Biomasses of Euphausiids and Smaller Zooplankton in the California Current—Geographic and Interannual Comparisons Relative to the Pacific Whiting, *Merluccius productus*, Fishery

M. M. Mullin and A. Conversi

ABSTRACT: We examined data on size-fractionated zooplankton biomasses from the California Current in summer to 1) verify that euphausiid and smaller zooplankton biomasses varied in similar ways geographically and interannually, and 2) test for increase in euphausiid biomass after 1966, concurrent with initiation of a fishery on Pacific whiting (a major predator of euphausiids), and distinct from general, interannual changes. We accomplished purpose 1, but were unable to detect a significant effect attributable to the Pacific whiting fishery.

On the scale of years to decades and thousands of square kilometers, variability in the biomass of zooplankton, or of taxonomic categories within the zooplankton, can result from physical and chemical causes, from biotic interactions (especially in closed, manipulated systems such as lakes) or from some combination of these. In nonmanipulated systems, a plausible hypothesis is that variability results from a change in the physical processes influencing the area (the ultimate cause) plus ecological responses or readjustments of the populations present (the proximate cause). For the zooplankton of the open ocean, it is difficult to assess, by examination of case histories, the relative roles of physical and biological processes, because manipulation on the scales of interest is extremely difficult.

The California Current is known to vary interannually in transport and in physical properties—in aggregate, the Current's climate—the most extreme warming and decrease in southward flow being called El Niño (Wooster and Fluharty 1985). Correlated with (and in some sense probably caused by) these changes are variations in the biomass of zooplankton (Wickett 1967; Reid 1962). These changes are coherent through a large area—when zooplankton biomass is anomalously large or small in one area within the region, it tends to be large or small in all areas during the same year (Chelton et al. 1982). Further, several major taxonomic groups of zooplankton have similar interannual changes (Colebrook 1977).

By examining the timing of maximal zooplankton biomass relative to that of maximal southward flow, Roesler and Chelton (1987) concluded that off northern California interannual variations in biomass are caused by variations in direct advection of biomass from more northern regions (where biomass is high); off Baja California, variations in advection of nutrients from the north, translated via the food chain into zooplankton biomass with some lag, are more important.

Even in the presence of natural interannual variability, rapid development of a major commercial pelagic fishery is an anthropogenic manipulation which might cause detectable change in the biomass and/or composition of zooplankton. Pacific whiting, *Merluccius productus*, (also called Pacific hake) is one of the dominant fish in the California Current (Smith 1978). Euphausiids, especially *Euphausia pacifica* and *Thysanoessa spinifera*, make up > 70% of the weight of gut contents of whiting, especially fish <45 cm long, aged 3–4 years (Livingston 1983). *Euphausia pacifica* is a vertical migrator, at least much of the year (Brinton 1967; Brooks and Mullin 1983). *Thysanoessa spinifera* apparently remains in the upper 150 m at all times (Youngbluth 1976). Another prey of whiting, especially offshore, is the pelagic shrimp, *Sergestes similis*, (Alton and Nelson 1970), which has a nocturnal distribution similar to that of *E. pacifica* (Omori and Gluck 1979). Whiting guts are most full of food in the evening and early night (Livingston 1983), when the fish tend to be dispersed near the surface (Bailey et al. 1982).

In 1966 a foreign (later joint-venture) fishery, conducted from spring through fall, began removing considerable quantities of whiting in coastal regions off Washington, Oregon, and

M. M. Mullin and **A. Conversi**: Institute of Marine Resources, A-018, University of California, San Diego, La Jolla, CA 92093-0218.

Manuscript accepted September 1988.
Fishery Bulletin, U.S. 87: 633–644.

northern California (Nelson 1985). The commercial catch of pandalid shrimp in Oregon increased markedly at the time the Pacific whiting fishery began; from this coincidence, Bailey et al. (1982) and Francis (1983) suggested that the shrimp no longer eaten by whiting were available to fishermen, even though these commercial shrimp are only a minor portion of the whiting's diet. [Livingston and Bailey (1985) pointed out, however, that most of the increase in shrimp catch was due to increased fishing effort on shrimp rather than to increased catch per unit effort; hence it is not certain that the shrimp population has increased.] Nevertheless, the result and evidence of zooplanktivory summarized above stimulated an analogous question—whether the biomass of euphausiids increased in summer samples of zooplankton from the California Current off northern California in 1966–69, relative to summers of earlier years.

The trophic dynamics of the Pacific whiting, and the implications of the fishery, have been calculated from a simulation model by Francis (1983). His results indicated that the fishery may have reduced the (calculated) virgin whiting stock by about 21% without changing the annual production significantly because the production/biomass ratio increased. This conclusion implies that any indirect impact of the fishery on the whiting's food resources should be less than the change in the whiting's biomass. Francis also reasoned that the geographical distribution of food consumption by whiting would shift towards central California from northern California and Oregon.

Since the climate of the California Current is known to be correlated with interannual changes in the biomass of zooplankton, any change in euphausiid biomass must be scaled against the biomass of other zooplankton which would (presumably) be affected by climatic change but not directly affected by the removal of whiting. To test the assumption that the biomasses of euphausiids and smaller zooplankton respond similarly to climatic change, we reexamined data from the late 1950s, when there was a major El Niño.

We then determined the biomass of euphausiids and other pelagic shrimps (a major whiting food) relative to small zooplankton (not eaten by adult whiting) before and after the initiation of the fishery, and in a northern area closer to the fishery compared to further south, and then tested for significant differences. We also analyzed a published set of data from the California Current off cental Oregon (Pearcy 1976), since this was closer to the center of impact of the Pacific whiting fishery than were the samples available to us. Finally, we calculated whether, given the variances observed in the zooplankton samples we analyzed, we should have been able to detect a change in euphausiid biomass owing to partial removal of a major predator by the fishery.

METHODS

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) yielded samples of zooplankton from the California Current from the mid-1940s to the present. Though the CalCOFI net is not a perfect sampler of euphausiids and other large, active, pelagic shrimp, samples taken at night (when most of these species migrate into surface waters) do contain euphausiids. From 1951 through 1968, the standard net was of mixed silk mesh—a large, forward portion of 0.55 mm and a small, rear portion of 0.25 mm—towed from the surface to a depth of 140 m. In 1969, the standard was changed to a net of uniform 0.505 mm nylon mesh, towed to 210 m (target depth). Though these procedures have been intercalibrated (Smith 1974; Hewitt 1980), care in interpretation of differences between pre-1969 and 1969 samples is necessary.

We divided nocturnal, summer (June–October) CalCOFI samples into the following space/time blocks or categories (Fig. 1): North of Monterey (CalCOFI line 70), 1960–65—41 samples (24 inshore); south of Dana Point (CalCOFI line 90), 1960–65—172 samples (103 inshore); north of Monterey, 1966–69—47 samples (25 inshore); and south of Dana Point, 1966–69—116 samples (73 inshore). "Inshore" samples, treated as a separate subset because of the inshore nature of the whiting fishery, thus constituted 53–63% of the samples in each block. Twenty-one other samples, in which no euphausiids were found, were excluded from statistical tests; at least two such samples occurred in each space/time block. The samples were from the following CalCOFI cruises (designated "aabb", where aa = year and bb = month): 6007, 6010, 6107, 6110, 6210, 6407, 6507, 6509 (southern area only), 6606, 6607, 6608 (southern area only), 6610, 6907, 6908, and 6910. We made analogous divisions into space/time blocks in the CalCOFI data set from the late 1950s and the set from Oregon.

Each sample consisted of formalin-preserved, unsorted zooplankton captured at one station by

a nocturnal tow. We fractionated each sample by sieving a subsample (≤0.5 of the sample) through a 4 mm screen, and counted and manually placed the euphausiids (and sergestids) retained on this mesh on a preweighed glass fiber filter. We then rinsed all or part of the same subsample sequentially through 1 mm and 0.5 mm meshes, using recirculating seawater, and then rinsed the plankton passing 1 mm but retained by 0.5 mm onto another preweighed glass fiber filter. We then rinsed both filters and their catches with 6% ammonium formate, dried them overnight at 50°–60°C, cooled them in a desiccator, and reweighed them. Blank filters (no zooplankton) were treated similarly. The dry weight of the sample, corrected for initial filter weight and any weight change of the blank filters, times the subsampling factor and divided by the volume of water filtered by the original net tow, is the biomass of "euphausiids" or of "small zooplankton" (that retained by the 0.5 mm mesh) for that station, and the weight of the euphausiids divided by their number is the dry weight per euphausiid.

With particular regard to the Pacific whiting fishery, which started in 1966 in the northern part of the California Current, and the expectation that biomass of whiting food might increase, we tested the following null hypotheses (stated in the "one-tailed" forms appropriate for our expectations).

H_{01}—Absolute biomass of euphausiids in the northern area was not greater from 1966 onward than that before 1966.

H_{02}—The ratio of biomasses (euphausiids/small zooplankton) in the northern area from 1966 onwards was not greater than a) this ratio before 1966, or b) that in the southern area. [The small zooplankton biomass is used to correct for the expected north-to-south differences, overall changes in the biomass of zooplankton, or change in sampling techniques, throughout the California Current for reasons other than the whiting fishery.]

H_{03}—The dry weight per euphausiid in the northern area was not greater from 1966 onward than before 1966.

Hypothesis H_{02}a, for example, was examined by a one-tailed rank sum (Mann-Whitney U) test of whether the median of all ratios at northern stations before 1966 was statistically indistinguishable from the median for all such stations beginning in 1966. The alternative which would be consistent with an effect of the whiting fishery would be, pre-1966 median <1966-and-later median. In some cases, analogous *t*-tests were also performed on data normalized by log-transformation to determine whether transformed means differed. In this approach, all stations within one block of geography and time are treated as equally valid estimates of the overall median, independent of location of the stations within the block.

There are significant inshore/offshore gradients in biomass (see below), and comparisons between years or between areas could be confounded by differences between groups being compared in the inshore/offshore locations of usable samples. We took several precautions to prevent this; first, we tested for such gradients in our own samples by comparing medians from inshore and offshore subsets of stations by rank sum tests. We also tested hypotheses H_{01}–H_{03} using only the inshore subsets of the stations (Fig. 1); this was done partly because the fishery for whiting is generally conducted in areas shallower than 500 m.

We tested analogously data from a transect off Oregon which was repeatedly sampled from 1962 to 1967 (see below).

Hypotheses H_{01} and H_{02}a were tested further by another approach which acknowledges that within each major space/time block, stations may differ systematically because of geography (e.g., an inshore/offshore gradient), so that the identity of each station should be retained in the test. The data from each northern California station which was sampled at least thrice before 1966 or in 1966–69, and at least once during the contrasting period, were ranked separately as for a rank sum test, but the summed ranks were then combined for testing against the expectation from the null hypotheses. There were 7 stations used in this test, and 21 data points from each period.

Falsification of these hypotheses implies that there was a significant increase in euphausiid biomass (and/or individual size) coincident with the whiting fishery and that this increase was unlikely to be caused by other factors affecting zooplankton in the whole California Current, including those types on which adult whiting do not feed.

In order to validate the assumption which underlies H_{02}—that small zooplankton and euphausiid biomasses vary in parallel in response to the California Current's climate—we

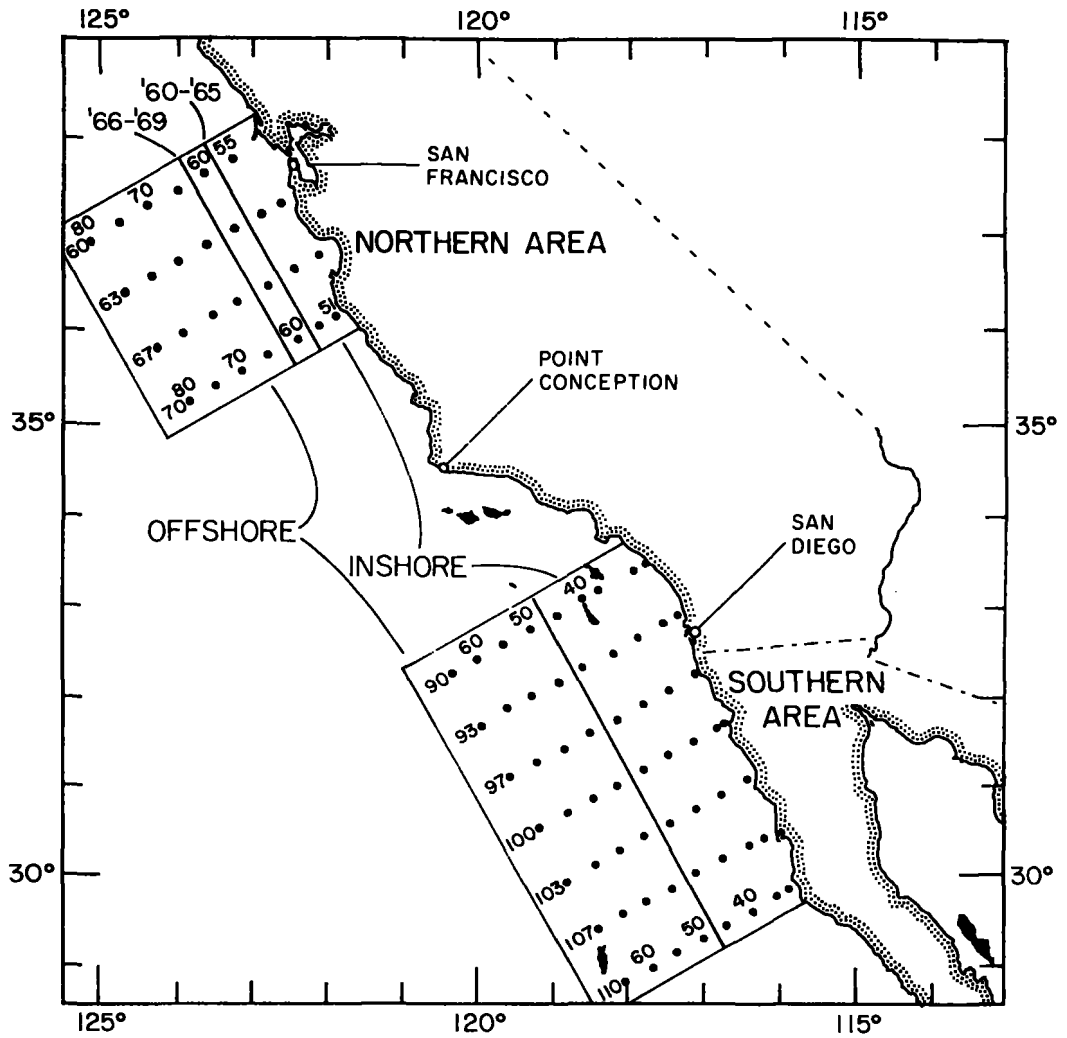

FIGURE 1.—Northern and southern areas, and CalCOFI transect line and station numbers. Each area is divided into "inshore" and "offshore" subsets of stations: the dividing line used in the northern area for 1960–65 was closer to shore than that for 1966–69 because the distribution of samples differed. The same areas were used for data from the 1950s, with same inshore/offshore divisions as in 1960–65.

used published data from 1958 and 1959, during which there was a major El Niño, compared with 1955–57. Zooplankton from the California Current during these years had been visually classified into 17 categories, and wet weight biomasses were assigned to each (Isaacs et al. 1969). We examined "euphausiid" and "copepod" categories of this data set (assuming from our visual examination that the "copepods" were most similar to our "small zooplankton" category), selecting those stations which were nocturnal and within the areas defined in Figure 1 during April, July, and October, and separating 1955–57 from 1958–59. This resulted in 21 northern, 1955–57 stations (13 of which were inshore); 49 northern, 1958–59 stations (30 inshore); 118 southern, 1955–57 stations (72 inshore); and 110 southern, 1958–59 stations (63 inshore). We then performed statistical tests analogous to those described above to test hypotheses concerning similarity of geographic and temporal variation of euphausiid and copepod biomasses, and constancy of their ratio.

RESULTS

Interannual Variation of Euphausiids and Copepods, 1955–59

Colebrook (1977) demonstrated by multivariate analysis overall north-to-south and inshore-to-offshore trends in the annual mean values of zooplankton biomass in the California Current. He found that the biomasses of euphausiids and

copepods particularly decreased moving offshore. The biomasses of both categories were larger in 1955 and 1956 (pre-El Niño years) than in 1958 and 1959 (El Niño years; see also Chelton et al. 1982). This suggests that biomasses of euphausiids and of the smaller copepods respond similarly to interannual climatic or environmental variation.

Our results, which are summarized in Figure 2, were

1) Biomasses of euphausiids and copepods were significantly less in the southern area than in the northern area, both before (1955–57) and during (1958–59) the El Niño, in agreement with Colebrook's (1977) conclusions, and the ratio of euphausiid to copepod biomasses did not change significantly. Analysis of data from only the inshore subareas yielded the same results, except that the euphausiid biomass did not differ significantly between northern and southern inshore areas during 1958–59.
2) Biomasses of euphausiids and copepods were significantly less during El Niño than before it, both in the complete areas and in the inshore portions (also agreeing with Colebrook's result), and the euphausiid/copepod biomass ratio did not change significantly.
3) Neither the euphausiid nor the copepod biomasses were significantly different between inshore and offshore subareas, nor were the ratios significantly different (comparison not shown in Figure 2); this result differs from Colebrook's conclusion.

Overall, we conclude that it is reasonable to use the biomass of small zooplankton to correct or scale the biomass of euphausiids for effects of geography or interannual climatic variation in order to test for changes due to factors specific to the euphausiids.

Interannual Variation in 1960–69 off California

Averaged over the entire decade, there were significantly lower biomasses of euphausiids and of small zooplankton offshore than inshore, both in the southern area by itself and in the combined areas (unlike our result for 1955–59). Thus, for testing hypotheses (such as H_{01}) concerning biomasses, the inshore/offshore distribution of samples should be similar in the sets being compared (as was true in our case). We were unable, however, to reject the null hypothesis that the median ratio of biomasses in the offshore subset of stations equalled the median

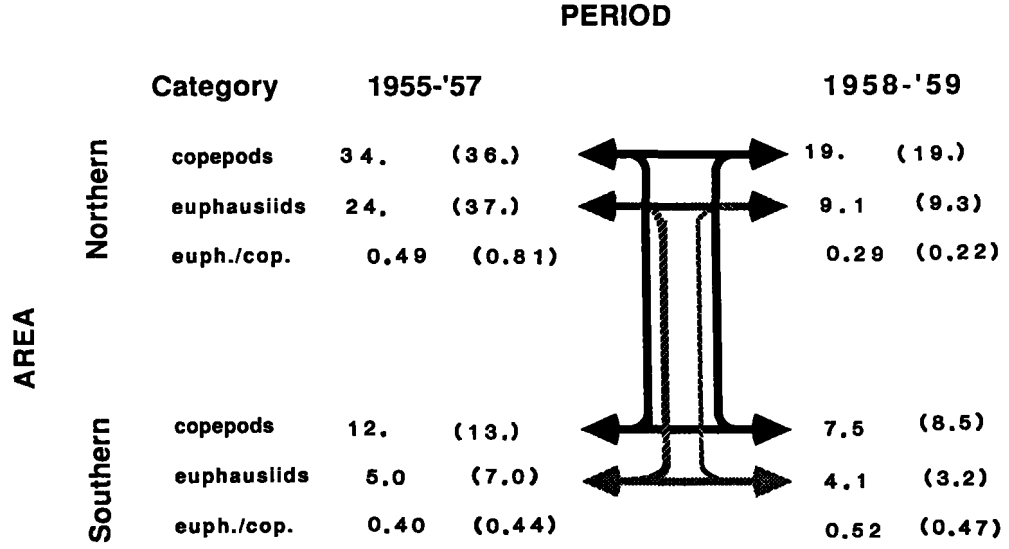

FIGURE 2.—Overall and (inshore subset) medians for each space/time block in the 1950s, for wet weight biomasses ($mg \cdot m^{-3}$) of copepods and euphausiids, and for the ratios at individual stations. Arrows connect medians which differed significantly ($P < 0.05$ for H_0 = no difference); a thick arrow indicates that the comparable medians of the inshore subsets of data also differed significantly. All comparisons were "vertical" or "horizontal"; no "oblique" comparisons were tested (e.g., no comparison between northern, 1960–65, and southern, 1966–69).

ratio at the inshore stations, either in the northern and southern areas separately or in the combined areas. Since we could not detect persistent gradients by this test (nor by analogous *t*-tests), we concluded that differences in the inshore/offshore placement of samples between two groups should not preclude the testing of hypothesis H_{02}, which concerns ratios.

In comparisons between periods or between areas (Fig. 3), the most significant difference was the greater biomass of the "small zooplankton" in the north in 1966–69 than the northern, 1960–65 or the southern, 1966–69 biomasses. These differences were significant ($P < 0.05$) even when the inshore subsets of data only were considered. Probably as a result of this, the ratio of euphausiid to small zooplankton biomasses was significantly lower in the northern, 1966–69 data set than elsewhere. This difference was also significant by *t*-test.

The biomass of small zooplankton was significantly greater in the northern than in the southern area in both periods, in fact (as in 1955–59). The null hypothesis that the biomass of euphausiids was the same in all sets of data could not be rejected. Nor did the weight per euphausiid in the northern area change.

These results were supported by the comparison of biomasses at specific northern stations which had been sampled several times. The biomass of small zooplankton was greater, and the euphausiid/small zooplankton ratio less, in 1966–69 than in 1960–65 ($0.05 < P < 0.1$ by two-tailed test in both cases), while the biomasses of euphausiids did not differ ($P > 0.1$).

The significant increase in median biomass of small zooplankton in 1966–69, relative to 1960–65, could have been due to the inclusion of data from 1969, when samples were taken differently (see Methods) if the different method itself resulted in increased catch. However, Smith (1974) reported that the method used in 1969 resulted in a *smaller* biomass (per unit volume filtered) than did the pre-1969 method. In our data, the biomass of small zooplankton was greater, and the euphausiid/small zooplankton ratio less, in 1966 than in 1969 (rank sum tests). Hence, the change in sampling in 1969 could hardly have been responsible, in itself, for the elevated biomass of small zooplankton in 1966–69 relative to the earlier years.

Thus, euphausiid biomass could not be shown to increase coincident with the onset of the whiting fishery, either in absolute units or relative to the small zooplankton. None of the null hypotheses relating to absence of change of euphausiids in the northern area at the time of the whiting fishery could be rejected, and in fact the ratio of

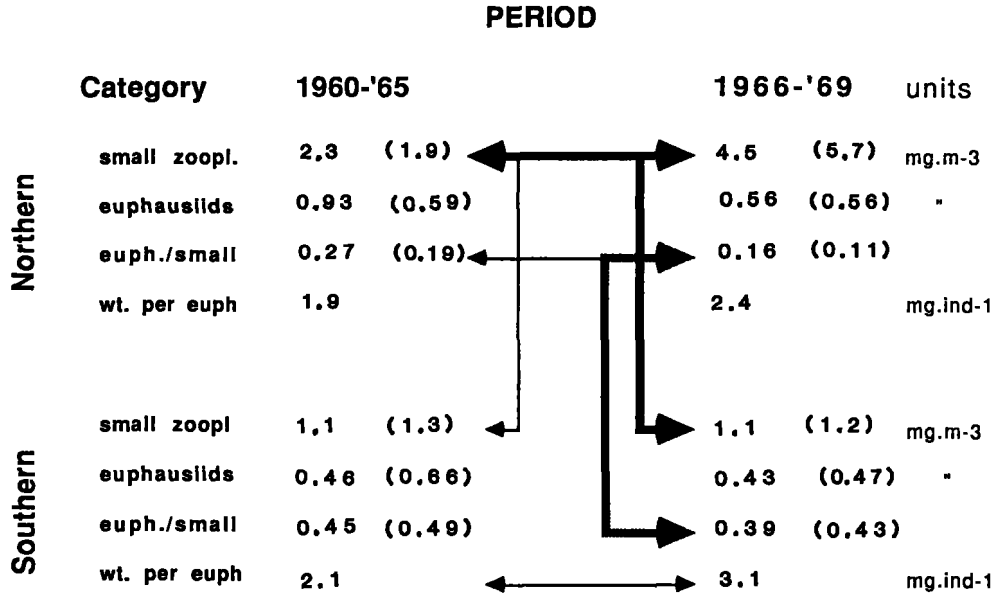

FIGURE 3.—Overall and (inshore subset) medians for each space/time block in the 1960s, for dry weight biomasses of small zooplankton and euphausiids, their ratios, and the dry weights per euphausiid. Arrows connect medians which differed significantly ($P < 0.05$ for H_0 = no difference); a thick arrow indicates that the comparable medians of the inshore subsets of data also differed significantly. All comparisons were "vertical" or "horizontal"; no "oblique" comparisons were tested.

euphausiid to small zooplankton biomass differed significantly in the direction opposite to that predicted.

Interannual Variation in 1962–67 off Oregon

We also examined similar hypotheses using data provided by W. G. Pearcy (see Pearcy 1976) for a repeatedly sampled transect from the Oregon coast seaward to 530 km, since this region is closer to the geographic center of the Pacific whiting fishery than was our California, northern area. The data set includes 89 values for dry weight biomasses of euphausiids and copepods from nocturnal samples from April to October 1962–67. By analogy to our treatment of California data, we defined inshore as the innermost 100 km, and offshore as the remainder of the transect; we therefore divided this set into subsets, 1962–65 (56 total samples, 34 inshore) and 1966–67 (33 samples, 20 inshore).

To compare results from this Oregon transect to one transect within the "southern" area, we chose CalCOFI line 93 (see Figure 1), and subdivided samples from it into similar subsets: 1960–65 (33 samples, 17 inshore) and 1966–69 (23 samples, 14 inshore). The direct comparison of biomass off Oregon to that on line 93 means little, since the methods differed (for instance, we measured "small zooplankton" and Pearcy measured copepods), but we could compare the patterns of variation shown on the two transects.

On line 93, biomass of euphausiids was significantly less offshore than inshore (as was true for the entire southern area), and the biomass of small zooplankton tended similarly, though the difference was nonsignificant. Neither the small zooplankton nor the euphausiid biomass, nor their ratio, differed between 1960–65 and 1966–69—conclusions which also characterized the entire southern area (Fig. 3). The Oregon transect revealed a similar spatial pattern (significant decreases of biomass offshore for both copepods and euphausiids) and a similar lack of temporal change (no significant changes for the entire transect, or its inshore portion, in copepod biomass, euphausiid biomass, or their ratio) between 1962–65 and 1966–67.

Therefore, the patterns off Oregon were very similar to those off southern California, and failed to indicate a change in the biomass of euphausiids concurrent with the whiting fishery off Oregon.

Expected Response of Euphausiid Biomass to the Pacific Whiting Fishery

Detection of a change in the biomass of euphausiids which could be caused by the start of the whiting fishery depends on 1) the magnitude of the change in the predatory impact on euphausiids due to change in the stock of whiting, 2) the rapidity with which the community readjusts to such changes, and 3) the variability among the available samples in which change is to be detected. Francis (1983) calculated the food consumption by the virgin and exploited whiting stocks in several standard regions of the North American west coast; these estimates can be applied to the areas we sampled by making various assumptions about the more detailed geography of the effect of the fishery on the whiting stock. The variances of the groups of samples we analyzed give an estimate of the "noise" against which this "signal" must be detected, and, as discussed above, we can use the biomasses of copepods to correct for long-term variability.

Since we were unable to detect a change in biomass of euphausiids attributable to the Pacific whiting fishery, we did a simple calculation to determine how many samples, with the same variances as the samples we did analyze, we would have had to analyze to detect an expected change at the 0.05 probability level, if 1) only the change in whiting stock affected the biomass of euphausiids, or 2) if changes in the biomass of small zooplankton were used to normalize the euphausiid biomass for nonfishery effects (i.e., using a simplified euphausiid/small zooplankton biomass ratio).

First, we assumed that the biomass of euphausiids was in equilibrium before the start of the fishery in 1966, such that the sum of mortality and growth was zero and immigration equalled emigration, and that subsequently a biomass of euphausiids simply accumulated, proportional to the decrease in whiting predation, without change of the population parameters. We averaged the biomasses of euphausiids from all samples in a given area from 1960 to 1965, and then calculated the expected biomass two years after the start of the fishery from the change in consumption by whiting in that area, using the estimates of Francis (1983) corrected for the fraction contributed by euphausiids to whiting gut contents (Alton and Nelson 1970; Livingston 1983; Rexstad and Pikitch 1986), for the dry/wet weight ratio, and for the volume represented by

that area. Thus, we calculated an "expected" biomass of euphausiids at the end of 1967, E_a, from the mean biomass before the start of the fishery, E_b. The maximum expected increase was 50% in the northern California inshore area.

To test for significant differences by two-sample t-test between the means of nonnormal data sets, we would transform to logarithms and verify that this normalized the data (as was true for our data sets) before performing the test. If the means of the log-transformed data are E_a^* and E_b^*, the critical value for the t-test, for given numbers of samples, then indicates how much E_a^* must exceed E_b^* for the difference to be significant, given the variance around E_a^* and E_b^*, and thus defines a critical ratio, $(E_a/E_b)_{cr}$, for nontransformed data (see Appendix A). Conversely, we can ask how many samples would need to be analyzed from a particular area such that $E_a/E_b > (E_a/E_b)_{cr}$.

We did this calculation for the entire areas, and the inshore portions, of northern California and Oregon. In order to detect significance, we would have had to analyze between 80 and 1,600 samples for each block of time within an area, depending on the area. Therefore, the numbers of samples we analyzed, and the data set from Oregon, were insufficient to detect the simplest expectation.

Next, to normalize the euphausiid biomasses, we multiplied the ratio, E_a/E_b, by the comparable ratio of means of observed, log-transformed, small zooplankton or copepod biomasses to obtain a ratio of euphausiid biomasses, $(E_a/E_b)_{corr}$, corrected for the environmental or climatic change reflected in these biomasses, which increased significantly off northern California (Fig. 3), and compared $(E_a/E_b)_{corr}$ to $(E_a/E_b)_{cr}$. In the Oregon data set, $(E_a/E_b)_{corr} < (E_a/E_b)_{cr}$, the expected change could not have been detected with the available data. In both inshore and total areas of northern California, however, $(E_a/E_b)_{corr} > (E_a/E_b)_{cr}$ meaning that a t-test should have been able to detect a significant increase in biomasses of euphausiids in northern California due to the combined effect of environmental change and the whiting fishery, if only these two factors operated in the most simple, additive fashion.

DISCUSSION

Our results, like those of Colebrook (1977), show considerable similarity in the large-scale geographic and interannual variations in biomass of euphausiids (at least those caught by the CalCOFI net at night) and smaller zooplankton. It is also clear that the impact of a climatic event like El Niño greatly exceeds, on these scales, any effect of the whiting fishery.

The failure to find greater biomasses of whiting prey after the beginning of the fishery in the Californian area north of Monterey, or off central Oregon, could result from undersampling, from a mismatch between the effect of the fishery on the whiting population and the zooplankton sampled by plankton nets, and/or from the complexity of the ecological relations affecting euphausiid biomass.

"Undersampling" means that variability within each space/time group of samples is so great that we cannot statistically detect differences between groups even though differences actually exist which would be detected if more samples were available. As we have shown, the change in euphausiid biomass calculated from a model of the biomass and food consumption of exploited and virgin Pacific whiting stocks could not have been detected statistically without at least three times the number of samples we had. Further, the actual biomasses of euphausiids off both northern California and Oregon tended to decrease, as did the ratios of euphausiid to small zooplankton (or copepod) biomasses. Therefore, we doubt that simply analyzing more samples of the same kind (i.e., from the same sampling pattern, using the same gear) would demonstrate the anticipated increase in the biomass of euphausiids.

Because CalCOFI stations north of San Francisco were not sampled after April of 1960 during that decade and because the whiting fishery was centered off Oregon and Washington, the samples in our northern California area (Fig. 1) were too far south to be ideal for this analysis, as well as extending too far offshore. The transect off Oregon was better placed latitudinally, but the number of samples in the inshore zone (where the Pacific whiting fishery was conducted) was rather small. Therefore, our effort to increase the number of samples to be analyzed resulted in inclusion of areas outside that where the predators had been reduced by the fishery; we were, in a sense, trying to detect advection or diffusion of the effect into a larger area.

Ecological complexity may have buffered the response to a reduction of a predator such as whiting in ways that do not ameliorate climatic effects. The relatively simple outcome—that euphausiids became absolutely or relatively

more abundant following the initiation of the fishery—could have been overshadowed by, e.g., 1) replacement of whiting by the increase of some other species of predator on euphausiids, even a species which is also prey for large whiting (Livingston 1983); 2) differential removal of large whiting by the fishery, leaving smaller whiting whose preference for euphausiids as food exceeded that of the larger fish, so that predation pressure did not decrease dramatically because of altered age structure of the whiting population; or 3) replacement of predator-limitation by food-limitation of euphausiid biomass.

We tried to minimize the effect of response 1) by restricting the post-1965 analysis to the years immediately following the initiation of the fishery, on the theory that this might have represented a period of abundant euphausiids before the ecosystem returned to a new equilibrium through the increase of a new, major zooplanktivore. Unfortunately CalCOFI coverage of the northern California Current in the summers of 1967 and 1968 was very small.

Response 3) is possible (indeed, euphausiid biomass may never have been limited by Pacific whiting's predation), but the increase in biomass of small zooplankton in the northern California area in 1966–69 (Fig. 3) suggests a food supply which could have supported an increased biomass of euphausiids—an increase which was not realized.

In considering the possible responses of the zooplanktonic community to the Pacific whiting fishery, it is worth remembering that there have been natural fluctuations in the whiting population as great as those caused by fishing. Oceanographic variation in the whiting's spawning area is important, higher temperatures being associated with greater, and more variable, recruitment (Swartzman et al. 1983; Bailey and Francis 1985). Judging from scales collected in an anoxic basin, whiting was much more abundant off Southern California in the 30 years around 1900 than in recent years (Soutar and Isaacs 1974). Such fluctuations in the stock of whiting are therefore only a manifestation or symptom of more general environmental variation in the California Current.

Overall, our results indicate that a major environmental perturbation, such as El Niño, acts on the California Current's ecosystem as a whole (though the mechanism of action may differ geographically; Roesler and Chelton 1987) and modifies the components we studied in similar ways. The system seems to adjust to more local, specific modifications, such as anthropogenic changes in biomass and age structure of one predator, so that widespread effects on planktonic prey populations are difficult to detect.

ACKNOWLEDGMENTS

We thank Elisabeth McEvoy and Michael Lindsey for the tedious analyses of many zooplankton samples, W. G. Pearcy for generously supplying data, Kevin Bailey and Paul Smith for advice, and two reviewers for comments. This work is a result of research sponsored in part by U.C.S.D. Academic Senate grants, and by NOAA, National Sea Grant College Program, Department of Commerce, under grant number NA85AA-D-SG140, project number R/F-111, through the California Sea Grant College Program, and in part by the California State Resources Agency. The U.S. Government is authorized to reproduce and distribute for governmental purposes.

LITERATURE CITED

Alton, M. S., and M. O. Nelson.
1970. Food of Pacific hake, *Merluccius productus*, in Washington and northern Oregon coastal waters. *In* Pacific hake, p. 35–42. U.S. Fish Wildl. Serv. Circ. 332.

Bagenal, M.
1955. A note on the relations of certain parameters following a logarithmic transformation. J. Mar. Biol. Assoc. U.K. 34:289–295.

Bailey, K. M., and R. C. Francis.
1985. Recruitment of Pacific whiting, *Merluccius productus*, and the ocean environment. Mar. Fish. Rev. 47(2):8–15.

Bailey, K. M., R. C. Francis, and P. R. Stevens.
1982. The life history and fishery of the Pacific whiting, *Merluccius productus*. CalCOFI Rep. 23:81–98.

Brinton, E.
1967. Vertical migration and avoidance capability of euphausiids in the California Current. Limnol. Oceanogr. 12:451–483.

Brooks, E. R., and M. M. Mullin.
1983. Diel changes in the vertical distribution of biomass and species in the Southern California Bight. CalCOFI Rep. 24:210–215.

Chelton, D. B., P. A. Bernal, and J. A. McGowan.
1982. Large-scale interannual physical and biological interaction in the California Current. J. Mar. Res. 40:1095–1125.

Colebrook, J. M.
1977. Annual fluctuations in biomass of taxonomic groups of zooplankton in the California Current, 1955–59. Fish. Bull., U.S. 75:357–368.

Francis, R. C.
1983. Population and trophic dynamics of Pacific hake

(*Merluccius productus*). Can. J. Fish. Aquat. Sci. 40:1925–1943.

Hewitt, R.
1980. Distributional atlas of fish larvae in the California Current region: Northern anchovy, *Engraulis mordax* Gerard, 1966 through 1979. CalCOFI Atlas 28:vii–xi.

Isaacs, J. D., A. Fleminger, and J. K. Miller.
1969. Distributional atlas of zooplankton biomass in the California Current region: spring and fall 1955–1959. CalCOFI Atlas 10:vi–xviii.

Livingston, P. A.
1983. Food habits of Pacific whiting, *Merluccius productus*, off the west coast of North America, 1967 and 1980. Fish. Bull., U.S. 81:629–636.

Livingston, P. A., and K. M. Bailey.
1985. Trophic role of the Pacific whiting, *Merluccius productus*. Mar. Fish. Rev. 47(2):16–22.

Nelson, R. E., Jr.
1985. Historical review of the coastal Pacific whiting, *Merluccius productus*, fishery. Mar. Fish. Rev. 47(2):39–41.

Omori, M., and D. Gluck.
1979. Life history and vertical migration of the pelagic shrimp *Sergestes similis* off the Southern California coast. Fish. Bull., U.S. 77:183–198.

Pearcy, W. G.
1976. Seasonal and inshore/offshore variations in the standing stock of micronekton and macrozooplankton off Oregon. Fish. Bull., U.S. 74:70–80.

Reid, J. L., Jr.
1962. On circulation, phosphate-phosphorus content, and zooplankton volumes in the upper part of the Pacific Ocean. Limnol. Oceanogr. 7:287–306.

Rexstad, E. A., and E. K. Pikitch.
1986. Stomach contents and food consumption estimates of Pacific hake, *Merluccius productus*. Fish. Bull., U.S. 84:947–956.

Roesler, C. S., and D. B. Chelton.
1987. Zooplankton variability in the California Current, 1957–1982. CalCOFI Rep. 28:59–96.

Smith, P.E.
1974. Distribution of zooplankton volumes in the California Current region, 1969. CalCOFI Atlas 20:xv–xvii.
1978. Biological effects of ocean variability: Time and space scales of biological reponse. Rapp. P.-verb. Réun. Cons. int. Explor. Mer 173:117–127.

Soutar, A., and J. D. Isaacs.
1974. Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediment off the Californias. Fish. Bull., U.S. 72:257–274.

Swartzman, G. L., W. M. Getz, R. C. Francis, R. T. Haar, and K. Rose.
1983. A management analysis of the Pacific whiting (*Merluccius productus*) fishery using an age-structured stochastic recruitment model. Can. J. Fish. Aquat. Sci. 40:524–539.

Wickett, W. P.
1967. Ekman transport and zooplankton concentration in the North Pacific Ocean. J. Fish. Res. Board Can. 24:581–594.

Wooster, W. S., and D. L. Fluharty (editors)
1985. El Niño North. Wash. Sea Grant Program, Univ. Wash., 312 p.

Youngbluth, M. J.
1976. Vertical distribution and diel migration of euphausiids in the central region of the California Current. Fish. Bull., U.S. 74:925–936.

Zar, J. H.
1984. Biostatistical analysis. 2nd ed. Prentice-Hall, Inc., Englewood Cliffs, N.J., 718 p.

APPENDIX A

Caution must be used when performing a logarithmic (ln) transformation [$y_i = \ln(x_i)$] on data (x_i) belonging to a nonnormal distribution. The resulting mean of the log-transformed data

$$\bar{y} = \frac{\sum_{i=1}^{n} \ln(x_i)}{n}$$

is equal to the logarithm of the geometric mean of the untransformed data

$$\bar{y} = \ln\left(\sqrt[n]{\prod_{i=1}^{n} x_i}\right).$$

Since the geometric mean is always less than the arithmetic mean (Zar 1984), the antilog of the mean of the log-transformed data must be corrected before it can be used as an unbiased estimation of the arithmetic mean of the untransformed data.

Bagenal (1955) showed a relationship between the means of transformed ($\bar{y}$) and untransformed ($\bar{x}$) data, which is valid when the transformed data belong to a normal distribution, with mean = $\bar{y}$ and variance = σ_y^2.

$$\bar{x} = e^{\bar{y} + \frac{1}{2}\sigma_y^2} \tag{1}$$

and

$$\bar{y} = \ln(\bar{x}) - \frac{1}{2}\sigma_y^2 \tag{2}$$

We applied this relation to our calculations of the critical differences between the means of log-transformed biomasses after and before the beginning of the fishery. The data had to be log-transformed in order to perform the two-sample t-test, since this assumes that the distributions underlying the two samples are normal.

The critical differences were so calculated, from the two-sample t-test formula:

$$E_a^* - E_b^* = t! \, s_p \sqrt{\frac{n_a + n_b}{n_a \, n_b}} \tag{3}$$

where E_a^*, E_b^* are, respectively, the means of the log-transformed biomasses after and before the beginning of the fishery, equal to $\bar{y}$ in Equation (2),
$t!$ is the critical t-value at $\alpha = 0.05$,
s_p is the pooled variance for the two samples, and
n_a,n_b are, respectively, the numbers of samples after and before the beginning of the fishery.

These differences were then related to the means of untransformed data by applying Equation (2):

$$E_a^* - E_b^* = \ln(E_a) - 0.5\, s_p^2 - \ln(E_b) + 0.5\, s_p^2 = \ln\left(\frac{E_a}{E_b}\right) \tag{4}$$

where $E_{a,b}$ indicate arithmetic mean of untransformed biomasses, analogous to $\bar{x}$ in Equation (1).

And therefore, from Equations (3) and (4), a critical ratio was defined:

$$\left(\frac{E_a}{E_b}\right) \text{cr} = e^{\left(t! \, s_p \sqrt{\frac{n_a + n_b}{n_a \, n_b}}\right)} \tag{5}$$

which is the minimum ratio necessary to reject the null hypothesis.

Note, however, that the correcting factors ($0.5 \, s_p^2$) cancel each other only when using a t-test with pooled s^2, i.e., when assuming the two samples belong to the same distribution.