PRIMARY PRODUCTION AND CHLOROPHYLL RELATIONSHIPS, DERIVED FROM TEN YEARS OF CALCOFI MEASUREMENTS

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ABSTRACT

On each CalCOFI cruise since 1984, primary production has been estimated at six depths on one station per day (the station occupied closest to noon). This is only 20% of the regularly occupied stations and leads to high variability in the estimate of mean production per cruise. We examine 500 stations occupied between 1984 (CalCOFI 8401) and 1994 (CalCOFI 9401) at which both production data and chlorophyll data were collected. A good relationship is found between the logarithm (base 10) of chlorophyll a integrated from the surface to 200 m (Chl) and integrated half-day primary production (*P*), standardized for potentially available half-day sunlight (L'):

$$P/L' = -617.3 + 495.3\,(\log_{10}\text{Chl})$$

where the light scaling factor, L', is approximated as

$$L' = 2.625 + 1.125\cos\left[\frac{360}{365}(\text{Julian day} - 173)\right]$$

This regression is highly significant and explains 64% of the variability of the standardized production. Thus the chlorophyll data may be used as a proxy for primary production, providing a more detailed map of the spatial distribution of production and a better cruise mean estimate than is possible from the productivity stations alone. The success of this regression is examined for CalCOFI cruises 9403, 9408, and 9410.

INTRODUCTION

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) has been surveying the California Current for more than forty years. In 1984 and 1985 there were major changes in spatial and temporal coverage of the cruises (Hewitt 1988). Since 1985, cruises have been conducted quarterly and have typically sampled 60–66 stations. It is important for our purposes that each cruise since January 1984 has included routine measurements of primary production and chlorophyll. Measurements made at each station now include temperature, salinity, oxygen, and nutrients above 500 m, and chlorophyll and macrozooplankton above 200 m. Estimates of primary production, however, are made at only one station per day, for a total of 14–16 estimates per cruise. Production measurements are not necessarily made on the same stations on each cruise.

High phytoplankton biomass and high production are usually restricted to a disproportionately small fraction of the survey area. Whether the complete grid of stations adequately samples this region is debatable. Almost certainly the restricted set of 16 noon stations does not.

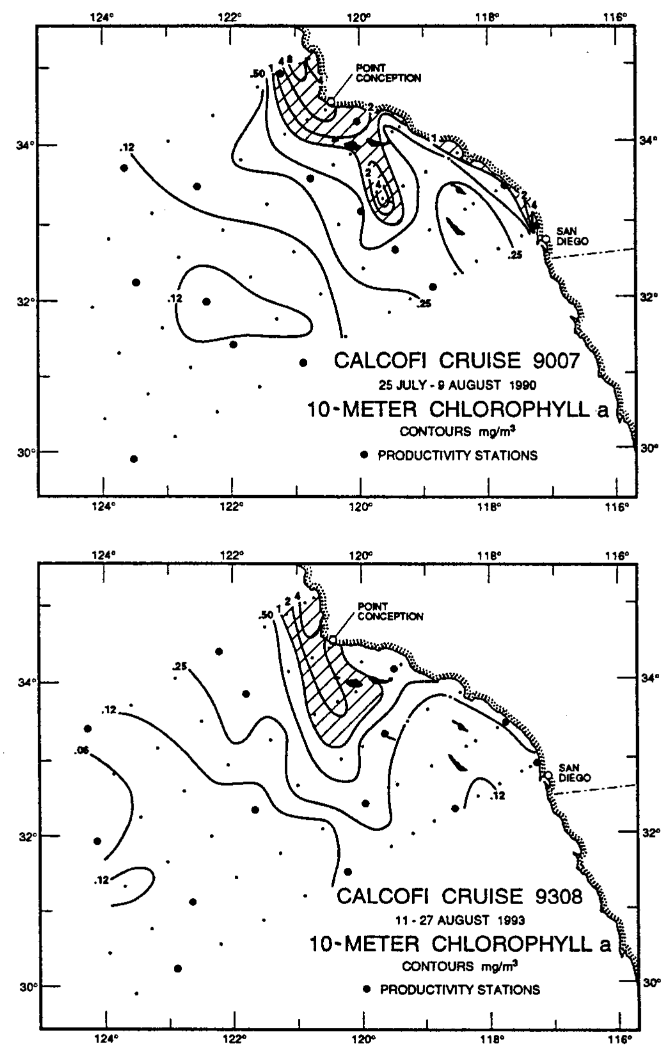

Figure 1. Locations of productivity stations on two summer cruises, and contours of chlorophyll concentration at 10 m. Contours are half or double the adjacent contour values. *Hatching* denotes chlorophyll ≥1 mg/m³.

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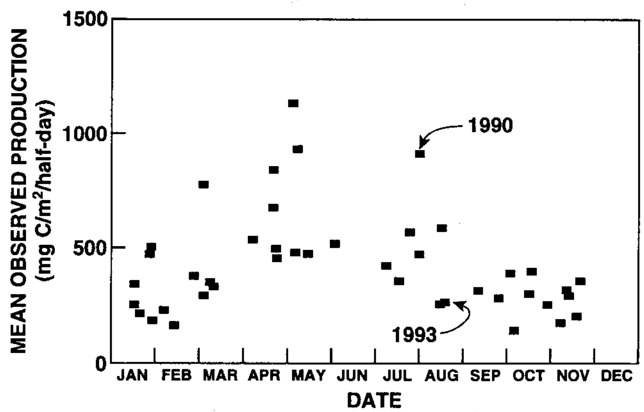

Figure 2. Seasonal cycle of measured production values, as cruise means, Jan. 1984–Jan. 1994, for data within the standard CalCOFI area, that region occupied by all cruises. Mean values for the summer cruises of 1990 and 1993 (figure 1) are indicated.

As a consequence, high sampling variability is associated with the mean production estimate on each cruise. This can be seen in a comparison of the summer cruises of 1990 and 1993 (figure 1). In both cruises, a tongue of elevated chlorophyll extended SE from Point Conception. In 1990, 3 of the 15 production stations were located in the region where near-surface chlorophyll exceeded 1 mg/m^3. The mean water-column production for that cruise is the highest observed in the months of July or August since measurements were started in 1984 (figure 2). In contrast, none of the production stations in 1993 were in the high-chlorophyll region. The mean production for 1993 is 29% of that measured in 1990 and is the second lowest observed in July or August.

The difference between these cruises seems due in large part to differences in the locations of the noon stations. This sampling variability might be reduced if a satisfactory relationship could be established between production and the measurements available for all stations. This relationship would allow more complete spatial coverage of production estimates, which would improve the mean estimates. The feasibility of this approach is suggested by an earlier study (Hayward and Venrick 1982), which established a linear relationship between production and chlorophyll on CalCOFI cruises 8105 J and 8105 NH. In this paper we develop an empirical relationship between total production, potential surface irradiance, and chlorophyll integrated through the upper 200 m. This algorithm appears to remove much of the variability between cruise mean production estimates.

METHODS

The Study Area

All of the observations come from within the region bounded by CalCOFI line 93 on the south, line 77 on the north, and stations XX.120 on the west (figure 3). This region roughly limits the two cruise patterns followed since 1985. However, a minor shift between patterns in 1986 (between cruises 8609 and 8611) introduced changes in spatial coverage that may increase the between-cruise variability of the data. In order to minimize this effect, several of the following analyses (e.g., figures 2 and 9 and table 1) include only data collected along lines 77, 80, 90, and 93 from the coast to station XX.100, and along lines 83 and 87 from the coast to station XX.70. Because this subset is common to both cruise patterns, it is referred to as the standard data set (figure 3), and the restricted region is referred to as the standard region. The spatial restriction of the data increases the calculated (unweighted) cruise mean by an average of 13%. No correction is made for stations missed because of weather or other unpredicted events.

To weight individual stations by area, the CalCOFI region is divided into 65 subregions, 47 in the standard region (figure 3). All data from within each subregion are pooled, and the resulting mean is weighted by the area of the subregion, indicated in figure 3 by the small numbers in the lower left corner of each region.

The Data

The chlorophyll data considered in this paper are those obtained from the standard hydrographic cast made at each station. Chlorophyll a concentrations are determined by the standard fluorometric method (Yentsch and Menzel 1963; Holm-Hansen et al. 1965). Before 1990, samples were filtered onto GF/C filters, which have a nominal retention size of 1.2 mμ. Thereafter, GF/F filters (0.7 mμ) were used. Comparison between the retention of the two filters, conducted in the central Pacific and in the CalCOFI study area on cruise 8105-J, indicated that GF/F filters retain about 15% more chlorophyll than GF/C filters at chlorophyll concentrations below 0.5 mg/m^3; at higher chlorophyll concentrations, this bias is negligible (Venrick and Hayward 1984). This filter change does not seem to influence the relationships discussed in this paper. The slopes of the regression lines before and after the filter change are not significantly different ($p >> 0.25$). The mean concentration of chlorophyll has decreased since 1990, but the effect of the filter change would be to increase recent values. Chlorophyll has been integrated to the deepest sample or 200 m, whichever is less, by means of the trapezoidal rule for numerical integration.

Primary production is estimated from the uptake of ^{14}C during half-day simulated in situ incubations (Scripps Institution of Oceanography 1994). Light penetration is estimated from the Secchi disk depth, assuming that the extinction coefficient is constant with depth and that the 1% light level is three times the Secchi depth. Samples for production estimates are collected with Niskin-type

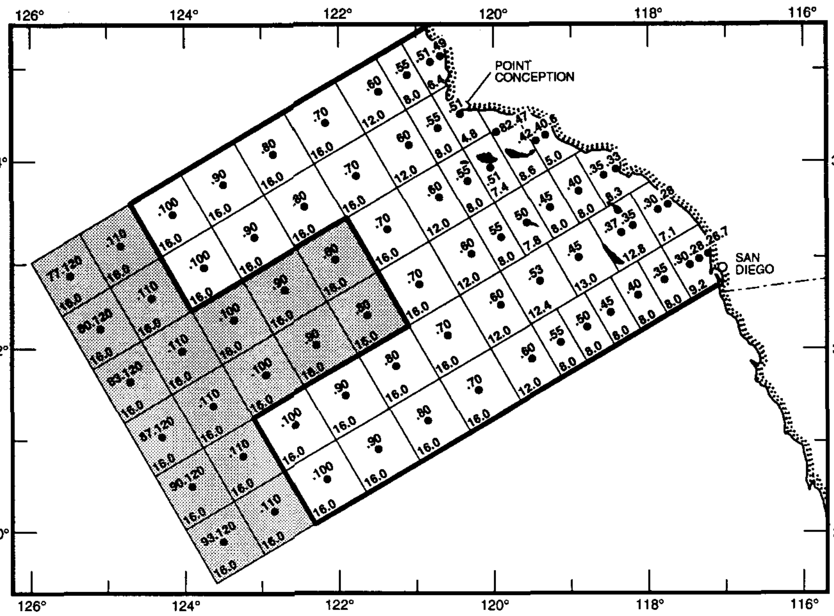

Figure 3. The general CalCOFI area since 1985, showing the 65 subregions used for weighting productivity data. Each subregion is centered around a station, indicated by the *dot* and station designation. All observations and estimates within each region are pooled and weighted by the spatial area, where the weighting factor (f) is indicated in the lower left corner of each box, and $f \times 10^2$ is the area in n.mi.^{2}. The *unshaded area* indicates the standard region, common to all cruise patterns; the *shaded area* indicates stations that were not occupied consistently.

bottles from six depths, the bottom depth being that reached by about 0.2%–0.5% of the surface irradiance (100–150 m in offshore waters). From each depth, samples are placed in two clear bottles and one dark (control) bottle. Each sample is inoculated with 10 µCi of ^{14}C as $NaHCO_3$. Incubations are carried out between local apparent noon and twilight in on-deck incubators cooled with surface seawater and equipped with neutral-density screens to simulate light intensities at the original depths of the samples. After incubation, samples are filtered through Millipore HA filters, acidified, and immersed in scintillation fluor until returned to SIO, where the radioactivity is determined with a scintillation counter. Uptake values are corrected for dark uptake and integrated to the deepest sample. Values are reported as carbon fixed per square meter per half-day. In the Southern California Bight, 24-hour production is approximately 1.8 times our half-day values (Eppley 1992).

Starting in August 1993, productivity casts have been merged with the standard hydrographic casts so that samples for productivity and chlorophyll come from the same bottles. Before that, the casts for productivity samples were separated from the standard hydrographic casts at the station by 0.5 to 3 hours.

Cloud cover is estimated as octas of sky cover at each daylight station. We have used the mean of cloud cover at the noon station and at the following station as an index of the sky conditions during incubation.

RESULTS

In the CalCOFI data, the most successful linear relation between integral chlorophyll and integral production is semilogarithmic. However, the parameters of the regressions vary seasonally (figure 4). Although the slopes of the regressions of spring and summer data are indistinguishable, as are those of fall and winter, the regression slopes of spring and summer are significantly greater than those of fall and winter ($p < 0.003$). This suggests an influence from seasonally varying parameters such as the light regime.

On CalCOFI cruises in 1969–72, direct measurements of daily incident radiation were made with an Eppley pyranometer (Owen and Sanchez 1974). Values from the study area are plotted in figure 5. There is considerable scatter in these measurements, presumably due to variable fog and cloud cover, but the maximum observed values approach those derived from the Smithsonian tabulated values for total daily solar radiation at 32.5°N corrected for 75% atmospheric transmission (List 1984, tables 132–135). A simple expression for potential irradiance is given by a cosine approximation to the Smithsonian values:

$$L(\text{cal} \times 10^{-6}/\text{m}^2/\text{day}) = 5.25 + 2.25\cos\left[\frac{360}{365}(\text{Julian day} - 173)\right]$$

where L is the potential daily irradiance. L is a function of both day length and sun elevation. We halve L to

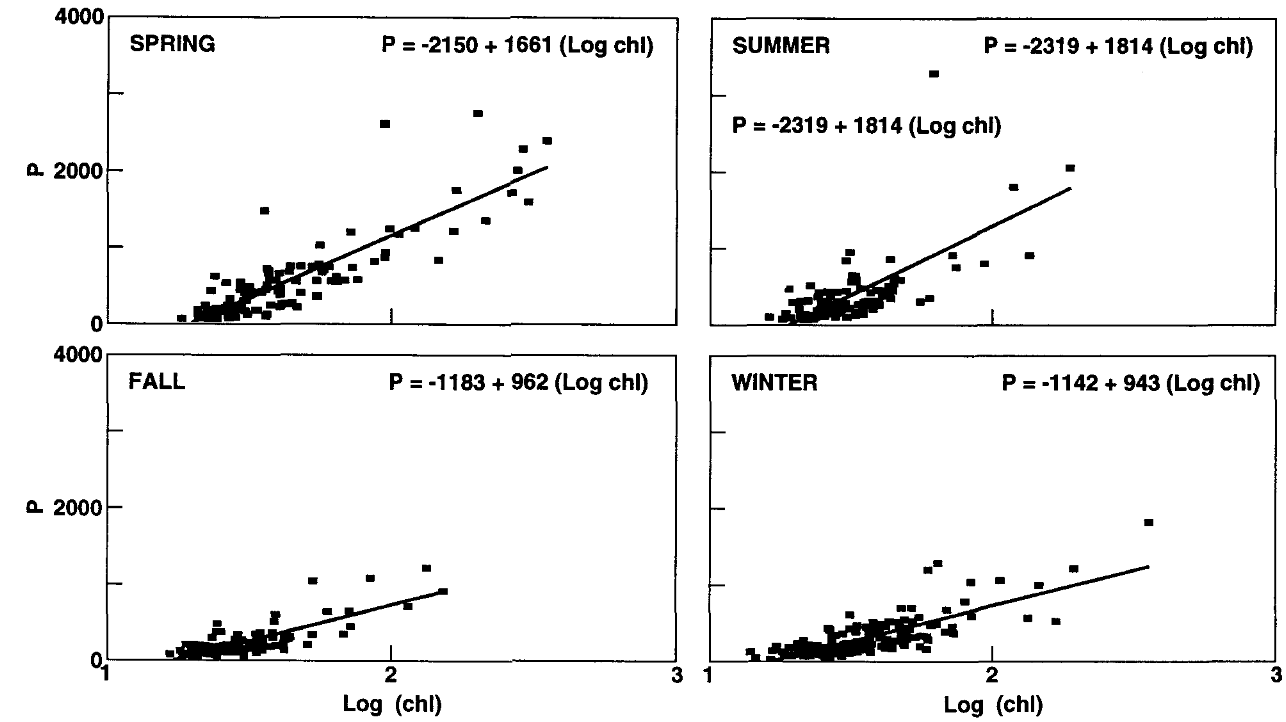

Figure 4. Regressions of observed integral production (P, mgC/m²/half-day) on log integral chlorophyll (Chl, mg/m²) for data divided into seasons: winter (Jan.–Mar.); spring (April–June); summer (July–Sept.); fall (Oct.–Dec.).

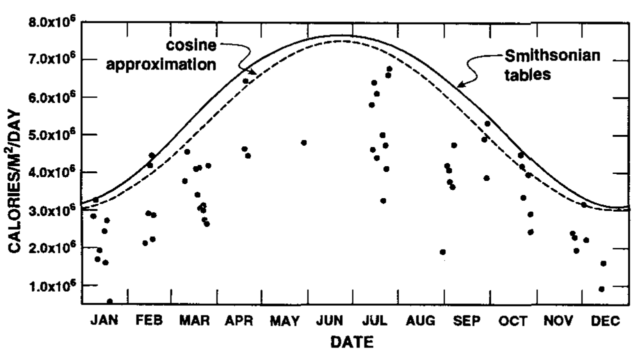

Figure 5. Measurements of total irradiance on CalCOFI cruises within the study area, 1969–72 (Owen and Sanchez 1974). The *dashed curve* indicates the Smithsonian tabulated values at 32.5°N adjusted for 75% atmospheric transmission (List 1984). The *solid curve* indicates the cosine function (L) used in this study to approximate the Smithsonian values.

make it comparable to our half-day production estimates:

$$L'(\text{cal} \times 10^{-6}/\text{m}^2/\text{half-day}) = 2.625 + 1.125\cos\left[\frac{360}{365}(\text{Julian day} - 173)\right] \quad (1)$$

Since L' is used only as a scaling factor, this half-day adjustment is not needed; but it may serve to avoid future confusion. At the equinox, L' changes by 12% of its annual range during a two-week period, the duration of a typical cruise. We have used daily values of L' in all of our calculations; close to the solstices it may be satisfactory to apply a constant value to the data from each cruise, using L' determined for the midpoint of that cruise.

When the observed rates of integral production (P, in mgC/m²/half-day) are standardized to potential irradiance by dividing by the cosine approximation for half-day irradiance (L', in cal × 10^{-6}/m²/half-day), the slopes of the seasonal regressions on log (base 10) chlorophyll (Chl, in mg/m²) become indistinguishable (slopes = 508, 536, 508, and 494 for spring, summer, fall, and winter, respectively; $p > 0.25$). Thus all the data can be combined into a single expression:

$$P/L'(\text{mg C/cal} \times 10^{-6}) = -617.3 + 495.3\,(\log_{10} \text{Chl}) \quad (2)$$

This regression accounts for 64% of the variability in standardized production and is highly significant (figure 6; $p < 0.001$). The regression will occasionally yield negative values of expected production. In the following applications, we have set such negative values to zero.

When this relationship is examined for the 43 individual cruises that make up the combined data set, a spectrum of fits is apparent. In some cases, regression 2 gives an excellent approximation of the relationship seen on a single cruise; in other cases the fit is poor. But in most instances in which the overall regression fails to describe the relationships within a cruise, all production stations were located in low-biomass regions, so there

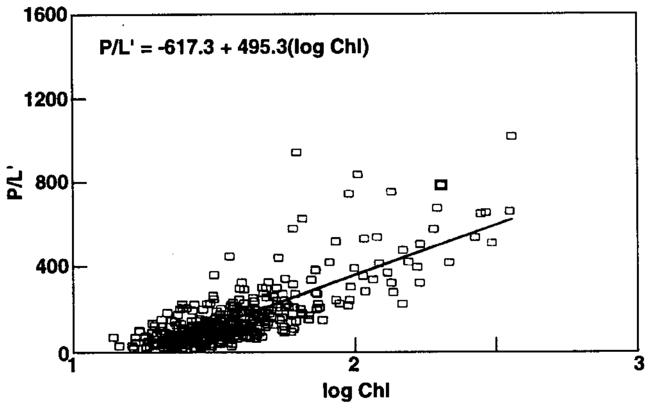

Figure 6. Regression 2: integral production (P, mgC/m²/half-day), standardized to potential irradiance (L', cal. × 10^{-2}/half-day) on the logarithm of integral chlorophyll (Chl, mg/m²) over all data; $n = 499$; $r^2 = 0.64$.

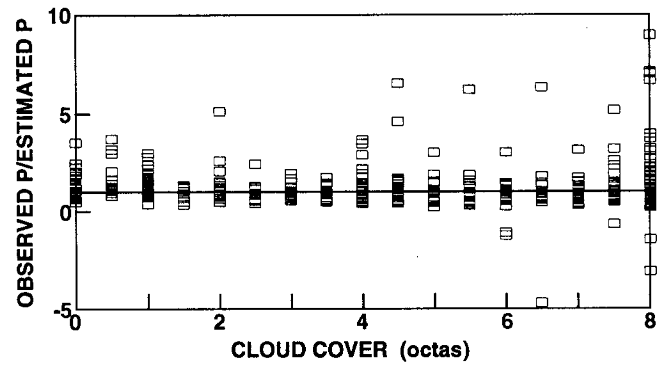

Figure 7. Relationship between local cloud cover (in mean octas, measured at the noon and the first afternoon stations) on the error about regression 2 (figure 6), where the error is expressed in relative terms as observed production/estimated production. A *horizontal line* at P/P' = 1.0 is provided for reference. A few points outside the range −5 to +10 are not shown.

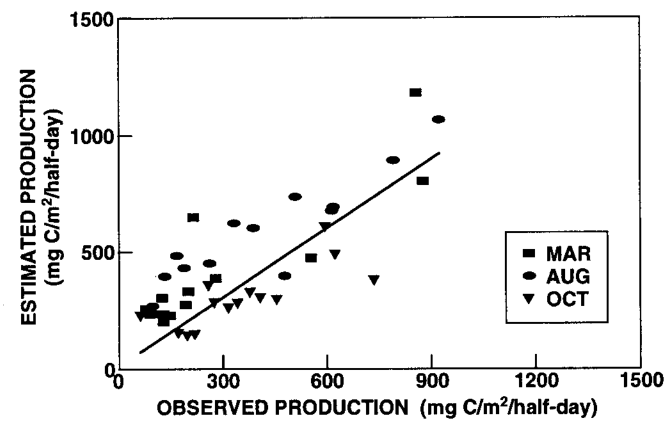

Figure 8. Performance of regression 2 on the three most recent CalCOFI cruises (9403, 9408, and 9410). The *solid line* indicates observed production = estimated production. These data were not used in the development of the regression.

are no observations of elevated production to define the relationship. To the extent that regions of elevated biomass and presumably production were present but not sampled at the noon stations, these cruises are precisely the ones for which this procedure is designed.

We have examined the residuals about regression 2 to see whether either nutrients or local cloud cover might explain some portion of the residual variability. There is a detectable positive influence of the surface nitrate concentration on production. Inclusion of surface nitrate (N, in μM/L) as an independent variable gives a regression:

$$P/L' = -572.9 + 462.2\ (\log_{10}\text{Chl}) + 11.7\ (N)$$

However, the coefficient of determination increases by less than 2% over that of regression 2. We do not believe that this level of fine-tuning is justified, and we have chosen not to include surface nitrate in our final regression. We have not explored the numerous other ways in which nutrient distributions might be incorporated into the regression.

Incorporation of local cloud cover is more of an intellectual exercise than a practical one, since local sky conditions are not available for stations occupied at night. Nevertheless, as figure 5 illustrates, the potential irradiance gives a poor estimation of actual incoming radiation, and much of the discrepancy is almost certainly due to local clouds and fog. However, neither the absolute nor relative magnitudes of the deviations of observed production from predicted production show any relationship with cloud cover other than a slight tendency for production to be overestimated (i.e., observed production depressed) when cloud cover is 100% (figure 7). This result is comparable to that reported by Eppley et al. (1985) from the Southern California Bight, where they found no relationship between production and incident radiation during 21 out of 22 cruises. The sole exception was a cruise during early March when several days were extremely foggy, and photosynthesis was correspondingly depressed.

To test the performance of regression 2, we apply it to data collected on cruises 9403, 9408, and 9410, which are not considered in the development of the regression equation. The production estimates derived from ^{14}C uptake experiments are compared with estimates of standardized production derived from chlorophyll measurements on the same station (i.e., regression 2), multiplied by the appropriate light factor (regression 1). For the data from March and August, the algorithm tends to overestimate the actual production (figure 8). In October, the reverse is true. Clearly, the estimate at any single station may be in error by a considerable amount, but as data are averaged, the overall agreement improves.

To illustrate the effect of our procedure on the spatial resolution of production, we apply regression 2 to the data from CalCOFI cruise 9308, a cruise in which

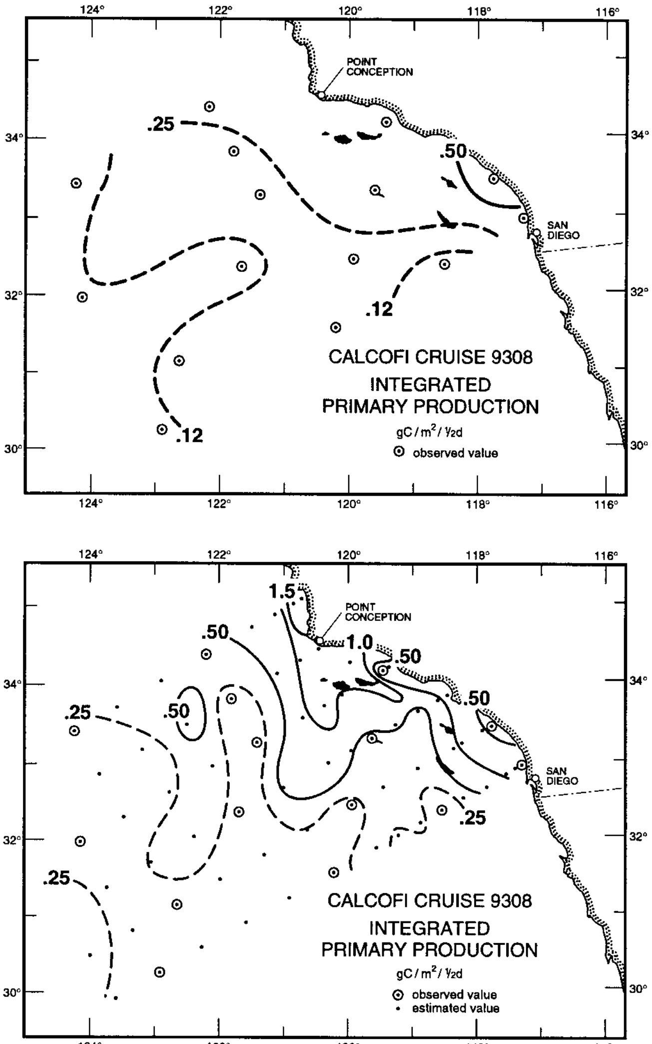

Figure 9. Spatial patterns of primary production on CalCOFI Cruise 9308 based on the 14 observed values of integral production (*top*) and on this set supplemented with 53 estimates derived from regression 2 (*bottom*).

there are no productivity measurements within the region of high chlorophyll extending south from Point Conception (figure 1, bottom). The 14 observed values of integral production are too widely spaced to properly contour, but they suggest nearly monotonic production values (figure 9, top). When these values are supplemented with the 53 estimates based upon integral chlorophyll and irradiance, a tongue of elevated production is indicated (figure 9, bottom), in agreement with the pattern of elevated near-surface chlorophyll. Although our procedure appears to perform as expected, we have no direct measure of the actual improvement in the estimate of cruise mean production.

A major motivation for this study is the reduction of error in our estimate of mean production per cruise, and hence a reduction in between-cruise variability. To examine how our procedure affects this variability, we apply

TABLE 1
Cruise Mean Production (mgC/m2/half-day): Observed Data (*P*, Unweighted) Compared with Values Supplemented by Estimates Derived from Chlorophyll Data According to Regression 2 (*P'*, Weighted by Area)

	All stations				Standard area			
	Observed		Supplemented		Observed		Supplemented	
Cruise	*P*	*n*	*P'*	*n*	*P*	*n*	*P'*	*n*
8401	307.0	18	167.2	62	336.7	15	174.5	56
8402–3	716.4	32	385.4	75	772.1	29	431.2	68
8404	762.0	18	695.6	62	839.4	16	751.3	56
8405	478.5	7	562.7	52	517.9	5	611.1	45
8407	338.4	17	403.1	59	356.8	15	442.3	53
8410	250.9	18	249.6	59	254.8	17	251.6	53
8502	346.8	10	295.8	52	374.1	9	328.6	47
8505	883.7	17	564.4	63	933.2	16	624.1	59
8508	224.8	13	237.6	65	252.4	11	273.8	56
8511	161.6	11	150.7	62	178.5	9	177.4	54
8602	152.1	12	169.2	56	161.2	11	187.6	52
8605	406.3	12	501.4	61	470.9	10	589.4	53
8609	244.4	12	282.7	65	284.2	10	335.4	55
8611	190.1	14	185.1	67	205.7	11	203.9	55
8703	305.0	13	306.2	70	346.5	10	349.1	59
8705	413.3	13	397.8	70	476.0	10	456.4	58
8709	267.5	13	284.1	69	318.7	10	336.5	57
8711	310.5	15	164.7	70	358.0	12	200.6	58
8801	427.3	12	352.2	65	469.0	9	381.5	53
8805	1076.2	11	676.6	59	1132.8	10	701.8	54
8808	495.8	15	465.3	69	589.3	12	563.1	57
8810	338.9	14	252.8	75	400.4	11	289.0	60
8901	425.7	14	316.5	67	499.1	11	358.4	54
8904	417.0	13	439.8	67	492.5	10	508.9	55
8907	477.9	15	501.2	65	570.0	12	561.0	55
8911	280.0	13	223.7	67	321.8	10	249.4	55
9003	314.1	13	478.0	65	327.7	12	505.0	58
9004	369.8	11	328.3	51	452.7	8	404.7	43
9007	774.1	15	488.0	65	911.7	12	556.7	53
9011	265.5	14	230.6	67	295.6	10	249.8	54
9101	236.2	14	264.6	63	250.1	12	279.8	54
9103	274.6	12	290.5	56	289.3	11	348.1	46
9108	420.3	14	393.6	69	475.2	11	445.6	56
9110	135.2	12	192.2	67	144.8	9	212.8	52
9202	225.2	13	177.8	64	225.2	10	197.5	52
9204	571.9	15	540.7	66	671.6	12	642.1	54
9207	366.3	14	410.5	66	422.9	11	451.6	54
9210	331.8	12	264.1	64	390.2	9	309.3	52
9301	189.9	13	144.9	66	209.0	10	169.1	54
9304	452.1	15	464.4	66	532.0	12	561.3	54
9308	235.5	15	376.2	66	265.8	12	425.2	54
9310	277.8	16	237.4	66	304.4	13	273.6	54
9401	170.8	16	179.3	66	182.6	13	201.2	54

our algorithm for standardized production to the past ten years of CalCOFI data. For those stations on which production was not directly determined, production (mgC/m^2/half-day) is estimated from chlorophyll and the appropriate light factor (L'). These estimates are combined with the observed data and weighted by area to reconstruct cruise mean values based upon all stations occupied within the study area (table 1).

When the reconstructed cruise means are plotted by season in a manner analogous to figure 2, much of the scatter about the emerging seasonal curve is removed (figure 10). The two cruises discussed earlier (9007 and

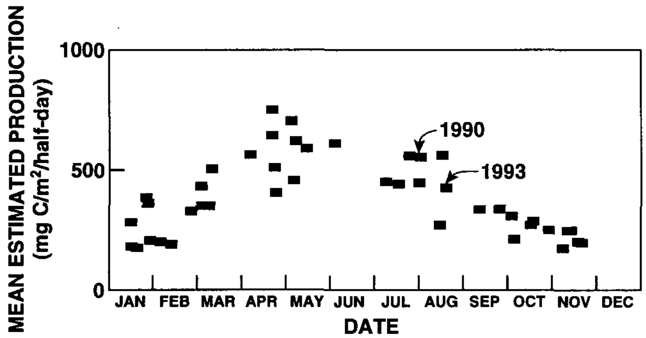

Figure 10. Seasonal cycle of supplemented production values, as cruise means, Jan. 1984–Jan. 1994, for data within the standard CalCOFI area (table 1). Mean values for the summer cruises of 1990 and 1993 are indicated for comparison with figure 2.

9308, figures 1 and 2) are no longer outliers. Thus we do accomplish a reduction of between-cruise variability, which is one indication of the success of our procedure for improving the spatial averages of production.

DISCUSSION

For nearly forty years, oceanographers have proposed algorithms relating primary production to pigments (e.g., Ryther and Yentsch 1957; Steele 1962). Many studies have one of two objectives. Some work toward developing a mechanistic, mathematical model relating photosynthesis to pigments and light, in the hopes that primary production can be determined directly from in situ measurements (Kiefer and Mitchell 1983; Bidigare et al. 1987; Smith et al. 1989). Such studies incorporate detailed information on the radiant energy field, pigment composition, and physiological parameters. Other studies are directed toward determining global production from satellites, and these studies emphasize parameters that can be remotely sensed, although many of the more successful of such studies also incorporate estimates of physiological parameters (but see the discussion of Occam's razor in Balch 1993). Balch et al. (1989, 1992) give a recent review of the development and performance of remote sensing algorithms. No previous study, however, is exactly comparable to the regression presented here because of differences in ultimate goals, parameters, or parameter formulations.

Most algorithms incorporate some measure of pigment and some measure of irradiance. Many, however, formulate the relationships in terms of production per unit pigment instead of production per unit light, as we have done. All combinations of linear and log-transformed relationships have been used. Other environmental parameters that have been useful in strictly empirical models such as ours include temperature or temperature anomaly (Smith and Eppley 1982; Eppley et al. 1985), mixed-layer depth (Collins et al. 1986; Eppley et al. 1987), and the diffuse attenuation coefficient (Smith and Baker 1978; Eppley et al. 1987). The success of a temperature function in empirical models has been attributed to temperature being a surrogate for nutrients. We have examined briefly, but directly, the influence of near-surface nitrate concentrations and have concluded that the effect is too slight to justify incorporation into our model, in agreement with the results of Banse and Yong (1990). We do not have measurements of recycled nitrogen, such as ammonium, but their influence on our regression would be interesting to examine.

A measure of diffuse attenuation is available to us through our Secchi disk depth determinations. But these are made only on daylight stations; so, like other daylight-dependent measurements, their usefulness to us is limited. We have not examined the mixed-layer depth.

In principle, the accuracy of the physiologically based bio-optical models is limited only by theoretical development and by our ability to determine the necessary parameters. Once developed, they should have broad generality and important advantages, since this approach is free of the contamination and containment effects that are thought to bias the conventional ^{14}C procedure; also, this approach may be amenable to long-term monitoring from moorings. We expect a bio-optical approach to be initiated on CalCOFI cruises in the near future.

In contrast, models that are primarily empirical seem to lack generality. The formulation and success of such models have varied both regionally and seasonally, and the more successful ones are calibrated to specific regional relationships (Eppley et al. 1985; Platt and Sathyendranath 1988; Morel and Berthon 1989; Balch et al. 1989). Coefficients of determination for relationships based primarily on shipboard measurements have ranged from less than 0.35 (e.g., Eppley et al. 1987; Balch et al. 1989; Banse and Yong 1990) to more than 0.80 (e.g., King 1986; Banse and Yong 1990). Except for studies based upon small data sets, which occasionally report very high coefficients (e.g., Hayward and Venrick 1982), most values of r^2 from studies in the CalCOFI region and the Southern California Bight are in the range of 0.55–0.62 (Smith and Eppley 1982; Smith et al. 1982; Eppley et al. 1985; Collins et al. 1986; Balch et al. 1989). Although the generality of our simple model remains to be examined in other environments, within the CalCOFI region it compares favorably with previous efforts.

ACKNOWLEDGMENTS

Without the CalCOFI program, these data would not exist. We particularly acknowledge the technicians, from both the Marine Life Research Group and the Southwest Fisheries Science Center, whose dedication and skill have insured the high quality of each measurement and calculation. In return for their contribution, we hereby offer them a party. R.S.V.P. by January 1, 1996.

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