SEASONAL CYCLE OF ZOOPLANKTON ABUNDANCE AND SPECIES COMPOSITION ALONG THE CENTRAL OREGON COAST

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ABSTRACT

Species composition of zooplankton collected during 3 yr of sampling close to the coast at Newport, Oreg., varied with season. In all seasons the most abundant plankters were copepods. Dominant species in summer were *Pseudocalanus* sp., *Acartia clausii*, *A. longiremis*, *Calanus marshallae*, and *Oithona similis*. These are primarily coastal forms with northern affinities, and they were present all year. Dominant species in winter were *Paracalanus parvus* and *Ctenocalanus vanus*, forms of southern affinities. They tended to disappear completely in summer. These geographic affinities are in correspondence with the source regions for surface waters that are implied by the direction of flow in the different seasons. Abundances are about one order of magnitude higher in summer than in winter. Copepod diversity is greater in winter than summer: the winter checklist contains 51 species, while the summer list contains only 38 species.

An analysis of differences in the zooplankton of the three winter periods of the study shows 1969–70 to have had much greater dominance by southern forms and a larger variety of them than 1970–71 or 1971–72. This corresponds with differences in the wind patterns between the years. Winds in the winter of 1969–70 were gentle and directly from the south, while the other winters had the more usual southwesterly storms. Gentle winds directly from the south were more effective at moving surface water northward alongshore than southwesterly storms, despite their lesser overall northerly component.

The hydrography and pelagic ecology of the Pacific Ocean very close to the Oregon coast are strongly seasonal. Winter winds from the southwest, which produce surface flow from the south and toward shore, alternate with summer winds from the north, which produce flow from the north and away from shore, generating coastal upwelling. These seasonal changes in the source of currents flowing through the area cause changes in the species of zooplankton that are present. In this paper we describe this cycle of change in species composition from a series of samples collected along a transect normal to the coast at Newport, Oreg., approximately every 2 wk from June 1969 through July 1972. In a previous paper (Peterson and Miller 1975) we have used these data to make a detailed comparison of the upwelling seasons of the years 1969, 1970, and 1971 with emphasis upon the differences between years. Here we consider the entire annual cycle with emphasis upon consistent aspects of the differences between seasons. The discussion includes a consideration of the differences between the three winters of the study.

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MATERIALS AND METHODS

Detailed description of collection and laboratory procedures are given in Peterson and Miller (1975, 1976). Plankton samples were collected with a 240-μm mesh net hauled obliquely from near the bottom to the surface at stations 2, 5, 9, and 18 km from the Oregon coast along a transect at lat. 44°40′N. The stations will be referred to as NH 1, NH 3, NH 5, and NH 10, respectively, which stand for Newport Hydrographic stations at 1, 3, 5, and 10 n.mi. from the shore. Water depths for the four stations were 20, 46, 55, and 80 m. Surface temperature and salinity measurements were made at most stations, and a bathythermograph was usually lowered. A total of 213 samples from 56 dates are included in the present analyses. Distribution of samples among stations, exact dates, and complete data for all samples can be found in Peterson and Miller (1976).

There are important limitations on the zooplankton data. We chose to express numerical abundance as numbers of individuals per cubic meter (no. m^{-3}). Because our nets were towed obliquely through the entire water column, the quantitative abundance estimates are actually abundances averaged over the water column. If an

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animal is equally abundant at all depths, then oblique tows will adequately estimate its abundance. If an animal is restricted to a narrow surface layer, then its abundance will be underestimated by deeper tows relative to shallower ones. Recent work by ourselves and Myers (1975) has shown that highest zooplankton abundances are found within the top 20 to 30 m of the water column. Therefore, our oblique tows from depths greater than about 30 m do underestimate zooplankton abundances. This becomes a problem for tows taken at stations farther from shore as the water depth increases, because an increasing fraction of the water column sampled contains few animals. Therefore, abundance gradients should not be considered to be real between stations NH 1 (water depth = 20 m) and NH 10 (water depth = 80 m) unless abundance differences are greater than a factor of four.

Abundances are also underestimated for many copepod taxa because the small copepodite stages could easily pass through our 240-μm mesh net. Copepodites of species of *Pseudocalanus* and *Acartia* younger than stage III were seldom seen in our samples. Probably only stages IV and V were sampled quantitatively.

The data set gains its value from being a 3-yr time series of samples collected in exactly the same manner at the same stations. As such, these are good baseline data to which future work can be compared. Point estimates of abundance have little meaning, but comparisons of abundances between seasons and years at a set of stations are valid and meaningful.

TABLE 1.—A checklist of copepod species taken off Newport, Oreg., in summer (S) and winter (W) months during the period of the study.

[C = Common, occurrence in >50% of the samples taken, U = Unusual, occurrence in <50% but >5 samples taken, R = Rare occurrence <5 samples.]

Copepod species	S	W	Copepod species	S	W
Calanus marshallae	C	C	*Metridia lucens*[2]	C	C
C. tenuicornis	U	C	*M. pacifica*[2]	U	
C. plumchrus	R	U	*Lucicutia flavicornis*	U	U
C. cristatus		R	*Candacia columbiae*		R
Rhincalanus nasutus	R	R	*C. bipinnata*	R	R
Eucalanus bungii	U	U	Immature *Heterorhabdus*		
Mecynocera clausii		U	spp.		R
Paracalanus parvus	C	C	*Pleuromamma borealis*		R
Calocalanus styliremis		U	*P. abdominalis*		R
C. tenuis		U	*Centropages abdominalis*	C	U
C. sp.		R	*Epilabidocera amphitrites*	U	U
Pseudocalanus sp.[1]	C	C	*Acartia clausii*	C	C
Microcalanus pusillus	U	U	*A. longiremis*	C	C
Clausocalanus masti-			*A. tonsa*	U	C
gophorus		U	*A. danae*		R
C. furcatus		R	*Eurytemora americana*	R	
C. arcuicornis	U	C	*Tortanus discaudatus*	U	U
C. jobei		R	*Microsetella* sp.	U	U
C. pergens	U	C	*Sapphirina* sp.	U	U
C. parapergens		U	*Oithona similis*	C	C
C. paululus		R	*O. spinirostris*	C	C
Ctenocalanus vanus	U	C	*Oncaea tenella*	R	R
Aetideus pacificus	U		*O. borealis*	R	R
Immature *Gaidius* spp.	U		*O. conifera*	R	R
Gaidius brevispinus		R	*O. mediterranea*	R	R
Immature *Gaetanus* spp.	R		*O. dentipes*		R
Gaetanus simplex		R	*O. subtilis*		R
Paraeuchaeta japonica	R	R	*O. media hymena*	R	
Racovitzanus antarcticas	U		*Corycaeus anglicus*	R	C
Scolecithricella minor	U	U	*C. amazonicus*		R

[1]Pacific representatives of the genus *Pseudocalanus* are not adequately described. They are being studied by B. Frost.

[2]Two morphs of the genus *Metridia* were separated on the basis of the shape of the prosome in lateral view. The *M. pacifica* type is more robust and has a steeply sloping forehead. Detailed morphological analysis of the two types has not been done.

RESULTS

Frequency of Occurrence of Zooplankton Taxa

Copepods were the most frequently occurring and the most abundant members of the zooplankton community in the nearshore region off Newport, Oreg. Fifty-eight species were seen in our samples (Table 1). Thirty-eight species were found in the summer samples and 51 species in the winter samples. During our study, species from the Subarctic, Transition, and Central Pacific faunal groups (McGowan 1971) were taken.

The copepods in Table 1 can be grouped on the basis of patterns of occurrence. Eight species occur commonly during both winter and summer months: *Calanus marshallae, Paracalanus parvus, Psuedocalanus* sp., *Metridia lucens, Acartia clausii, A. longiremis, Oithona similis*, and *O. spinirostris*. Seven species were found only during the summer months and probably have northern affinities: *Aetideus pacificus, Gaidius* immatures, *Gaetanus* immatures, *Racovitzanus antarcticas* s.l., *Metridia pacifica,* and *Oncaea media hymena. Eurytemora americana* occurred very rarely in the sample series, but it is a common form in all of the local estuaries (Frolander et al. 1973). Only one species was common during the summer and uncommon during the winter: *Centropages abdominalis*. This species has northern affinities. A group of six species had the opposite characteristic; that is, they were common during the winter but uncommon or rare during the summer: *Calanus tenuicornis, Clausocalanus arcuicornis, C. pergens, Ctenocalanus vanus* s.l., *Acartia tonsa*, and *Corycaeus anglicus*. All of these species are common in warmer water south of Oregon.

The majority of the copepod species (43) were always uncommon or rare in our samples and probably have unimportant roles in the community. However, taxonomic study of these rare or uncommon species is important because in many cases their presence indicates the presence of a particular water type or mixture of types. Most of the species that are found off Newport only during winter months have southern affinities (Central Pacific waters). They are transported north along the continental shelf by the Davidson Current and are probably very near the extreme northerly limit of their range. These species were *Mecynocera clausii, Calocalanus styliremis, C. tenuis, Calocalanus* sp., *Clausocalanus mastigophorus, C. furcatus, C. jobei, C. parapergens, C. paululus, Acartia danae, Corycaeus amazonicus, Oncaea dentipes*, and *O. subtilis*. Other species that were found only during winter months have northern affinities and are usually found in deep water over the continental slope. They were probably transported shoreward as a result of onshore winds. These species were *Calanus cristatus, Gaidius brevispinus, Gaetanus simplex, Candacia columbiae, Heterorhabdus* immatures, *Pleuromamma borealis*, and *P. abdominalis*. The 16 species that were rare or uncommon in both summer and winter include representatives of both northern and Central Pacific faunal groups.

Seasonal Cycle of Total Zooplankton Abundance

The annual cycles of total zooplankton abundance for stations NH 1, NH 3, NH 5, and NH 10 are shown in Figures 1, 2, and 3. Abundance is high during the upwelling season and often remains high during the autumn period of hydrographic transition. Abundance is low during the period from November through April. All four stations have this basic pattern, but there are important changes with distance offshore. Table 2 gives several indices of cycle amplitude. The amplitude

TABLE 2.—Some indices of the amplitude of the seasonal cycle of zooplankton density off the Oregon coast. Median density estimates for summer and winter seasons at the four stations on the Newport, Oreg., transect, the ratio of median densities between seasons, and the number of dates with densities >5,000 m^{-3}.

Station	Summer (May–Oct.)	Winter (Nov.–Apr.)	Summer–winter ratio	No. dates with density >5,000 m^{-3}
NH 1	4,350 m^{-3}	850 m^{-3}	5.1	17
NH 3	2,250 m^{-3}	800 m^{-3}	2.8	8
NH 5	1,550 m^{-3}	530 m^{-3}	2.9	4
NH 10	1,000 m^{-3}	365 m^{-3}	2.7	0

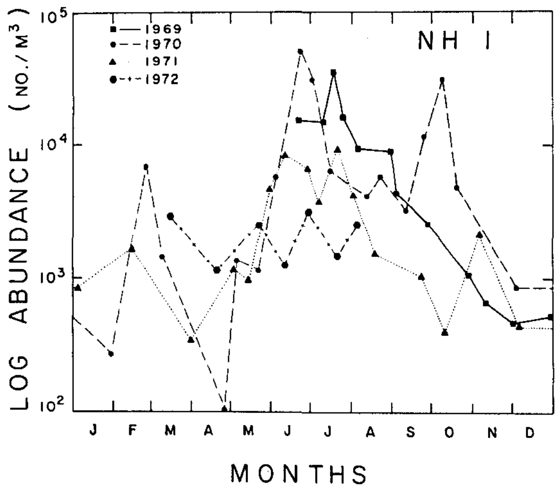

FIGURE 1.—Annual cycle of totaled zooplankton abundance 2 km from the Oregon coast at Newport (NH 1) during the 3-yr study period.

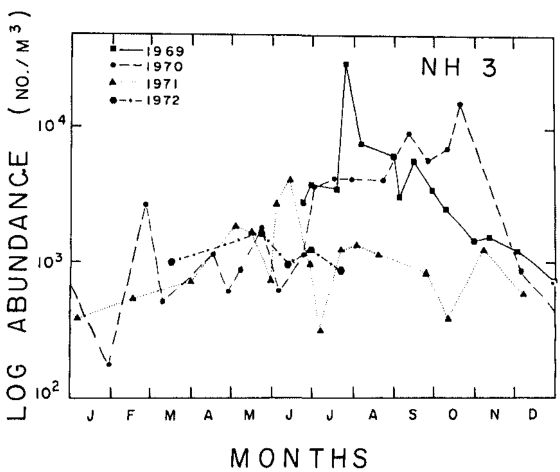

FIGURE 2.—Annual cycle of totaled zooplankton abundance 5 km from the Oregon coast at Newport (NH 3) during the 3-yr study period.

of the cycle is greater inshore. First, there are more dates at NH 1 and NH 3 with densities in excess of 5,000 m^{-3} (an arbitrary value). Second, the absolute difference between summer and winter density decreases with distance from shore. All of the decrease in the ratio of the densities in the two seasons occurs between 2 and 5 km from shore (NH 1 to NH 3).

There is a suggestion in the data for NH 1 (Figure 1) that the annual cycle of zooplankton abundance is more complex than just a summer high

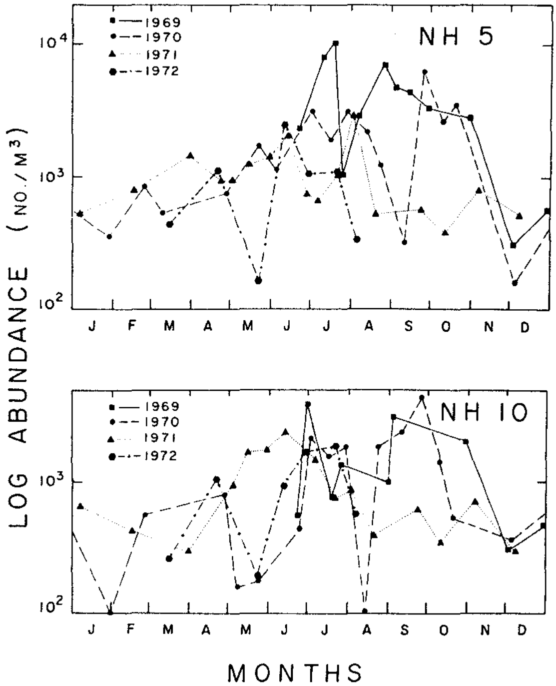

FIGURE 3.—Annual cycle of totaled zooplankton abundance 9 and 18 km from the Oregon coast at Newport (NH 5 and NH 10) during the 3-yr study period.

and a winter low. In addition to that basic cycle, there are peaks in total abundance at NH 1 in each year of the study in either February or March. The 25 February 1970 sample had high numbers of copepod nauplii other than *Calanus* (1,840 m^{-3} = 27% of the total zooplankton). This indicates the presence of an actively reproducing adult copepod population. A diatom bloom was in progress at that time as well. Our nets were clogged with the diatom *Thalassiosira*. The 16 February 1971 peak had high numbers of *Pseudocalanus* sp. (680 m^{-3} = 41% of the catch), *Calanus marshallae* (240 m^{-3} = 15%), and *Calanus* nauplii (192 m^{-3} = 12%). The *Pseudocalanus* sp. population was almost entirely stage I copepodites. These facts again indicate actively reproducing adult copepod populations in late winter. In both of these years, abundances decreased after the February peak to lower values in March or April. In 1972 no samples were collected in January or February. The 15 March sample at NH 1 had high numbers of *Pseudocalanus* sp. (1,844 m^{-3} = 62%), *Oithona similis* (690 m^{-3} = 23%), and *Acartia longiremis* (265 m^{-3} = 9%). Half of the total catch were immature *Pseudocalanus* sp. and half of the *A. longiremis* were immature. Again, there is some evidence of a late winter cycle of reproduction of the species of copepods permanently resident in the nearshore zone and dominant later in the year. There is evidence of this late winter peak in copepod abundance at NH 3 only in 1970, and it is not seen at all in the data for NH 5 and NH 10.

The months of April and May are periods of transition in the direction of the prevailing wind. An atmospheric high pressure cell begins to form over the North Pacific Ocean, and the winds begin to blow from the north with greater frequency. In all years of this study, heavy phytoplankton blooms were observed at NH 1 during this period. The blooms are probably associated with the replenishment of nutrients within the photic zone by the earliest brief episodes of upwelling. Dates with dense blooms were 27 April 1970, 3 and 14 May 1971, 20 April 1972, and 22 May 1972. Zooplankton abundances were low at these times.

Seasonal Cycle of Relative Species Abundance

The seasonal cycle of relative abundance of the most abundant species of copepods is shown in Figure 4 for all four stations. The graphs for each station represent cumulative percentage of the total catch for the species as labelled. The result is complex but deserves careful study because some interesting patterns are present. The simplest pattern is the sinusoidal annual cycle. This pattern is in phase with the seasonal cycle of total abundance. It can be concluded from comparison of the zooplankton abundance plots (Figures 1, 2, 3) and from the relative species abundance plot (Figure 4), that low numbers during winter months are coincident with 1) a decrease in relative abundance of the endemic copepod species and 2) an increase in importance of warmwater species and noncopepod taxa. In addition to copepods with southern affinities, *Oikopleura* spp. and chaetognaths become important during the winter.

There is marked seasonality in the relative abundance of each taxon. This will be discussed station-by-station. At NH 1 *Pseudocalanus* sp. were numerically important during the upwelling season, usually through August. *Acartia clausii* and *A. longiremis* were always important during the autumn after the cessation of upwelling. *Centropages abdominalis* was never a major component after August, with the exception of 1971. *Calanus marshallae* copepodites and nauplii were

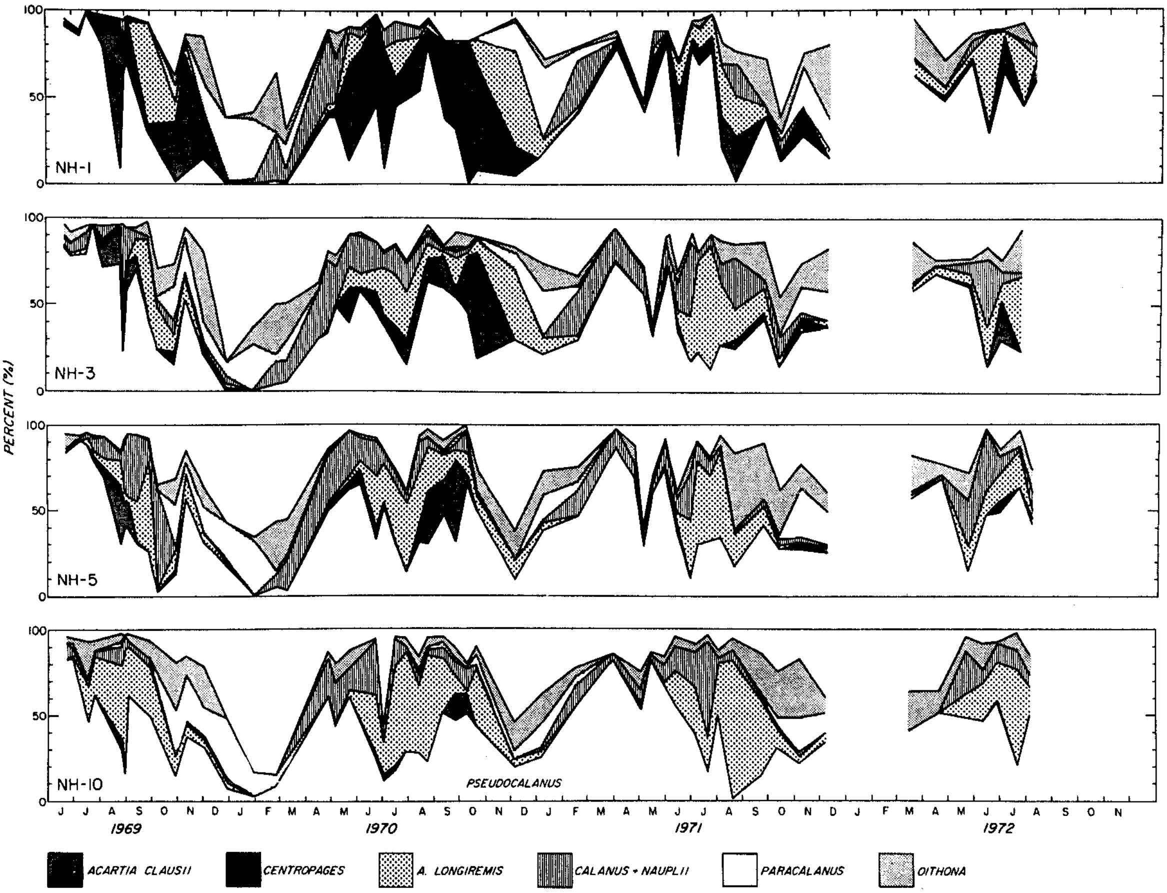

FIGURE 4.—Seasonal cycle of relative abundance (percent of total catch) of the most abundant zooplankton species (all copepods) at stations NH 1, NH 3, NH 5, and NH 10 along the Newport, Oreg., transect over the 3-yr study period. *Centropages* were *C. abdominalis*, *A. longiremis* were *Acartia longiremis*, *Calanus* were *C. marshallae*, *Paracalanus* were *P. parvus*, and *Oithona* were *O. similis*. *Pseudocalanus* sp. are represented by the white area at the bottom of each graph. All remaining zooplankton are represented by the white area at the top of each graph.

most dominant during the spring. *Paracalanus parvus* and *Oithona similis* have their highest relative abundance during the winter.

Different years were different at NH 1, as previously noted (Peterson and Miller 1975). *Pseudocalanus* sp. had a much higher relative abundance during the 1969 and 1971 upwelling seasons than in 1970. During the 1970 upwelling season, *A. clausii* and *Pseudocalanus* sp. shared numerical dominance in many samples. *Centropages abdominalis* was less important during the 1971 upwelling period than in earlier years. *Acartia longiremis* was about equally dominant at various times during all three upwelling seasons. *Oithona similis* was more important during the summers of 1969 and 1971. *Paracalanus parvus* was a significant fraction of the plankton over broader time intervals in 1969 and 1970 than in 1971.

At NH 3 the most striking aspect of the annual cycle compared with NH 1 is the greatly decreased importance of *Acartia clausii* and generally increased importance of *A. longiremis* and *Calanus marshallae*. *Acartia clausii* made up a large fraction of the catch only during October 1970. *Acartia longiremis* and *C. marshallae* were major components over broader intervals in 1970 and 1971 at NH 3 than at NH 1. The annual cycle of *Pseudocalanus* sp. relative abundance at NH 3 was about the same as for NH 1, except for two periods: July of 1970 and 1971. During both times *Pseudocalanus* sp. was dominant at NH 1, whereas *A. longiremis* was dominant at NH 3.

The NH 5 plot is similar to that for NH 3, particularly between November 1969 and May 1970 and between January and July 1971. Similarly to NH 3, the importance of *A. clausii* is greatly reduced and the importance of *A. longiremis* and *C. marshallae* are increased relative to NH 1. The NH 10 plot follows the NH 5 plot closely during 1970 and 1971 with one exception: in September 1970 *A. clausii* was a significant component at NH 5 but not at NH 10.

DISCUSSION

The annual cycle in the species composition of the zooplankton community along the Oregon coast must result from the annual cycle of the nearshore circulation, which is well described by Huyer et al. (1975). There is an exact correspondence between the sources of currents implied by the direction of flow in each season and the geographic affinities of the species occurring in the water. In summer, when the net water transport is to the south, species with northern affinities dominate. In winter, when transport is northward, species with southern affinities are mixed with the indigenous fauna. Abundances are about an order of magnitude higher in summer than winter, presumably because of production stimulated by coastal upwelling. We term the summer dominants "indigenous" both because they are present throughout the year and because they are the forms which reproduce and complete their life cycles in the Oregon nearshore zone. None of these forms is endemic, however, in that the distributions of all of them extend north around the rim of the Gulf of Alaska and into the Bering Sea. New studies now in progress are intended to describe the distributions within the upwelling ecosystem of the life cycle stages of the summer dominants, and to explain the maintenance of their populations within the system of nearshore currents.

A similar interpretation of seasonal changes in zooplankton species present off Oregon was offered by Cross and Small (1967). They used *Acartia danae* as an indicator of transport from the south (following Frolander 1962), and *Centropages abdominalis* (called *C. mcmurrichi* in their paper) as an indicator of flow from the north. In the present study *A. danae* was very infrequent, and a variety of other species (*Paracalanus parvus*, *Ctenocalanus vanus*, *Clausocalanus pergens*, etc.) appear to be much better indicators of southern sources. The studies were different in that the earlier one sampled farther offshore, and it began with the notion that *A. danae* would be an indicator, rather than examining the fauna as a whole.

While there is a generally similar sequence each year in the changes of the copepod species and their abundance, there are also marked differences in these changes between years. These were discussed for the upwelling season by Peterson and Miller (1975). We would like to add to that a brief evaluation of some differences between the winters of our study. Temperature–salinity diagrams including all of the data collected at our inshore stations during the months of October through March are shown in Figure 5. The winter of 1969–70 was warmer than the other winters. Progressive vector diagrams of the winds in each of the winter periods of our study are shown in Figure 6. The winds during 1969–70 were different from those of 1970–71 and 1971–72. During the fall and winter months of 1969–70 there were

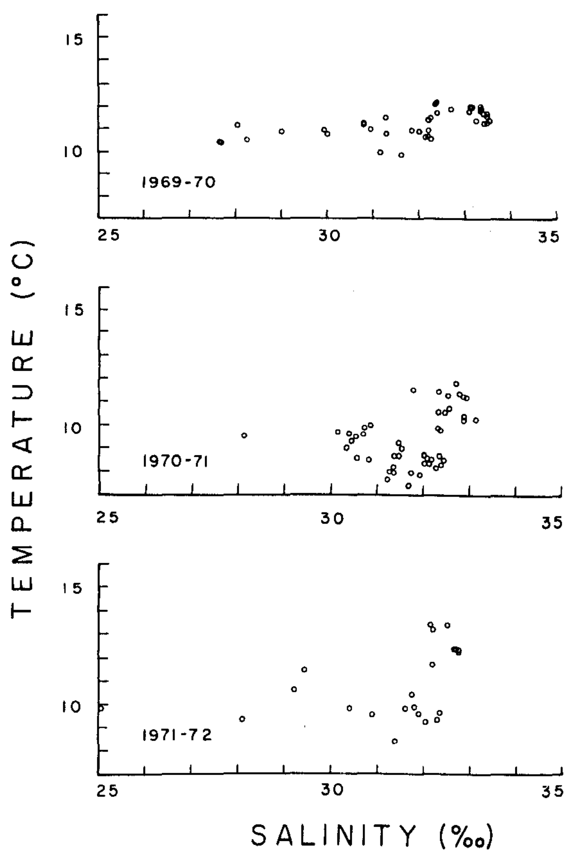

FIGURE 5.—Temperature–salinity scatter diagrams combining data from stations NH 1, NH 3, NH 5, and NH 10 along the Newport, Oreg., transect for the winters of 1969–70, 1970–71, and 1971–72 from October through March.

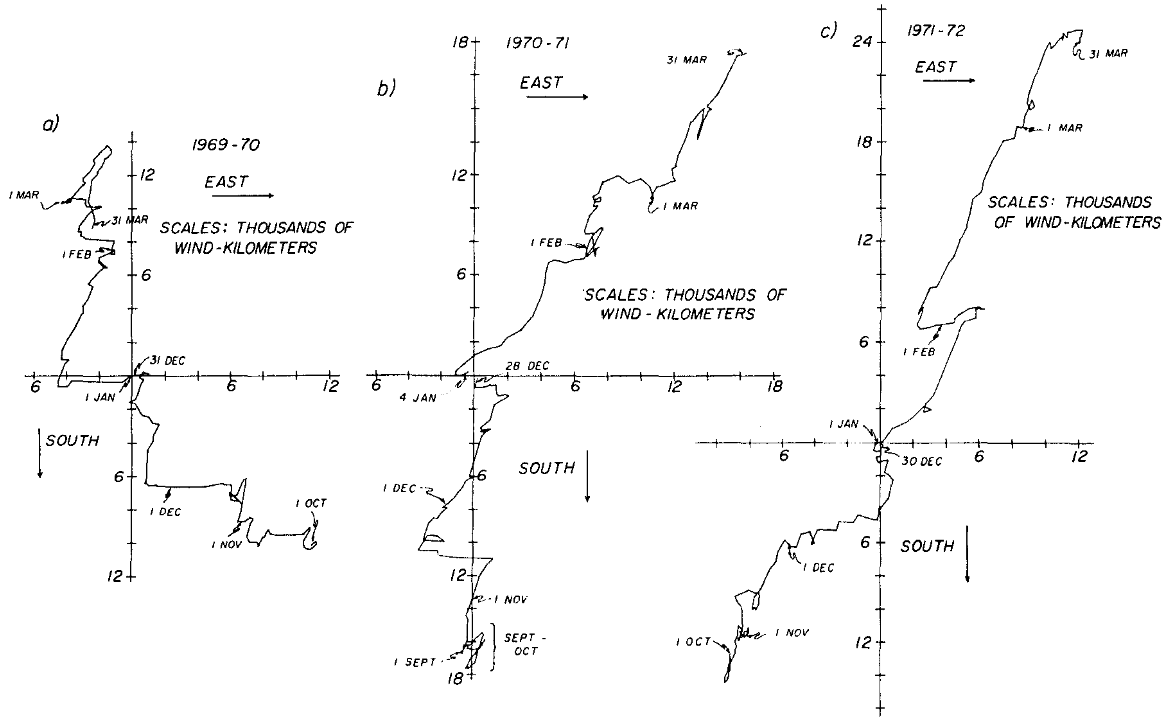

FIGURE 6.—Progressive vector diagrams for the wind at Newport, Oreg., for the winters of 1969–70, 1970–71, and 1971–72.

three intervals with winds from the east: most of October, 23 November to 8 December, and 30 December to 12 January. The entire 6-mo period of winter winds lacked the southwesterly storms that are characteristic of most winters. The other two winter wind patterns shown in Figure 6 are more typical on the basis of comparisons to the winters of later years (1972–73, 1973–74, 1974–75).

Upwelling index data taken from Bakun (1973) for the winters of our study are presented in Table 3. Negative values of the index indicate winds that will produce shoreward convergence of surface waters on the average over the month. Negative values of the anomaly indicate greater-than-usual shoreward convergence. Indices for winter 1969–70 are quite different from those of the other two winters. Onshore convergence was anomalously high in 1969–70 and anomalously low in 1970–71 and 1971–72.

The zooplankton data (see Peterson and Miller (1976) for detailed tabulations) indicate that the northward flow of the Davidson Current probably was much greater in 1969–70 than in the other two years. A number of southern zooplankton species had their greatest abundance during that

TABLE 3.—Monthly upwelling index values from Bakun (1973) for midwinter period at lat. 45°N, just north of the Newport, Oreg., transect, during the years of our study.

Month	20-yr mean index for month	1969–70 Index	1969–70 Anomaly	1970–71 Index	1970–71 Anomaly	1971–72 Index	1971–72 Anomaly
Nov.	−74	−53	+21	−54	+19	−40	+34
Dec.	−93	−157	−64	−106	−12	−27	+66
Jan.	−94	−98	−4	−32	+62	−19	+75
Feb.	−47	−71	−24	−16	+32	−103	−56
Total			−71		+101		+119

winter: *Clausocalanus jobei, C. paululus, Oncaea dentipes,* and *O. subtilis.* All of the above 16 copepod species are indicators of water originating south of at least Cape Mendocino, Calif. (Olsen 1949; Fleminger 1964, 1967; Frost and Fleminger 1968).

The physical implication of this set of biological observations is that winter periods of gentle winds directly from the south (Figure 6a) are much more effective at moving water northward alongshore than winter periods of violent southwesterly storms (Figures 6b, c), even though the total northward component of the winds during the stormy winters might be much greater. This is in agreement with the temperature results (Figure 5) and with the anomaly in the upwelling indices.

Bakun (1973) pointed out that winters of extreme shoreward convergence of wind-drifted surface waters (negative index anomaly) should cause the density structure to be depressed toward the coast and should accelerate northward flow or decelerate southward flow. "Either situation would favor an anomalous warm advection," according to Bakun.

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