PRODUCTION OF EGGS BY THE COPEPOD *CALANUS PACIFICUS* IN THE SOUTHERN CALIFORNIA SECTOR OF THE CALIFORNIA CURRENT SYSTEM

MICHAEL M. MULLIN
Marine Life Research Group
Scripps Institution of Oceanography
University of California, San Diego
La Jolla, California 92093-0218

ABSTRACT

Production of eggs by female *Calanus pacificus* during two years was determined by shipboard incubations in ambient seawater plus seston and in seawater enriched with cultured phytoplankton to detect the extent of food limitation. In all seasons, there was some production in the unenriched water at some stations. In winter and spring, production exceeded 30 eggs·(female·day)$^{-1}$ near Point Conception and along the southern California coast and the Santa Rosa–Cortes Ridge; in summer and fall, however, this rate was less widespread, or attained only by females with enriched food. At the stations farthest offshore, production was frequently <10 eggs·day^{-1} even after two days of supplemental food. The geographic patterns of the ratio of production in ambient and in food-supplemented water also indicated seasonality in food limitation. Although egg production was generally correlated with concentrations of chlorophyll, this relation was quite imprecise.

RESUMEN

La producción de huevos por hembras de *Calanus pacificus* fue determinada durante dos años en incubaciones a bordo de barco, empleando agua de mar con concentraciones ambientales de seston y agua de mar enriquecida con cultivos de fitoplanton, con el fin de detectar el grado de limitación alimentaria. Durante todas las estaciones del año se encontró producción de huevos en algunas estaciones no enriquecidas. En invierno y primavera una producción >30 huevos (hembra día)$^{-1}$ fue observada en Point Conception y a lo largo de la costa del sur de California y de la cadena de Santa Rosa–Cortés. En verano y otoño, este nivel de producción fue menos extendido, o alcanzado solamente por hembras con refuerzo alimentario. En las estaciones más alejadas de la costa, la producción fue generalmente de <10 huevos (hembra día)$^{-1}$, incluso despues de dos días de comida suplementaria. Los patrones geográficos de la proporción de producción en aguas ambientales con respecto a la producción en aguas con comida suplementaria también indicaron estacionalidad en la limitación de comida. Aunque la producción de huevos se correlacionó en términos generales con las concentraciones de clorofila, esta relación fue bastante imprecisa.

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INTRODUCTION

Varying sizes of planktonic populations (as biomasses or abundances) can result from changes in the physical processes influencing an area (frequently the ultimate, and sometimes also the proximate, cause) plus ecological responses or readjustments of the populations themselves. Such variability is particularly well documented in the California Current because of the venerable California Cooperative Oceanic Fisheries Investigations (CalCOFI). For example, there is now clear evidence (e.g., Reid 1962; Chelton et al. 1982) that the biomass of zooplankton responds coherently on the interannual scale throughout the California Current to variations in southward transport, and Colebrook (1977) showed that the biomasses of most major planktonic groups — copepods, euphausiids, and particularly salps and doliolids — changed coincident with an extreme climatic event: the 1958–59 El Niño. By more closely examining the timing of maximal zooplanktonic biomass relative to maximal southward flow, Roesler and Chelton (1987) concluded that off northern California such interannual variations in biomass are caused by variations in direct advection of biomass from more northern regions (where biomass is high). Off Baja California, a time lag in response suggests that variations in advection of nutrients from the north, translated via the food chain into zooplanktonic biomass (probably after recycling within the euphotic zone), may be more important. Whether this is equally true for all taxa, or whether some vary more as a direct result of advection and others more as a result of biotic interactions, is not known.

Even when physical variation in a region includes advection of exotic species, physiological and demographic rate processes (proximate causes for biomass variation) of indigenous species may also be

altered. Particularly on smaller spatial-temporal scales, such alterations may be correlated with food or predators. For example, Hakanson (1987) has shown that the lipid contents of copepodite stage V *Calanus pacificus* are geographically positively correlated in the California Current with chlorophyll (though on smaller scales or at other times this may not be so [Ohman 1988]). The immediacy of demographic response to variations in food probably varies with species (Dagg 1977), but at some scales any species will vary in growth or reproductive rate per capita. Reproductive variation, times the abundance of females, results in variation in the rate of population increase. Even for an indigenous, planktonic population there can be ambiguity as to cause, however; demographic rates in a particular area can change because of physiological response to environmental changes, or because another population of the same species but with different properties has been advected into the area.

The rate at which females produce eggs has been widely used to indicate secondary production for particular species; to determine how production varies in response to food, temperature, etc.; and particularly to test for food limitation of growth rate (e.g., Ambler 1986; Beckman and Peterson 1986; Bellantoni and Peterson 1987; Borchers and Hutchings 1986; Checkley 1980a,b; Dagg 1978; Durbin et al. 1983; Hirche and Bohrer 1987; Kimmerer 1984; Kiørboe et al. 1985; Peterson 1985; Runge 1985a,b; Smith and Lane 1987). Applying this approach to assess a coastal front's effect on rate processes as well as abundances, Kiørboe and Johansen (1986) showed that per capita egg production was higher on the unstratified side of the front, where the chlorophyll concentration was elevated, than on the stratified side, but the abundances of late copepodites and adults were independent of the front, indicating that the pattern of abundance alone did not reveal "where the action was."

In my assessment, this body of literature has shown both the utility of this means of efficiently assessing ecological relations, and the (probably real) complexities: the immediate response depends on past history of the females, the season, and the size or quality of the food. To put the last point another way, the biomass of food should best be assessed in terms of the nutritional factor that most limits egg production (though, in fact, this is seldom known).

For an example of variation in a zooplanktonic population's demographic rates, I investigated the seasonal and mesoscale spatial variability in the production of eggs by an important pelagic copepod, *Calanus pacificus*, in the southern California sector of the California Current. I designed the study to make inexpensive use of sampling, and of data generated concurrently, by the ongoing CalCOFI cruises, and to be eventually interpretable in the context of the historical record of interannual variations in zooplanktonic biomass and physical processes already established by this program.

METHODS

CalCOFI cruises on the *New Horizon* and *David Starr Jordan* cover a sector of the California Current off southern California quarterly; these cruises are designated *XXYY*, where *XX* represents the year and *YY* the month. Each cruise includes stations in the coastal zone, in the relatively oligotrophic Southern California Bight, in the relatively eutrophic tongue extending SSE from Point Conception along the Santa Rosa–Cortes Ridge, and in the offshore California Current beyond (see Mullin 1986 for summaries of the Southern California Bight, and Peláez and McGowan 1986 and McGowan 1985 concerning areas farther offshore). Each station is sampled whenever the ship arrives at it, so there is no purposely maintained relation between a particular station and time of day.

CalCOFI sampling includes water bottle casts for particulate and dissolved properties at standard depths, typically with seven samples within the euphotic zone. Temperature was determined from reversing thermometers; I have plotted temperature at 10 m, based on data reports for each cruise (published in the SIO Reference Series). Because the vertical distribution of the copepods used in experiments was unknown, both within the upper 200 m (the region sampled) and below this depth, and probably differed between stations, the temperature at 10 m should not be interpreted as that experienced by the copepods *in situ*. Rather, it indicates the geographical pattern of temperature over the sampled region, and is approximately the temperature relevant to incubations that I set up on ship to measure egg production.

The biomass of phytoplankton was determined at the standard depths by extraction of chlorophyll from cells retained on a GF/C or GF/F glass fiber filter, followed by fluorometric analysis (Venrick and Hayward 1984). Because the concentration of chlorophyll is correlated with other properties of the seston (Eppley et al. 1977), I have assumed that it represents, or at least is linearly proportional to, the food for the copepod *Calanus pacificus*, even though this genus is known to ingest nonphytoplanktonic

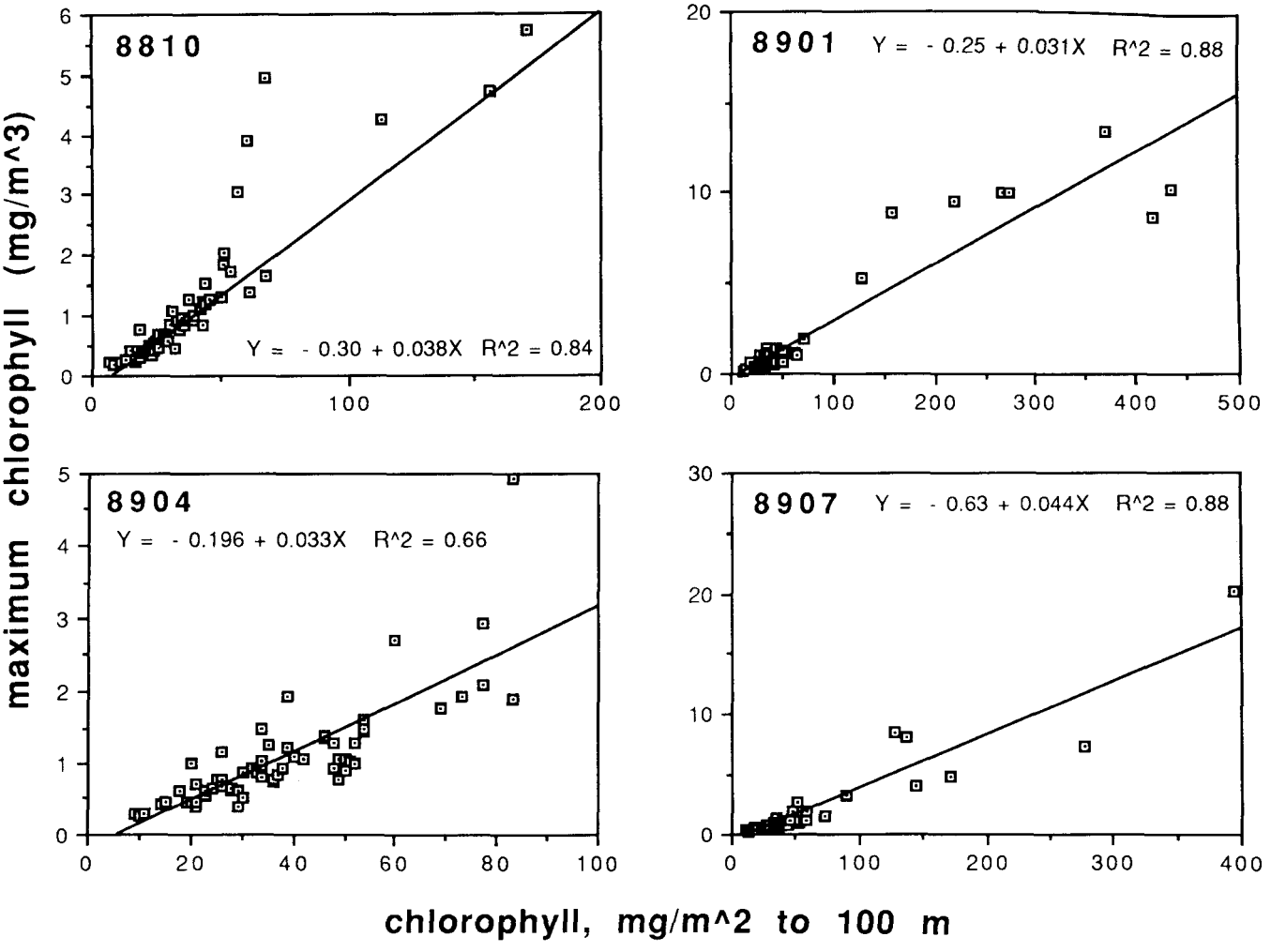

Figure 1. Relations between phytoplanktonic biomass as chlorophyll in $mg \cdot m^{-2}$ to 100 m (integrated from concentrations at seven standard depths) and maximum concentration of chlorophyll ($mg \cdot m^{-3}$) actually measured at each station, for four cruises. All correlations are significant at $p << 0.01$.

particles and to feed inefficiently, if at all, on the smallest particles (1–2-μm) nominally retained by the filters. Also, the depth range within which there is significant biomass of phytoplankton, the variability in concentration within this range (notably, the degree of a subsurface maximum), and the distribution of types and sizes of particles at each depth vary seasonally and with location offshore (Eppley et al. 1977; Reid 1983). Thus the concentration of food as perceived by the copepods depends on their depth distribution relative to that of the particles they eat. Arguably, the maximal concentration of particles of suitable types may be more significant to *Calanus* than is the biomass of total chlorophyll per unit of sea surface if this maximum is where feeding occurs (e.g., Napp et al. 1988a). Nevertheless, I have mapped total chlorophyll as $mg \cdot m^{-2}$, from the surface to 100 m or the bottom, based on the concentrations measured or interpolated at 0, 10, 20, 30, 50, 75, and 100 m (published in the SIO Reference Series). This estimate of biomass correlates closely with the maximal concentration of chlorophyll actually measured at the same stations, however, and the relation was similar for different cruises (figure 1).

CalCOFI sampling at each station also includes an oblique net tow from 200 m to the surface with paired nets of 505-μm mesh, only one of which is used for a quantitative, Formalin-preserved sample. After briefly narcotizing the catch from the other net, or the catch from a 1-m-diameter, 505-μm-mesh net, in seawater plus methane tricaine sulfonate, I picked out living female *Calanus* for incubation.

If egg production varies vertically, females from specific depths should be incubated in water (and

food) from those depths to assess production. However, because stations are occupied at whatever time of day they are reached; because *Calanus* migrates dielly in some seasons; and because the depth at which eggs are laid may not match the daytime depth at which females are found (because of nocturnal egg laying and diel migration [cf. Peterson 1985]), I simplified by using water (and seston) from 10–20 m at each station for incubations.

At selected stations, I placed female *Calanus* in each of three shaded containers, which were placed in seawater flowing from the ship's through-hull intake. Each container was a plastic cylinder with a mesh screen and a funnel attached to the bottom so that eggs could fall through the mesh (reducing cannibalism) and be drawn off without removing females from the container (cf., e.g., Hirche and Bohrer 1987). I filled each cylinder with seawater and natural seston from the euphotic zone at the station; one cylinder ("unfed") had only this. The copepods, because they were more concentrated in the containers than *in situ*, were able to graze down the natural seston during the incubation. To test for maximal egg production without food limitation, I added excess food as the diatom *Thalassiosira weisflogii* (maintained in nutrient-enriched cultures on shipboard) to a second cylinder ("fed") at the start of the incubations (cf. Durbin et al. 1983), as well as to a third cylinder after 24 hours. I removed eggs (and nauplii, if any) for counting after 24 and 48 hours, and preserved, recounted, and retained the female copepods after the second assessment to verify identity and measure size with an ocular micrometer.

I assumed that any difference between the initial and final number of copepods in a container was due to linear change during the experiment. However, if fewer than 33% of the copepods were recovered alive at the end of an experiment, I assumed that damage during capture or toxicity during incubation had affected egg production severely enough to reject the results. In fact, in 89% of 375 48-hour incubations, at least 67% of the copepods survived.

I modified the basic design in simple ways to examine the two critical issues of interpretation in this experiment: (1) Is the production of eggs in the containers of ambient seawater ("unfed") during the first 24 hours equal to the daily rate of reproduction *in situ*? (2) Is the production of eggs in water enriched with *T. weisflogii* a suitable measure of the maximal rate, unlimited by food?

The first issue results from the following assumptions: (a) that the rate is not altered by either temperature or light during the incubation, nor because the containers prevent diel vertical migration, nor as a result of stresses imposed on the females by the sampling and sorting; (b) that all the eggs counted are viable (nauplii were often present in addition to eggs, but I did not test for viability of all eggs); (c) that the concentration of natural food in the container is the same as that experienced *in situ* by the "typical" copepod, i.e., that the copepods do not preferentially produce eggs at depths where food is more concentrated (see above); and (d) that egg production in the first 24 hours is not depressed by reduction of food in the containers because of the unnaturally elevated concentration of copepods (reduction surely occurs, but egg laying may not be immediately inhibited), nor are eggs removed by unnaturally high cannibalism. Grazing down of food in experimental containers could lead either to an underestimation of overall reproductive rate (i.e., equivalent underestimation at all stations) or to an accentuation of real differences in rates between females from moderately oligotrophic and eutrophic regions. In many ways, this issue is similar to concerns over the potential artifacts in measuring primary production by incubations in containers (e.g., Peterson 1980).

Limitation of station time and the complexity of communities of copepods from which female *Calanus* (which were sometimes quite rare) had to be selected dictated my methods of sampling (standard CalCOFI tow) and sorting (narcotizing with MS222, removal by forceps). Nevertheless, to assess the possibility that these procedures adversely affected egg laying, I used a 2-way ANOVA to compare egg production in the presence of *Thalassiosira* by females collected in a standard tow to that of females captured in a shorter, slower tow. I also compared the production of those sorted under a microscope after narcotization to that of females picked by pipette from a beaker without narcotization. I repeated each collection-sorting combination four times.

There were no significant differences between these treatments ($p >> 0.1$ in all cases). This does not mean that collection had no adverse effect (see Results below), merely that reasonable alternative procedures caused no difference in the rate of egg laying, given the variability within each treatment.

I tested the effect of the size of experimental container (influenced by convenience) and the concentration of female copepods. Females lay clutches (batches) of eggs, and the rate of production of clutches by an individual is at least as variable as the number of eggs per clutch (Runge 1985a; Peterson 1988). Therefore, if an experiment is shorter than the interval between clutches, having a larger number of females in a container will yield a more precise

estimate of mean rate of egg production through averaging over more individual vagaries in whether or not a clutch was produced. (This also means that average clutch size will be underestimated by the average rate, unless all females produce clutches.) However, the more females there are in a given volume, the faster they eat the suspended particles in the water. This can affect the number of eggs recovered (relative to the number of females) either if the rapid depletion of food causes egg laying to stop in less than one day, or if the females eat eggs. If either problem is serious, the apparent rate of egg production per female should decrease as the concentration of females increases.

At three stations on cruise 8901, I placed various concentrations of female *Calanus* in the 500-ml containers of unenriched (ambient) seawater, and measured the production of eggs over 24 hours. The trends varied among the individual experiments (figure 2A), and none of the correlation coefficients was high. When I standardized the data by adjusting the rates for stations 90.53 and 87.35 to match those of station 93.30 (by assuming that 20 females per 500 ml produced eggs at the same mean rate at all stations), there was no discernable relation between egg production per female and concentration of females (figure 2B). I repeated the experiments at three stations on cruise 8904, except that the lowest concentrations of females were established in 1-l containers. In this case, the apparent rate of egg production decreased with increasing concentrations in all experiments (figure 2C), and the production standardized to station 90.30 also showed a significant ($p < 0.01$) depression (figure 2D). Egg production tended to be greater in 1-l than in 500-ml containers when the concentration of copepods was the same (tested separately on cruise 8907), but the difference was nonsignificant ($0.05 < p < 0.10$, 2-tailed).

The result shown in figure 2D, and the augmentation of egg production within 24 hours which almost always resulted from adding *T. weisflogii* (see Results), suggest that assumption d might be incorrect, so I examined it further. To directly test how fast egg laying declined after depletion of food, I compared in three experiments the 24-hour egg production of 5–7 groups of female *Calanus* in ambient water with or without added *T. weisflogii*. All of the females had already been maintained in excess *T. weisflogii* for 24 hours (cf. Borchers and Hutchings 1986; Peterson 1988). The interesting alternative to the null hypothesis (no difference) would be reduced egg laying by the females that had been returned to ambient water.

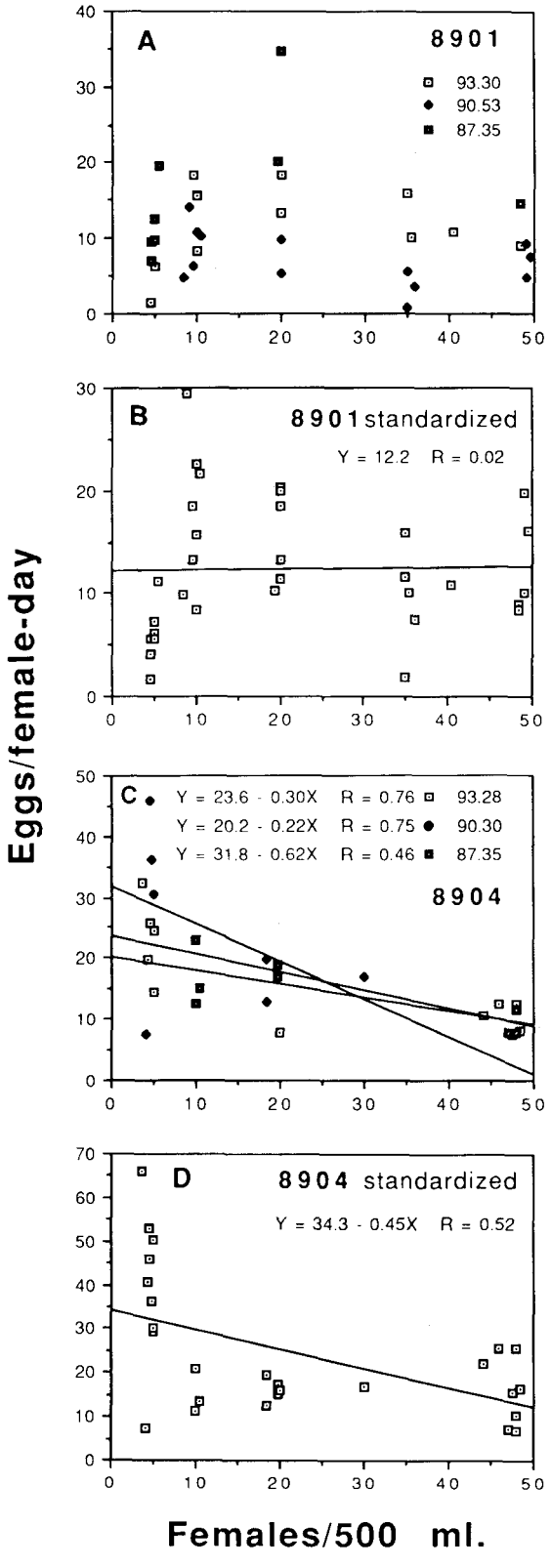

Figure 2. Rate of daily egg production per female in ambient seawater as a function of concentration of females in experimental containers, for three stations on each of two cruises (*A*, *C*). Rates were standardized (*B*, *D*) by assuming that at all three stations the mean rates at 20 females (500 ml) ⁻¹ equalled that at station 93.30 of cruise 8901 or 90.30 of cruise 8904. Linear fits are presented only to illustrate negative relations, not to imply linearity throughout the range measured.

In all three cases, the median production of females deprived of *T. weisflogii* on the second day was significantly reduced ($p < 0.05$ by rank sum test) relative to those continued in the enriched water. The overall reduction in the combined tests was significant at $p << 0.01$. Therefore, drastic change from a plentitude of available food caused production to be reduced from 32 to 20 eggs·(female-day)$^{-1}$. Whether this would also happen when food was reduced more gradually at natural concentrations by grazing during the first day of an experiment is not proven, nor is it clear whether reduced production or increased cannibalism when females are deprived of *T. weisflogii* is the cause, but the results at least indicate that a problem exists.

Overall, there eventually was enough evidence to conclude that the concentration of females in experimental containers can, when ambient seston is not enriched, apparently reduce the rate of egg production by some amount with respect to that when females are dilute enough that they do not deplete the food supply. Therefore, although I had incubated approximately 20 females in each 500-ml cylinder during cruises 8810–8907, I conducted the incubations on cruises 8911–9008 in 1-l rather than 500-ml cylinders, with no more than 15 *Calanus* per cylinder. The rates of egg production reported below for the "unfed" cases may underestimate the natural rates, particularly for cruises 8810–8907 (figures 3–6). In principle, chemostats could obviate this difficulty in the experimental design.

The assessment of how food limits egg production also deserves comment. If *T. weisflogii* had failed to increase egg production, this would not necessarily rule out food limitation (since it may not be a "satisfactory" food, though *Calanus* has been cultured through its life cycle on this food alone: Mullin and Brooks 1970); enhancement of production is, however, strong evidence for some sort of food limitation.

I used rank sum tests to compare the 48-hour egg production per female for incubations in which *Thalassiosira weisflogii*; brine shrimp (*Artemia*) nauplii; the chrysophyte flagellate *Monochrysis lutheri*; the coccolithophorid *Emiliania huxleyi*; the smaller diatom *Thalassiosira pseudonana*; or a senescent culture of the large diatom *Lauderia borealis* was provided as food. *T. weisflogii* and *Artemia* resulted in similar production rates ($p > 0.1$, 2-tailed); for both, production exceeded that in unsupplemented water. But *Monochrysis*, *Emiliania*, *T. pseudonana*, and the senescent *Lauderia* were significantly inferior to *T. weisflogii* ($p < 0.01$), though *Emiliania*, *T. pseudonana*, and *Lauderia* were themselves superior to natural seston. Other foods may be superior to *T. weisflogii* in stimulating egg production, but I have not found them.

The absolute magnitudes of egg production rates provide some information on the extent of limitation by food, but are also affected by temperature, size of females, etc. Therefore, I tested several ratios of rates as indicators of food limitation, as described in table 1.

The ratio of rates of unfed and fed females is a measure of realized production relative to potential production over the short (ratio a) or medium (ratio b) term. Ratio c would be high, and ratio d low, if food limitation was so severe that females needed a full day's feeding before beginning to lay eggs at the maximal rate. These ratios are mapped for each cruise. Ratio e would be close to 1.0 only in the absence of food limitation.

The calculation of several ratios would be redundant if ratios a, b, d, and e were strongly positively intercorrelated, and all were strongly negatively correlated with ratio c. However, correlations among these ratios were weak (though of the right sign); either the different ratios correspond to different aspects of limitation by food, or some of them are meaningless. In fact, production of eggs on the second day in unsupplemented seston was sufficiently rare (except in January) that ratio e proved of little discriminatory use.

RESULTS

Figures 3–10 are maps covering two years (October 1988; January, April, July, and November 1989; and March, April, and August 1990) of temperature at 10 m, chlorophyll in the water column, daily production of eggs by female *Calanus* in natural and

TABLE 1
Ratios Used to Assess How Severely Food Limitation Affects Egg Production by *Calanus*

Ratio	Interpretation
a. (unfed females)/(fed females), egg production rate on 1st day	The *greater* the ratio, the less severe is food limitation (unless both rates are 0, when females are unripe, spent, or extremely food-limited).
b. (unfed females)/(fed females), total egg production on both days	Same as above
c. (2nd-day rate)/(1st-day rate) fed females.	The *less* the ratio, the less severe is food limitation.
d. (females fed 2nd day only)/(females fed both days), 2nd-day rate	The *greater* the ratio, the less severe is food limitation.
e. (2nd-day rate)/(1st-day rate), unfed females	The *greater* the ratio, the less severe is food limitation.

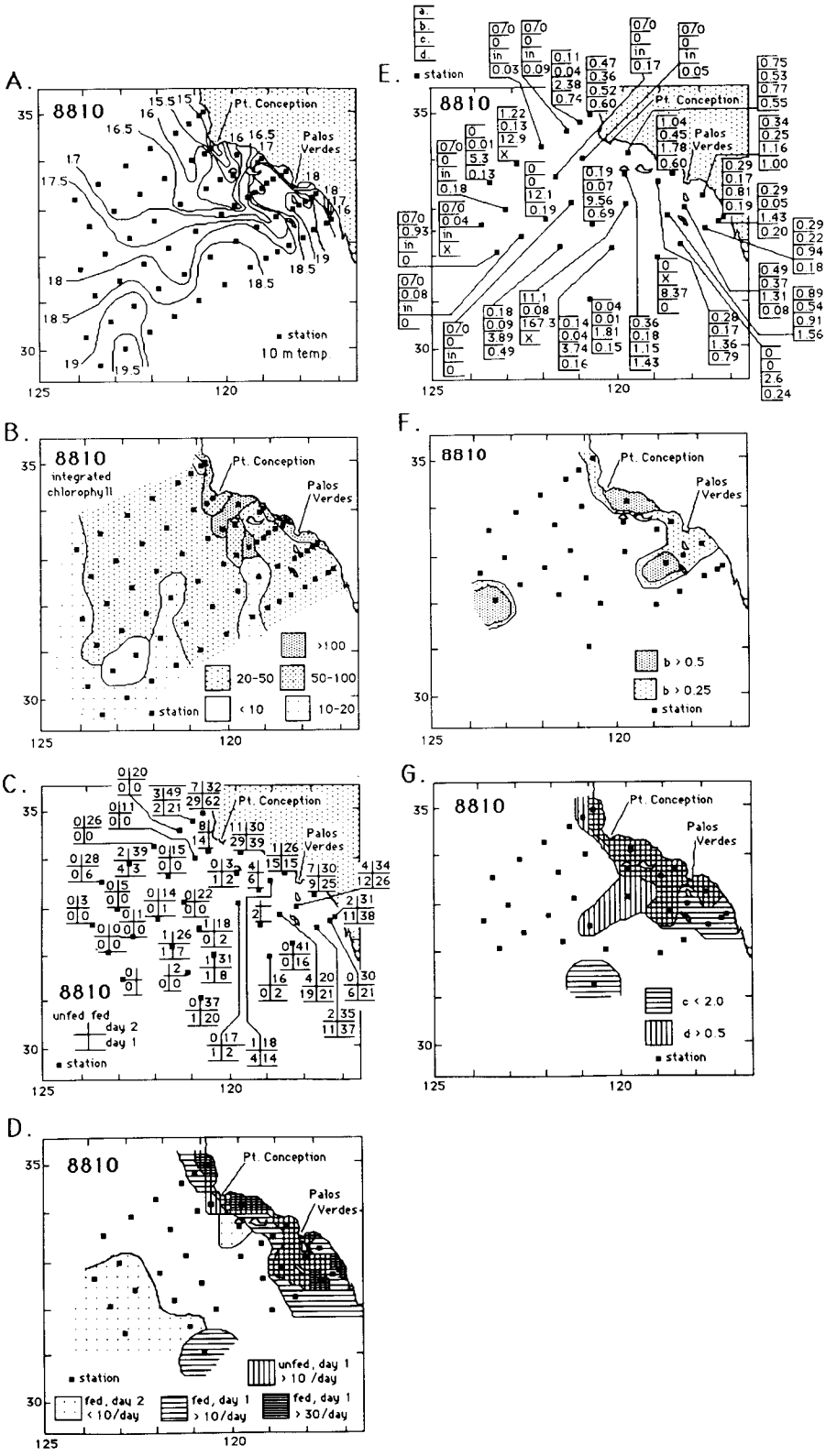

Figure 3. Maps for cruise 8810. *A*, Temperature (°C) at 10 m. *B*, Integrated chlorophyll, mg·m^{-2}. *C*, Eggs produced per female on first and second days in ambient and food-enriched conditions (blank means no data). *D*, Contours of daily egg production (no shading means <10·day^{-1} on day 1). *E*, Ratios a–d (see Methods text for definitions and interpretations): 0/0 means numerator and denominator 0; "in" means only denominator 0; X means no data. *F*, Contours of ratio b, higher values meaning less food limitation of production. *G*, Areas of low food limitation of production as shown by relatively low values of ratio c and high values of ratio d.

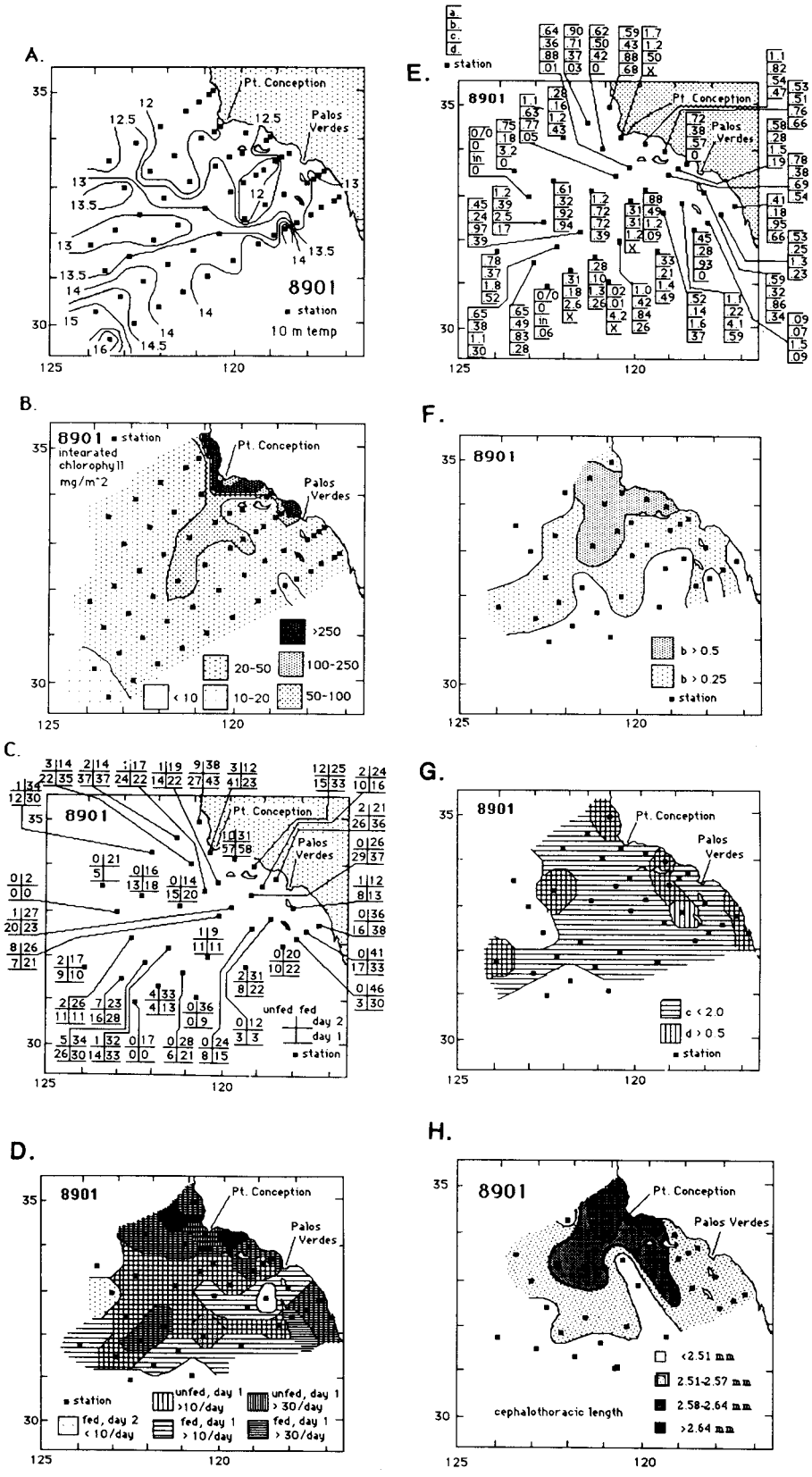

Figure 4. Maps for cruise 8901. See figure 3 for explanation of *A–G*. *H*, contours of cephalothoracic (prosomal) length of female *Calanus* from stations where experiments were conducted.

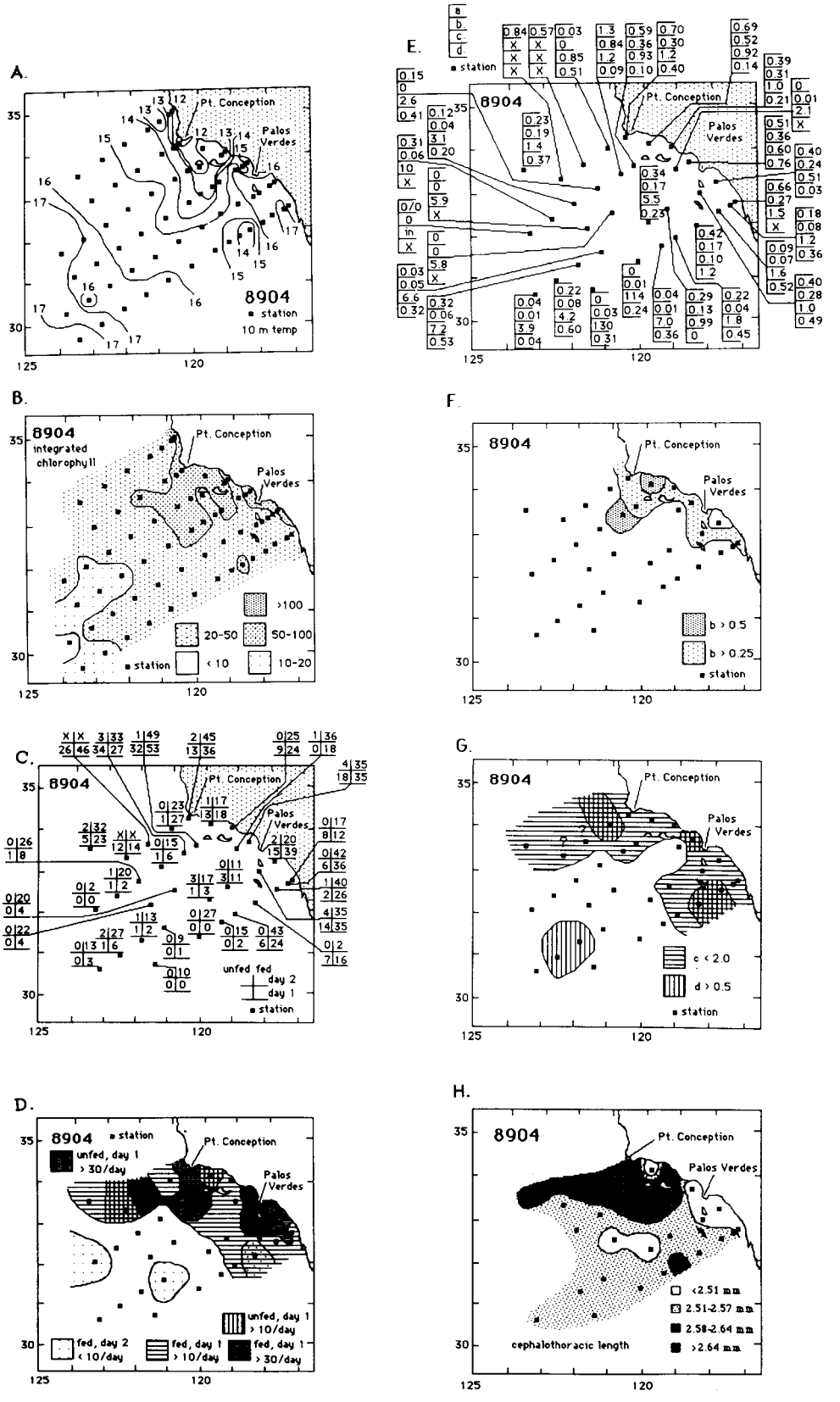

Figure 5. Maps for cruise 8904. See figures 3 and 4 for explanation. Note that there are no stations north of Point Conception.

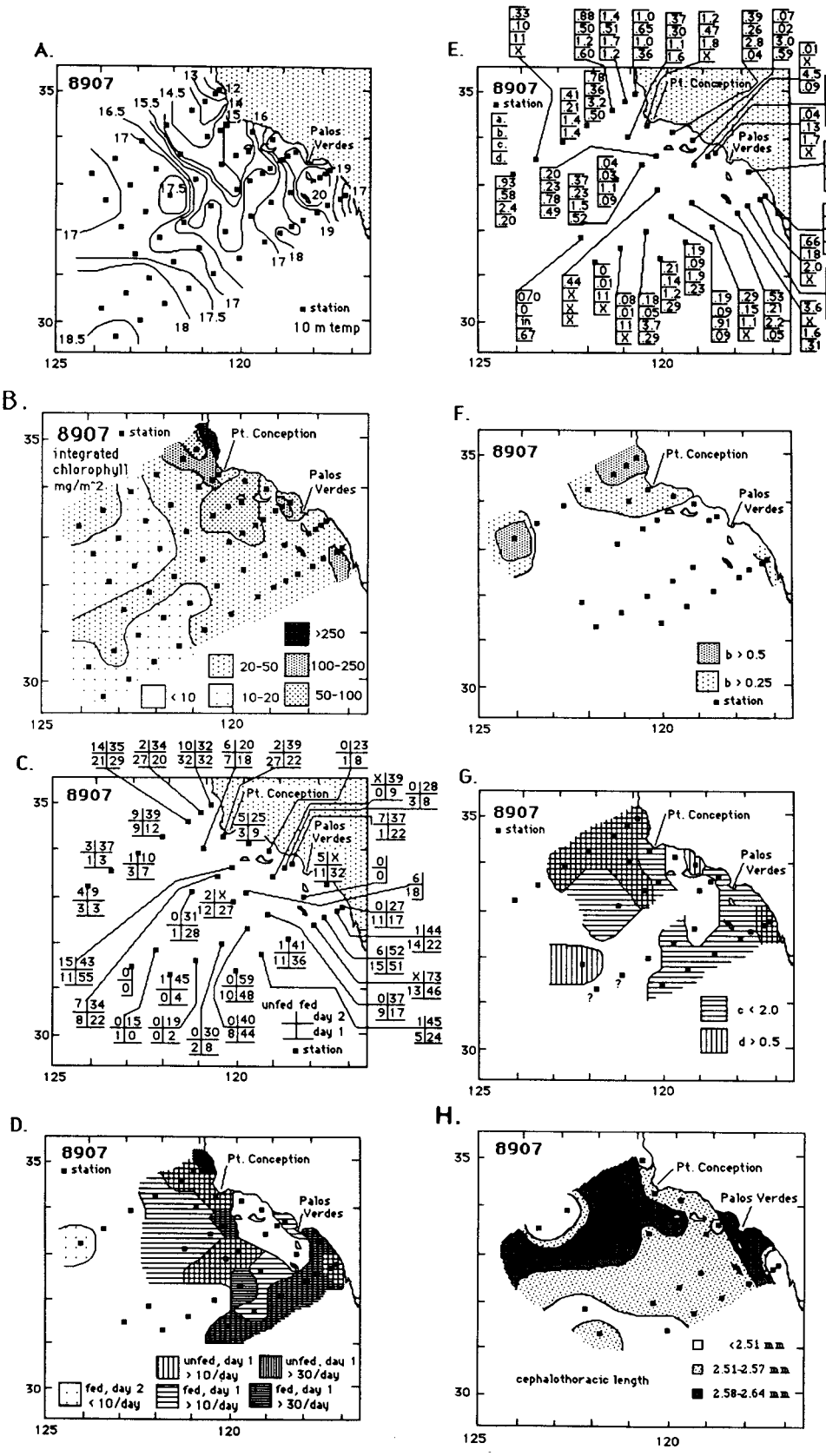

Figure 6. Maps for cruise 8907. See figures 3 and 4 for explanation.

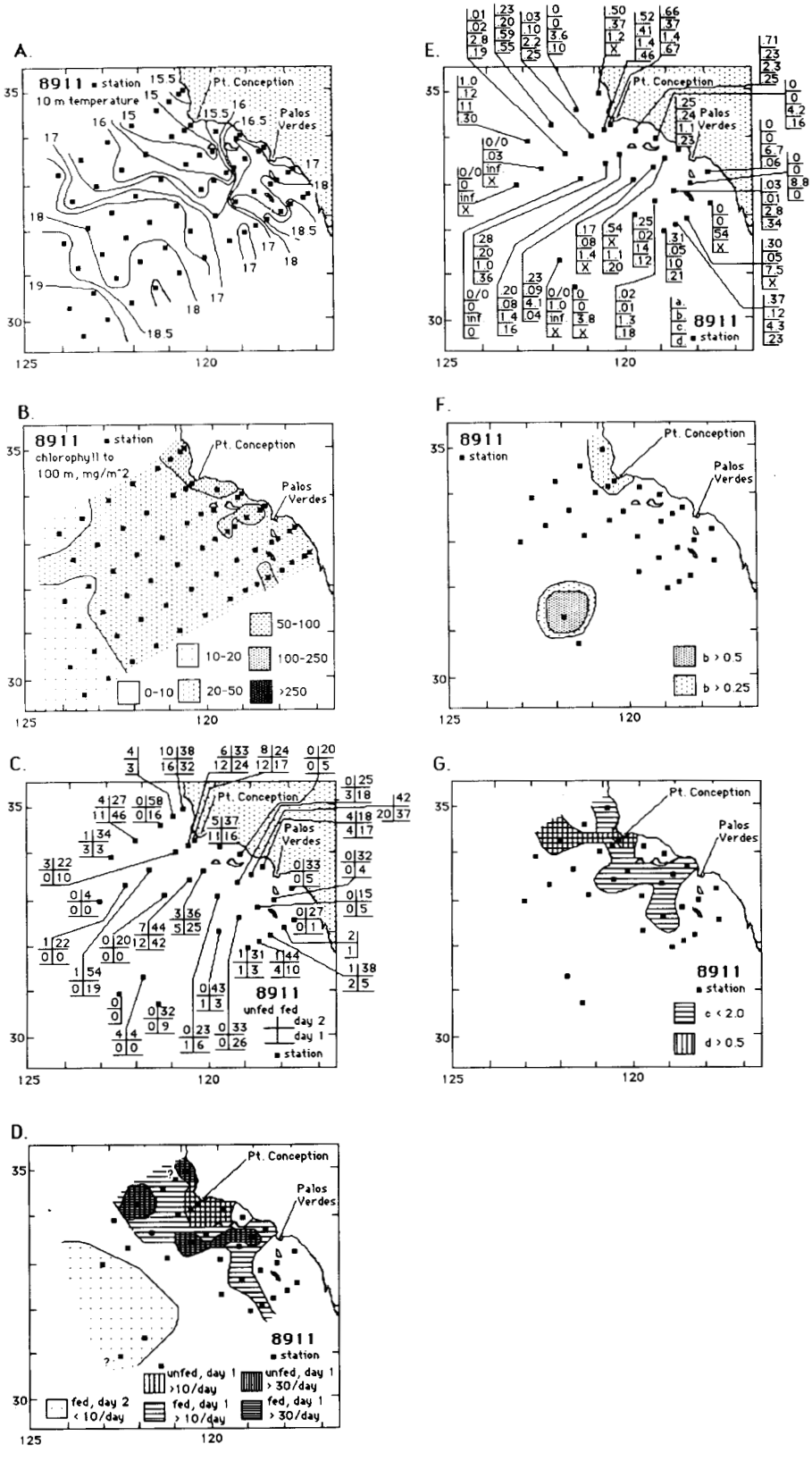

Figure 7. Maps for cruise 8911. See figure 3 for explanation.

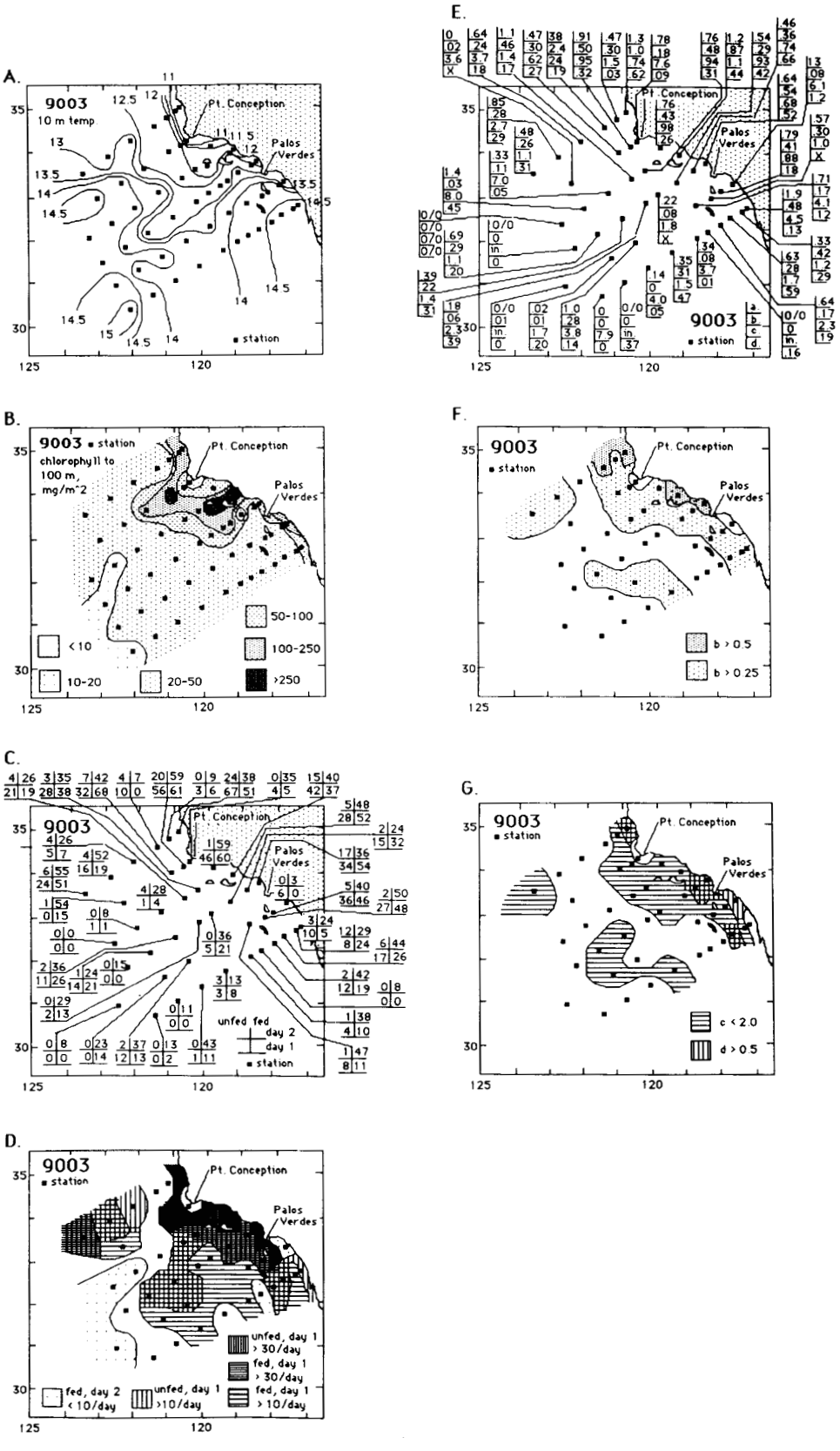

Figure 8. Maps for cruise 9003. See figure 3 for explanation.

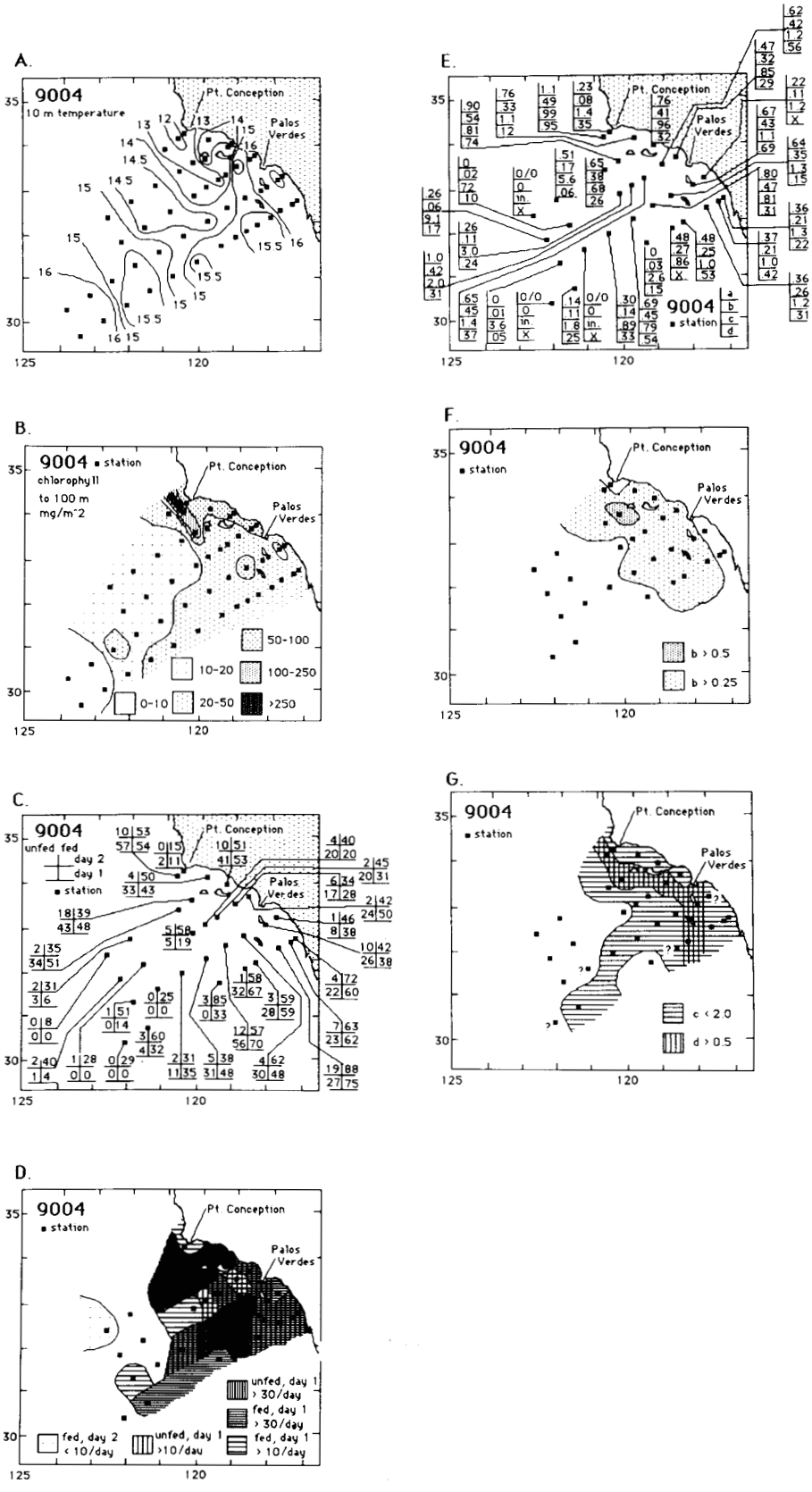

Figure 9. Maps for cruise 9004. See figure 3 for explanation. Note lack of northerly stations.

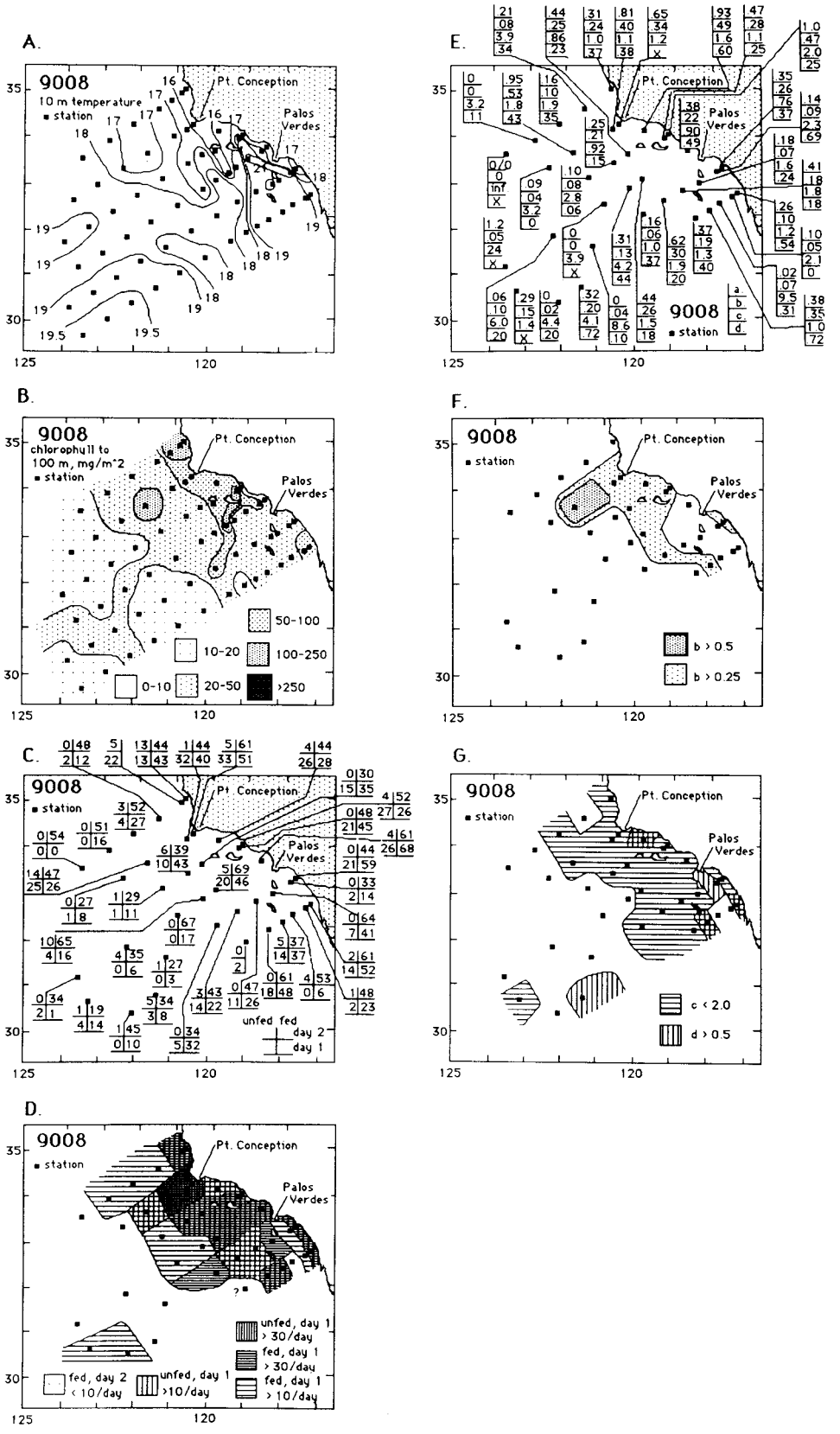

Figure 10. Maps for cruise 9008. See figure 3 for explanation.

Thalassiosira-enriched seawater on each of the two days of incubation, and ratios a–d (see Methods), together with more easily comprehended contour maps of the egg production and ratios b, c, and d. The sizes of females, as cephalothoracic (prosomal) lengths, are also shown for three 1989 cruises.

Large-scale features appearing on most cruises include the following.

1. The coolest water was in the northern, nearshore region and (on 8901) in the Southern California Bight; the warmest water was in the southwestern, offshore region and (in summer–fall) in the Southern California Bight (A in each figure).
2. The biomass of chlorophyll was consistently high nearshore in the vicinity of Point Conception (except immediately off Point Conception on 8901 and 9003); this relatively eutrophic region often extended southward along the nearshore and offshore edges of the northern half of the bight (B in each figure).
3. Both realized (in ambient seston) and potential (in *Thalassiosira*-enriched incubations) production of eggs were greatest nearshore and to the north, except on 8907 and 9004, when potential production was also high in the south. Perhaps the most variable region was the southern portion of the bight. Greatest absolute limitation by food (i.e., low production even on the second day with supplemented food [dotted areas of D in each figure]) occurred offshore; only on cruise 8810 were there more than four such stations (though three such stations represented a large area on 8911), meaning that there are few locations or seasons where females occur in the upper 200 m but are unable to reproduce because of infertility or exhaustion of oocytes or sperm. Only a more prolonged exposure to augmented food would reveal whether low fecundity on cruise 8810 was due to severe limitation by food or to infertility.
4. Egg production was consistently least limited by food nearshore, in relative terms (shaded areas in F and G of each figure); areas of only modest food limitation (as indicated by ratio b) extended far offshore on 8901 because of high reproductive rate even in unenriched water, and sporadically on other cruises because of poor production even when food was added.

Generalizations 3 and 4 mean that there is a pattern, though a variable one, to per capita reproductive rate of *Calanus* in the California Current off southern California; figures 3–10 (D, F, and G) are not random mosaics. Qualitatively, the patterns are related to the mesoscale distributions of phytoplanktonic biomass (figures 3–10, B), though there are some interesting differences.

There are also some clear differences, which may be seasonal, between cruises. For example, absolute production was poorest, and relative food limitation most widespread, on 8810; on 8901, both strong production and regions approaching food-independence were the most widespread (figures 11–13). (8904 and 9004 are difficult to compare to the other cruises because of the paucity of data along the northernmost line.) Compared to the seasonality of reproduction of *Calanus* spp. in more polar latitudes, however, the year-round reproduction off southern California is the interesting feature (cf. Mullin and Brooks 1967, figure 2).

Egg production of unfed females was significantly, positively correlated with that of females from the same stations provided with *Thalassiosira* (figure 14). This is because there were some stations on each cruise where even fed females produced few eggs on the first day (i.e., food limitation was sufficiently severe that at least a day's active feeding was necessary to elevate the rate of production, so ratio c was much greater than 1.0), and other stations where even ambient seston sustained relatively high rates, and where fed females also had high rates. The interesting variability is in the middle range, where fed females frequently produced eggs at moderately high rates, but unfed females did not.

Though the patterns of egg production qualitatively resembled those of the distribution of chlorophyll, on all cruises the rate of production by both unfed and fed females varied considerably with respect to chlorophyll (figure 15). The expected relations should include (1) increasing production with increasing biomass of chlorophyll, quasi-linearly at small biomasses and asymptotically at large ones (i.e., a saturation of the rate at large biomasses); (2) some "maintenance level"—a minimal biomass of chlorophyll at which no production by unfed females occurs (i.e., a positive abscissal intercept); (3) at any biomass below saturation, production by fed females exceeding that by unfed ones; and (4) stronger correlation between the production and biomass of chlorophyll, and a more pronounced difference in production between "poor" and "rich" stations, for unfed females than for fed ones.

Expectation 3 was met in all cases. Data from 8901 and 8907 failed to meet expectation 1, in the sense that egg production was not significantly correlated with integrated chlorophyll ($p > 0.01$ by 1-tailed test, this probability level chosen because of the multiple tests) for these two cruises. Expectation 4 was met in the sense that R^2 values for relations of

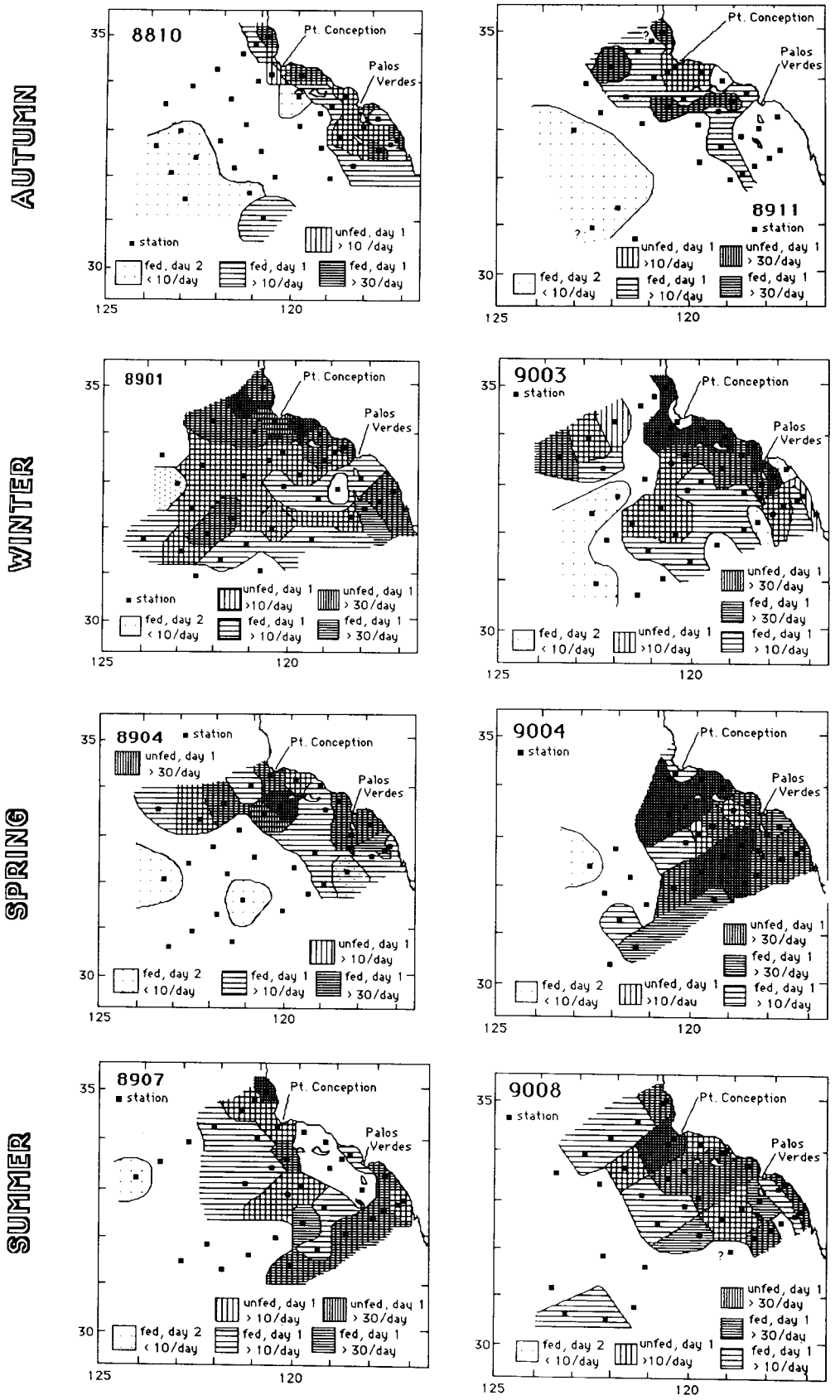

Figure 11. Maps of egg production for all cruises, arranged seasonally.

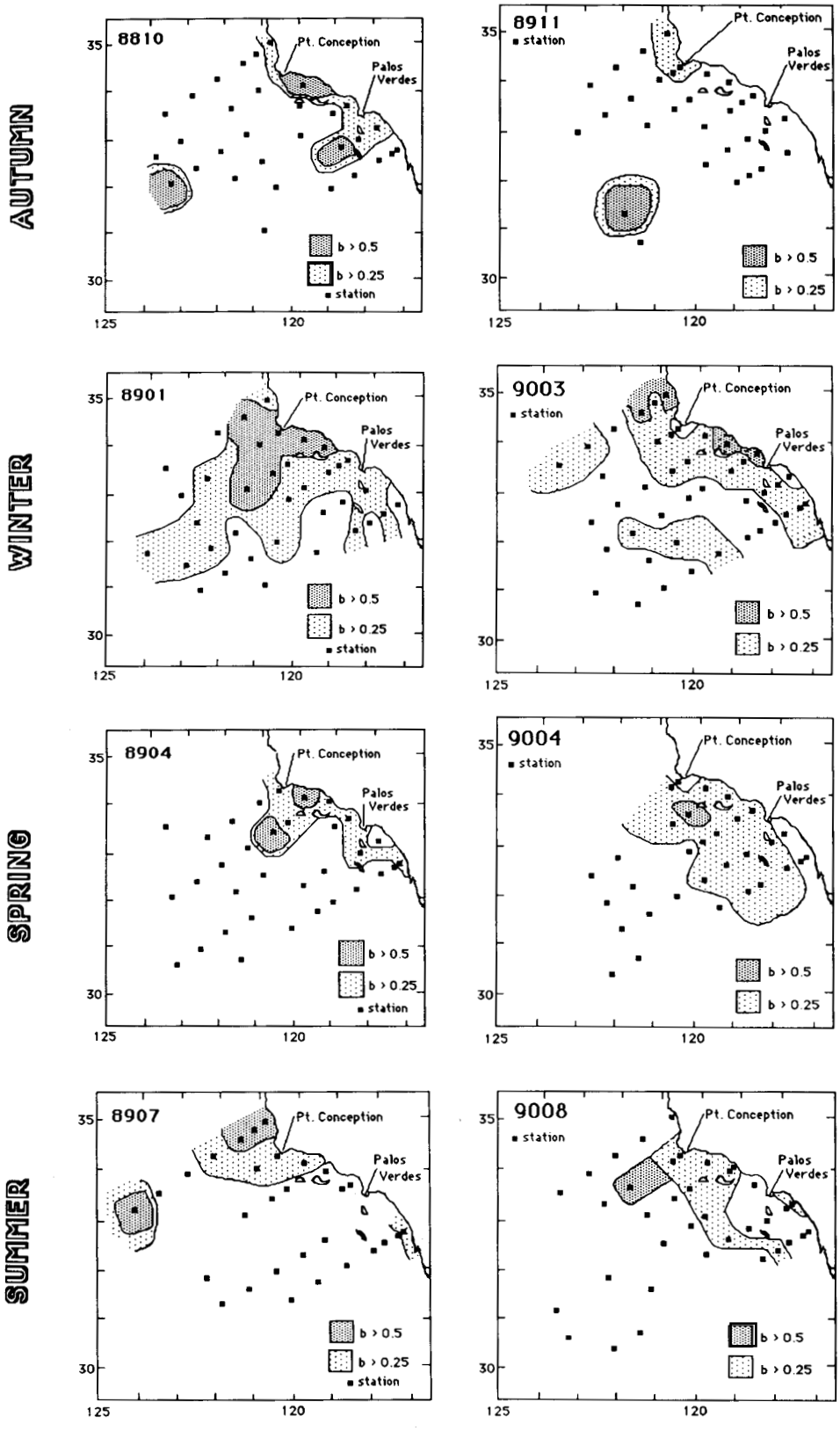

Figure 12. Maps of ratio b (2-day egg production, unfed:fed females), arranged seasonally.

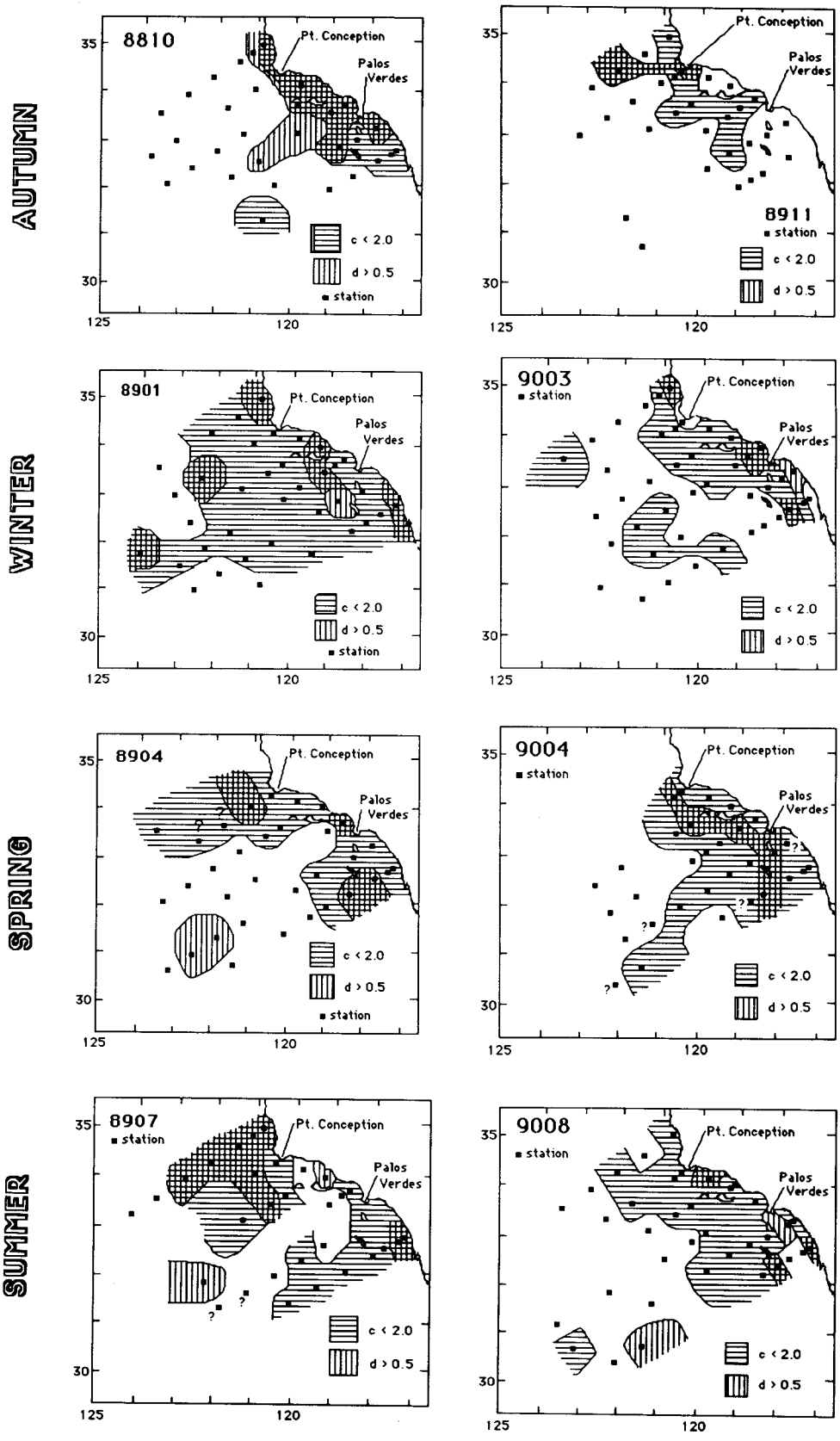

Figure 13. Maps of ratios c and d, arranged seasonally.

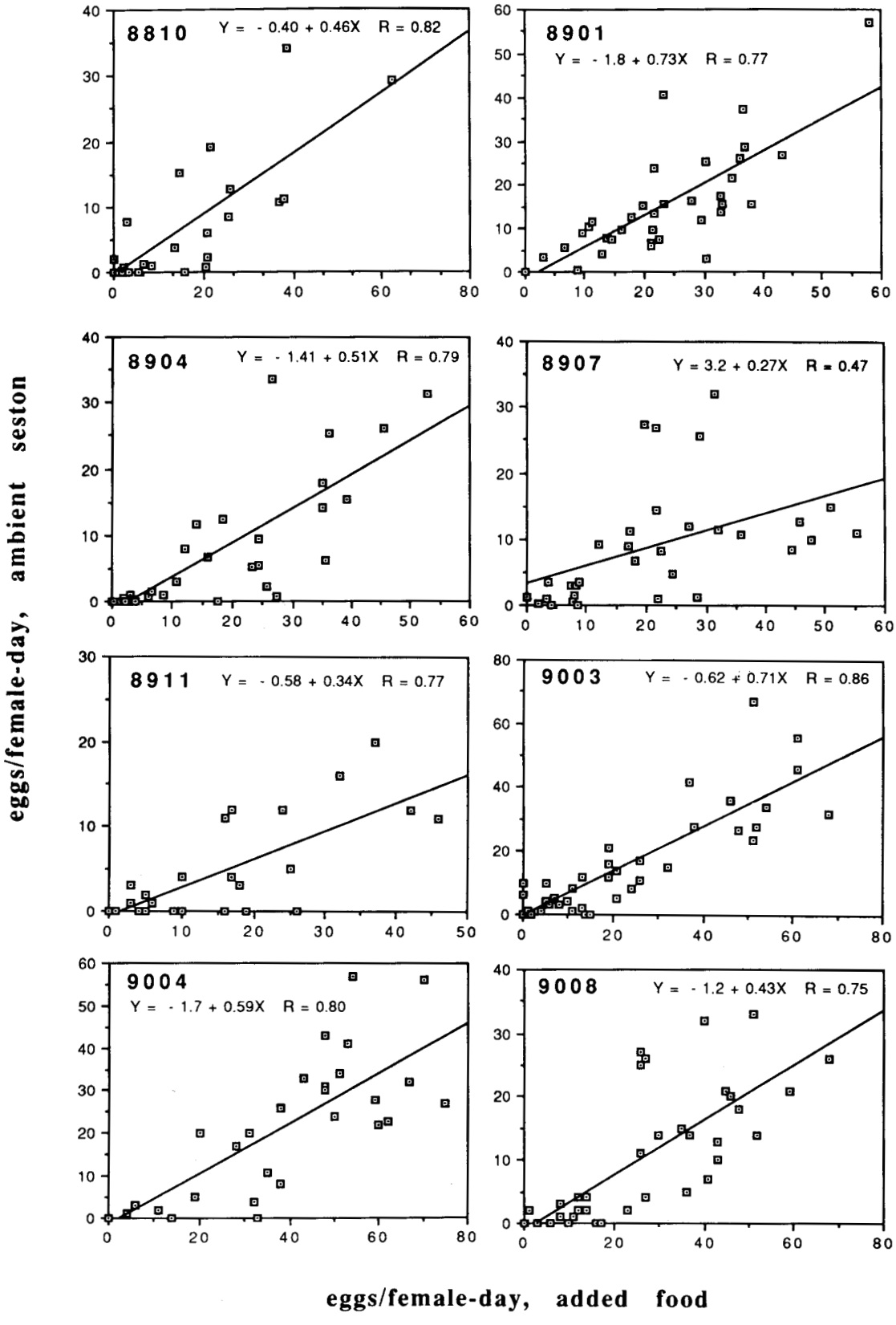

Figure 14. Rates of egg production of female *Calanus* for first 24 hours with excess phytoplankton added as food, and in unsupplemented seawater and seston from each station, for eight cruises. All correlations are significant at $p < 0.01$.

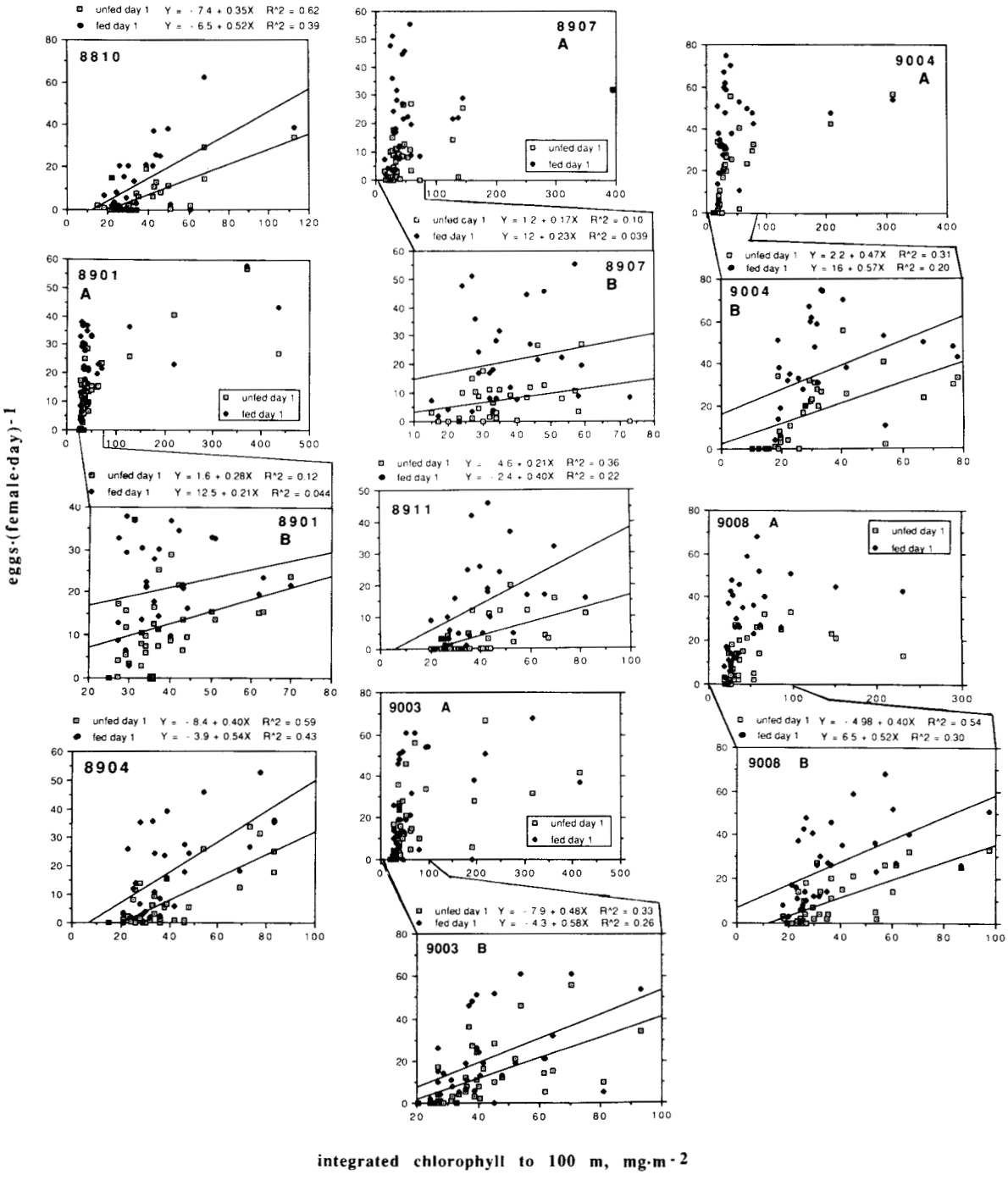

Figure 15. Rates of egg production over the first 24 hours for unfed (i.e., ambient seston) and fed (seston augmented with *Thalassiosira*) female *Calanus* as functions of chlorophyll biomass. October 1988: both correlations are significant at $p < 0.01$.
January 1989: *A*, all data; *B*, data for stations where biomass of chlorophyll was <100 mg·m^{-2}, and linearity might be expected. The correlation for unfed females is marginally significant ($0.025 < p < 0.05$, 1-tailed), and the correlation for fed females is not significant ($p > 0.05$, 1-tailed).
April 1989: both correlations are significant at $p < 0.01$.
July 1989: *A*, all data; *B*, data for stations <100 mg·m^{-2}. The correlation for unfed females is marginally significant ($0.025 < p < 0.05$, 1-tailed), and the correlation for fed females is not significant ($p > 0.05$, 1-tailed).
November 1989: both correlations are significant at $p < 0.01$, 1-tailed.
March 1990: *A*, all data; *B*, data for stations <100 mg·m^{-2}. Both correlations are significant at $p < 0.01$, 1-tailed.
April 1990: *A*, all data; *B*, data for stations <100 mg·m^{-2}. Both correlations are significant at $p < 0.025$, 1-tailed.
August 1990: *A*, all data; *B*, data for stations <100 mg·m^{-2}. Both correlations are significant at $p < 0.01$, 1-tailed.

unfed females exceeded those for fed females (i.e., the regression explained more of the variance in production by unfed females than by fed ones). I expected that production of unfed females would range from 0 to some maximum as a function of chlorophyll, while that of fed females would range from low (but >0) to the same maximum. Thus the former would have the greater slope. However, contrary to this expectation, the slopes for the regressions of egg production against ambient chlorophyll were generally greater for fed than for unfed females. (I did not determine the statistical significance of these differences.) Further, the expectation (2) that the abscissal intercept for data from unfed females would be positive (i.e., that the ordinal intercepts in the regression equations would be negative) was not met by the data from cruises 8901, 8907, and 9004. It is conceptually possible that production of eggs could occur in the absence of chlorophyll, fueled by ingestion of detritus or heterotrophs. However, the extrapolations indicating slight egg production by unfed females at 0 chlorophyll are more likely to be artifacts resulting from the linear regression fit to (probably) curvilinear relations (even though I restricted the analyses to stations where concentration of chlorophyll was low enough that linearity should pertain). In summary, the relations of production to chlorophyll met some but not all of the expectations for the relations between a food-limited reproductive rate and the biomass of usable food.

In principle, the best measure of potential production rate (a rate not limited by food) should be the production by females during the second day of feeding, and an effect of the size of the females on the rate of production might be detectable. For example, Runge (1984) showed that the clutch size of *C. pacificus* increased approximately from 22 to 50 eggs·female^{-1} as prosomal length increased from <2.1 to 2.8 mm. In my incubations, *Calanus* produced approximately 38 eggs·(female·day)$^{-1}$ on the second day when provided with *Thalassiosira*, suggesting that clutches are produced daily, but there was still considerable variation, and no significant increase for larger females within the range of sizes I encountered (figure 16). Analysis of variance showed that temperature at each station explained little of this variability.

It is possible that production of eggs by copepods injured during capture, anesthesia, or sorting is inhibited (or stimulated before the incubation, leaving the females spent), though the tests of capture and anesthesia reported above did not demonstrate this. If the incidence of such injury varied between stations, and if it reduced survival as well as egg production, there might be a positive correlation between production by well-fed females (i.e., those on the second day in supplemented food) and their survivorship in the incubations. I examined data from all eight cruises for such correlations; there were significant (1-tailed p <0.025), positive correlations for cruises 8904, 8907, and 8911. This may indicate that injury contributed to variable production of eggs, but the evidence is still ambiguous, since such positive correlations might also exist because of naturally variable states of health, even without injury.

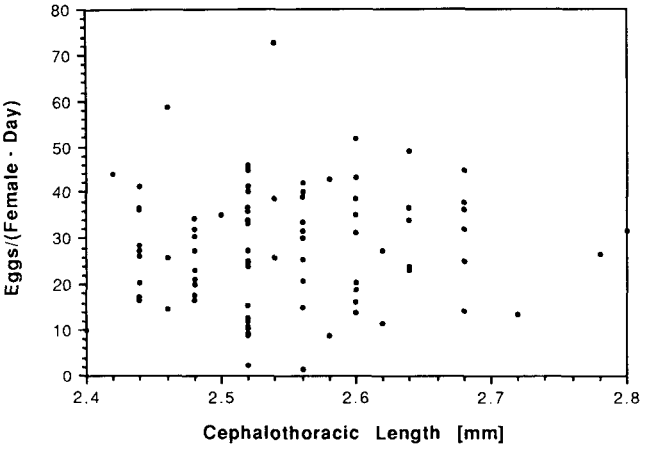

Figure 16. Production of eggs during the second day by female Calanus fed Thalassiosira, as a function of cephalothoracic (prosomal) length, in mm, for three 1989 cruises. The relation is nonsignificant.

As noted in Methods, ratio b should increase, and ratio c decrease, as limitation of egg production by the ambient food supply becomes less severe. Figure 17 shows that variation in these ratios supports the hypothesis that chlorophyll in the water column generally relates to the effective supply of food, but that the variability is again considerable. This means that either the experimental manipulations caused great variability as an artifact, or else that there are sources of food limitation (and its alleviation) which are poorly related to the areal distribution of total chlorophyll.

DISCUSSION

The mesoscale geography of growth rates of the *Calanus* population is the product of the maps in figure 11 and maps of the abundance of females. This geography is significant with respect to the locations of food production for larval fish (many of which rely on copepod nauplii for much of larval life), to the areas and seasons where the population

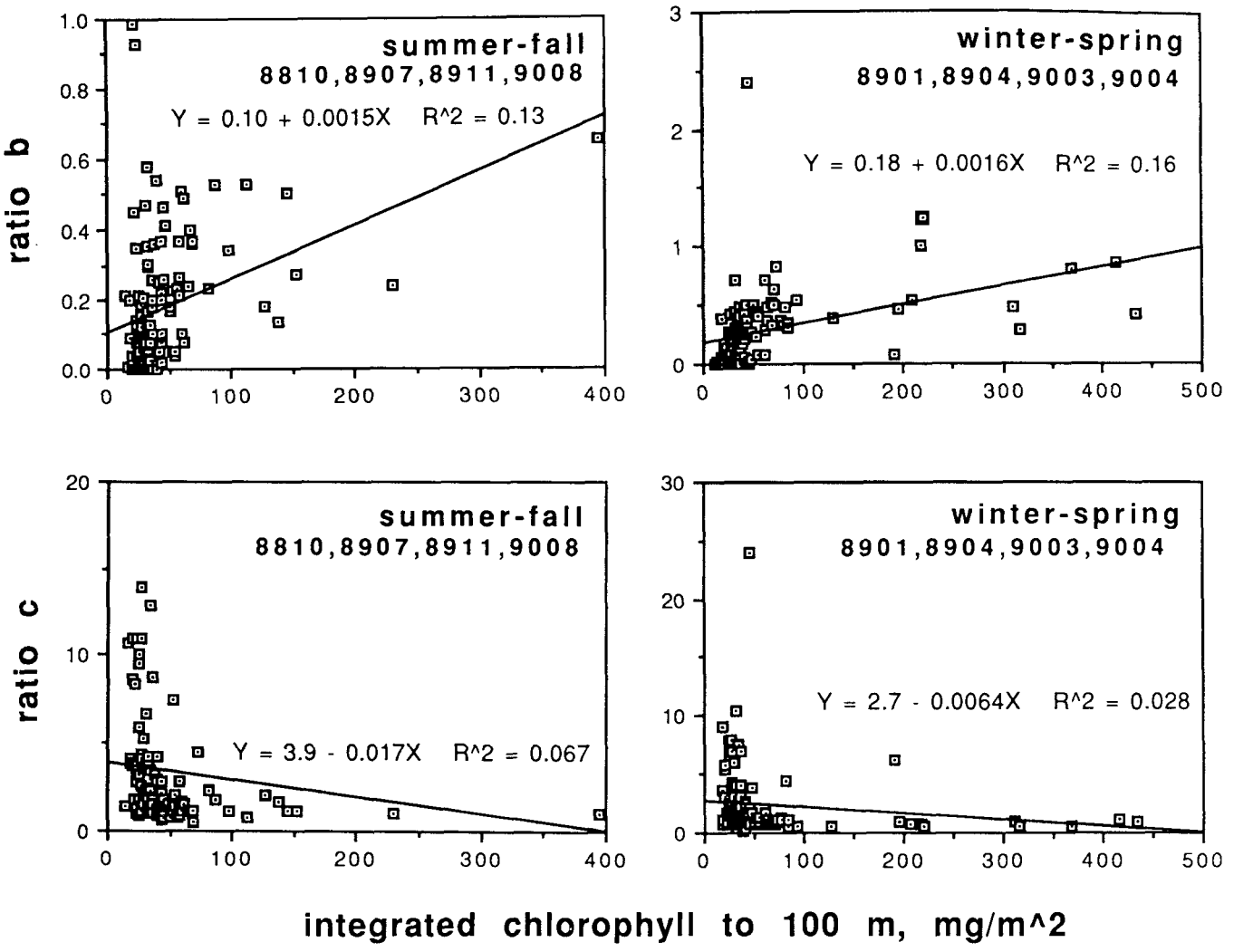

Figure 17. Ratios b (*top*) and c (*bottom*) versus integrated chlorophyll, for cruises grouped by season (four cruises per season). See Mullin 1991 concerning the relations for ratio b on four individual cruises. For ratio c, two summer-fall and three winter-spring values >50 have been eliminated; curvilinear (logarithmic and exponential) fits explained approximately twice as much of the variability. In all of the four cases, $p < 0.05$, 1-tailed.

will wax or wane (natality–mortality), and to the relative importance of immigration and emigration by advection, which also has a mesoscale structure (e.g., Roemmich 1989).

The great areal extent of egg production in January 1989, and the generally high rates in the northern and inshore regions on other cruises indicate that low temperature near the surface is not the rate-limiting factor for reproduction in the studied area. If anything, per capita reproductive rates are low in the areas and seasons of elevated temperatures, though because these are also areas of low biomass of chlorophyll the actual cause is ambiguous. *Calanus pacificus* ranges as far south as Cabo San Lázaro in Baja California (Fleminger 1964, as *C. helgolandicus*), but is most abundant south of Point Conception in nearshore regions, and the southern limit of reproduction is not known. Cool temperatures, but not phytoplanktonic food, can be found below the euphotic zone, and much of the population of late copepodite stages of *Calanus* off southern Baja California is deep-living and nonmigratory, at least at times (Longhurst 1967).

Some mesoscale relations are suggested, in spite of the coarseness of the pattern of sampling. On cruise 9003 (figure 8) in particular, the station immediately adjacent to Point Conception was characterized by low temperature, moderately low chlorophyll concentration, and low egg production. These are probably symptoms of, and responses to, intense localized upwelling, since near-surface O_2 concentration was only about 50% of saturation, and salinity was 0.2–0.4 ‰ higher than at adjacent stations.

On both conceptual and empirical grounds, the relation between per capita rate of egg production and concentration of food should be quasi-hyperbolic (the rate increasing with increasing concentration until some other environmental or physiological limit becomes crucial), possibly with a positive abscissal intercept (a threshold concentration necessary to initiate egg release). Figure 4 of Mullin 1988 summarizes most of the relevant measurements that have previously been reported. Within the range of natural concentrations of seston in the open ocean, however, saturating concentrations may seldom be approached, so a linear increase in rate with increasing biomass of seston might adequately describe such data.

Runge (1984) found experimentally that the relation between rate of egg production of *Calanus pacificus* (from Washington waters) and food indicated saturation above approximately 250 mg $C \cdot m^{-3}$. This is approximately 4 mg chlorophyll$\cdot m^{-3}$; as shown in figure 1, such concentrations were present at only a few stations — those where the integrated biomass exceeded 100 mg chlorophyll$\cdot m^{-2}$. In Runge's study, egg production ceased if the concentration of phytoplankton was less than 50 mg $C \cdot m^{-3}$, or 0.8 mg chlorophyll$\cdot m^{-3}$. Peterson (1988) found experimentally that still higher concentrations of phytoplankton were necessary to saturate egg production of the related species *Calanus marshallae*, from Oregon.

Comparison of figure 15 with Runge's and Peterson's data is inexact for two major reasons. First, non-phytoplanktonic organic seston is available to *Calanus* throughout the California Current, and some fraction of this, such as microzooplankton and some part of the detrital carbon, is likely to be nutritious (e.g., Eppley et al. 1977). Second, at least half of the total chlorophyll is likely to be in phytoplankters too small to be grazed readily by *Calanus* (e.g., Mullin and Brooks 1976), and this fraction is likely to be greater offshore and where total biomass is low than nearshore where it is high (Eppley et al. 1977; Reid 1983). Because of these opposing problems, the biomass of chlorophyll could either overestimate or underestimate the concentration of food as perceived by *Calanus* (or both, in different locations or times), even if the copepods were distributed uniformly through the upper 100 m so that the vertical structure was unimportant.

If other measures of seston were available for these cruises, it would be interesting to attack this problem "in reverse," by determining the size category or measure of sestonic biomass with which the rate of egg production was most tightly correlated (cf. Mullin and Brooks 1970; Checkley 1980b). Based on the experimental studies with other species of copepods (Checkley 1980a; Kiørboe 1989), particulate nitrogen would be a particularly valuable addition, since it is more limiting to egg production than is carbon when phytoplankton cultured so as to differ in C/N ratio is used as food. However, Eppley et al. (1977) reported that ratios of organic carbon to nitrogen were relatively invariant in the seston of the Southern California Bight, and close to the ratio that, when phytoplankton is the food, results in maximally efficient use of ingested carbon as well as nitrogen in production of eggs. Thus particulate nitrogen may covary so closely with chlorophyll that distinguishing it as a more precise predictor of egg production by goodness of fit (rather than by controlled experiments) would be difficult (though Checkley [1980b] concluded that food limitation was better estimated by phytoplanktonic than by total particulate nitrogen).

Because there was a strong relation between integrated chlorophyll per unit surface area and the maximal concentration in the water column (figure 1), the relations of reproductive rate to maximal chlorophyll were no more precise than those to integrated chlorophyll: in only three of the eight cruises (8901, 8907, and 9008) did a regression against the maximal concentration of chlorophyll account for more of the variability in egg production rate than did the regression against integrated chlorophyll. Moreover, Napp et al. (1988b) showed that at stations in the Southern California Bight there was little vertical variation in the nutritional quality per unit biomass of the seston, at least as indicated by analysis of protein, carbohydrate, and lipid. Thus it is difficult to argue that a strong vertical association between female *Calanus* and a particularly nutritious layer, obscured by the vertically integrated sampling, caused the scatter observed in figure 15.

Even assuming that the biomass of chlorophyll is correlated with what a female copepod perceives as food, a relevant question is the degree to which the chlorophyll biomass measured at a single station is representative of the surrounding area, and therefore also of the recent past biomasses experienced by the copepods captured there. If horizontal patches of chlorophyll of high intensity but small spatial scale (and therefore small temporal persistence) were characteristic, females captured at different stations with similar concurrent chlorophyll biomasses could have had quite different nutritional histories, and hence reproduce at quite different rates in both ambient and food-enriched incubations.

There are several reasons for believing that this is not the dominant source of variability shown in figure 15. First, there is large-scale pattern to the chlorophyll distribution (panel B in figures 3–10); the maps are not mosaics of different individual stations, and regions of similar biomasses tend to be contiguous. Second, horizontal patchiness within the distance integrated by a net tow, which might create variability between the females within one incubation, can be almost as great as that between adjacent stations. For instance, Mullin (1979, figure 2) found relatively little increase in horizontal, longshore heterogeneity of chlorophyll in the euphotic zone of the Southern California Bight on scales from 100 m to 10 km in March, and Star and Mullin (1979, 1981) found that horizontal patchiness of near-surface chlorophyll in the coastal zone (in the longshore direction), offshore California Current, and North Pacific Central Gyre in July was either relatively minor or not statistically detectable. Certainly there are some fronts or other steep gradients in the horizontal distribution of chlorophyll in the region surveyed, but the results summarized above, though limited to specific times, imply that such fronts are not common enough to cause great variability in rate of egg production between females from stations with similar biomasses of chlorophyll at the time of sampling.

Finally, figure 2 (upper panels) shows that reproductive rates estimated from parallel incubations of females from the same station in the same unsupplemented seawater can vary considerably. This variability is unexplained, but patchiness of chlorophyll around a station could play a role only if it caused female copepods of differing nutritional states to be present (this is certainly possible because of the integrative nature of the collecting tow) *and* if these different states were quite unevenly distributed among the replicate incubations. Alternatively, artificial differences between incubations in the incidence of injured females, or chance differences in the proportion of females releasing batches of eggs, could be responsible.

In a larger-scale study, Hakanson (1987) compared the wax ester and triglyceride contents of CV *Calanus* to chlorophyll in the water column of the California Current system; he found that these two lipid types (representing long- and short-term storage, respectively) were strongly correlated. *Calanus* could be lipid-rich or lipid-poor where the concentration of chlorophyll was relatively small (the lipid-rich copepods presumably having recently grazed down larger concentrations of chlorophyll, or fed on non-plant food), but were always lipid-rich where concentrations of chlorophyll were large. This would not be likely if the patches of elevated concentration were very small. Nor did the variability in lipid content of *Calanus* at a station relate to the vertical variability of chlorophyll there, again suggesting that small-scale patchiness of chlorophyll is not reflected in storage lipids.

Variation in per capita reproduction by *Calanus* within the Southern California sector of the California Current suggests that limiting factors vary geographically. The poor correlations between reproduction by unfed females and ambient biomass of chlorophyll (figure 15) and between ratios b and c and chlorophyll (figure 17) therefore mean either that chlorophyll is an imprecise measure of the rate-limiting food (though, as noted above, it is strongly correlated on some scales with other possible "bulk" measures), or that there are factors other than concurrent nutrition which also affect reproductive rate but vary geographically quite differently from chlorophyll. Even after a day of feeding in excess food, when all females might be expected to produce eggs at nearly the same rate, there is a large scatter (figure 16), which supports the latter explanation.

If the source of variability was food limitation that could be negated by a day's feeding, one would expect egg production during 24–48 hours in excess food to be either uncorrelated with that during 0–24 hours (i.e., variability during the second period removed by one day's feeding) or negatively correlated with it (well-nourished animals would produce eggs during the first 24 hours and be spent during the second 24, while poorly nourished ones would not produce eggs until the second period). In fact, the per capita egg production of well-fed animals during the second 24 hours was positively correlated with their production during the first 24 (figure 18, $p << 0.01$), and had almost as great a range (though failure to lay any eggs was much more common on the first than on the second day). This persistence of variability again suggests that small-scale patchiness of food around a station is not the sole cause of the variability shown in figure 15. Though there was a geographic pattern to body size (panels H in figures 4–6), this did not explain variability in maximal reproductive rate (figure 16). Analysis of the geographical pattern of population genetics might be revealing, but the possible role of injury on egg production must be assessed first.

In any case, a consequence is that maps of integrated chlorophyll concentrations, whether derived from shipboard or remotely sensed data, may be of little value in predicting the per capita reproduction by *Calanus* at particular stations. Such maps will also

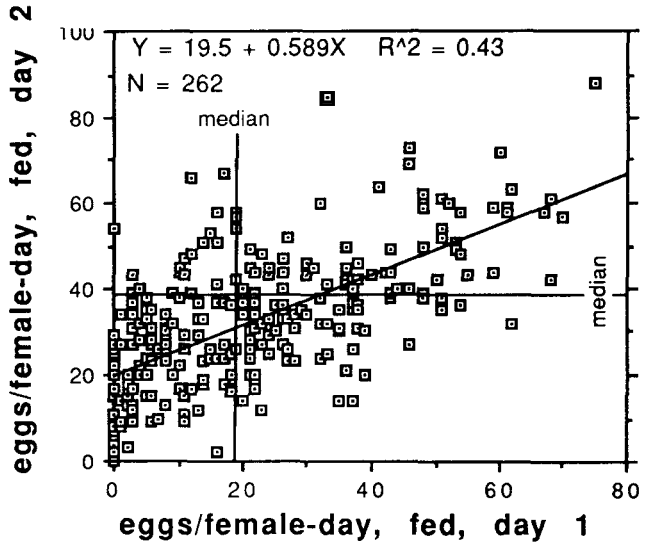

Figure 18. Production of eggs during the second day by female *Calanus* fed *Thalassiosira*, as a function of that on the first day, for all eight cruises. Medians for each day are shown. The correlation is significant at $p << 0.01$, 2-tailed.

not help predict the population's reproductive rate unless the abundances of females are more strongly correlated with chlorophyll than are the per capita rates. Other species will differ in geographical pattern, of course; if the per capita reproductive rate of females represents secondary productivity per unit biomass generally (reproduction plus somatic growth), it is possible that total secondary production by mesozooplankton (those large enough to be retained in the 500-μm mesh) is correlated with biomass of chlorophyll (which is often correlated with primary production: e.g., Hayward and Venrick 1982; Eppley et al. 1985; Mullin 1991). It would be rash, however, to conclude from present evidence that rates of primary and secondary production are tightly linked, except on the largest scales.

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