REPRODUCTION BY THE OCEANIC COPEPOD *RHINCALANUS NASUTUS* OFF SOUTHERN CALIFORNIA, COMPARED TO THAT OF *CALANUS PACIFICUS*

MICHAEL M. MULLIN
Marine Life Research Group
Scripps Institution of Oceanography
University of California, San Diego
9500 Gilman Drive
La Jolla, California 92093-0218

ABSTRACT

Measuring zooplankters' rate of egg production can provide estimates of secondary production and of the availability of food for many larval fish. Superficially, *Rhincalanus nasutus* and *Calanus pacificus* have similar ecologies; conditions for successful rearing in the laboratory are similar, as are rates of egg production when females are held in the laboratory with excess food; also, the abundances of the two species are positively correlated through space and time. Rates of egg production by these two species in the southern California sector of the California Current were measured in the winters and springs of 1991–93 by holding females in the ambient seawater and in seawater enriched with phytoplanktonic food. At many locations, female *Calanus* produced eggs when in the unenriched seawater; they almost always did so when food was enhanced with cultured phytoplankton. In contrast, *Rhincalanus* seldom produced more than 10 eggs·(female·day)$^{-1}$ except when incubated with excess food for 2 days, and even then, the spatial/temporal patterns of egg production differed from those of *Calanus*. Future work should focus on whether there are conditions (season, food, etc.) permitting high reproductive rates in *Rhincalanus* feeding on the natural seston off southern California; i.e., >10 eggs·(female·day)$^{-1}$.

RESUMEN

La disponibilidad de alimento para muchas larvas de peces, así como la producción secundaria, pueden ser estimadas con mediciones de tasas de producción de huevos de zooplancton. Superficialmente, las ecologías de *Rhincalanus nasutus* y *Calanus pacificus* se asemejan. Las condiciones para su cultivo en laboratorio son similares y las tasas de producción de huevos en laboratorio (con dietas de saciedad) son asimismo similares. Además, la abundancia de éstas especies se encuentran correlacionadas positivamente, espacial y temporalmente. En los inviernos y primaveras de 1991–93, en la corriente de California (frente a California sur), se midieron las tasas de producción de huevos de las dos especies; se pusieron hembras en aguas "no tratadas" y en "aguas enriquecidas con fitoplancton cultivado". *Calanus* hembra produjeron huevos en varias estaciones con "aguas no tratadas". Por otro lado, hubo producción de huevos en casi todas las estaciones con "aguas enriquecidas con fitoplancton cultivado". En contraste, *Rhincalanus* raramente produjeron más de 10 huevos (hembra·dia)$^{-1}$. La excepción fué el tratamiento de dieta de saciedad durante dos días, y aun así, los patrones espacio-temporales de producción de huevos difirieron a los de *Calanus*. Estudios futuros deberán enfocarse en discernir si para *Rhincalanus* (con dieta de seston natural) existen condiciones (estación del año, alimento, etc.) en los mares de California sur que produzcan altas tasas de reproducción; es decir, >10 huevos (hembra·día)$^{-1}$.

INTRODUCTION

The rate of reproduction by planktonic copepods is an important indicator of population growth and secondary production. Comparing rates in ambient seawater and in the presence of excess food indicates how much these demographic rates are limited by the natural food supply (e.g., Durbin et al. 1983; Ayukai 1988). But it is difficult to determine the effective natural concentration of food because neither the small-scale spatial distribution of copepods relative to where point samples of seston (potential food) are taken nor the property of seston that is most significant to reproduction (e.g., chlorophyll, particulate organic carbon or nitrogen, a critical amino acid, a particular size and type of particle) are usually known. Further, the genetic constitution and past nutrition of female copepods used in experiments is also unknown, though both can affect reproduction and the response to food. Finally, different species may respond differently to the supply of food, or to the proxy variable for food, even if their trophic type, seasonality, and biogeography seem the same.

To compare the reproductive geography of two similar species of large, planktonic, particle-graz-

ing, calanoid copepods, as well as their responses to chlorophyll biomass, I measured the egg production of female *Rhincalanus nasutus* at several locations in the southern California sector of the California Current system, and contrasted the patterns of reproduction to those of the more intensively studied species *Calanus pacificus* (see Mullin 1991a, and references therein) at the same locations.

Earlier work (Mullin and Brooks 1967, 1970; Hakanson 1987) compared metabolic and demographic properties of the two species, including feeding and growth when the diatom *Thalassiosira weisflogii* (= *fluviatilis*) was provided as food. In these studies, the similarities between the two species were more striking than their differences. Both extend into the southern California sector from farther north, not south or west, and both can range farther south to the tip of Baja California (Fleminger 1964), but the southern limits of reproduction and recruitment are not known. This zoogeography led me to expect that *Rhincalanus* would reproduce most readily in the northern part of the region I studied.

Longhurst et al. (1966) found the vertical distribution of *Rhincalanus* to overlap that of *Calanus* in the upper 150 m off San Diego in May, but to extend deeper, to at least 500 m. Populations of the two species were studied concurrently off La Jolla, California, in 1967. From this set of data, Koslow and Ota (1981) found indirect evidence of a difference between the species in the seasonal pattern of diel vertical migration relative to diatom blooms, and Mullin (1991b) found that though rates of juvenile mortality of both populations were density-dependent, the space/time distributions of these rates were uncorrelated between the species.

METHODS

Similarity in the mesoscale distributions of *Rhincalanus* and *Calanus* imply ecological similarity. I therefore counted females of both species in samples taken by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) from January and April 1989 and March and April 1990 (cruises 8901, 8904, 9003, and 9004) and tested whether the abundances correlated.

In June 1969, I found spermatophore-carrying (i.e., newly mated) female *Rhincalanus* in net tows made off La Jolla. I placed 13 of these individually in 1-liter beakers of filtered seawater with cultured *Thalassiosira* added as food. No precautions were taken against cannibalism. The beakers were kept at 15°C for up to 4 months, and every 1–4 days I removed and counted eggs and nauplii, replaced the seawater, and added fresh food.
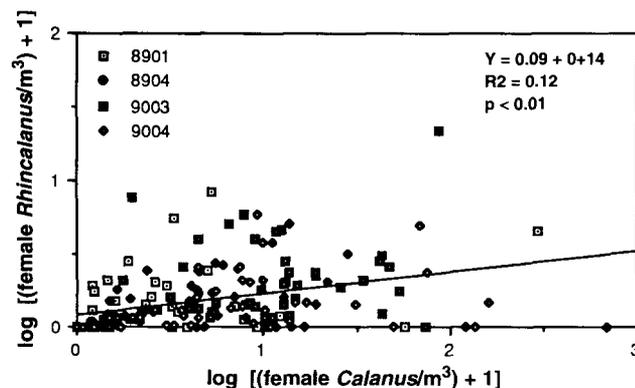

Figure 1. Abundances (log-transformed) of female *Rhincalanus* and *Calanus* in the upper 200 m of the region of study in January and April 1989 and March and April 1990 (cruises 8901, 8904, 9003, and 9004). See figure 3 for region. The correlation is significant at $p < 0.01$.

On several CalCOFI cruises, I measured the production of eggs during 2 days' incubation in seawater plus natural seston ("unfed"), and in the same seawater enriched with *Thalassiosira* ("fed"), by female *Rhincalanus* captured in net tows at various stations, with methods described in Mullin 1991a. The measurements were made irregularly in April and August of 1990 (cruises 9004 and 9008), and at all stations where sufficient animals were captured in January and March 1991 (cruises 9101 and 9103), February and April 1992 (cruises 9202 and 9204), and January 1993 (9301). I measured the per capita reproduction of *Calanus* similarly. In addition to determining the daily production rate of both species with and without supplemental food, I used two ratios (from Mullin 1991a) to express the degree by which food limited production: the ratio (b) of the total production over 2 days of unfed females to that of fed ones, and the ratio (c) of the production of fed females during the second day to that of the same copepods during the first day. Ratio b increases, and c decreases, as food becomes less limited.

Female *Rhincalanus* eat the dinoflagellate *Gymnodinium splendens* and naupliar *Artemia* (Mullin and Brooks 1967, 1970), so I tested how these two alternate foods stimulate fecundity, although neither is as convenient to use at sea as is *Thalassiosira*. Neither resulted in egg-laying rates as high as those when *Thalassiosira* was the supplemental food.

RESULTS

As shown by the example in figure 1, the areal distributions of the two populations in the southern California sector of the California Current are similar on the large scale (the statistically significant trend) but far from identical on smaller scales (the scatter). *Calanus* is the more widespread (fewer absences) and generally the more abundant of the two.
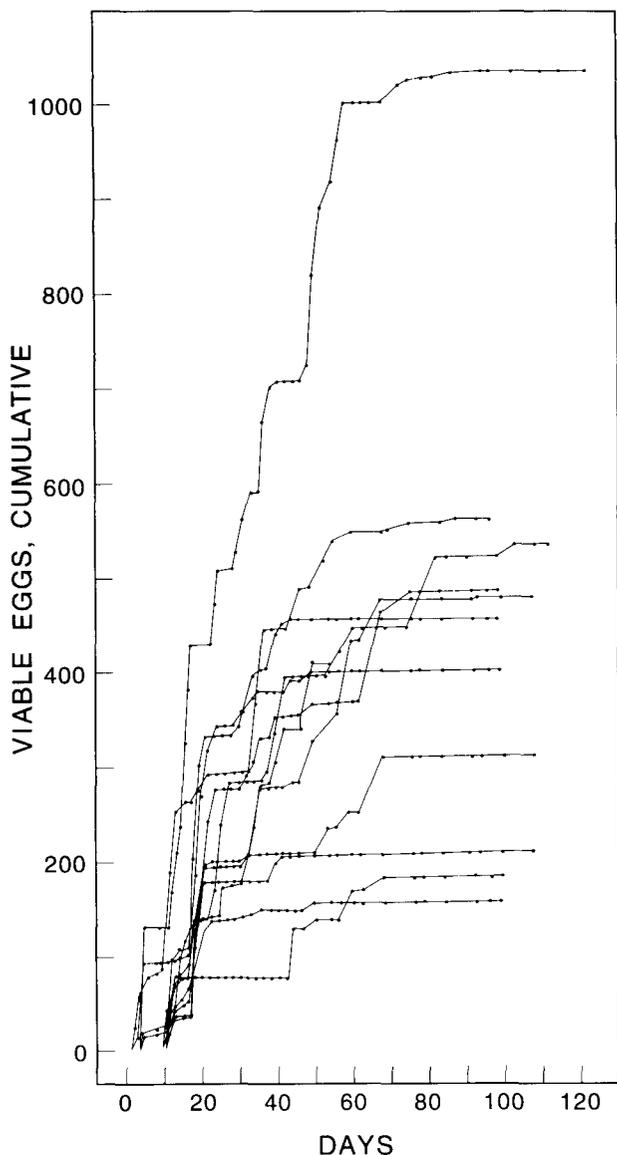
Figure 2. Cumulative production of eggs by 12 newly mated female *Rhincalanus nasutus* fed *Thalassiosira* in the laboratory. The history of another female which produced a total of 1042 eggs is not shown.

Individual female *Rhincalanus* maintained in the laboratory could produce up to 95 eggs in 1–2 days, and over 1000 eggs during adult life (figure 2). The maximal daily production rate slightly exceeded greatest rates by *Calanus* from the same area (Mullin 1991a, figure 18). Mean lifetime fecundity of *Rhincalanus* was 478 eggs; the median was 449 (compared to about 650 for *Calanus*; Mullin and Brooks 1967). Because of the possibility of cannibalism in the 1-liter containers in which females were held, these estimates must be considered minimal. Thus, female *Rhincalanus* are reproductively active at 15°C as far south as La Jolla, at least at times, when fed *Thalassiosira* over long periods.

In April 1990 *Rhincalanus* produced very few eggs south of Palos Verdes unless food was supplemented, and even then did not approach the reproductive rate of *Calanus* at these stations (Appendix). Reproduction did not equal that of *Calanus* even farther north (unfortunately, no samples were taken north of Point Conception during this cruise). Similarly, there was little reproduction by *Rhincalanus* south of Palos Verdes in August, and only one station in the entire area where eggs were laid in the absence of added food, although *Calanus* was reproductively active at several stations (Appendix). With one exception on the two cruises, *Rhincalanus* produced ≥ 10 eggs·(female·day)$^{-1}$ only when fed for more than 24 hours. The impressions resulting from these two cruises, where sampling of *Rhincalanus* was sporadic, are that conditions at many stations (or the condition of the females themselves), though suitable for *Calanus* to reproduce, were unsuitable for *Rhincalanus*, especially in August.

Figures 9 and 10 of Mullin 1991a show the reproductive geography of *Calanus* during these two periods more completely. They also show the temperatures at 10 m (approximately the temperature of the shipboard incubations) and integrated biomasses of chlorophyll; comparison with the Appendix table suggests that *Rhincalanus*'s reproduction was more inhibited by scarcity of food (as indicated by sparse chlorophyll) or high temperature than was *Calanus*'s reproduction. In April there was no clear relation between *Rhincalanus*'s reproduction and the chlorophyll biomass at the same stations; in August the only reproduction was at three stations where chlorophyll exceeded 80 mg·m^{-2}. As noted above, this could be either an experimental artifact or a symptom of longer-term limitation: perhaps reproduction would have been greater with other conditions of incubation, or perhaps the females were physiologically incapable of intensively producing eggs within two days under any conditions.

I will present the more extensive measurements of egg production made in January and March 1991 (cruises 9101 and 9103) and February and April 1992 (9202 and 9204) as if they had been made in consecutive months of one year, thus emphasizing seasonality and suppressing interannual variability. Interannual variability might well be important, since the winter of 1992 was characterized by El Niño conditions (Hayward 1993). The distributions of temperature and chlorophyll biomass during these cruises are shown in figure 3, and the actual daily rates of per capita egg production in the Appendix.

In only one case in January 1991 did unfed *Rhincalanus* produce eggs; only once did fed *Rhincalanus*
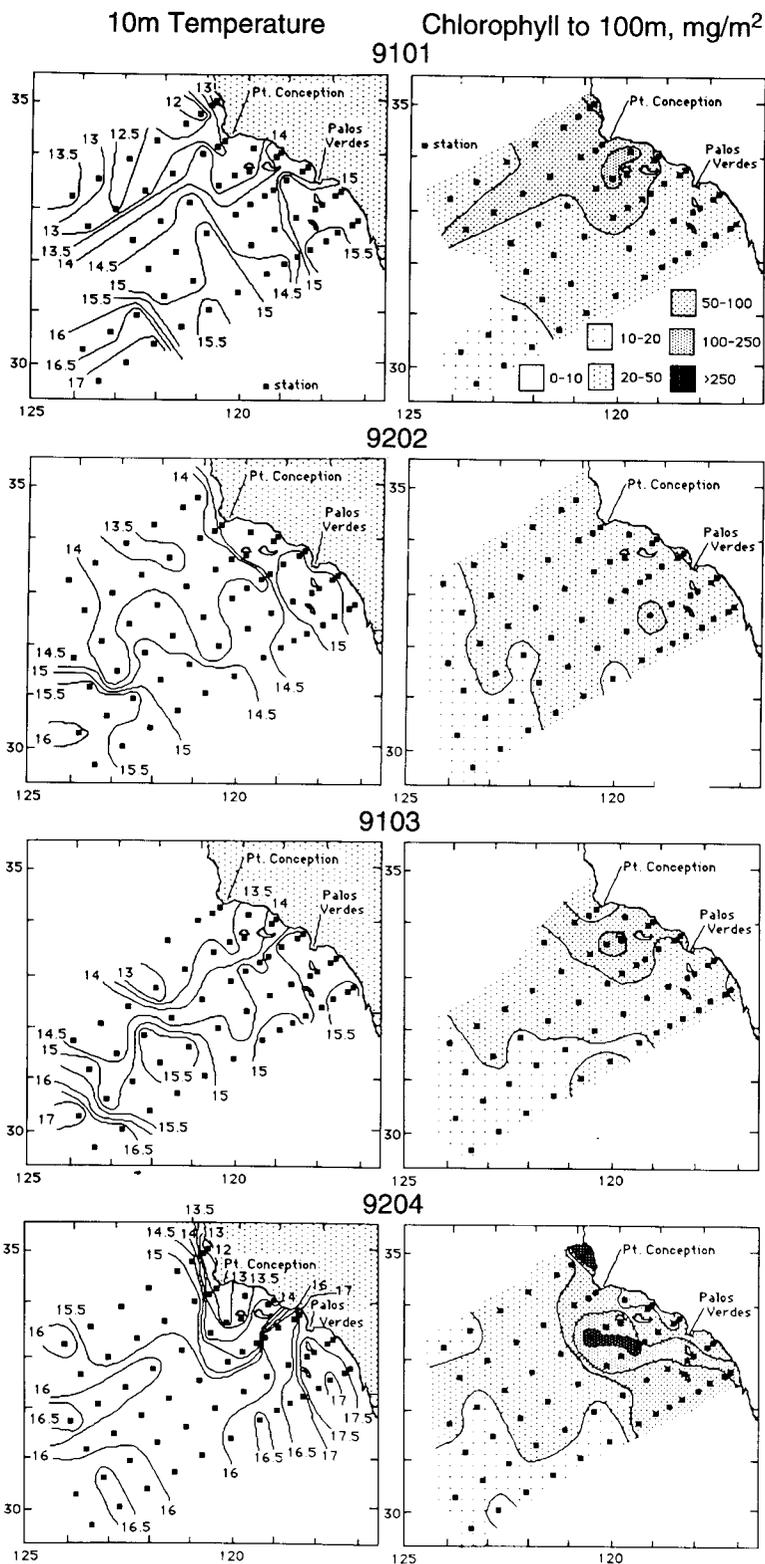
Figure 3.   Distributions of temperature at 10 m, and integrated chlorophyll (mg·m⁻², to 100 m) in January 1991 (9101), February 1992 (9202), March 1991 (9103), and April 1992 (9204).
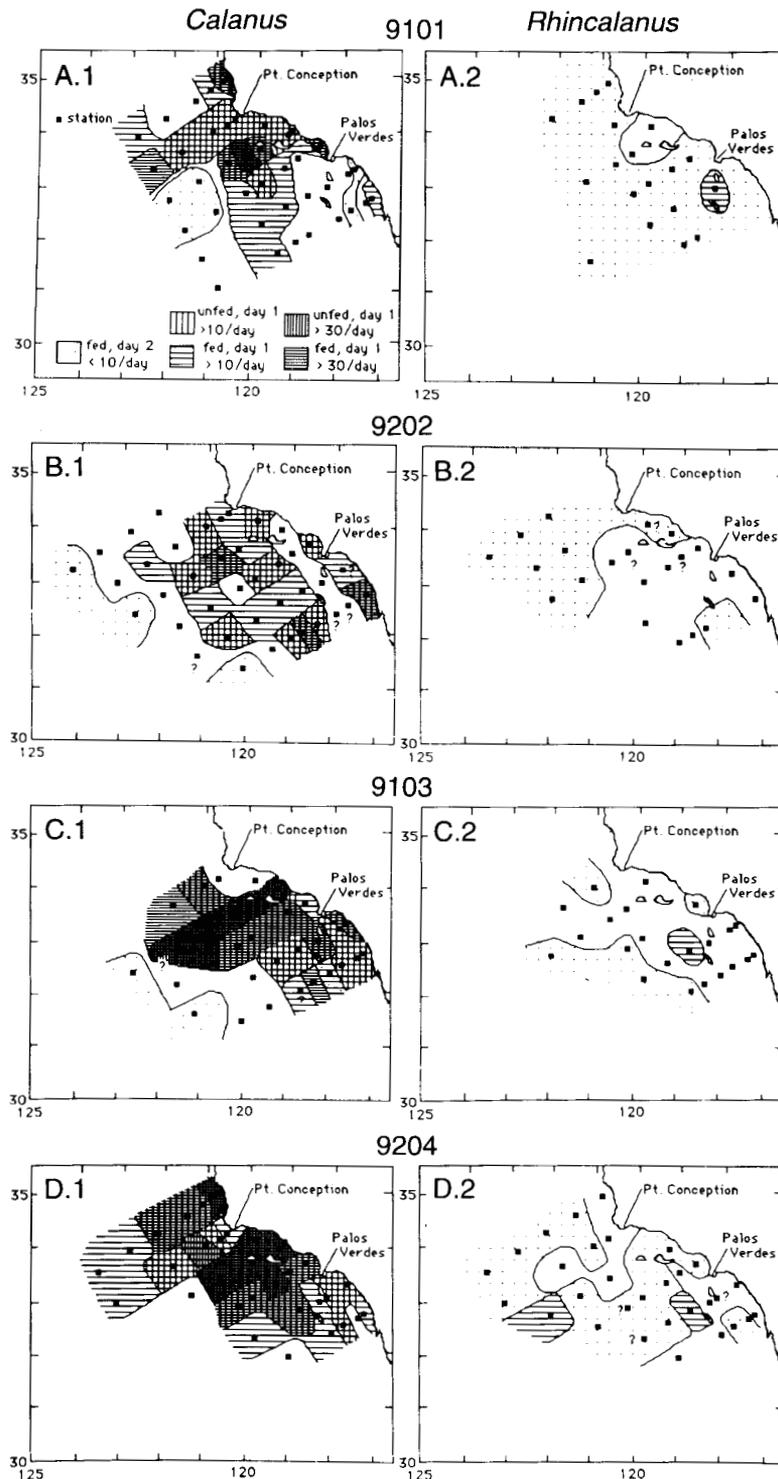
Figure 4.   Contour maps of egg production by *Calanus* (*1*) and *Rhincalanus* (*2*) on cruises 9101 (*A*), 9202 (*B*), 9103 (*C*), and 9204 (*D*). Poorest production is in stippled regions; clear regions represent rates of <10 eggs·(female·day)⁻¹ on the first day, with or without supplemental food, but production exceeding this on the second day with food.

produce as many as 10 eggs·(female·day)$^{-1}$ on the first day (horizontally striped area in figure 4A.2), and at only two additional stations did the per capita rate exceed this value on the second day (nonstippled areas in figure 4A.2). The rate of production by *Calanus* in unsupplemented seawater south of Palos Verdes was generally small, but, unlike *Rhincalanus*, female *Calanus* were ready to reproduce at much

EGGS/FEMALE-DAY, FED, DAY 2
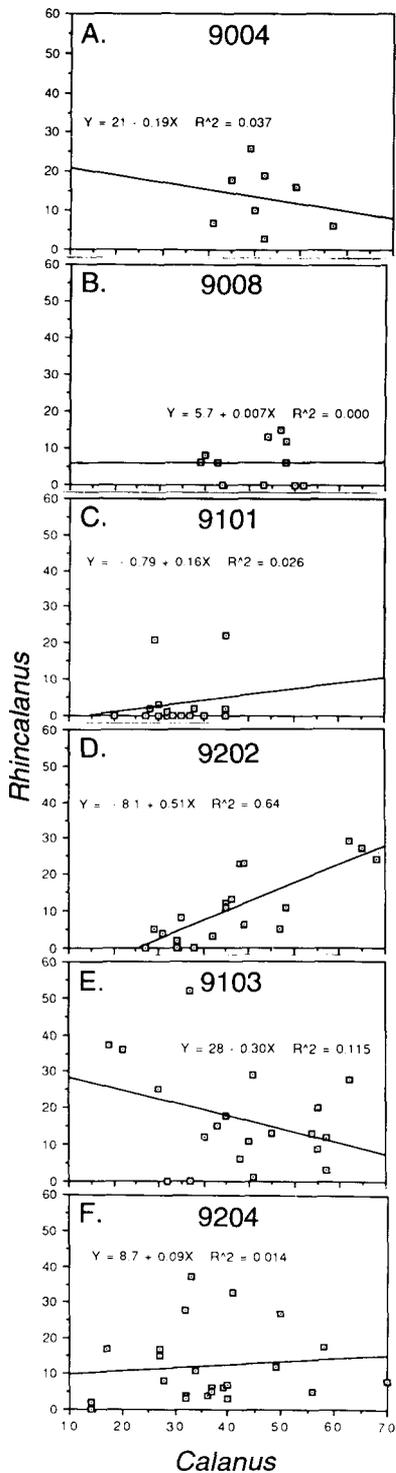
Figure 5. *A–F*. Egg production of fed *Rhincalanus* on the second day of incubation versus that of *Calanus*, for 6 cruises. Only the correlation for cruise 9202 was statistically significant ($p < 0.01$).

greater rates in the presence of excess food (horizontal striping in figure 4A.1). North of Palos Verdes, *Calanus* was reproductively active at many stations,

even in the unsupplemented seawater, where *Rhincalanus* was not (figure 4A.1 and 2; see also figure 5C). *Rhincalanus*'s reproduction was food-limited everywhere; food limitation affected *Calanus*'s reproduction much less north of Palos Verdes than south of it (figure 6A.1 and B.1).

The lack of egg production by *Rhincalanus* at even the northernmost stations of 9101 makes it unlikely that high temperature, per se, caused *Rhincalanus*'s failure to reproduce at many southern stations where *Calanus* did reproduce.

In February 1992 (9202; figure 4B.1 and 2) no measurements were made north of Point Conception. The distribution of chlorophyll was relatively uniform (figure 3), the absence of elevated biomass around Point Conception perhaps being due to El Niño. There were no stations at which female *Rhincalanus* produced ≥ 10 eggs·day^{-1} on the first day of incubation, with or without supplemental food, even though *Calanus* exceeded this rate at several stations. When food was supplemented for 2 days, however, *Rhincalanus* produced ≥ 10 eggs·(female·day)$^{-1}$ at almost half the stations (nonstippled areas in figure 4B.2), primarily those in the Southern California Bight where *Calanus*'s reproduction was also strong (see also figure 5D). *Calanus*'s reproduction was food-limited more often than in January, at least as indicated by ratio b (figure 6C.1), but there was less obvious geographic pattern to this limitation. *Rhincalanus*'s reproduction was again food-limited over much of the area (figure 6C.2 and D.2).

Again in March 1991 (9103; figures 4C.2 and 5E) *Rhincalanus* on their second day of supplemental food (but, with one exception, only then) produced more than 10 eggs·(female·day)$^{-1}$ at several stations. This was true even at rather warm temperatures along the southernmost line of stations, again suggesting that temperature had not caused the poor reproduction there two months earlier (9101). Also, females incubated at 12.5°–13°C were no more fecund than those incubated at ambient surface temperatures in the southern part of the area. As on cruise 9202, no measurements were made north of Point Conception. *Rhincalanus* reproduced at stations where the concentration of chlorophyll was <80 mg·m^{-2}, a range in which little or no reproduction had occurred on cruises 9008 and 9101 (compare figure 4C.2 with 3; figure 7C.2). Again, however, *Rhincalanus* produced many fewer eggs on the first day of incubation than *Calanus* at most stations (figure 4C.1 and 2), and *Rhincalanus* was more food-limited (figure 6E and F).

Similar results were obtained in April (9204; figure 4D.2), even though several stations north of
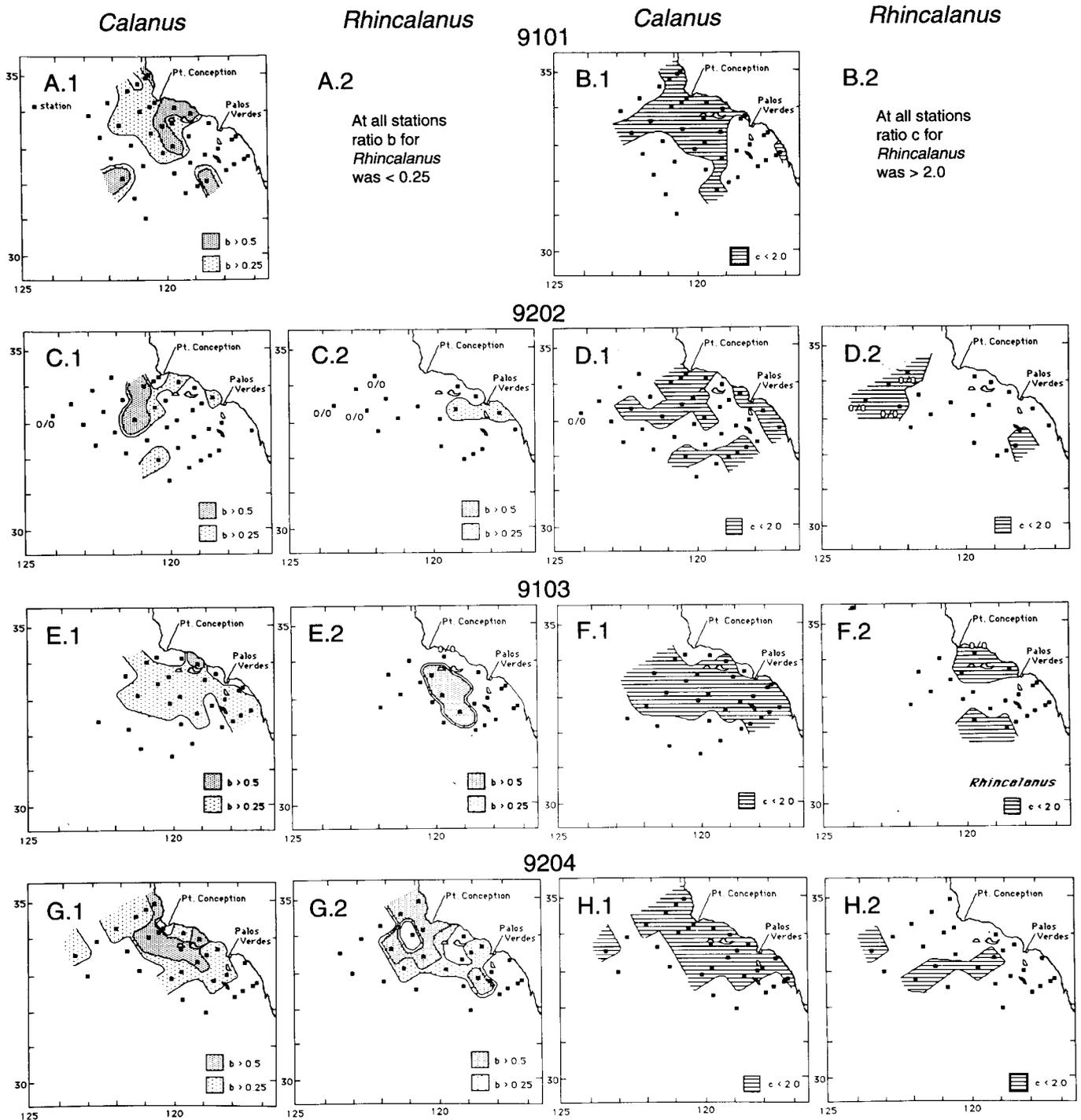
Figure 6. Maps of food limitation of egg production in *Calanus* (1) and *Rhincalanus* (2). In each case, shaded areas mean less limitation by food, as measured by ratios b (A, C, E, and G) and c (B, D, F, and H). See text for explanation of ratios.

Point Conception were sampled, and the biomass of chlorophyll was relatively great north and south of Point Conception. *Rhincalanus*'s rate of egg production was $\geq 10 \cdot \text{day}^{-1}$ at a minority of stations, and then generally as a result of two days' feeding. Again, reproduction was more likely to be stimulated by supplemental food (nonstippled areas in fig-

ure 4D.2) in the Southern California Bight than elsewhere. The reproductive rate of *Calanus* was high over much of the area (figure 4D.1).

At three northern, inshore stations of cruise 9204, *Rhincalanus* on the second day in unsupplemented seawater produced >10 eggs·(female·day)$^{-1}$ (the same rate as with supplemental food), and more than

Rhincalanus
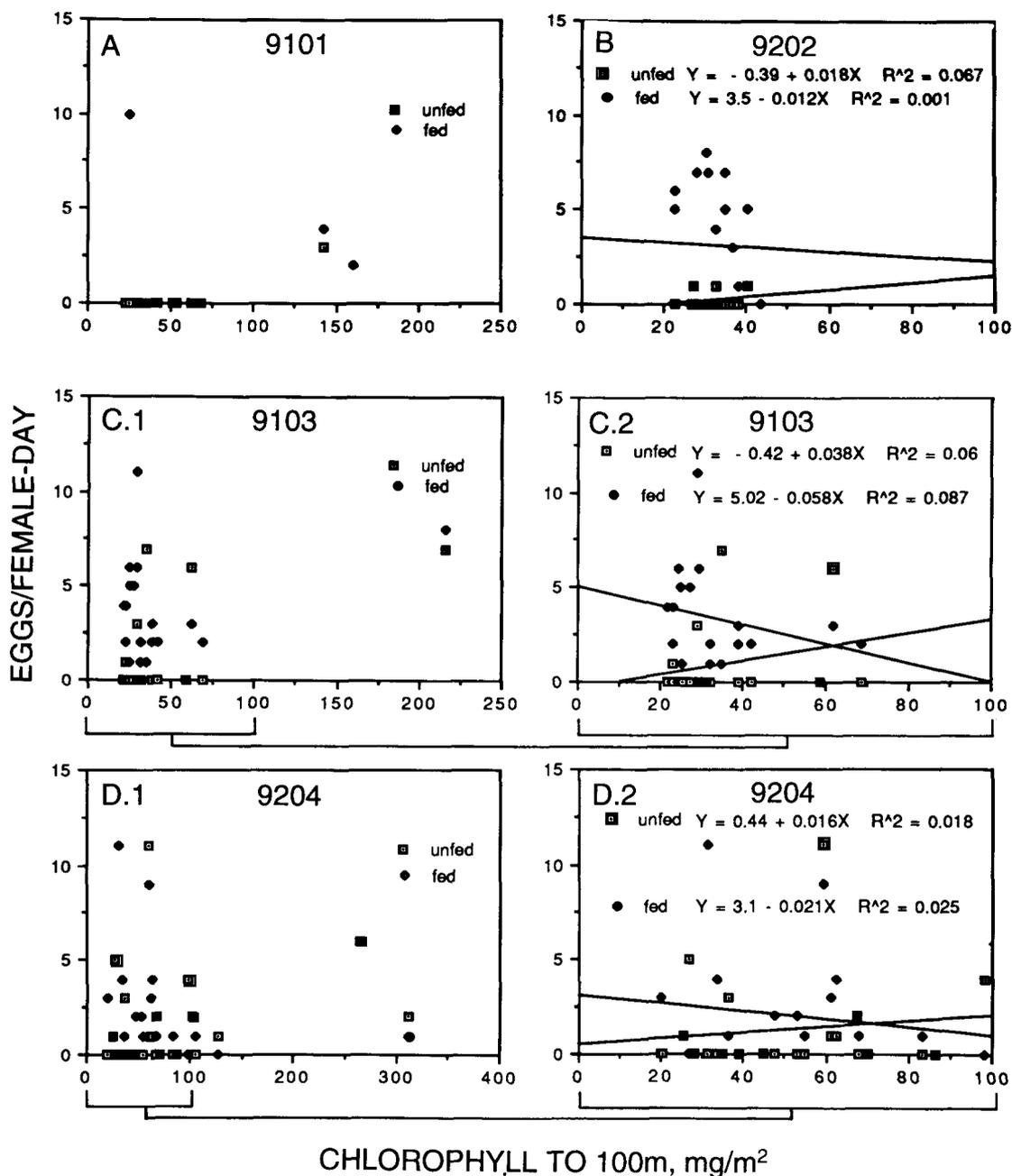
Figure 7. Relations of egg production by *Rhincalanus* on the first day of incubation, with (fed) or without (unfed) supplemental food, to the biomass of chlorophyll (see figure 3) in *A*, January 1991 (9101); *B*, February 1992 (9202); *C*, March 1991 (9103); and *D*, April 1992 (9204). For cruises 9103 and 9204, correlations were calculated only for those stations where the biomass of chlorophyll was ≤ 100 mg·m^{-2} (graph 2 in each case), because nonlinearities might occur at greater biomasses. All correlations are nonsignificant ($p > 0.05$).

five times the first-day rate. This increase virtually never occurs in *Calanus* (Appendix, and Mullin 1991a, figures 3–10), in which depleted food in unsupplemented seawater by the second day results in a rate that is either less than the first-day rate, or <10 eggs·(female·day)$^{-1}$, or (most often) both. A single station on cruise 9204 near Palos Verdes was the only

exception for *Calanus*. This result suggests that *Rhincalanus*'s reproduction is more divorced from the immediate supply of food than is that of *Calanus*.

Based on the ratios indicating the extent that the ambient food supply limits egg production at each station, *Rhincalanus*'s reproduction was more widely limited by food (unshaded areas in figure 6) on all

cruises than was that of *Calanus*. Further, most of the shaded areas for *Rhincalanus* in figure 6 were not due to strong reproduction by unfed females (as the shaded areas for *Calanus* usually were), but to very low rates even after two days with supplemental food. Since the measures of food limitation were based on the copepods' response to supplemental phytoplankton, this conclusion depends on the assumption, drawn from experimental rearing, that both species are particle-grazers, eating primarily phytoplankton.

Egg production by *Calanus* usually correlates positively with chlorophyll biomass, though there is much unexplained variability (Mullin 1991a, figure 15). However, on none of the four cruises in 1991–92 was there a significant relation between production of eggs on the first day of incubation by female *Rhincalanus*, either with or without supplemental food, and the chlorophyll biomass in the water column (figure 7). Analogous relations for *Calanus* were highly significant ($p < 0.01$) for cruises 9101 and 9103, and positive but nonsignificant for cruises 9202 and 9204. Only on 9204 was there a significant relation between *Rhincalanus*'s egg production on the second day of feeding and the biomass of chlorophyll; this relation was positive.

In January 1993 *Rhincalanus*'s reproduction was poor over much of the region, as it had been in January 1991 (compare figure 8A with 4A.2; stippled areas represent poorest reproduction) and was again food-limited at most stations (figure 8B). Unfed *Calanus* produced >10 eggs·day^{-1} at fewer stations in 1993 than in 1991, and food limitation was more widespread, but *Calanus*'s reproduction was as strong in 1993 in the presence of excess food as in 1991. Had I made more extensive measurements of *Rhincalanus*'s reproduction in April 1990 (Appendix), it might have been possible to discuss interannual variability caused by anomalies in physical properties during winter-spring 1992 (Hayward 1993). In fact, the reproductive rates of *Calanus*, and their food limitation, did not differ greatly from the situation in springs of other years (compare figures 4D.1 and 7G.1 and H.1 with figures 11, 12, and 13 of Mullin 1991a).

DISCUSSION AND CONCLUSIONS

Though additional months and years should be sampled to test the seasonality of reproduction in *Rhincalanus*, the present results suggest that it may be more marked than in *Calanus*, which produces eggs in at least the coastal parts of the region in all seasons (Mullin 1991a). In January 1991 and 1993,

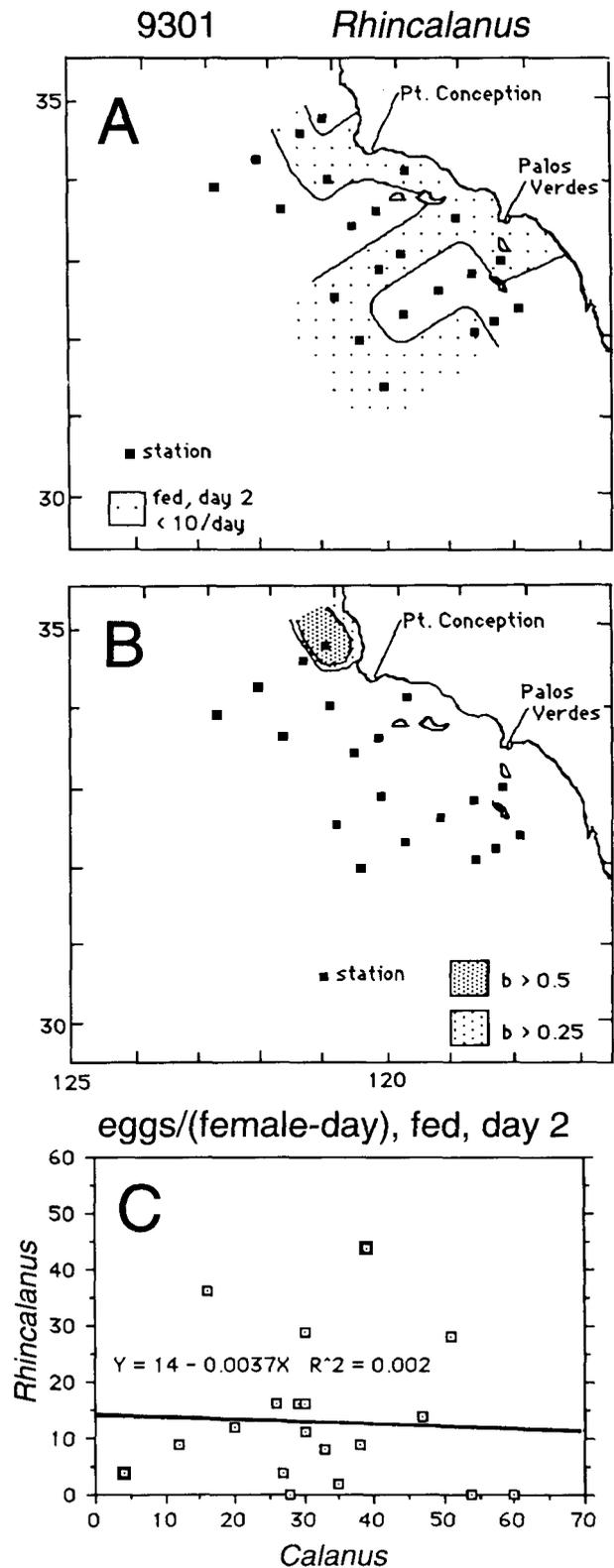Figure 8.   January 1993. *A*, Contour maps of per capita egg production by *Rhincalanus*; *B*, degree of limitation by food as reflected in ratio b. *C*, relation of egg production by *Rhincalanus* to that of *Calanus* after 2 days' feeding. Compare to figures 4A.2, 6A.2, and 5C.

Rhincalanus not only failed to lay eggs in unsupplemented seawater, but also failed, over much of the area, to respond to the presence of excess food. February–April seems to be a more favorable season, at least in terms of the potential to respond to excess food (nonstippled areas in figure 4A–D.2), and late summer is somewhat less favorable (Appendix). However, figure 2 shows that females can be stimulated to reproduce as late as June.

The production of eggs on the second day of incubation with supplemental food, more than the other measurements I made, is a measure of the reproductive potential not limited by food, reflecting the effects of the females' nutritional history and reproductive state over a longer term. If *Rhincalanus* is reproductively affected by the environment in the same way that *Calanus* is, a testable (alternative) hypothesis is that the second-day rates of production by fed females of the two species are positively correlated. As shown in figure 5A–F and 8C, this was the case only on cruise 9202, suggesting that in spite of the overall zoogeographic similarity in the area (figure 1), the two populations often differ on the scale sampled in respect to the aspects of the environment that lead to the most fecund females. On smaller scales, Mullin (1991b) concluded that the two populations also differed in sources of juvenile mortality.

These relations could arise simply from differing rates of response to food if *Calanus* females responded on the first day, *and* were to some degree spent on the second, while *Rhincalanus* required two days to respond (as seems to be the case). But since the relation between the rates of production by fed female *Calanus* on the first and second days of incubation is never negative (e.g., Mullin 1991a, figure 18), this alternative explanation is untenable.

Though the positive relation between *Calanus*'s egg production and the local biomass of chlorophyll varies considerably, the lack of any positive relation between *Rhincalanus*'s production and chlorophyll is striking, given the apparent similarities in the two species and the fact that food availability frequently limits production (figure 6), as shown by the stimulatory effect of supplementary phytoplankton.

Smith and Lane (1991) argued that reproduction in another large copepod, *Eucalanus californicus*, off central California depends in the summertime on females living in the cold, chlorophyll-rich waters of coastal upwelling or in jets originating in the coastal zone. The CalCOFI stations are too coarsely spaced to define such mesoscale features off southern California, where upwelling is generally weaker than off central California. But the results shown in

figure 7 are not consistent with a similar dependency by *Rhincalanus* in winter and spring.

For the reproductive rate of *Rhincalanus* to approach that of *Calanus* in the studied region, the females must encounter supplies of food (or perhaps other conditions) generally not represented in my experiments, or at times must respond differently. The adequacy of *Thalassiosira* for long-term production (figure 2), and for rearing from egg to adult, demonstrates that *Rhincalanus* can thrive solely on plants, but there may be other food sources, perhaps highly patchy ones in time or space, that were not present in most of my incubations but that some *Rhincalanus* can locate in the natural water column to achieve high rates of production. Future work obviously should focus on this issue — whether there are conditions (season, food, etc.) permitting *Rhincalanus* to reproduce at a high rate on the natural seston; i.e., >10 eggs·(female·day)$^{-1}$; vertical striping in figure 6A.2–D.2. Alternatively, the distribution of *Rhincalanus* off southern California must be explained either by very low mortality rates or by advective immigration of immature stages.

ACKNOWLEDGMENTS

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APPENDIX

Station*	Day	9004				9008				9101				9103			
		Calanus		*Rhincalanus*		*Calanus*		*Rhincalanus*		*Calanus*		*Rhincalanus*		*Calanus*		*Rhincalanus*	
		Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed
93.100	1	0	0	—	—	0	10.2	—	—	—	—	—	—	—	—	—	—
	2	0	29.2	—	—	1	44.9	—	—	—	—	—	—	—	—	—	—
93.90	1	4.6	32.4	—	—	2.7	8.4	0	0	—	—	—	—	—	—	—	—
	2	3.3	59.6	—	—	5	34.3	0	0	—	—	—	—	—	—	—	—
93.80	1	—	—	—	—	—	—	—	—	0	0	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	0	35.8	—	—	—	—	—	—
93.70	1	—	—	—	—	—	—	—	—	—	—	—	—	0	0	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—	0	25	—	—
93.60	1	0	32.9	—	—	—	—	—	—	6.4	17.5	—	—	0	3.6	—	—
	2	3.1	85.3	—	—	—	—	—	—	0.8	20.7	—	—	0.8	31.9	—	—
93.55	1	—	—	—	—	1.5	—	—	—	0.3	2.7	0	0	—	10.9	0	2
	2	—	—	—	—	0	—	—	—	0	23	0	0	—	40.9	0	0.7
93.50	1	31.9	66.8	—	—	—	—	—	—	1.2	0	0	0	—	—	—	—
	2	1.1	57.6	—	—	—	—	—	—	4.2	9.8	0	0	—	—	—	—
93.45	1	28.4	58.7	—	—	17.8	48.3	—	—	—	—	—	—	4.5	34.5	0	4.2
	2	3	58.7	—	—	0	61.1	—	—	—	—	—	—	0.5	45.4	0	13.1
93.40	1	—	—	—	—	14	37	—	—	0	0	—	—	5.5	11	0.8	4.1
	2	—	—	—	—	5.4	37.2	—	—	0	20	—	—	4.6	9.3	2.8	37.1
93.35	1	26.8	75.3	—	—	0.2	5.6	—	—	0	0	—	—	19.3	24.8	—	2.4
	2	19.5	87.8	—	—	4.3	53	—	—	0	1.5	—	—	2	20	—	25.4
93.30	1	22.4	61.7	—	—	2.4	23.2	—	—	0	—	—	—	12.3	21.8	0	5.6
	2	6.8	63.1	—	—	1	48.3	—	—	0	—	—	—	0.5	11.5	0	35.9
93.28	1	21.7	60.3	—	—	13.3	52.2	—	—	6.3	22.7	—	—	12.5	—	0	5.6
	2	3.8	75.8	—	—	1.6	60.7	—	—	0.3	29.7	—	—	0.5	—	0	36.8
90.110	1	—	—	—	—	4	13.8	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	0.9	19.1	—	—	—	—	—	—	—	—	—	—
90.90	1	0	14.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	2	1	51.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—
90.80	1	0	0	—	—	0	3.1	—	—	0	1.4	0	0	0	0	—	—
	2	0	24.9	—	—	1.2	27	—	—	0	26	0	0.4	0	3.7	—	—
90.70	1	10.6	34.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	2	1.9	30.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—
90.60	1	31	47.9	—	—	5.4	32.3	0	0	5.8	16.3	0	0.2	6.8	4.8	0	0.7
	2	4.6	37.8	—	—	0.1	33.9	0	0	2.3	35.1	0	1.7	0	26.7	0	0
90.53	1	56.6	70.5	0	0.4	13.7	22.2	0	0	3.4	16.7	0	0	16.1	21.2	6.8	0.7
	2	11.8	56.9	0.3	6.2	2.7	43.1	0	0	0.4	20	0	3.3	5.8	30.3	3.9	12.4
90.45	1	30.7	48.1	—	—	10.8	26.3	—	—	1	8	—	—	11.3	26.4	3	11.4
	2	3.5	61.5	—	—	0.4	47.4	—	—	0	22.5	—	—	0	26.8	7	52.5
90.37	1	—	—	—	—	7.2	40.9	—	—	0.3	0	0	10	15.4	33.9	0.2	5.9
	2	—	—	—	—	0	64.2	—	—	0.9	19	0	20.7	4.1	41.3	0	29.5
90.35	1	25.9	38.4	0	3.5	—	—	—	—	—	—	—	—	—	—	—	—
	2	9.8	42.1	0	2.9	—	—	—	—	—	—	—	—	—	—	—	—
90.30	1	8.4	38.2	—	—	2	14.3	0	0	0.7	2.5	—	—	14.7	23	0	5.4
	2	1.1	46.4	—	—	0	33	0	6	1.2	38.9	—	—	0.7	32.6	0	15.1
90.28	1	—	—	—	—	20.7	58.6	—	—	0.9	1.2	—	—	15.5	31.4	0	0.2
	2	—	—	—	—	0.4	44.5	—	—	0	9	—	—	0	35.4	0	17.8
87.110	1	—	—	—	—	1.7	1.5	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	0	34.6	—	—	—	—	—	—	—	—	—	—
87.90	1	1.2	4.3	—	—	0.4	5.8	—	—	—	—	—	—	—	—	—	—
	2	2.4	39.5	—	—	4	34.8	—	—	—	—	—	—	—	—	—	—
87.80	1	0	0.4	—	—	—	—	—	—	6.3	0	—	—	0	0.3	—	2.7
	2	0.5	28	—	—	—	—	—	—	0.6	0.1	—	—	0	36.7	—	16.4
87.70	1	—	—	—	—	—	—	—	—	0	0	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	0	0	—	—	—	—	—	—
87.60	1	5	19.2	—	—	3.8	15.7	—	—	6.6	14.9	0	0	27.7	36	0.1	1.9
	2	5.2	58.1	—	—	10.1	65.4	—	—	1.8	17.3	0	0	3.1	39.8	0	11.4
87.55	1	20.3	20.3	0	1.3	20.5	45.7	—	—	11.5	15.7	0	0	17.8	39.4	6.4	2.7
	2	4.4	40	0	10.4	5.4	68.5	—	—	1.5	10.1	0	0	7.3	38.5	5.9	5.9
87.50	1	20.4	30.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	2	2.2	44.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—
87.45	1	—	—	—	—	—	—	—	—	5.7	19.8	—	0	—	—	—	—
	2	—	—	—	—	—	—	—	—	4.2	30.3	—	0	—	—	—	—
87.39.5	1	17.2	27.8	—	—	—	—	—	—	0	—	0	—	11.7	30.8	—	—
	2	5.9	34	—	—	—	—	—	—	0	—	0	—	15.6	24.7	—	—

*For CalCOFI Basic Station Plan, see inside back cover.

| | | 9202 | | | | 9204 | | | | 9301 | | | |
| | | Calanus | | Rhincalanus | | Calanus | | Rhincalanus | | Calanus | | Rhincalanus | |
Station	Day	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed
93.100	1	—	—	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—
93.90	1	—	—	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—
93.80	1	—	—	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—
93.70	1	0	0	—	—	—	—	—	—	0	0	—	0
	2	0	8.5	—	—	—	—			0	4.2	—	4.3
93.60	1	0	0	—	—	—	—	—	—	—	—	—	—
	2	0	11.3	—	—	—	—	—	—	—	—	—	—
93.55	1	10.6	21.6	0	6.9	3.3	7.9	0	2.4	—	—	—	—
	2	0	39.3	0	23.4	1.9	49.8	0.5	26.6	—	—	—	—
93.50	1	17.2	42.4	0	7.3	—	—	—	—	12.4	20.1	0	1.4
	2	2	67.9	0	24.3	—	—	—	—	2.9	37.7	0.1	9.3
93.45	1	11.7	25.9	0	7.6	—	—	—	—	12.8	58.4	0.5	5.8
	2	1.5	39.5	0	5.6	—	—	—	—	6.4	50.7	0	27.9
93.40	1	—	6.8	—	—	0	16.7	0	0.7	0	7.9	0	0
	2	—	19.3	—	—	0.5	58.2	0.2	18.5	2.7	46.9	1.2	13.8
93.35	1	1.8	—	—	—	15	27	0	0	0	0	—	—
	2	0	—	—	—	0.3	69.6	0.2	8	0	21.1	—	—
93.30	1	—	—	—	—	0	0	0	0	2.7	2.3	—	—
	2	—	—	—	—	2.3	40	0	3.3	0	11.3	—	—
93.28	1	14.2	53.7	0	5	0.5	19.9	1.2	0	0	0	—	—
	2	3.6	61.8	0	28.7	3.6	34.4	0	10.8	0	31.8	—	—
90.110	1	—	—	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—
90.90	1	—	—	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—
90.80	1	0	—	—	—	—	—	—	—	—	—	—	—
	2	0	—	—	—	—	—	—	—	—	—	—	—
90.70	1	15.8	23.5	—	—	—	—	—	—	0	18.7	0	0
	2	0.2	41.4	—	—	—	—	—	—	0	53.6	0	0
90.60	1	5.5	26	0	6.3	7	20.3	0.2	—	0	15.1	0	0.6
	2	0	64.7	0	26.8	8.6	46.7	0	—	0	28.8	0.5	15.5
90.53	1	0	12.9	—	—	—	—	0.3	1.3	0	—	0	3.9
	2	0	69	—	—	—	—	0.3	9.3	0	—	0.6	18.2
90.45	1	0	20.4	—	—	24.8	41.1	10.6	8.8	0	0	0	1.6
	2	0.5	51.7	—	—	5.7	40.7	27.3	32.6	0	16.1	0	35.7
90.37	1	0	4.6	—	—	9.1	16.5	0	0.9	6.2	18.7	0	0
	2	0	40.8	—	—	7	26.6	0.1	14.9	0	32.9	0.1	9.8
90.35	1	—	—	—	—	—	29.2	0	—	—	—	—	—
	2	—	—	—	—	—	27.9	0.1	—	—	—	—	—
90.30	1	—	27.6	1.4	0.9	—	—	—	—	2.7	11	—	—
	2	—	48.2	1.6	10.6	—	—	—	—	0	33	—	—
90.28	1	—	—	—	—	21.1	33.5	0	2.4	—	—	—	—
	2	—	—	—	—	6	32.6	0	36.7	—	—	—	—
87.110	1	—	—	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—
87.90	1	—	—	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—
87.80	1	1.2	0	—	—	—	—	—	—	—	—	—	—
	2	0.6	32.8	—	—	—	—	—	—	—	—	—	—
87.70	1	7.4	11.7	—	—	—	—	0	0	1.4	5.6	0	0
	2	1.4	33.7	—	—	—	—	0.2	2.2	0	27	0	4.2
87.60	1	4.2	1.5	—	—	27.8	60.8	0.8	—	0.5	5	0	0.8
	2	0	22.7	—	—	0.4	37.9	5.6	—	0	33	0	7.7
87.55	1	11.9	35	0	7.5	9.9	44.3	1.8	2.3	2.4	15.8	0	0
	2	3.9	38.2	0	23.3	6.4	14.1	2.9	1.7	0.5	60.3	0	0
87.50	1	—	—	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—
87.45	1	11.3	17.4	1.4	3.5	42.7	48.2	0.6	3.1	—	—	—	—
	2	1.1	35.2	4.8	11.6	14.4	32.2	0.8	4.2	—	—	—	—
87.39.5	1	1.6	5.1	0	—	14.9	30.6	1.3	3.6	0	14.6	0	0
	2	0	31.6	0	—	1.5	27.3	7.4	17.2	0	28.3	0	0

APPENDIX (*continued*)

Station	Day	9004				9008				9101				9103			
		Calanus		*Rhincalanus*		*Calanus*		*Rhincalanus*		*Calanus*		*Rhincalanus*		*Calanus*		*Rhincalanus*	
		Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed
87.35	1	23.8	49.6	8.3	6.3	26.2	67.7	—	—	0	11.6	—	—	6.2	21.2	0	2.9
	2	1.5	42	9.3	19.3	4.1	61.2	—	—	0	27.6	—	—	0.2	45.8	0	4.3
87.33	1	—	—	—	—	—	—	—	—	—	56.6	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	30.4	—	—	—	—	—	—
83.90	1	0	0	—	—	—	—	—	—	—	—	—	—	0.2	2.1	—	—
	2	0	7.5	—	—	—	—	—	—	—	—	—	—	0	6.2	—	—
83.80	1	2.8	5.5	1.2	0	—	—	—	—	0	1.9	—	—	—	35.5	0	0.4
	2	1.7	30.6	0	6.8	—	—	—	—	0	7.6	—	—	—	57.1	0	3.1
83.70	1	—	—	—	—	1	10.5	0	0	0	3.9	0	0	37.1	57.5	0	0.7
	2	—	—	—	—	1.4	29.3	0	6	0	8.1	—	—	2.5	56.6	0	12.5
83.60	1	33.8	51.3	5.6	12.8	10.4	42.6	—	—	15.8	34.4	0	0	35.5	49.6	0.2	1.5
	2	2.3	34.7	10	18.5	5.6	39	—	—	3.1	22.1	0	0	4.5	55	0.8	19.8
83.55	1	43.3	48.1	2.7	9	15.4	35.3	0	9	48	68.8	—	2.5	39.6	62.7	7.5	7.8
	2	18.5	39.1	3.8	26.5	0	30.2	0	8	5.4	17.8	—	20.9	6.3	54.5	13.2	13
83.51	1	—	—	—	—	—	—	—	—	23.1	46.7	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	6.7	32.3	—	—	—	—	—	—
83.42	1	40.9	53.2	—	—	21.4	45	0	0	26.1	27.4	—	—	50.6	53.3	—	—
	2	10.1	50.9	—	—	0	48.3	0	6	20.7	38.2	—	—	8.6	28.5	—	—
83.40	1	—	—	—	—	—	—	—	—	16	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	2.5	—	—	—	—	—	—	—
82.47	1	32.9	43.4	1.1	1.2	25.6	27.7	—	—	29.8	23.6	3.3	4.2	0	0	0	0
	2	3.7	49.6	1.7	15.6	4.4	44.3	—	—	4.7	35.3	3.8	22.5	0	22.3	0	0
80.90	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
80.80	1	—	—	—	—	0.7	8.3	—	—	8.1	40.8	—	—	—	—	—	—
	2	—	—	—	—	0	26.7	—	—	3.3	28.1	—	—	—	—	—	—
80.70	1	—	—	—	—	25	26.4	0	1	19	18.9	—	—	8.4	62.8	0	3.3
	2	—	—	—	—	13.5	47	0	15	0.8	28.8	—	—	0	62.5	0	27.9
80.60	1	—	—	—	—	—	—	—	—	23.8	29.6	—	—	26.1	47.7	0.3	2.2
	2	—	—	—	—	—	—	—	—	1.7	42.1	—	—	1.1	55.2	2.1	9.4
80.55	1	57.4	53.5	—	—	32.4	40	—	—	13.6	20.4	0	0	1.7	0	—	—
	2	9.6	52.8	—	—	1	43.7	—	—	7.8	35.1	0	0	0	25.5	—	—
80.51	1	2.5	10.6	—	—	32.9	27.7	—	—	18	24.8	—	—	—	—	—	—
	2	0.1	15.2	—	—	4.9	44.3	—	—	0	35.3	—	—	—	—	—	—
77.100	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
77.90	1	—	—	—	—	0	0	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	0	54.3	—	—	—	—	—	—	—	—	—	—
77.80	1	—	—	—	—	0	15.7	—	—	0	12.5	0	—	—	—	—	—
	2	—	—	—	—	0	50.9	—	—	0	36.7	0	—	—	—	—	—
77.70	1	—	—	—	—	4.3	27.5	0	0	0.3	7.3	0	0	—	—	—	—
	2	—	—	—	—	2.8	52.1	0	0	2.8	24.5	0	0	—	—	—	—
77.60	1	—	—	—	—	2.5	12.3	0	0	8.6	8	0	0	—	—	—	—
	2	—	—	—	—	0	47.6	·0	12	1.7	28.1	0	1.8	—	—	—	—
77.55	1	—	—	—	—	—	—	—	—	1.7	16.9	0	0	—	—	—	—
	2	—	—	—	—	—	—	—	—	0	27.2	0	0	—	—	—	—
77.51	1	—	—	—	—	22	—	0	1	26.7	38	0	0	—	—	—	—
	2	—	—	—	—	5.1	—	0	2	2.3	22.3	0	0	—	—	—	—
77.49	1	—	—	—	—	13.2	43	4	3	9.4	55.3	—	—	—	—	—	—
	2	—	—	—	—	13	43.8	5	13	13.5	38.7	—	—	—	—	—	—

| | | 9202 | | | | 9204 | | | | 9301 | | | |
| | | Calanus | | Rhincalanus | | Calanus | | Rhincalanus | | Calanus | | Rhincalanus | |
Station	Day	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed
87.35	1	17.5	21	0.1	2.7	13.8	45.2	0	0.1	0.8	1.6	—	—
	2	3.6	35.8	0	13.3	22.6	36.6	1.3	5	0.3	24.7	—	—
87.33	1	—	—	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—
83.90	1	0	0	—	—	—	—	—	—	—	—	—	—
	2	0	4.1	—	—	—	—	—	—	—	—	—	—
83.80	1	0.9	1.2	0	0	—	—	0.3	11.2	—	—	—	—
	2	0.7	21.2	0	3.9	—	—	0	13.2	—	—	—	—
83.70	1	13.4	17.8	0	0	4.3	9.4	0.2	4.2	—	—	—	—
	2	9	25.7	0	8.2	2.8	35.8	1.8	3.8	—	—	—	—
83.60	1	13.7	30.7	1.1	5.4	53.2	—	5.7	5.6	11.7	28	0	3.3
	2	7.2	35.3	1.6	12.5	13	—	28.5	38.5	2.9	30	1.1	29.1
83.55	1	0	24.8	0	—	—	—	—	—	0	23.8	0	2.1
	2	0	38	0	—	—	—	—	—	0	29.8	0	11.2
83.51	1	—	—	—	—	51	51.5	—	—	9.3	26.8	—	—
	2	—	—	—	—	6.8	27.2	—	—	0	40	—	—
83.42	1	0	5.7	0	0.3	48.6	72.8	0	1.4	1.5	3	—	—
	2	0	47.3	0	5.2	8	37.1	0.1	5.6	0	15	—	—
83.40	1	—	—	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—
82.47	1	12.6	28.3	—	0	38.4	41.9	—	—	0	3.9	0	0.3
	2	1.7	24.1	—	1.8	0.2	46.6	—	—	0	34.7	0.3	2.2
80.90	1	0	5.4	—	—	3.7	16	1	0.6	—	—	—	—
	2	0	33.8	—	—	1.1	39.8	0	7.1	—	—	—	—
80.80	1	8.7	26.5	0	0	—	—	—	—	—	—	—	—
	2	0	17.8	0	0	—	—	—	—	—	—	—	—
80.70	1	0	4.8	0	0.5	11.1	24.4	4.6	0.4	16	12.2	0	0
	2	0	18.7	0	4.9	0.2	49.1	2.4	11.6	0.1	29.9	0.1	15.8
80.60	1	20.2	20.1	—	—	30.8	24.6	2.1	1.7	3.7	10	0	0
	2	8	28.7	—	—	9	28.2	0.2	7.6	0.1	28.1	0	0
80.55	1	2.6	18.3	—	—	24	21.8	3.8	0.3	7.6	18.8	—	—
	2	1	16	—	—	6.9	32.1	28.2	28.4	0.7	16.8	—	—
80.51	1	9.2	19	—	—	5.8	24.6	—	—	0	4.7	—	—
	2	0	21.4	—	—	0.1	21.9	—	—	0	21.4	—	—
77.100	1	0	0	—	—	—	—	—	—	—	—	—	—
	2	0	0	—	—	—	—	—	—	—	—	—	—
77.90	1	0	1.3	0	0.4	4.7	13.5	0	0	—	—	—	—
	2	0	24.2	0	0	6.7	14.2	0	0.3	—	—	—	—
77.80	1	0	1	0	4.6	1.6	14.9	0	0	6.2	36	0	1.4
	2	0	32.5	0	3.3	4.7	39.1	0	6.3	1.2	26.3	1.5	15.7
77.70	1	0.4	5.9	0	0	18.3	34.1	0	0.4	32.4	66.3	0.4	4.1
	2	0	28.4	0	0	8	50.4	0	5	2.3	19.9	0.6	12
77.60	1	—	—	—	—	20.2	33.4	3.1	0.6	18.3	28.4	0.8	0.1
	2	—	—	—	—	6.2	31.6	4.2	2.6	7.3	11.7	0.5	9.2
77.55	1	—	—	—	—	11.6	29.6	—	—	29.5	24.2	4.7	6.6
	2	—	—	—	—	8.4	18.8	—	—	5.6	38.9	14.4	44.3
77.51	1	—	—	—	—	31.2	33.2	2	1.4	0.2	11.8	—	—
	2	—	—	—	—	11.5	17.2	15.4	16.5	0.1	23	—	—
77.49	1	—	—	—	—	65	—	—	—	0	11.8	—	—
	2	—	—	—	—	9.4	—	—	—	0.3	28.5	—	—