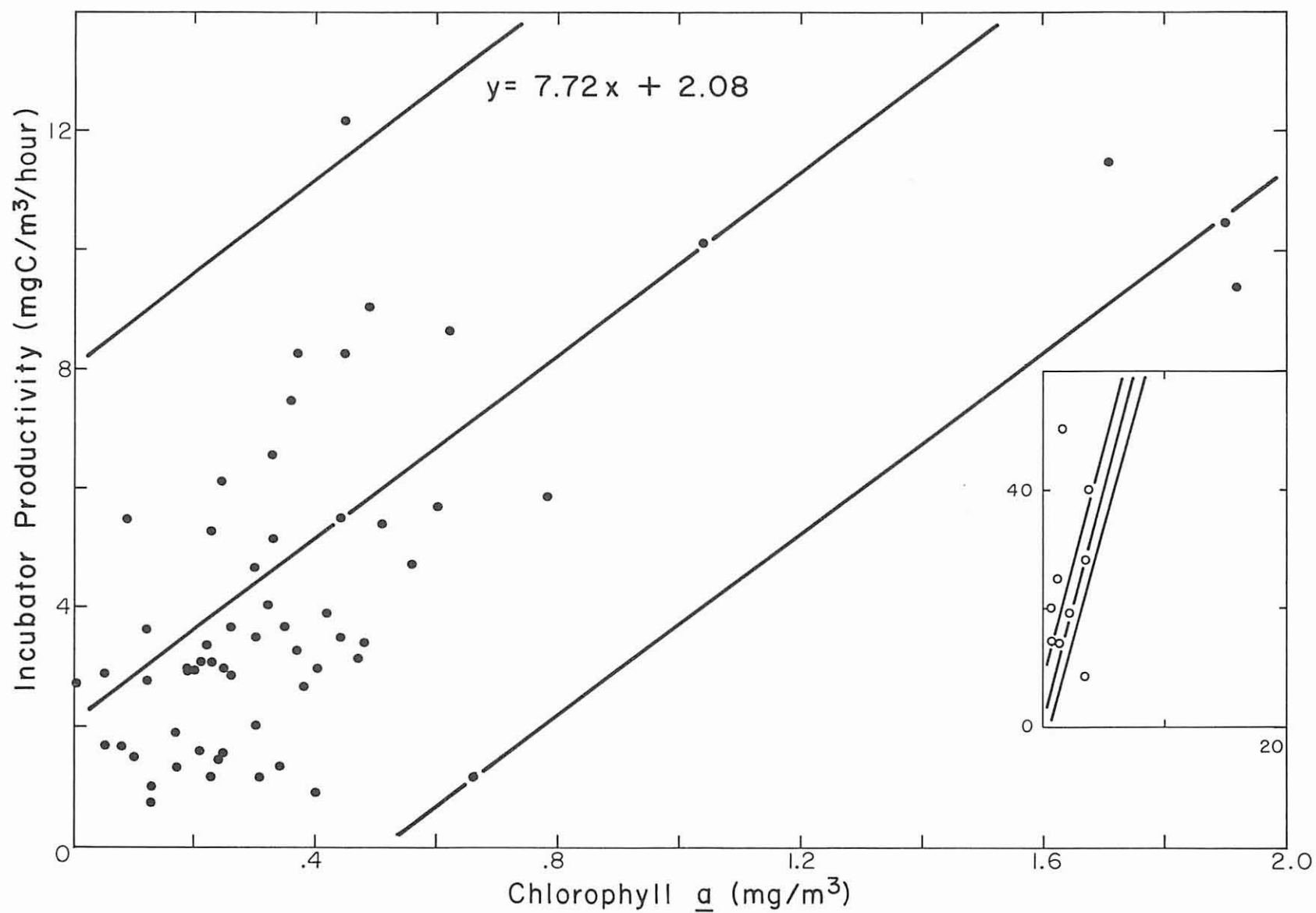
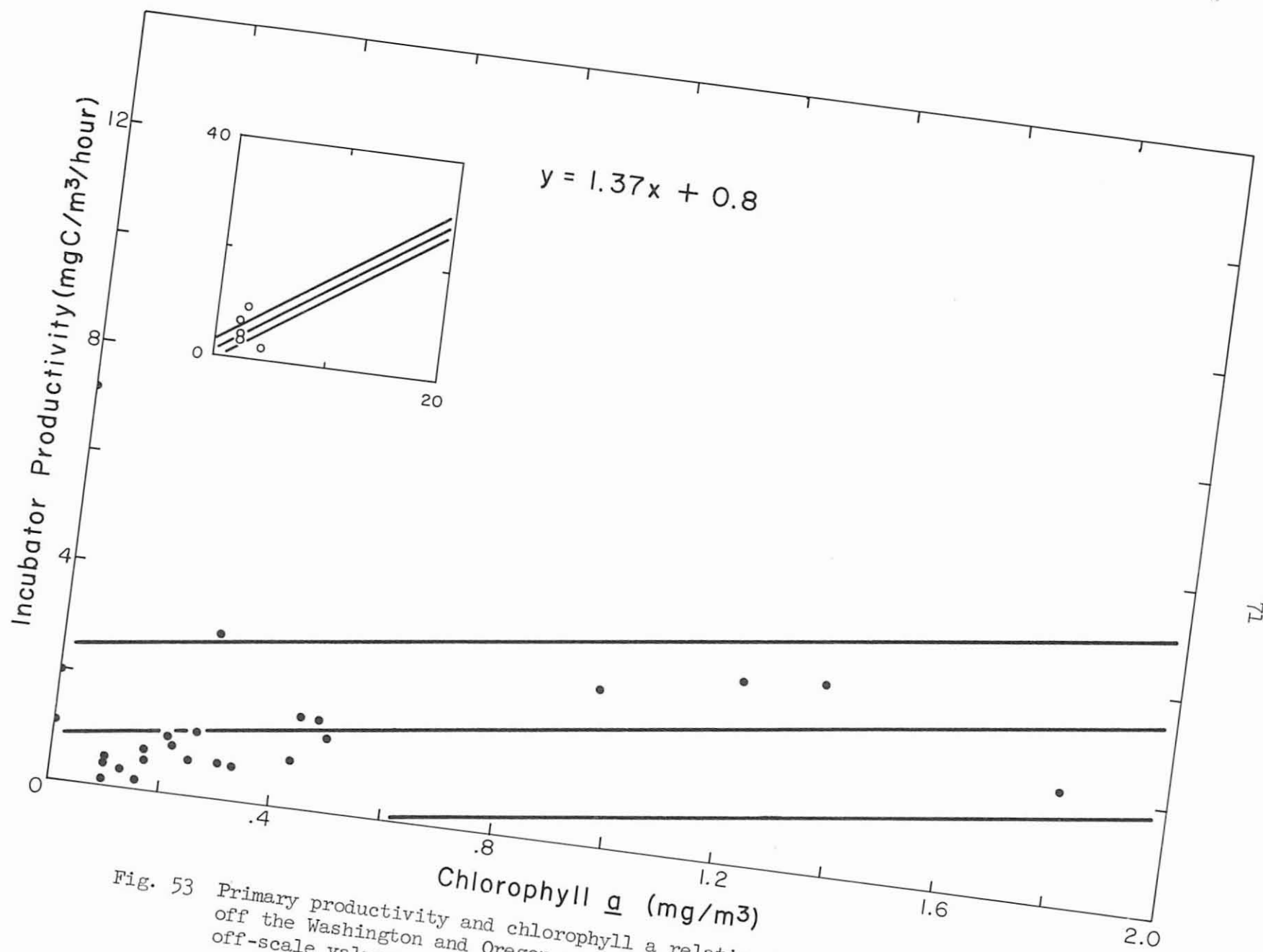


Fig. 52 Primary productivity and chlorophyll a relationships in surface waters off the Washington and Oregon coasts, May, 1961. The insert contains off-scale values.



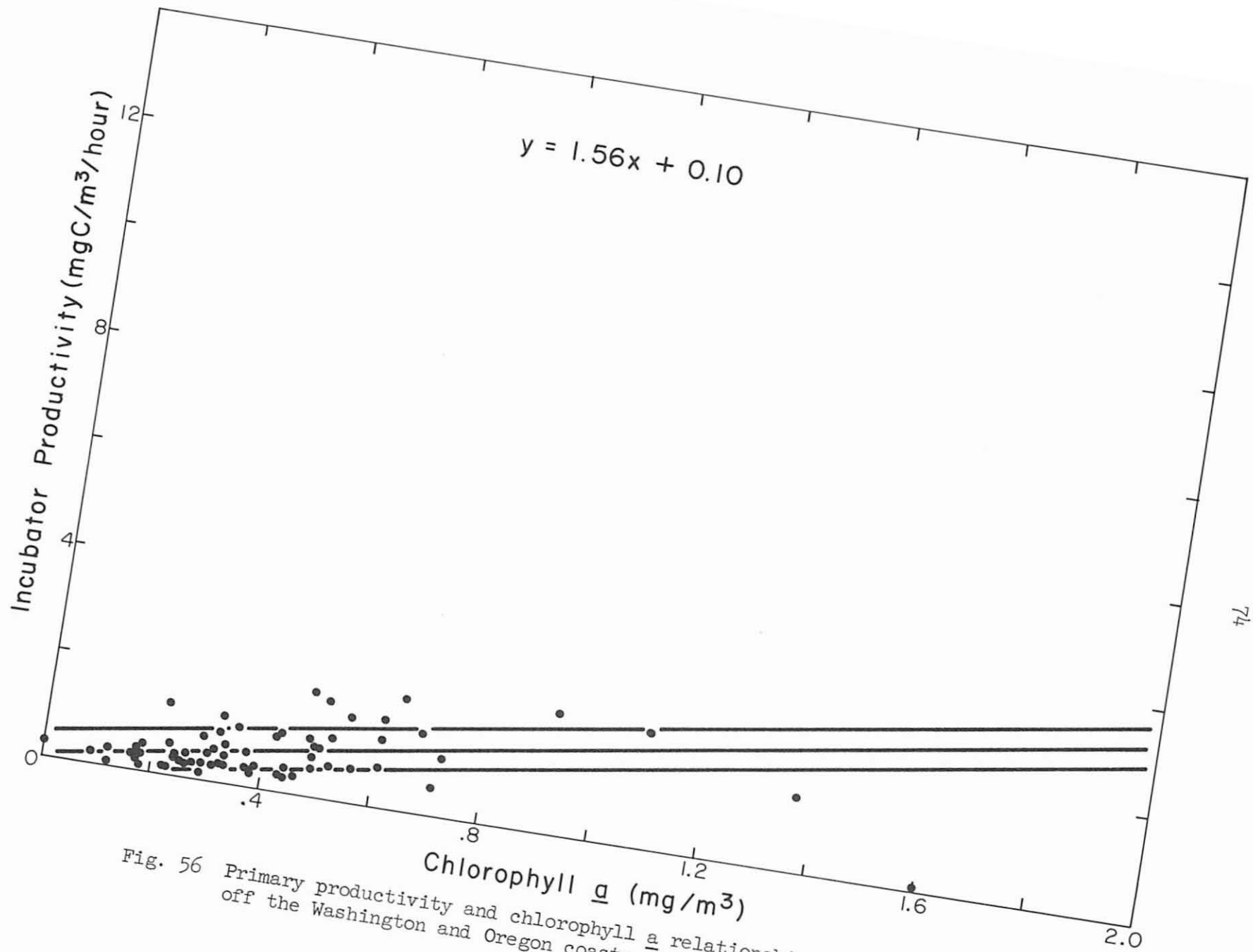


Fig. 56 Primary productivity and chlorophyll a relationships in surface waters off the Washington and Oregon coasts, November-December, 1961.

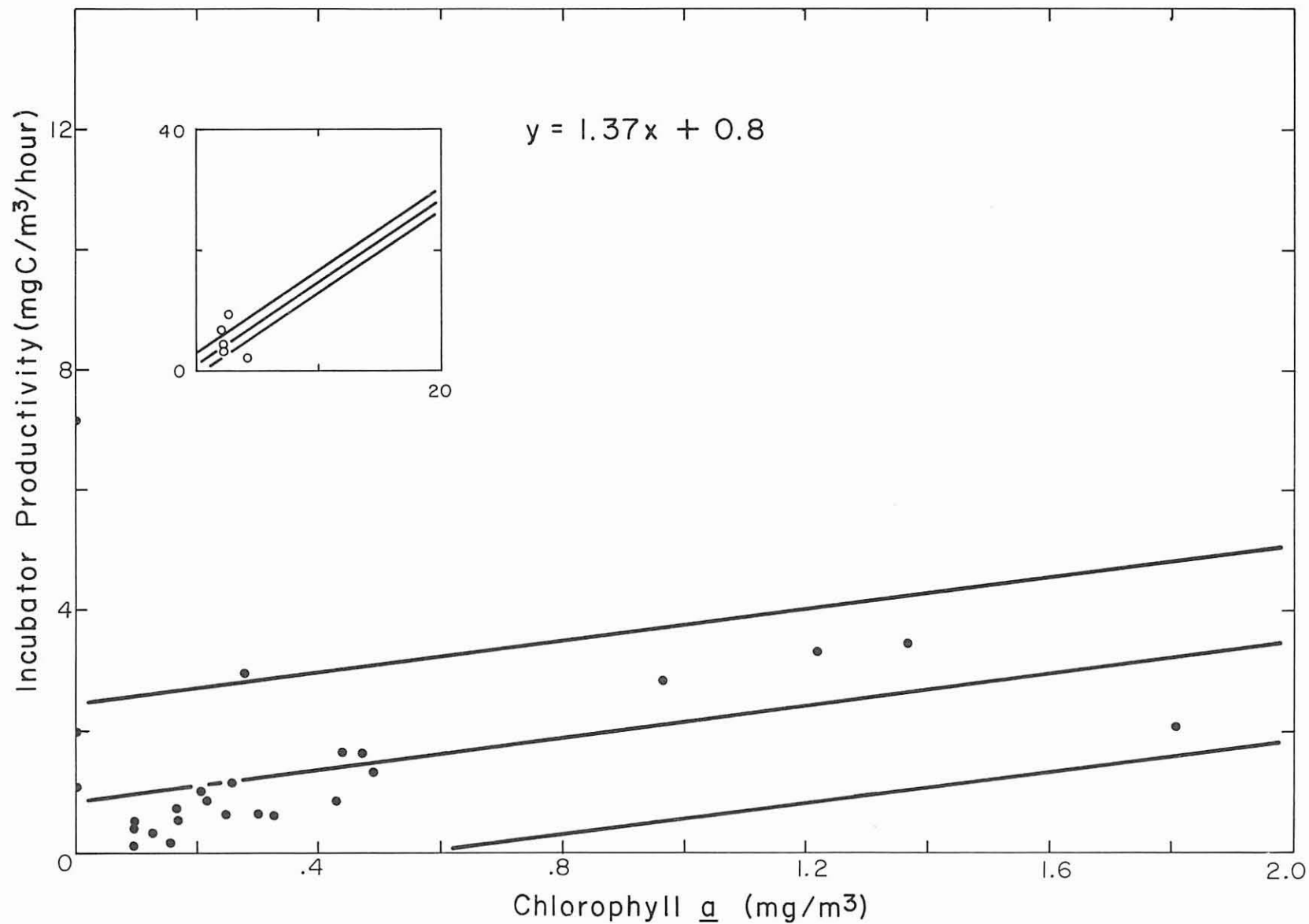


Fig. 53 Primary productivity and chlorophyll a relationships in surface waters off the Washington and Oregon coasts, June, 1961. The insert contains off-scale values.

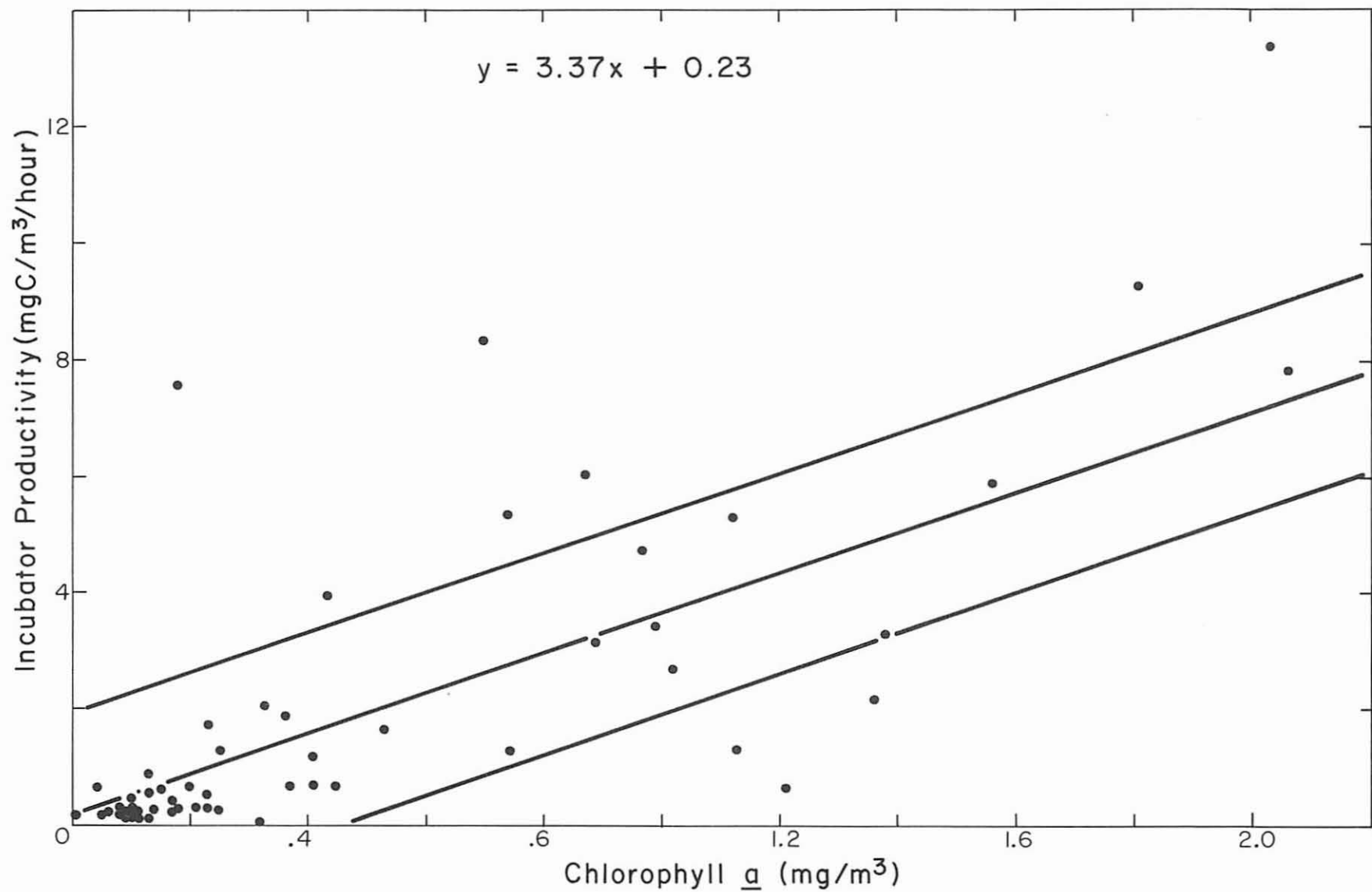


Fig. 54 Primary productivity and chlorophyll a relationships in surface waters off the Washington and Oregon coasts, July, 1961.

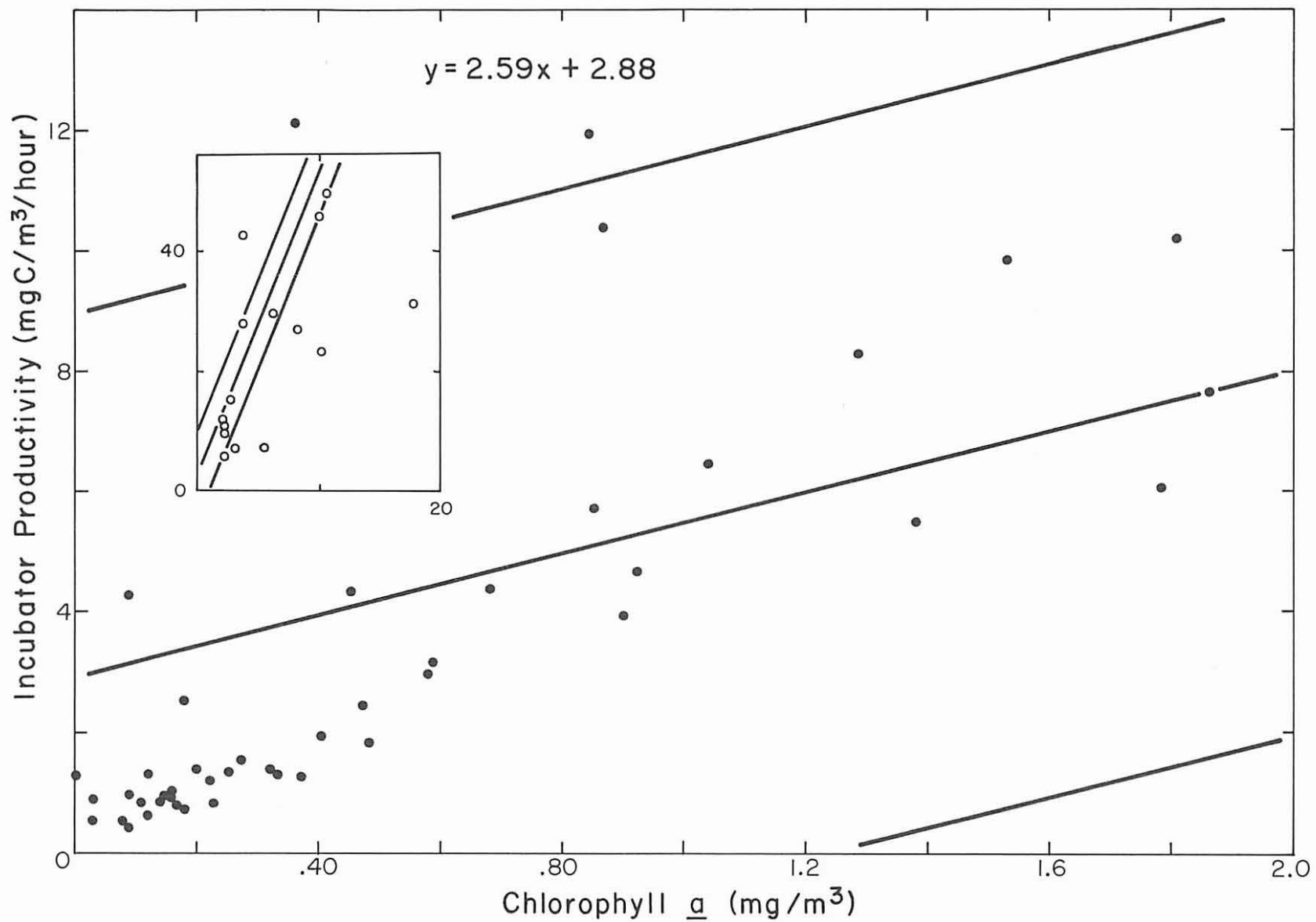


Fig. 55 Primary productivity and chlorophyll a relationships in surface waters off the Washington and Oregon coasts, August, 1961. The insert contains off-scale values.

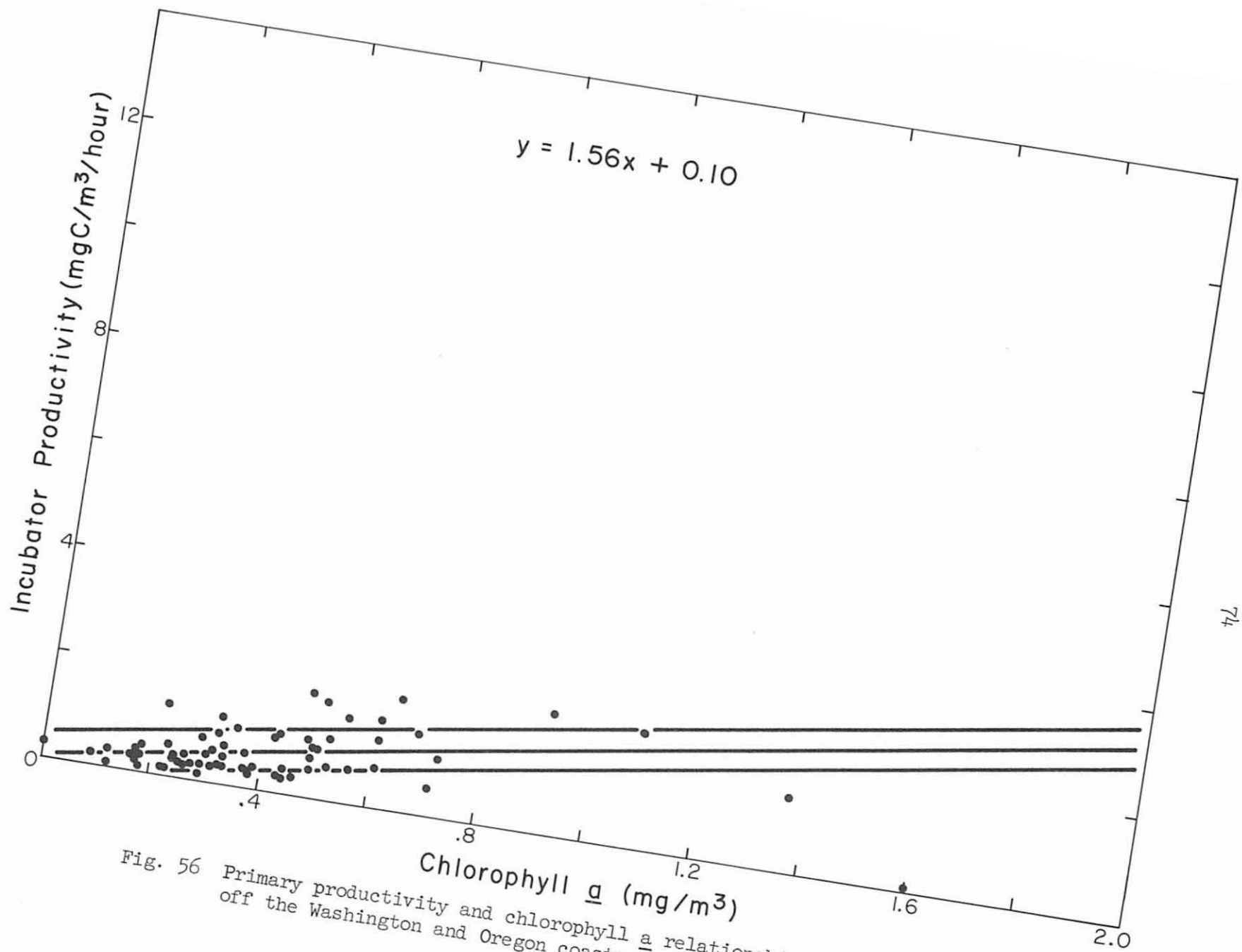


Fig. 56 Primary productivity and chlorophyll a relationships in surface waters off the Washington and Oregon coasts, November-December, 1961.

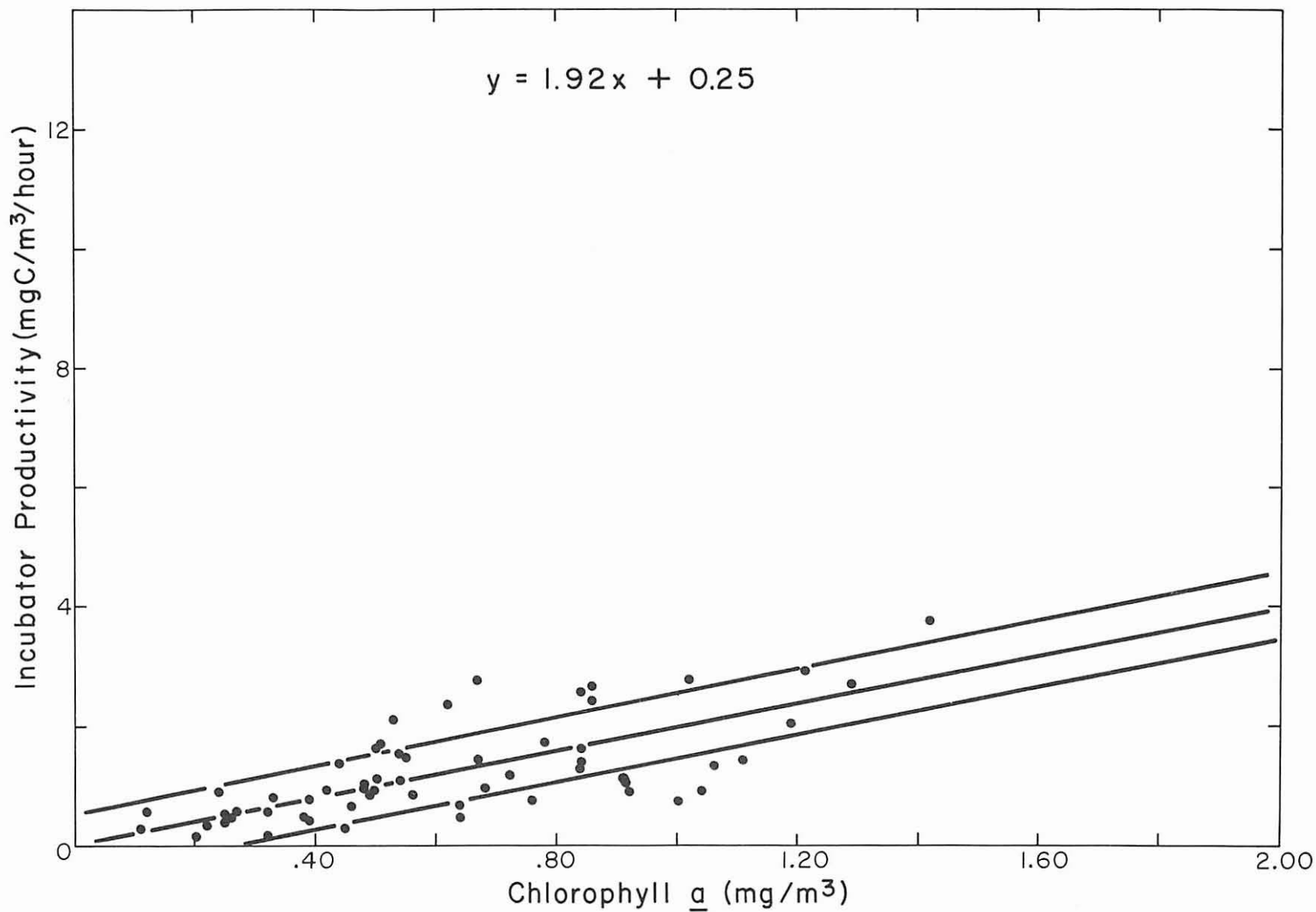


Fig. 57 Primary productivity and chlorophyll a relationships in surface waters off the Washington and Oregon coasts, January-February, 1962.

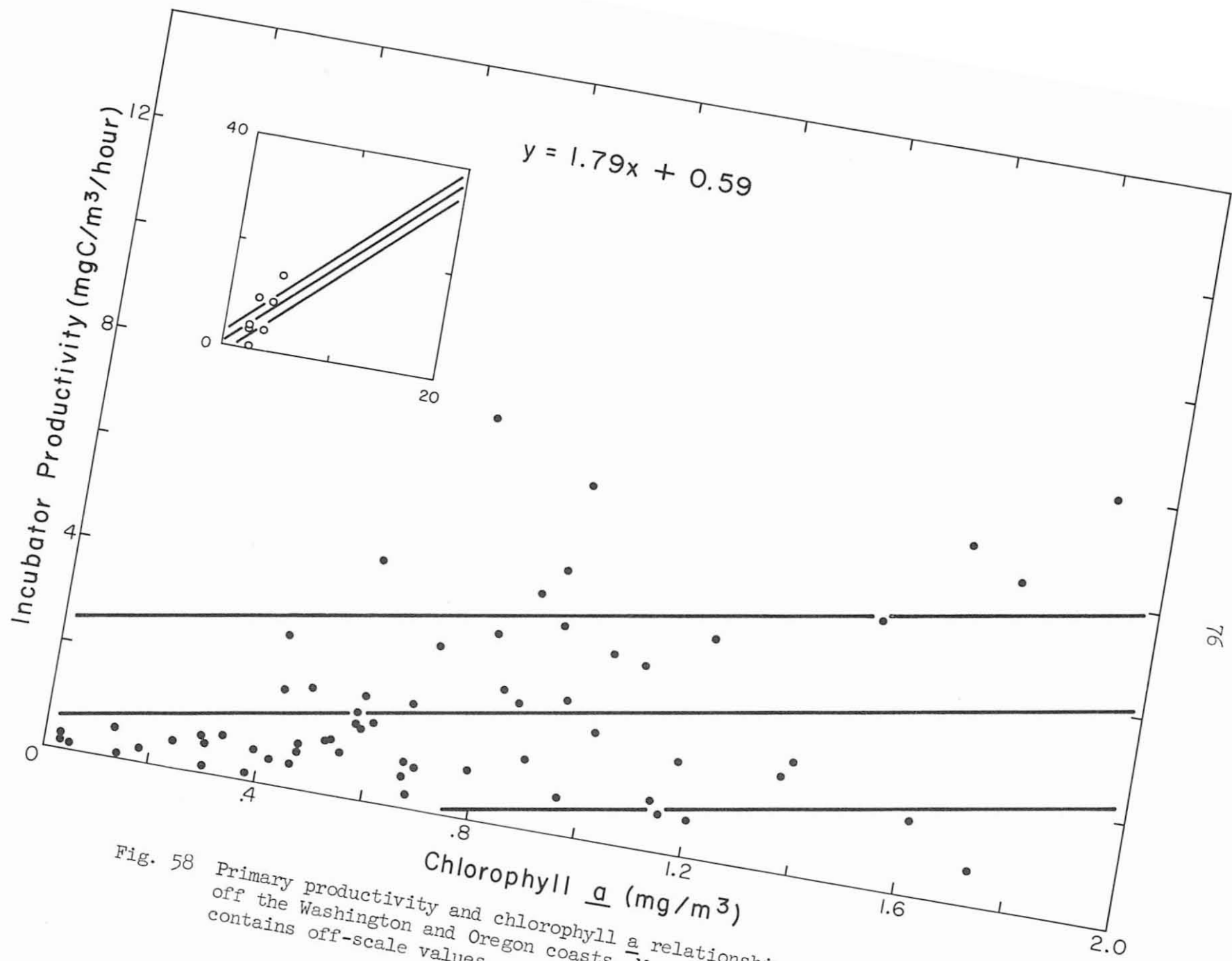


Fig. 58 Primary productivity and chlorophyll a relationships in surface waters off the Washington and Oregon coasts, March-April, 1962. The insert contains off-scale values.

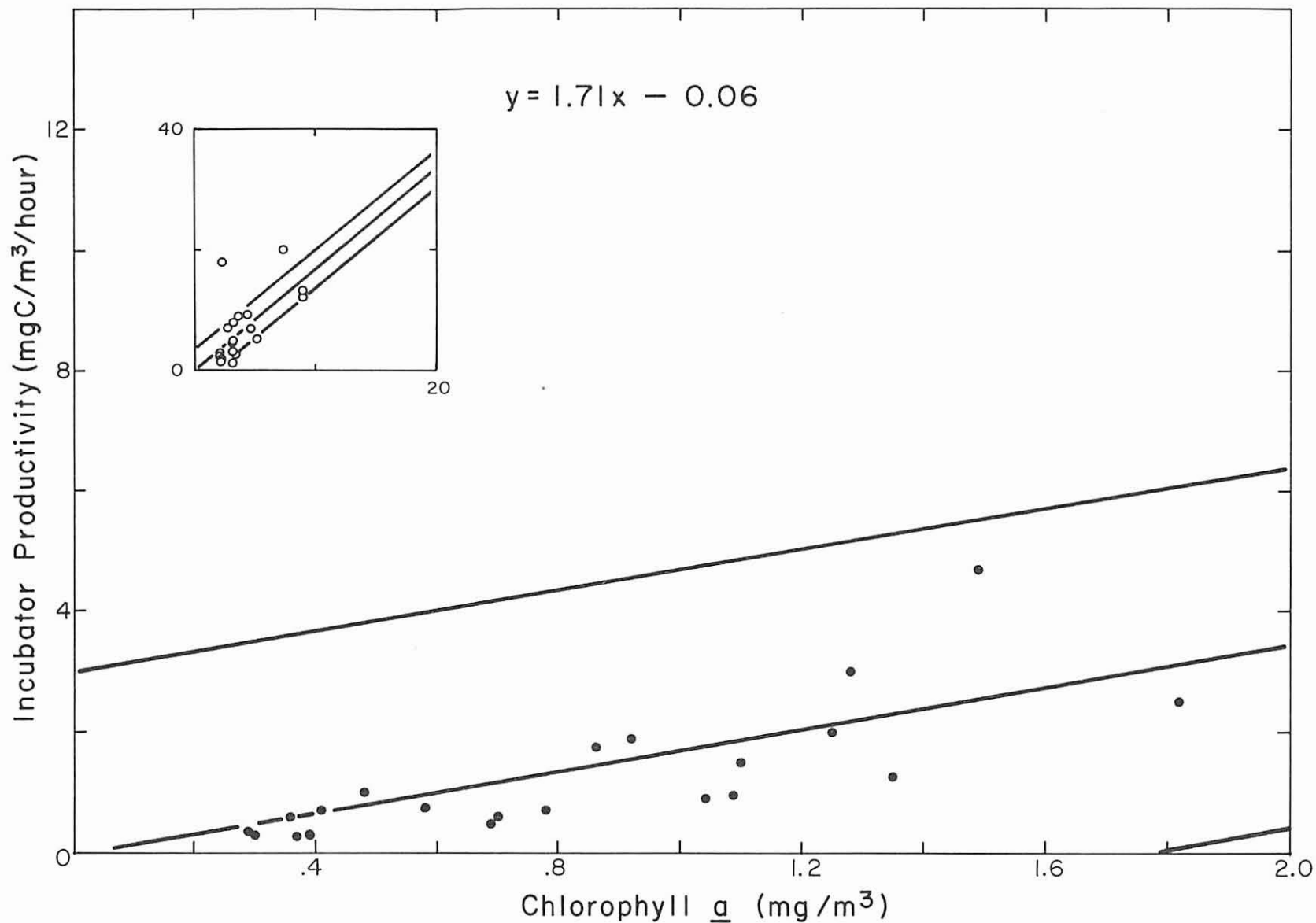


Fig. 59 Primary productivity and chlorophyll a relationships in surface waters off the Washington and Oregon coasts, June, 1962. The insert contains off-scale values.

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