

## INTERANNUAL VARIATIONS IN ZOOPLANKTON BIOMASS IN THE GULF OF ALASKA, AND COVARIATION WITH CALIFORNIA CURRENT ZOOPLANKTON BIOMASS

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### ABSTRACT

Large-scale atmospheric and oceanographic conditions affect the productivity of oceanic ecosystems both locally and at some distance from the forcing mechanism. Recent studies have suggested that both the Subarctic Domain of the North Pacific Ocean and the California Current have undergone dramatic changes in zooplankton biomass that appear to be inversely related to each other. Using time series and correlation analyses, we characterized the historical nature of zooplankton biomass at Ocean Station P (50°N, 145°W) and from offshore stations in the CalCOFI region. We found a statistically significant but weak negative relationship between the domains. We investigated whether such a relationship arises from different forcing mechanisms or as an opposite response to the same mechanism. We found that the seasonal peak of both data sets occurred in the summer but that the CalCOFI data lagged the Ocean Station P data. A surface-drift simulation model showed that winter trajectories started at Ocean Station P and along 145°W drifted more into the California Current before the 1976–77 regime shift, and more into the Alaska Current after the 1976–77 shift. We examined physical and biological conditions which may lead to this inverse relationship between the two ecosystems, and we discuss the implications of these results for higher trophic levels.

### INTRODUCTION

Substantial temporal and spatial heterogeneity occurs in the production of oceanic ecosystems. Much of this heterogeneity results from seasonal and geographic variations in nutrient availability, mixed-layer depths, or solar radiation. Processes that enhance productivity (e.g., upwelling, wind and tidal mixing) tend to be localized and transient. Physical forcing in the form of the large-scale circulation pattern redistributes the elevated production to areas less favorable for in situ production. Thus production at any location can be affected by both local and remote processes, and it is often difficult to dis-

tinguish their relative contributions (Wickett 1967; Chelton et al. 1982; Roessler and Chelton 1987).

It has become increasingly apparent that atmospheric and oceanic conditions are likely to change due to a buildup of greenhouse gases in the atmosphere (Graham 1995). Although there has been much interest in predicting the effects of climate change, especially on fisheries resources (e.g., see papers in Beamish 1995), different scenarios exist for future trends in basic physical processes such as upwelling (Bakun 1990; Hsieh and Boer 1992). Biological processes are more laborious to monitor and difficult to predict because of their inherent complexity.

There are numerous examples showing that large-scale physical and biological changes have occurred throughout much of the Northeast Pacific Ocean over the last few decades (Francis and Hare 1994; Miller et al. 1994). Indices which showed these changes include atmospheric (Trenberth 1990; Trenberth and Hurrell 1994), oceanographic (Royer 1989; Hsieh and Boer 1992; Miller et al. 1994; Lagerloef, 1995; Polovina et al. 1995), productivity (Venrick et al. 1987; Polovina et al. 1994), and biomass of various trophic levels (Brodeur and Ware 1992, 1995; McFarlane and Beamish 1992; Beamish 1994; Hare and Francis 1995; Roemmich and McGowan 1995a, b). A number of studies have suggested that biological changes occurred rather suddenly sometime around 1976–77, concurrent with a dramatic shift in physical regimes (Francis and Hare 1994; Miller et al. 1994).

Documenting the effects of climate change on marine ecosystems requires long time series of sampling to examine low-frequency periodicity. In the Northeast Pacific Ocean, two series are notable not only for their length, but also for the broad suite of biological and physical measurements made at each location. The first of these, Ocean Station P (50°N, 145°W; hereafter called Station P), nominally represents a subarctic oceanic ecosystem that was sampled almost continuously from 1956 to 1980 but only sporadically since then. The second, the CalCOFI grid, is an eastern boundary current

ecosystem that has been sampled since the late 1940s, although not always with the same geographic and temporal intensity. Although Ekman pumping of deep, nutrient-rich water is a feature common to both these ecosystems, the mechanisms behind biological production in the two systems differ (Ware and McFarlane 1989).

Over the past few decades, there has been much speculation on the nature of the eastern bifurcation of the Subarctic Current into the Alaska Current and California Current and its possible effects on biological production in these two large ecosystems (figure 1). Wickett (1967), Chelton and Davis (1982), and Chelton (1984) have speculated that the intensities of the flows in the Alaska and California Currents fluctuate in opposition to one another. They hypothesized that north-south shifts in the bifurcation of the Subarctic Current (West Wind Drift) could be forced by physical factors occurring in the western or central Pacific Ocean.

Using environmental indices and fish-recruitment data, Hollowed and Wooster (1992) and Francis (1993) have characterized two alternating interdecadal states of atmospheric and oceanic circulation in the Northeast Pacific Ocean which result in very different components of fisheries production (e.g., groundfish, salmon) in the Alaska Current and California Current domains. Hollowed and Wooster (1992) have characterized these states as

lasting 6 to 12 years each. A cold era (Type A) is associated with a weak Aleutian Low, relatively weak circulation in the Alaska Gyre, strong upwelling inshore of the California Current, negative sea-surface temperature (SST) anomalies throughout the coastal Northeast Pacific Ocean, and positive SST anomalies in the central North Pacific Ocean (centered at 40°N). A warm era (Type B) is associated with a strong Aleutian Low, strong gyral circulation, and reduced upwelling and high temperatures to the south (figure 2).

Francis (1993), Francis and Hare (1994), and Hare and Francis (1995) find similar although longer (20–30 year) periods of oscillating “warm” and “cool” regimes, which they relate to the production dynamics of Alaska salmon. In addition, Francis (1993) speculated that the interdecadal variations in salmon production in these two oceanic domains are inversely correlated.

This paper examines factors related to long-term changes in production in the subarctic Pacific Ocean, using examples mainly from Station P. We examine, in particular, trends in zooplankton biomass as an indicator of changes in productivity in this oceanic ecosystem. Using time-series analysis, we then compare these trends to those evident in the offshore region of the California Current to examine the hypothesis of Wickett (1967) that production in both systems may be affected by an

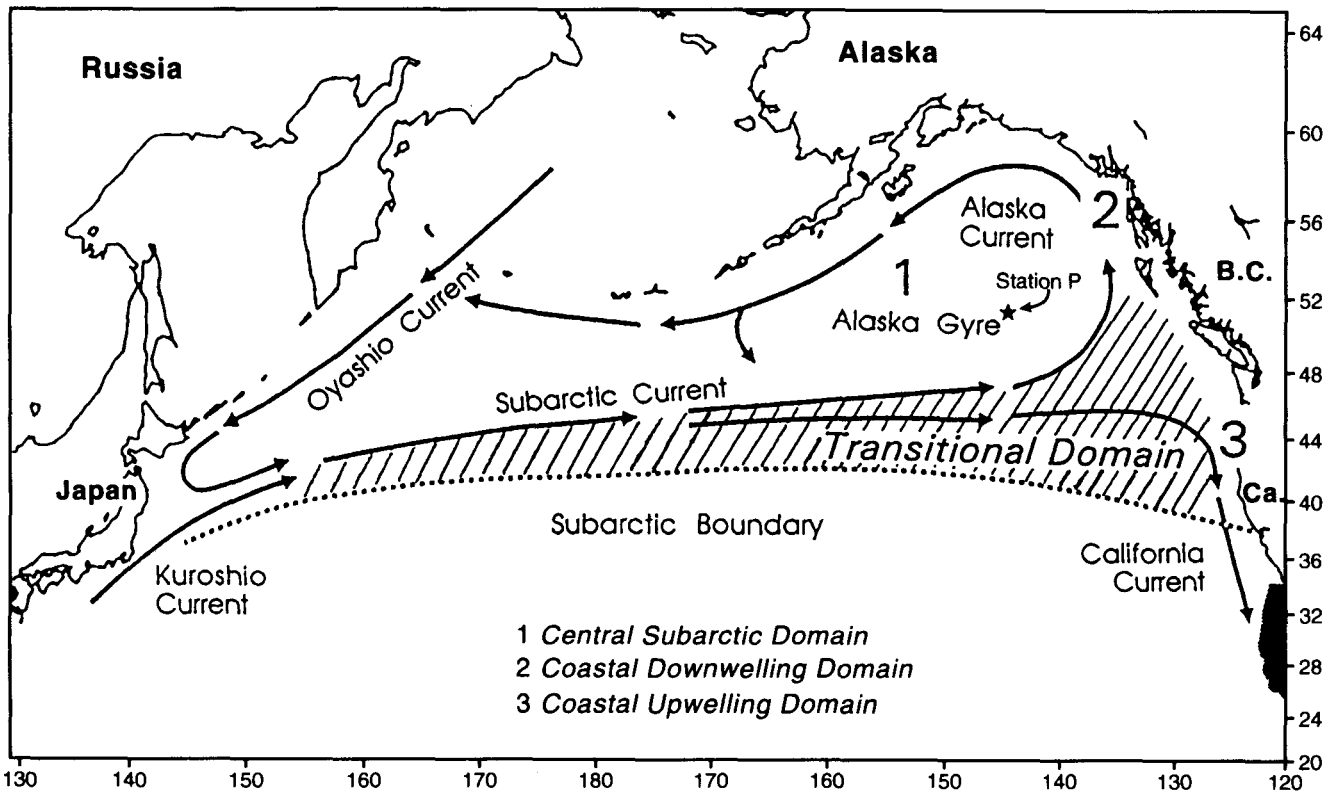


Figure 1. Large-scale near-surface circulation in the North Pacific Ocean, and Ocean Station P (star) and the CalCOFI sampling region (shaded area). Also shown are the different ocean production domains of Ware and McFarlane (1989) and Percy (1991).

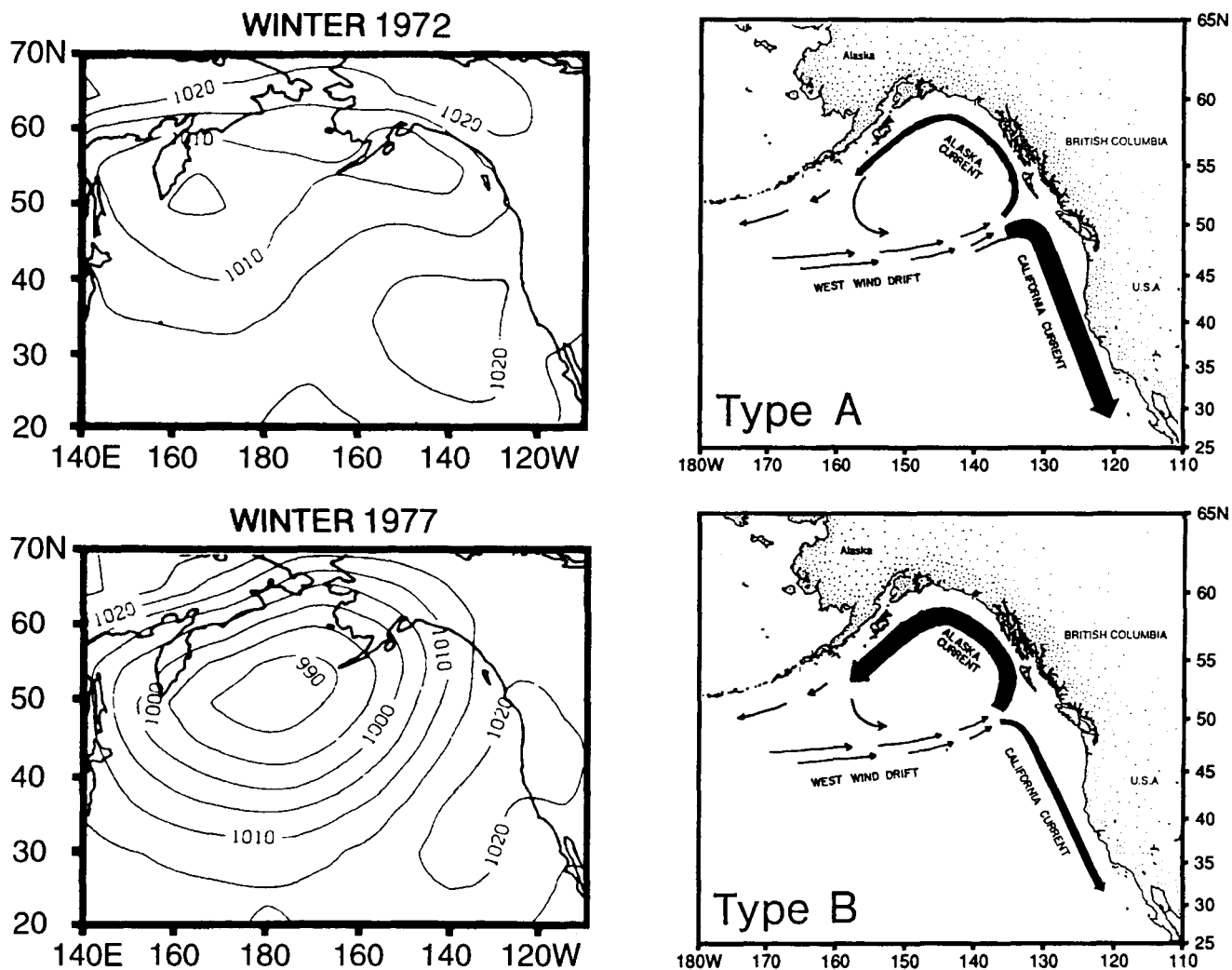


Figure 2. Winter mean sea-level pressure from Emery and Hamilton (1985) for two contrasting years, and the alternate states of atmospheric and oceanic circulation patterns in the eastern North Pacific Ocean proposed by Hollowed and Wooster (1992).

influx of water from the same source—the Subarctic Current. We examine physical data relevant to regime-shift changes in flow between the Alaska Current and California Current. Finally, we discuss implications of regime shifts to higher trophic levels and suggest new hypotheses and further studies that could be undertaken to address these hypotheses.

## DATA SOURCES AND METHODS

### Zooplankton Data Sets

Zooplankton biomass data from 24 years (1956–80) of vertical net sampling at Station P were used in our analyses (figure 1). Before 1969, sampling was conducted over alternate 6-week periods, but after this time, sampling was continuous (Fulton 1983). Sampling frequency varied from 1 to 29 samples per month over 8 to 12 months of the year (Frost 1983). Hauls were mainly done during daytime, and all were from 150 m to the surface.

Sampling gear was changed from a 0.42-m-diameter NORPAC net to a 0.57-m SCOR net in August 1966, although the mesh size remained the same (0.351 mm). Fulton (1983) estimated that the catching efficiency of the SCOR net was 1.5 times greater than the NORPAC net, based on a series of intercalibration tows. But a new estimation based on the original data presented by Fulton (1983) suggests that the correction factor should be higher, somewhere in the range of 1.6–2.1 $\times$ , with 1.77 $\times$  being the most likely value (Waddell and McKinnel 1995; Frost, Ware, and Brodeur, unpubl. data), which is what we used in this analysis.

Zooplankton displacement volumes from the central part of the CalCOFI grid (lines 77–93) over a longer time frame (1951–94) were provided by Paul Smith (NMFS, SWFC, La Jolla). The gear and maximum haul depths changed during this period from a bridled 1-m-diameter ring net fished obliquely to 140 m (1951–68) or to 212 m (1969–78) to an unbridled bongo net fished

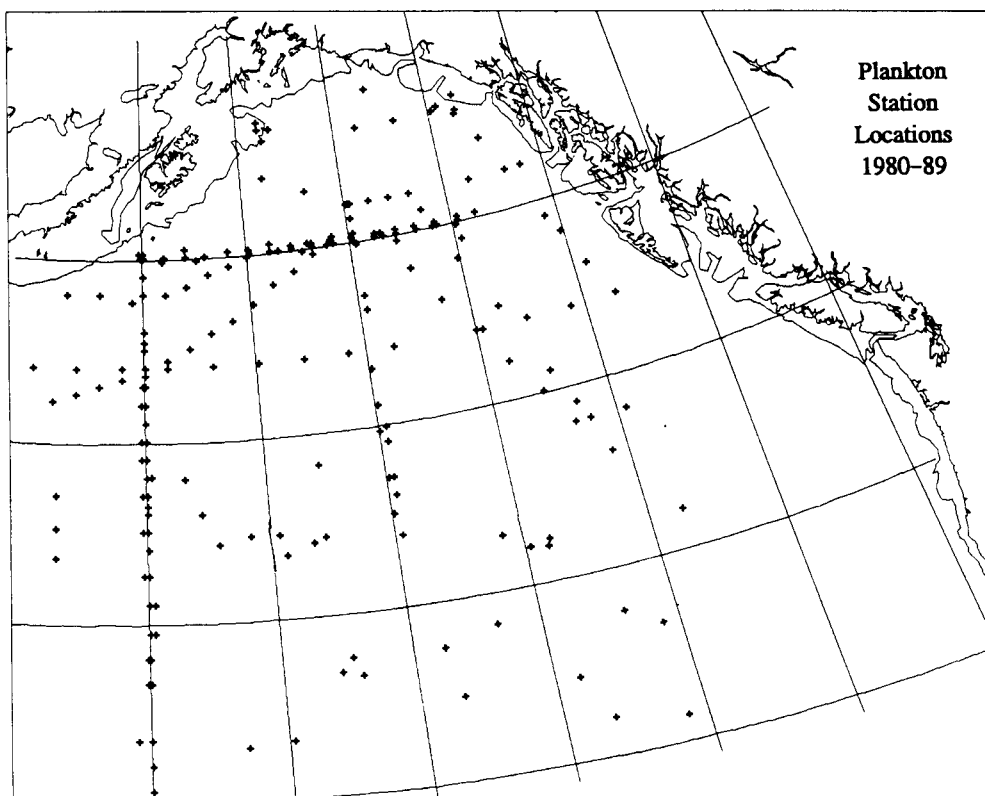
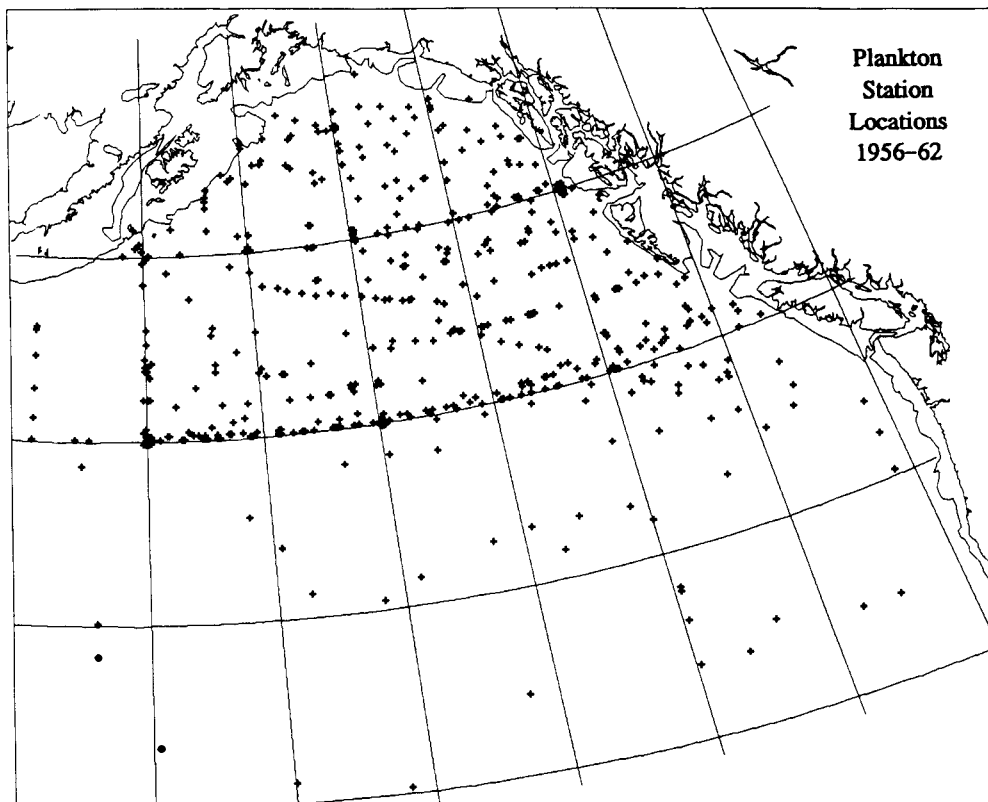


Figure 3. NORPAC zooplankton sampling stations (*plus signs*) during 1956-62 and 1980-89.

down to 212 m (1978–94). An analysis by Ohman and Smith (1995) has determined that the deeper tows with the 1-m net are low by a factor of 1.366 compared with the shallower 1-m nets and the deep bongo tows without bridles, and we adjusted the data accordingly.

Since we were interested in advective rather than local production processes (Chelton et al. 1982), we trimmed the data set to include only those stations farther than 60 km offshore. We initially aggregated the data in several ways, such as by the northern (north of CalCOFI line 80), middle (line 80 to line 90), and southern (south of line 90) parts of the region, as well as by working with only the most frequently sampled transects (lines 80 and 90). We found, however, that the time series utilizing all the data was highly correlated with almost all other combinations of data. Therefore, the CalCOFI data for a given year were combined spatially for all analyses. In addition, the number of missing data points was reduced, though large gaps still existed.

Additional zooplankton biomass data from oceanic areas of the Northeast Pacific Ocean besides Station P exist for two time periods (1956–62 and 1980–89, except for 1986), and are more fully described in Brodeur and Ware (1992). In this analysis, we extended the geographic range of values to 40°N to include the transition region south of the subarctic boundary (Pearcy 1991) for both time periods (see figure 3 for sampling locations). Contour maps of zooplankton biomass ( $\text{g}/1,000 \text{ m}^3$ ) were generated for both time periods with a raster-based GIS program (Compugrid, Geo-spatial Ltd.). Yearly interpolated means were computed for each year. Since the earlier analysis, an additional 5 years (up to 1994) of data collected by Hokkaido University have become available. Although there is not enough coverage for this later period to map the overall distribution of biomass, many of the same transects were sampled each year so that the interannual variability can be examined. As before, only biomass data collected from 15 June to the end of July and in the same geographic area described by Brodeur and Ware (1992) were included.

### Time Series Analyses

We examined the temporal relationship between the Station P zooplankton data and the offshore CalCOFI data using time series cross-correlation analyses (Box and Jenkins 1976). We investigated monthly, seasonal, and annual lagged relationships. The time series of available data for each region shows incomplete temporal overlap, especially for the CalCOFI region, which was intermittently sampled during the 1970s and 1980s (figure 4). The distribution of both the Station P and offshore CalCOFI zooplankton data was highly skewed, and a log-transformation of the data was performed before the time-series analysis. In addition, a pronounced seasonal

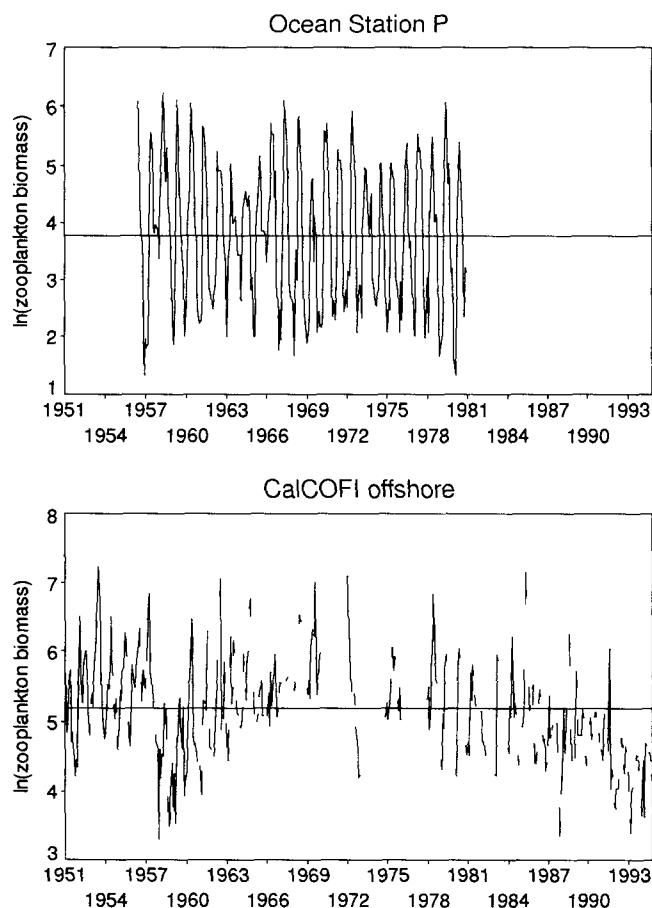


Figure 4. Log-transformed zooplankton biomass time series for Ocean Station P and offshore CalCOFI sampling areas.

signal is evident in each region (figure 4). This signal was removed by calculating a yearly average biomass for each month and season (spring = March–May; summer = June–August; fall = September–November; winter = December–February). Both monthly time series exhibited substantial lag-1 autocorrelation, which can result in spurious cross-correlations (Box and Jenkins 1976; Myers et al. 1995). Therefore it was necessary to filter both series by a process known as prewhitening (*sensu* Box and Jenkins 1976) before computing the cross-correlation function (CCF) at lagged periods.

### Ocean Surface Current Simulations

Due to a lack of time series of open-ocean current data, we used a model developed for the North Pacific Ocean which provided a continuity of surface mixed-layer currents through space and time. The OSCURS (Ocean Surface CURrent Simulations) model uses gridded daily sea-level pressure fields to compute daily winds, and from them to compute daily ocean surface currents (Ingraham and Miyahara 1988). The long-term mean geostrophic current vectors computed from existing temperature and salinity versus depth data are added

vectorially to these daily currents, and the model is then tuned to existing satellite-tracked drifter data.

## PRODUCTION TRENDS IN THE CENTRAL SUBARCTIC DOMAIN

### Phytoplankton and Primary Productivity

Nearly 30 years of observations at Station P indicate no major seasonal variation in phytoplankton biomass (figure 5; see also Wong et al. 1995). There are generally no phytoplankton blooms, and the mean phytoplankton biomass is always very low, averaging about  $0.4 \text{ mg chlorophyll m}^{-3}$  (figure 5; Banse 1994). There are no indications of long-term increases in chlorophyll over this time period (figure 6) similar to those documented for the central North Pacific Ocean by Venrick et al. (1987).

However, as model studies show (Frost 1993; Fasham 1995), phytoplankton biomass is not necessarily a sensitive indicator of either seasonal or interannual variations of phytoplankton productivity. Depth-integrated productivity at Station P shows a pronounced seasonal cycle, increasing in early spring with the seasonal increase in insolation and peaking in midsummer at levels 4–8 times as high as in winter (Sambrotto and Lorenzen 1987; Welschmeyer et al. 1993; Boyd et al. 1995; Wong et al. 1995). Estimates of phytoplankton production rate at Station P also suggested higher rates in the 1980s than in the 1960s and 1970s, but this is considered inconclusive evidence for interdecadal variation in phytoplankton production rate because of methodological problems prior to the 1980s (Welschmeyer et al. 1993; Wong et al. 1995). Moreover, indirect evidence of changes in phytoplankton productivity based on nitrate removal during the spring-summer period provides no sugges-

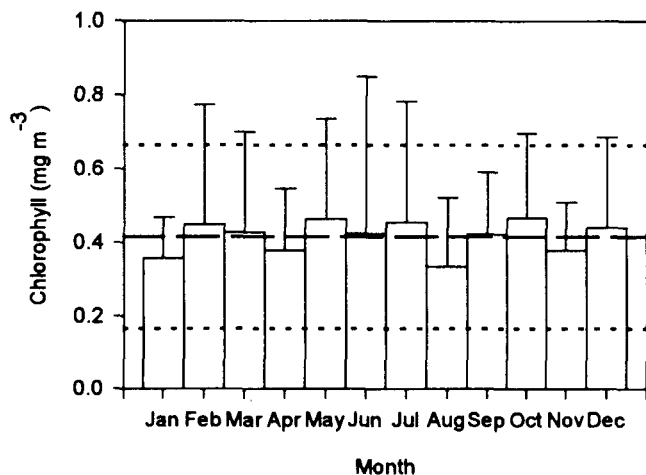


Figure 5. Monthly mean surface chlorophyll a concentration at Ocean Station P. Error bars are standard deviations (s.d.) of the mean. Also shown is the overall annual mean (dashed line) and  $\pm 1$  s.d. of the annual mean (dotted lines).

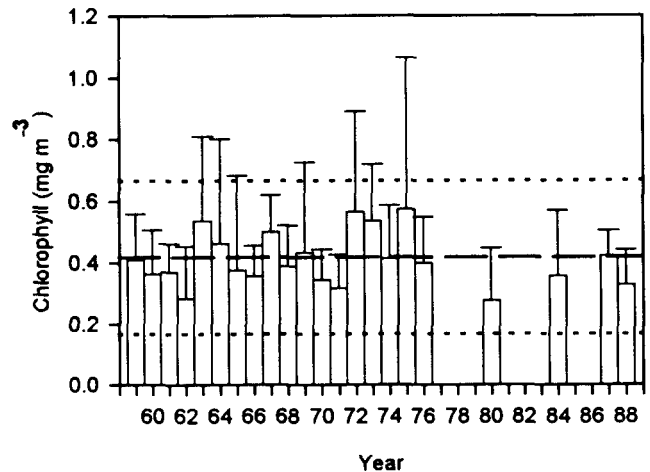


Figure 6. Annual mean and standard deviation of surface chlorophyll a concentration at Ocean Station P. Means for the period 1959–76 are based on data in McAllister et al. (1959), McAllister (1962), and Stephens (1964, 1966, 1968, 1977); two very high values in 1975 (21 June, 26 October) were excluded from the analysis because of lack of supporting evidence from either subsurface depths or preceding and subsequent dates. Sources of other data: 1980 (C. B. Miller, pers. comm.); 1984 (C. J. Lorenzen, unpubl. data rep.); 1987 and 1988 (N. A. Welschmeyer, pers. comm.). Also shown are the long-term mean value (dashed line) and  $\pm 1$  s.d. of the mean (dotted lines) for the entire data set.

tion of interannual trends (C. S. Wong, IOS, Sydney, B.C., pers. comm.). Wong et al. (1995) noted that because availability of dissolved iron may affect phytoplankton production rate at Station P (Martin and Fitzwater 1988), interannual variations in atmospheric input of iron could produce parallel changes in phytoplankton production, but any significant interdecadal changes in phytoplankton production rate induced by this mechanism also should be evident in seasonal nitrate removal.

### Zooplankton

**Seasonal variability.** Zooplankton biomass is highly seasonal at Station P, peaking in May and June and decreasing almost an order of magnitude from late fall to early spring (October to March; figure 7). This contrasts with the situation for the offshore CalCOFI grid, which shows some seasonality but only about a doubling between winter and summer (figure 7). With each month given equal weighting, the annual mean weight of zooplankton at Station P is  $82 \text{ g}/1,000 \text{ m}^3$ . The annual mean displacement volume ( $260 \text{ ml}/1,000 \text{ m}^3$ ) for the CalCOFI region converts to a higher wet weight (using wet weight =  $0.8$  displacement volume; Wiebe 1988) than that seen for Station P.

**Interannual variability.** In the entire data set of zooplankton biomass from Station P (figure 4), there appears to be no discernible trend over the 26-year period. However, Brodeur and Ware (1992) found a significant long-term increase in biomass for a 6-week period in early

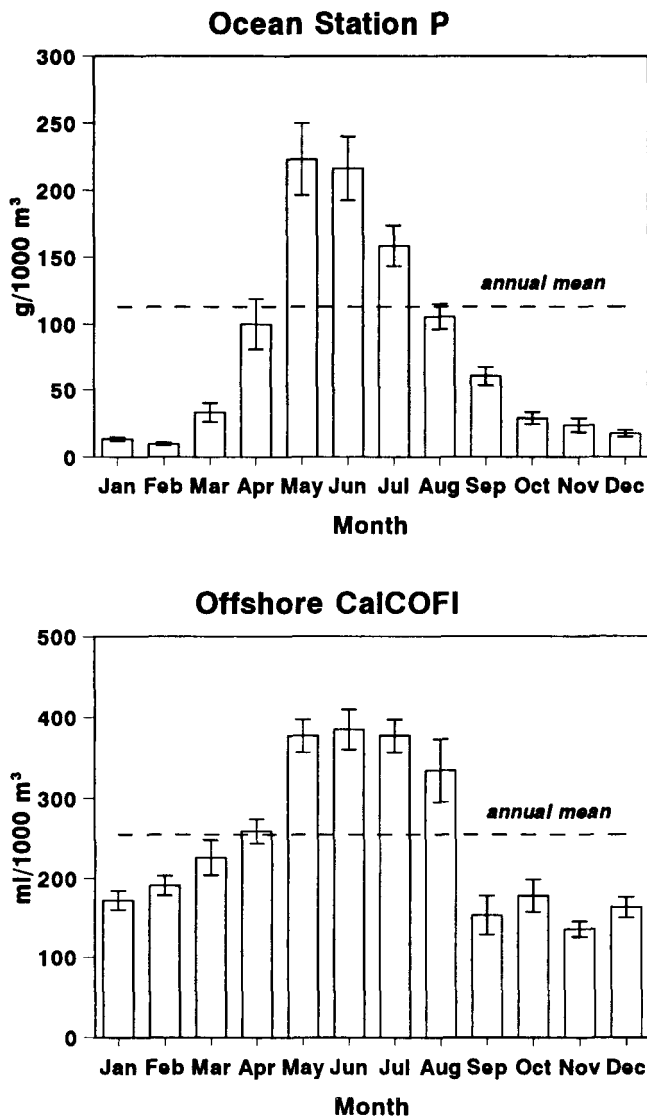


Figure 7. Monthly values of zooplankton biomass at Station P and in the offshore region of CalCOFI. The bars represent the means, and the error bars represent  $\pm 1$  standard error. We calculated the Station P data as means of the monthly means for each year (17–23 values per month) rather than using all data within a month (range 104–339 observations per month). The annual means for each area are shown as a dashed line.

summer, when biomass is near its annual peak. We re-analyzed these data using the new gear-correction factor (see Methods) and still found a significantly positive relationship ( $p = 0.003$ ) despite the high annual variability and the fact that so few years are represented beyond the 1976–77 regime shift (figure 8). For the large-scale sampling (figure 9), a discernible shift in zooplankton biomass was observed between the earlier period (1956–62) and most of the 1980s (up to 1988). The mean zooplankton biomass for the years after 1988, although above the long-term mean, was generally intermediate relative to the other periods examined, and showed more interannual variability (figure 9).

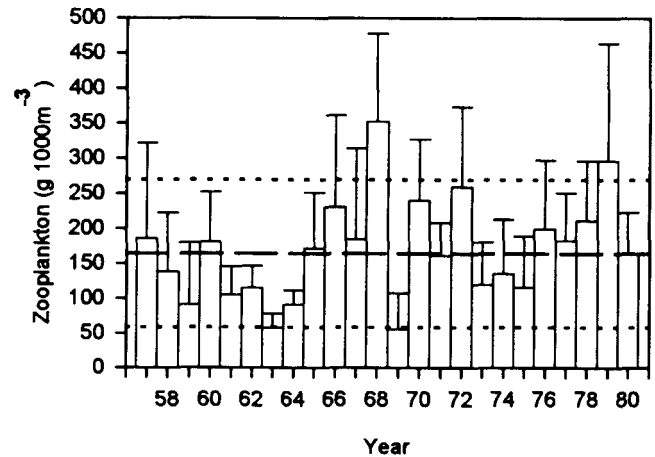


Figure 8. Annual values of zooplankton biomass (means  $\pm 1$  s.d.) at Station P from 1956 to 1980 for the 6-week period beginning June 1. Also shown are the long-term mean value (dashed line) and  $\pm 1$  s.d. of the mean (dotted lines) for the entire data set.

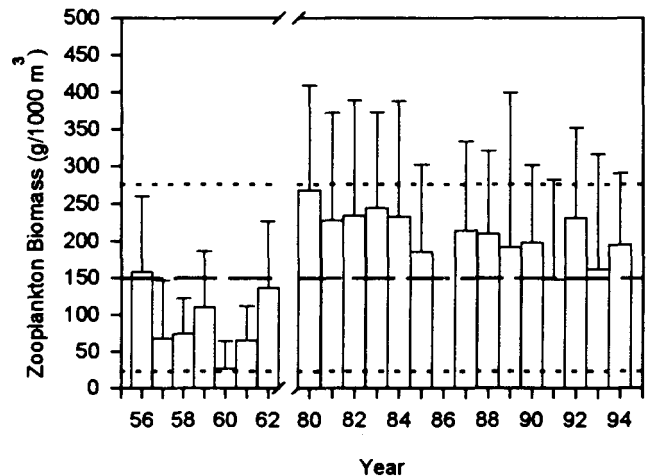


Figure 9. Annual values of zooplankton biomass for the large-scale sampling in the subarctic and transition regions of the North Pacific. Shown are the annual mean (histograms) and  $\pm 1$  s.d. (error bars). The dashed line is the mean for all years, and the dotted lines are  $\pm 1$  standard deviation of the long-term mean.

**Geographic variability.** The large-scale zooplankton biomass distributions showed dramatic differences between the two periods not only in the overall biomass, as described previously, but also in the distribution patterns for each time period (figure 10). High biomass in the 1956–62 period occurred mainly in the central part of the Gulf of Alaska, with much lower concentrations nearer to the coast. Conversely, during 1980–89 elevated biomass occurred in a continual band from the Transition Zone up to the northern coast of Canada and Southeast Alaska, and then extended westward along the shelf edge (figure 10). The overall pixel distribution of biomass between the periods showed that almost all the biomass values in the later period were above the mean value for the earlier period (figure 10).

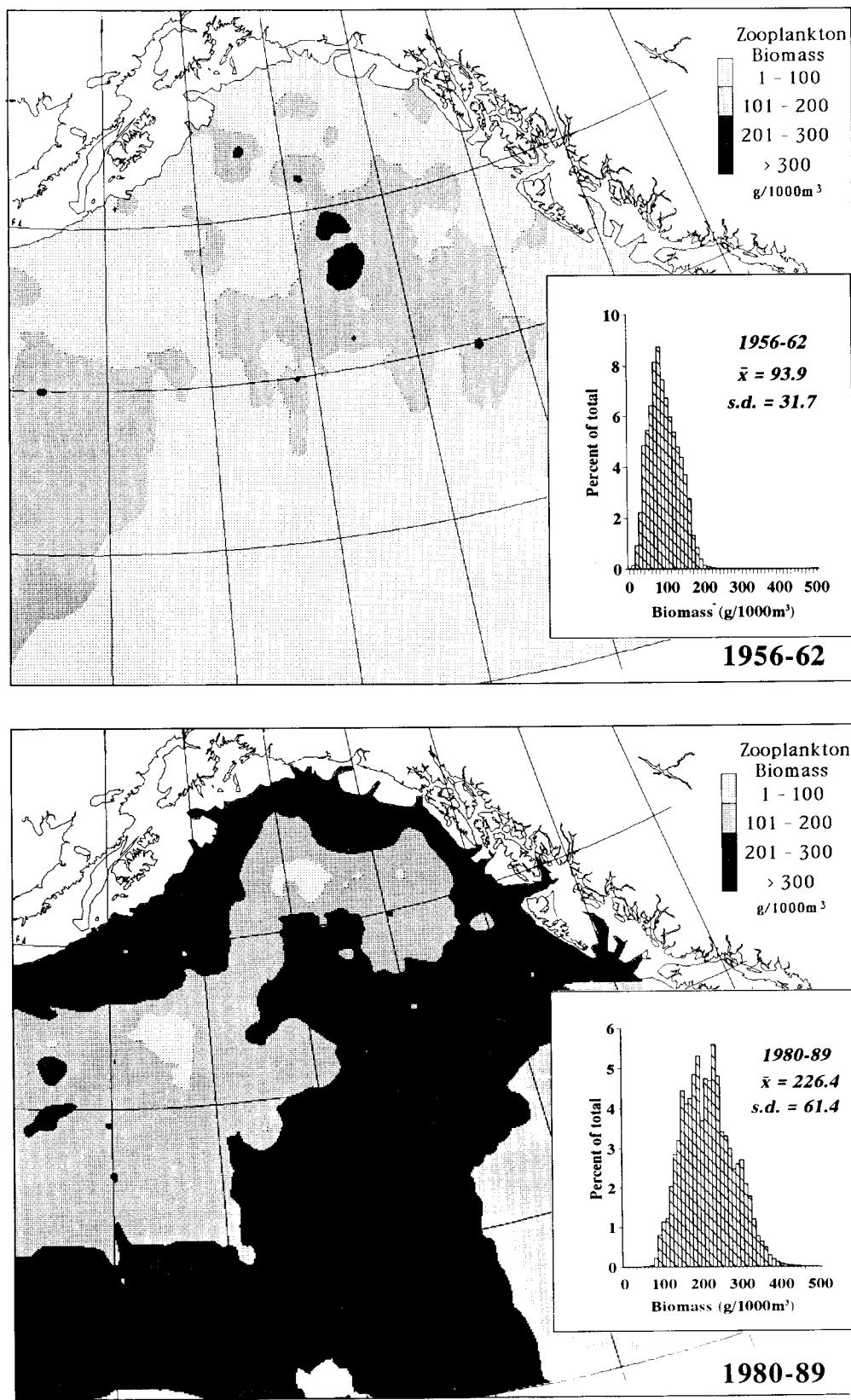


Figure 10. Large-scale distribution of zooplankton biomass from sampling during the 6-week period beginning June 1 for 1956-62 and 1980-89. See figure 1 for locations of sampling stations for each period. The insets show the zooplankton biomass pixel distributions as a percentage of the total number of pixels for each time period. The overall mean and standard deviation of biomass for the time period are given.



### ANALYSIS OF COVARIATION IN STATION P AND CALCOFI DATA SETS

The magnitude of anomalous values was similar in both regions, but the CalCOFI data showed an apparent long-term decline in zooplankton biomass over the last two decades (figure 4). Autocorrelation plots were examined to determine whether serial autocorrelation exists within each region (figure 11). Both monthly time series show significant autocorrelation. The CalCOFI data are significantly autocorrelated up to 12 months, and all correlations up to 24 months are positive. Conversely, the Station P data show that anomaly events are much more short-lived (lasting 2–3 months), and little temporal pattern is evident after this time.

The cross-correlation between the autocorrelated data sets shows highly significant lagged correlations in both directions (figure 12). The presence of autocorrelation within both time series, however, renders this relationship highly suspect (Katz 1988; Newton 1988). To ascertain whether there is a real relationship, it is necessary to prewhiten both series—that is, remove the autocorrelation structure—and then plot the CCF of the residual series. Both series were adequately described by

a lag-1 autoregressive (AR1) model. Separate filters were used for the two series (“double prewhitening”), and the coefficients were approximately equal to the lag-1 autocorrelation values—0.412 for CalCOFI and 0.524 for Station P. After filtering, almost all the significant lag correlations disappeared (figure 12). The only one that remained (CalCOFI leading Station P by 2 months) was quite small (−0.203) and possibly spurious.

The effect of prewhitening, while statistically justified, may also have the side effect of overcompensating for autocorrelation and removing evidence of an actual signal. As an alternative to prewhitening, an “effective degrees of freedom” is sometimes employed when calculating the confidence intervals around the cross-correlation estimates (Trenberth 1984). In the case of two AR1 time series, the true standard deviation at lag 0 is inflated over the no autocorrelation case by

$$f = [(1 + \phi_X * \phi_Y) / (1 - \phi_X * \phi_Y)]^{0.5},$$

where  $\phi_X$  and  $\phi_Y$  are the lag-1 autocorrelation coefficients (Katz 1988). Thus at lag 0, the standard deviation is approximately 1.25 times greater than that computed on an assumption of independent data points.

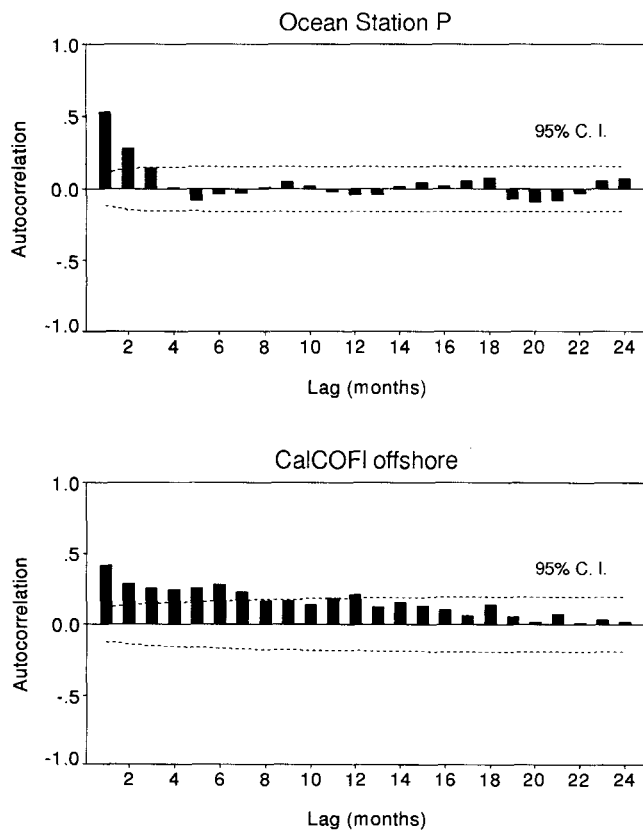


Figure 11. Serial autocorrelation of Station P and offshore CalCOFI zooplankton biomass at various time lags. Upper and lower 95% confidence intervals are indicated as *dashed lines*.

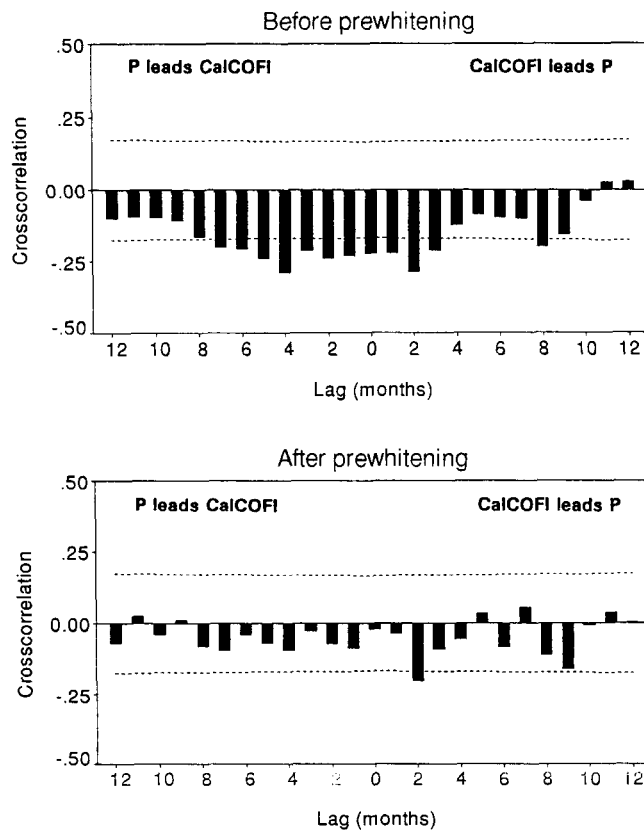


Figure 12. Cross-correlation between Station P and offshore CalCOFI zooplankton biomass at various time lags before and after prewhitening. The upper and lower 95% confidence intervals are indicated as *dashed lines*.

Assuming an approximately equal inflation at other lags, only lags -4 (Station P leads CalCOFI by 4 months) and +2 (CalCOFI leads Station P by 2 months) are significant at the 0.05 level. The -4-month lag is interesting in that it is interpretable in terms of ocean physics. A parcel of water originating upstream in the Subarctic Current would arrive at Station P approximately 4 months ahead of a particle diverted to the CalCOFI region (see next section). The +2-month lag may or may not be spurious, but it has no obvious physical explanation (though see below).

We next examined within- and between-area lag correlations for the yearly 3-month seasonal averages. The seasonal data exhibited almost no autocorrelation among years, a result that can be deduced from the monthly correlations, which die out by 12 months. Therefore, the cross-correlations between seasonal averages did not require a prewhitening step. Most within-region correlations were positive (10 of 12), with the CalCOFI data showing much stronger between-season coherence than the Station P data (table 1).

TABLE 1  
**Within-Region Correlation Matrices of Ocean Station P and Offshore CalCOFI Seasonal Biomass Time Series (Log-Transformed and Zero-Centered)**

	Winter	Spring	Summer	Fall
<b>Ocean Station P</b>				
Winter	1.000	0.221	0.005	0.387
Spring		1.000	<u>0.474</u>	-0.163
Summer			1.000	-0.032
Fall				1.000
<b>Offshore CalCOFI</b>				
Winter	1.000	<u>0.498</u>	0.242	0.351
Spring		1.000	<u>0.590</u>	<u>0.376</u>
Summer			1.000	<u>0.411</u>
Fall				1.000

Single underline indicates significance at the 0.05 level, double underline at the 0.01 level.

TABLE 2  
**Cross-Region Lag-Correlation Matrices of Ocean Station P and Offshore CalCOFI Seasonal Biomass Time Series: Cross-Region Correlations Are Shown up to 4 Seasons Later**

Ocean Station P leads CalCOFI								
	C winter	C spring	C summer	C fall	C winter+1 <sup>a</sup>	C spring+1	C summer+1	C fall+1
P winter	-0.205	-0.315	-0.343	-0.039	-0.182			
P spring		<u>-0.615</u>	-0.397	-0.463	-0.218	-0.172		
P summer			-0.342	<u>-0.506</u>	-0.269	-0.055	0.256	
P fall				-0.009	-0.210	-0.376	<u>-0.617</u>	-0.062
CalCOFI leads Ocean Station P								
	P winter	P spring	P summer	P fall	P winter+1	P spring+1	P summer+1	P fall+1
C winter	-0.205	-0.263	0.121	-0.011	-0.018			
C spring		<u>-0.615</u>	-0.309	-0.026	-0.004	-0.217		
C summer			-0.342	-0.123	-0.322	<u>-0.571</u>	-0.412	
C fall				-0.009	-0.112	<u>-0.610</u>	-0.068	0.328

<sup>a</sup>+1" indicates a season in the following calendar year.

Underlined values are significant at the 0.05 level. The cross-correlations with no lag are repeated in each section of the table for consistency (first diagonal row).

We examined cross-region correlations lagged up to a year in each direction (table 2). Out of a total of 36 separate correlations, 32 were negative. Of those 32, 5 were significant at the 0.05 level. There are a few details worth noting about the pattern of correlations. Those where Station P leads CalCOFI tend to be stronger than the converse set, particularly for the winter and spring seasons. If we focus only on the spring months, which is the time when these ecosystems are most likely to respond to variations in the north-south diversion from winter Aleutian Low intensity (figure 13), there is indication of a strong, lag-0 inverse relationship between Station P and offshore CalCOFI ( $r = -0.62$ ;  $n = 16$ ;  $p = 0.011$ ). This relationship remains strong even after the weak autocorrelation in the California Current data is removed ( $r = -0.58$ ).

### COMPARISON TO ENVIRONMENTAL VARIABLES

In order to examine variability of surface flow into the Gulf of Alaska, we started OSCURS model runs at Station P on December 1 and ran them for 3 months

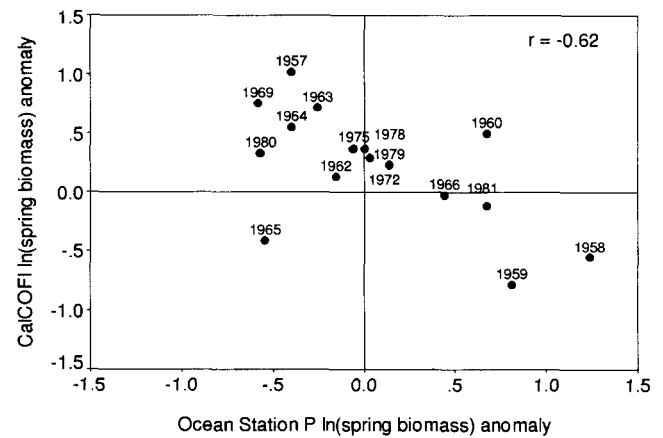


Figure 13. Relationship between Station P and offshore CalCOFI biomass anomalies for the spring quarter (March-May) by year.

for all years from 1946 to 1994. A substantial divergence of the tracks occurred in the eastern part of the gulf, with some tracks going north into the Alaska Current and others heading into shore or turning south. When the tracks are partitioned into pre-1975 and 1975 and later, some decadal changes become evident (figure 14). In the earlier period, flow into the Alaska Current was more relaxed, and a substantial number of the trajectories veered southward. The later period appeared to show stronger flow into the Gulf of Alaska, and relatively few trajectories went south. The occurrence of either northward or southward flow tends to run in series of various lengths (table 3). Simulations started 5° south of Station P (45°N, 145°W) showed more directed eastward and southward flow but again showed some differences between the two time periods (figure 15).

The model was then used to simulate the north-south divergence of the Subarctic Current along its eastern boundary for equivalent 5-year time periods before and after the regime shift (1971–75 vs. 1976–80) in order to assess changes in circulation between the two regimes. Long-term mean flow tracks begun in January along 145°W showed a more southern diversion before the regime shift than after, with the primary differences in the trajectories starting at or north of 48°N (track 5 in figure 16).

## DISCUSSION

For oceanic waters of the eastern subarctic Pacific Ocean, direct evidence for interannual and decadal variations in biological production—that is, phytoplankton production—is weak. However, zooplankton standing stock, when viewed on a basinwide scale, has varied and seems to be higher since the 1976–77 regime shift. Recognizing that primary production might not have changed between the regimes, Brodeur and Ware (1992) hypothesized a causal link between increased wind stress and increased zooplankton stock and production, in that intensified wind mixing would result in deeper mixed-layer depths (MLD) in winter. This would slow the growth rate of the phytoplankton, retard the spring increase in primary production, and allow grazers to make more efficient use of phytoplankton production. Experiments with an ecosystem model (Frost 1993) do not provide support for such a mechanism. Indeed, just the opposite effect should occur. A deeper mixed layer in winter should result in decreased balance between phytoplankton growth and grazing in spring, when the surface layer restratifies. Phytoplankton production should be less efficiently utilized by grazers, and more production should be lost to mixing and sinking below the surface layer.

But, in fact, there is not much interannual variation in MLD at Station P because of the halocline, and over

TABLE 3  
 Yearly Anomalies of Simulated OSCURS Trajectories  
 from Ocean Station P North or South of the Long-Term  
 Mean Trajectory, in Three-Month (Dec.–Feb.)  
 Trajectories for 1946 to 1994

North	South
	46
47	48
	49
	50
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52	
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the observed interannual range of winter MLD (80–130 m), Frost's (1993) model suggests that such variations would have relatively little effect on biological production or zooplankton biomass at Station P (Frost, unpubl. data). Using a 1-D dynamic mixed-layer model (modified Garwood model) coupled to a nitrate-phytoplankton-zooplankton (NPZ) model, McClain et al. (1996) found surprisingly little interannual variation in phytoplankton production rate at Station P.

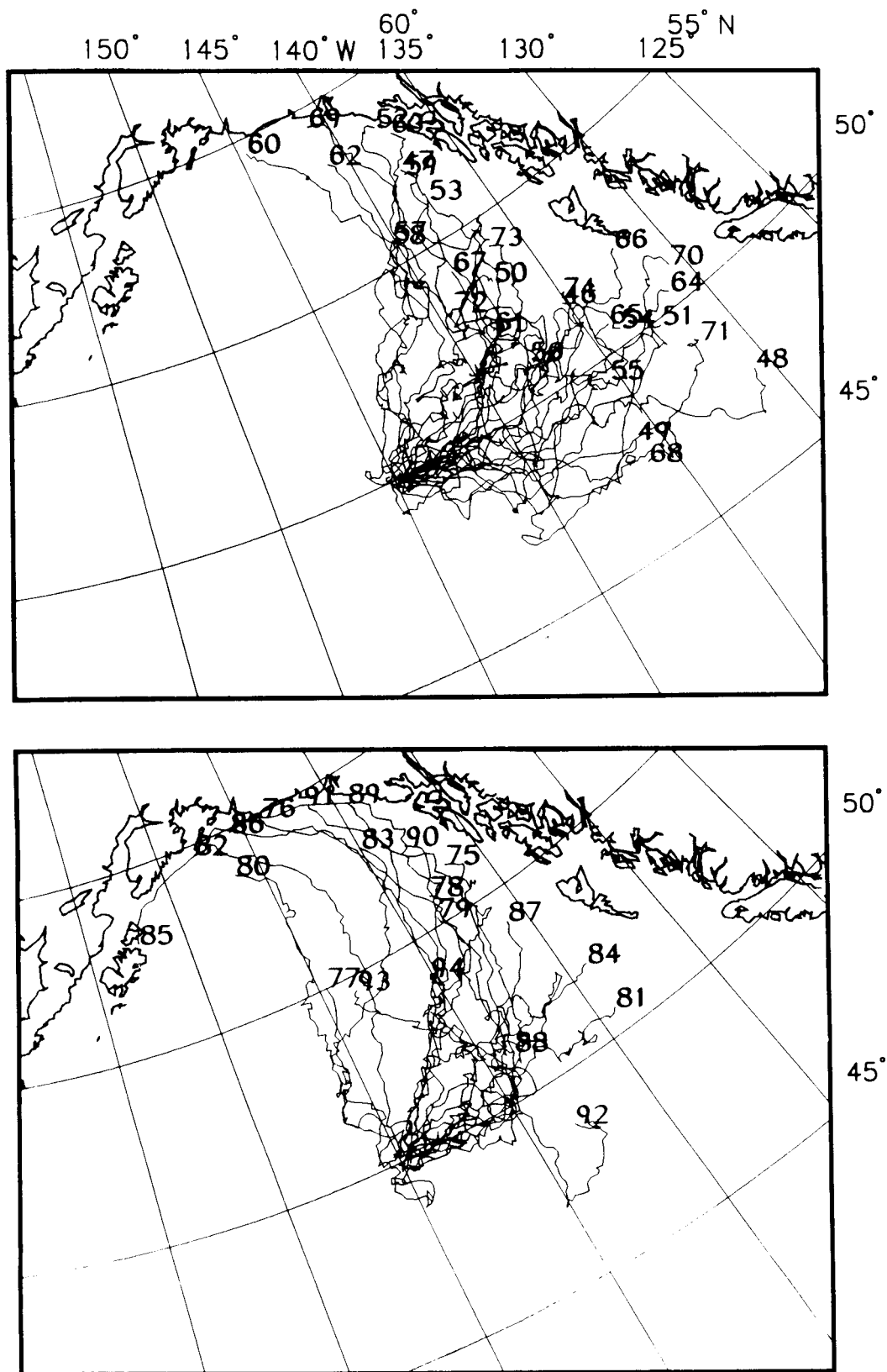


Figure 14. Simulated flow trajectories for the OSCURS model runs from 1946 to 1974 (top) and 1975 to 1994 (bottom). Each trajectory was started at Station P (50°N, 145°W) on December 1 and run for 3 months, incrementing the positions daily. Each year is marked at the endpoint of its trajectory.

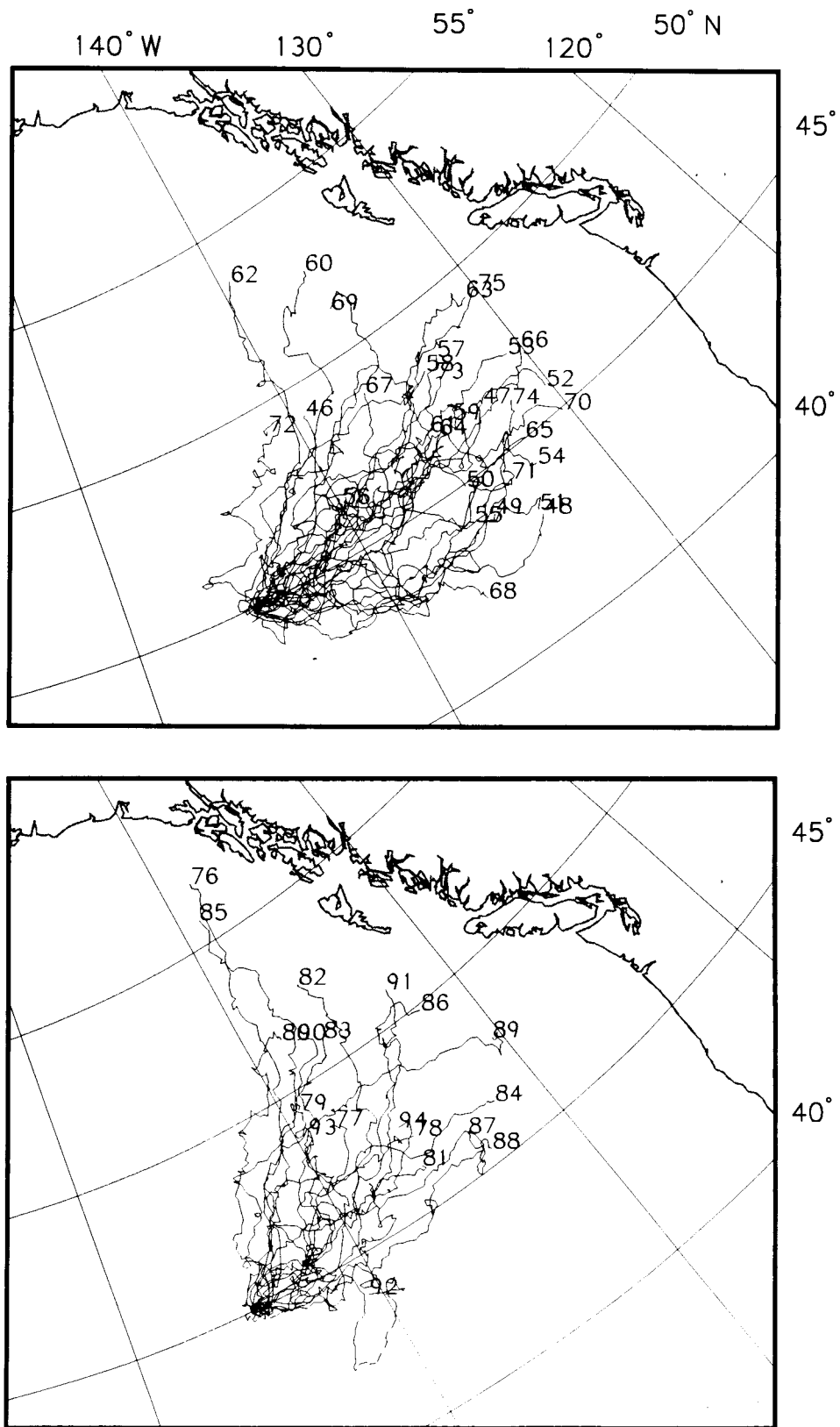


Figure 15. Same as figure 14 but with the simulations started 5° south of Station P (45°N, 145°W).

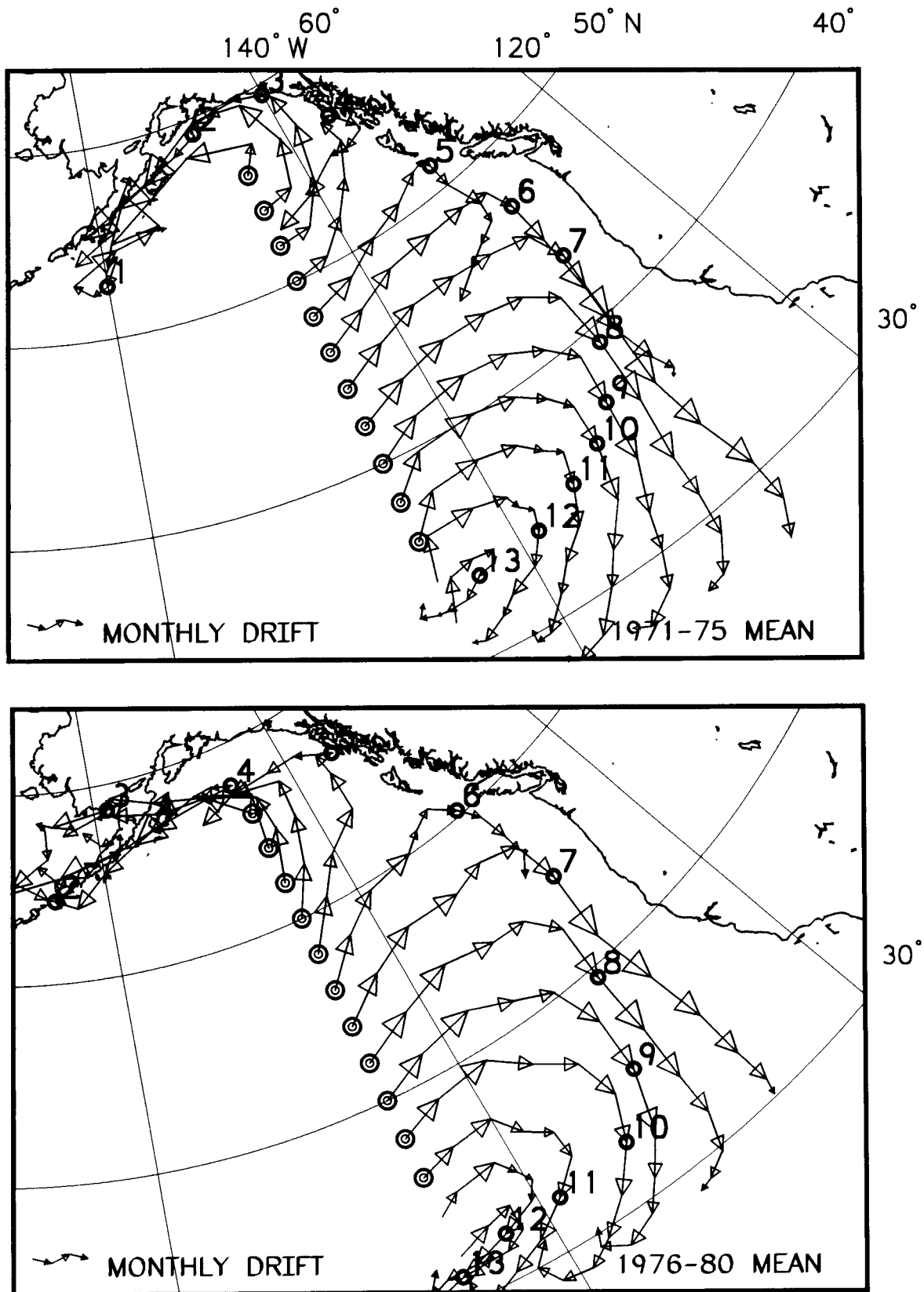


Figure 16. Mean simulated flow trajectories for OSCURS model runs for the 5-year period before (*upper*) and after (*lower*) the regime shift. Model runs were started at 145°W on January 1 and run for 12 months. The size of the arrow head and the length of the shaft indicate the relative current speed. Each trajectory is marked with a circle after 6 months.

It is likely that events at Station P are not generally representative of the entire open Gulf of Alaska, due both to the singularity of the station and its location. Polovina et al. (1995) reported on interannual changes in winter-spring mixed-layer depth throughout the North Pacific Ocean. There was considerable spatial variation in change in MLD, with the region of Station P showing little long-term change but other areas showing rather large changes (e.g., the northeast Gulf of Alaska). Polovina et al. (1995) used an NPZ model to look at the effects of their modeled changes in MLD. The model predicts that large changes in MLD will have little effect on phytoplankton stock, but potentially large effects on phytoplankton production rate and zooplankton stock in the mixed layer. Thus, spatial variation in the processes controlling production rate may explain the apparent increase in zooplankton stock evident on a large spatial scale in the eastern subarctic Pacific Ocean during the 1980s. This hypothesis is difficult to test because there are no basinwide data on nutrient concentrations and biological observations.

To our knowledge, there is no extensive time series of phytoplankton standing stock for the California Current region comparable to the data set from Station P. However, the analysis by Fargion et al. (1993) of Coastal Zone Color Scanner data and in situ chlorophyll measurements indicates little seasonal variation in phytoplankton stock in the offshore area represented by the zooplankton data presented here (30° to 35°N). Moreover, phytoplankton pigment concentrations are similar to those at Station P (cf. Chavez 1995). Because the California Current region covered by the zooplankton data is at considerably lower latitude than Station P, it is probable that higher phytoplankton production accounts for the higher zooplankton standing stock observed (figure 7).

Two factors hinder definitive identification of a lead/lag or "out-of-phase" relationship between zooplankton productivity at Station P and the CalCOFI region. First, as noted earlier, there is a great deal of missing data in both regions. Secondly, the high observed autocorrelation, the robust estimation of which is also hindered by data gaps, needs to be removed. Despite these difficulties, there is evidence that the two regions are negatively related. It is less clear whether there is a consistent lag time between the two regions. The evidence points more toward anomalies at Station P leading anomalies at CalCOFI. It is possible that the inverse relationship is due to differential (i.e., inverse) flow from the Subarctic Current, but that the flow speed within each regime is highly variable, hence the lack of a consistent lag relationship.

El Niño–Southern Oscillation (ENSO) events are another factor that may play a role in the timing and in-

tensity of anomalous zooplankton production. During ENSO events, positive SST anomalies are propagated poleward in the form of coastally trapped Kelvin waves. Roemmich and McGowan (1995a, b) attributed the decline in CalCOFI region zooplankton biomass to sea-surface warming, part of which resulted from a large number of ENSO events since the mid-1970s. While sea-surface temperature anomalies associated with ENSO events have occurred in the Gulf of Alaska (Wooster and Fluharty 1985), as often as not, there has not been any North Pacific Ocean response (Freeland 1990; Bailey et al. 1995). Thus, depending on the magnitude and northward extent of the ENSO event and the Station P zooplankton response to surface warming, there is the potential for a Station P response to lag a CalCOFI response. At the very least, the ENSO factor serves to cloud the relative effects on zooplankton productivity from variations in the Subarctic Current.

It may not be coincidental that the increase in zooplankton shown here in the Subarctic Pacific is opposite to the trend for California Current zooplankton reported by Roemmich and McGowan (1995a, b). Although there is some indirect biological evidence for the ocean-circulation model proposed by Hollowed and Wooster (1992), the hydrographic evidence is more limited. However, several recent papers shed some light on the issue and suggest considerable modification to the model. Tabata (1991), in reexamining the Chelton and Davis (1982) premise, found a correlation between the coastal component of the Alaska Current and California coastal sea levels, particularly during El Niño years. He attributed this correlation, however, to the coastal currents being in phase from Canada to California rather than to changes in the bifurcation of the Subarctic Current. Kelly et al. (1993) analyzed sea-surface height anomalies for the Northeast Pacific Ocean over a 2.5-year period. Their results tended to support those of Chelton and Davis (1982) that the California and Alaska Current systems fluctuate "out of phase," coinciding with variations in wind-stress curl in the North Pacific Ocean and subsequent diversion of flow from the Alaska Gyre into the California Current, as well as with some correlation with ENSO dynamics. Van Scoy and Druffel (1993), in an analysis of tritium (<sup>3</sup>H) concentrations in seawater from Ocean Station P and a station in the southern California Current, suggest that there is increased advection of sub-polar water into the California Current during non-El Niño years and that ventilation of the Alaska Gyre (intensification) occurs during El Niño years.

Lagerloef (1995), in his analysis of dynamic topography in the Alaska Gyre during 1968–90, suggested that after the well-documented climatic regime shift of the late 1970s, the Alaska Gyre was centered more to the east and that its circulation appeared weaker after the shift

than before. The implication is that the intensification of the winter Aleutian Low associated with the regime shift did not result in a spin-up of the Alaska Gyre.

Finally, Miller (1996) reviews some recent advances in large-scale modeling of the California Current and its interaction with basin-scale circulation and forcing. He reports the significant deepening of the thermocline off California after the 1976–77 regime shift similar to that described by Roemmich and McGowan (1995a) and attributes this to basin-scale changes in wind stress curl. This is achieved at two time scales—the first at the decadal and North Pacific Gyre scale, forced by significant deepening and weakening of the Aleutian Low, and the second at the interannual ENSO scale, forced by waves propagating through the ocean from the tropics. Miller (1996) also reported that after the 1976–77 regime shift there appeared to be a stronger than normal northward flow into the central Gulf of Alaska but little change in the flow into the California Current system.

If zooplankton biomass is advected preferentially to either region, as the current-simulation model suggests, then this allochthonous biomass should be higher than that produced locally for our results to be valid. There are few comparable measurements of zooplankton biomass in both the Transition Domain and Subarctic Domain. Our data for the large-scale sampling during the 1980s suggest that levels were high in the Transition Domain and are somewhat higher than in the central part of the Alaska Gyre. Data taken in summer for several years from north-south transects in the western subarctic (155°E, 170°E, 175.5°E, and 180°E) show elevated zooplankton wet weights in the transition zone compared with those in the subarctic (Shiga et al. 1995). Sampling along 180° and in the Gulf of Alaska during June and July of 1987 revealed higher zooplankton biomass in transition zone waters than in the central Subarctic Domain, especially in the 150–300-m depth strata (Kawamura 1988).

An alternative explanation for the inverse relationship in zooplankton might be that similar large-scale changes in thermal structure of the western North Pacific (Venrick et al. 1987; Royer 1989; Roemmich and McGowan 1995a; Miller 1996) could have radically different effects on biological production in the two regions. At Station P, the slightly warmer temperature of the mixed layer could directly affect increased zooplankton production rate and standing stock, as suggested by Conversi and Hameed (1996). The same warming and associated deepening of the upper mixed layer (Miller 1996) could cause decreased zooplankton production and standing stock in the California Current region by impeding the supply of nutrients to the surface layer (Roemmich and McGowan 1995a). Our data are not sufficient to allow examination of this alternate hypothesis.

## IMPLICATIONS FOR HIGHER TROPHIC LEVELS

The dramatic increase and change in distribution of mesozooplankton biomass seen in the subarctic Pacific Ocean between the periods 1956–62 and 1980–89 would be expected to have important ramifications for higher trophic levels dependent on these food sources. Brodeur and Ware (1995) documented substantial increases in the catch rates of most pelagic nekton (fishes, squids, and elasmobranchs) caught in research gill nets over roughly the same time periods. The only species that showed a decline in catch rates (jack mackerel, *Trachurus symmetricus*) is primarily a California Current species which migrates into the Gulf of Alaska only during periods of peak abundance. Although these authors were not able to convert catch rates to abundance or biomass because of the paucity of collaborative time series of abundances for the noncommercial species, Brodeur and Ware (1995) estimated that total salmon abundance nearly doubled between these two periods.

For the present study, we combined catch data of the 14 species examined by Brodeur and Ware (1995) and plotted nekton catch-rate distributions for roughly the same two time periods over the same geographic range examined previously for zooplankton. Although there are differences between them, the nekton distribution plots (figure 17) showed some similarities to the zooplankton distribution in that most concentrations are offshore in the Alaska Gyre during the 1950s and occur in a band around the outside of the gyre in the 1980s. The magnitude of the increase in catch rate (figure 17 inset) is also similar to that of the plankton. Although this is not cogent evidence of a strong link between these trophic levels, since there is often an additional trophic level (macrozooplankton and micronekton) between the mesozooplankton and the larger nekton, there is enough commonality in the distribution patterns to suggest that the distribution and abundance of zooplankton is positively related to that of higher-level predators.

Coastal fishes in the Gulf of Alaska would be expected to benefit most from the increase in zooplankton biomass that we observed during the 1980s. High rates of upwelling in the center of the Alaska Gyre would push nutrients and subsequent phytoplankton and zooplankton production onto the shelf along the edge of the gulf, thereby stimulating coastal production. Cooney (1986) has suggested that large oceanic species of copepods (*Neocalanus* spp. and *Eucalanus bungii*) are transported onto the shelf in the northern Gulf of Alaska, providing rich food resources for the coastal community. A direct link between atmospheric circulation, oceanic copepod production, and sablefish (*Anoplopoma fimbria*) recruitment has been hypothesized by McFarlane and Beamish (1992), but such mechanisms have not been explored for other demersal fishes.



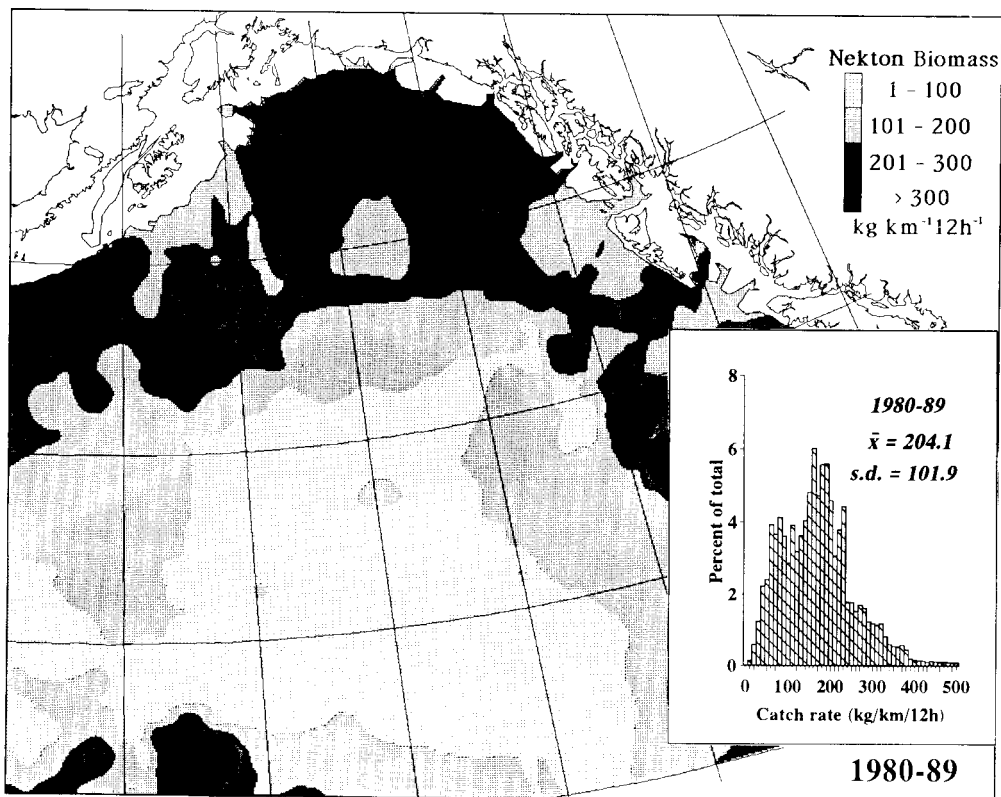
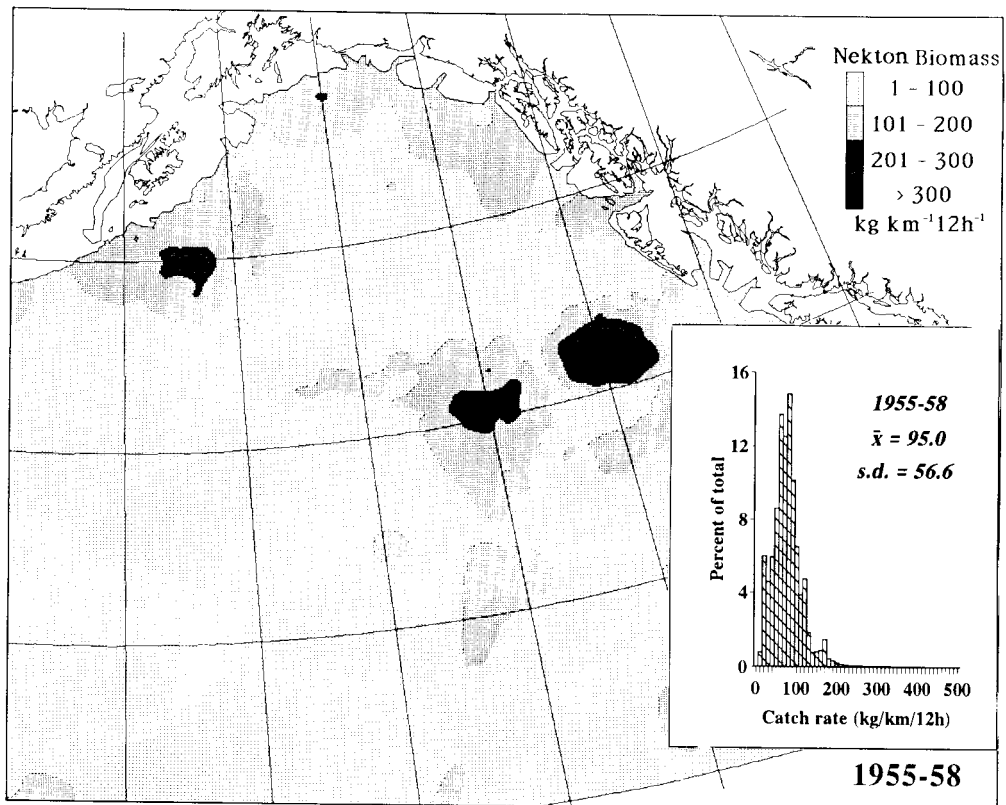


Figure 17. Large-scale catch-rate distribution for 14 species of nektton commonly caught in research gill nets during the periods indicated. See Brodeur and Ware (1995) for sampling methodology, locations of sampling stations, and species included. Insets show nektton biomass pixel distributions as a percentage of the total number of pixels for each time period. The overall mean and standard deviation of biomass for the time periods are given.

For an investigation of ocean effects on fish species, Pacific salmon are an attractive group to study, since they have a relatively short life span, show substantial inter-annual variability in marine survival, and can be reliably censused at least several times during their life history. As discussed previously, Pacific salmon stocks have substantially increased in abundance since the mid-1970s in Alaska waters, whereas southern stocks have shown opposite trends (Pearcy 1992; Beamish 1994; Hare and Francis 1995). In some cases, the inverse relation between stocks in the two domains is striking (Francis and Sibley 1991). Our analyses suggest that zooplankton biomass in the subarctic region is inversely related to that in the California Current region. A combination of increased transport into the Alaska Current and advection of nutrients and zooplankton onto the shelf would probably increase the carrying capacity for juvenile salmon entering Alaska coastal waters (Cooney 1984).

By studying time lags between atmosphere/ocean and salmon statistics, Francis and Hare (1994) indicated that this regime-scale effect on Alaska salmon production is most likely to be felt during the early ocean life history. If salmonid production and survival are limited by factors occurring early in their marine life history, then the relative flow into the California Current and Alaska Current may profoundly affect their dynamics by enhancing prey production for smolts in the coastal zone. However, the increasing number of salmon surviving to maturation in the open ocean after the regime shift may have imposed an excess burden upon the oceanic zooplankton, which did not appear to increase as dramatically as those in the coastal zone (figure 10). It is likely that the amount of zooplankton available per individual salmon has decreased over this period, as suggested by Peterman (1987), which may be manifested in the long-term decreases in size at age and the older age of maturity witnessed in several salmon stocks (Ishida et al. 1993; Helle and Hoffman 1995).

#### SUGGESTIONS FOR FURTHER STUDY

1. Examine taxonomic composition of zooplankton over time to see if shifts in species composition have occurred along with the decadal-scale biomass shifts. This objective has been facilitated by the entry of the entire Station P detailed zooplankton data set in digital format that may be amenable to analyses (Waddell and McKinnel 1995).
2. Construct more spatially-explicit coupled physical and NPZ models to account for geographic variability in ocean conditions, nutrient input, and phytoplankton and zooplankton species composition (e.g., as in McGillicuddy et al. 1995).
3. Use models to examine potential top-down control on phytoplankton and zooplankton populations, extending—if possible—some of the presently available models (e.g., Frost 1993) to include nekton.
4. Establish new oceanic sampling sites for comparison with Station P to see whether processes occurring at Station P are representative of the subarctic region as a whole.
5. Continue any present time series sampling, and—if possible—revive discontinued sampling. It is imperative that the methodology does not change substantially during any time series. If it becomes necessary to make changes, then at least a sufficient number of intercalibration studies between old and new methodologies should be conducted to provide a seamless time series.
6. Examine factors that control the production of phytoplankton in the open subarctic Pacific. A major uncertainty concerns the rate of supply of iron, which may stimulate the growth rate of large phytoplankton species, enhance the growth rate of large zooplankton, and produce favorable feeding and growth conditions for pelagic fish.

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