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Oscillations of macrobenthos in shallow waters of the Peruvian central coast induced by El Niño 1982-83

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ABSTRACT

Macrozoobenthos was sampled at 15 m (January 1982–October 1984) and 34 m depth (September 1981–September 1984) in the Bay of Ancón, north of Lima. Fluctuations in density, biomass, species composition and diversity of the fauna as well as oscillations in the density of several dominant species were studied in relation to temperature, salinity and dissolved oxygen. El Niño (EN) 1982–83 induced marked positive effects at both depths. Some of these changes prevailed in 1984 due to the increase of oxygen close to the seafloor and the persistence of higher O₂ values during and after the phenomenon.

The number of species at 15 m, which before EN fluctuated between 3 and 17, increased to >26 (max. 45) during EN and in the months following the event. Biomass, before EN always <1 g, reached 18.4 g AFDW per m² in December 1982. Density, normally <4000 per m², increased to 1724, and diversity nearly doubled and remained high until September 1984.

The number of species at 34 m (≤5 before EN) fluctuated between 15 and 24 from December 1982 to February 1983 and returned to ≤5 by June 1984. Biomass reached 6.9 g AFDW per m² in December 1982. Density, normally <425 per m², increased to 13550, and diversity at this depth nearly tripled in February 1983.

1. Introduction

Investigations on marine macrobenthic communities off the Peruvian coast have in the past been sporadic, based on scattered sampling without temporal continuity. The determination of species has in many cases not been possible (see summaries in Paredes and Tarazona, 1980; Rosenberg *et al.*, 1983). Only recently were long-term studies started on sandy beach communities (Tarazona *et al.*, 1985a, 1986; Arntz *et al.*, 1987) and on rocky shores (Tarazona *et al.*, 1985b), revealing that the zoobenthos communities in the Peruvian upwelling area undergo marked changes in time similar to those encountered in temperate European waters (Buchanan *et al.*, 1974; Rachor and Gerlach, 1978; Ziegelmeier, 1978; Glémarec, 1979; Arntz and Rumohr, 1986) and in similar environments off North America (Lie and Evans, 1973; Levings, 1975; Boesch

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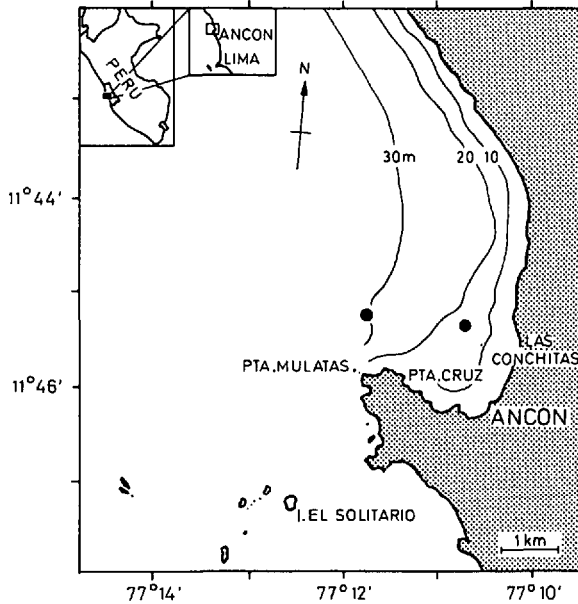


Figure 1. Map of Ancón Bay (Peru) showing the localities of the two sampling stations (●).

et al., 1978; Maurer *et al.*, 1979; Holland, 1985; Nichols, 1985; Stull *et al.*, 1986). The principal ecological factor behind the changes in Peru is “El Niño” (EN) which drastically alters environmental conditions such as water temperature and oxygen saturation at the seafloor, and temporarily converts the cool upwelling zone into an area which resembles a subtropical or even tropical environment (Arntz, 1986; Barber and Chávez, 1986). This effect extends to deeper waters along the continental shelf (Arntz *et al.*, 1985; Salzwedel *et al.*, 1986) and to some degree affects benthic communities off northern and central Chile (Soto, 1985; Tomicic, 1985; Gallardo, 1985).

This paper reports on macrozoobenthos oscillations from two shallow-water soft bottom stations in the Bay of Ancón (Peru) before, during and after the strong EN 1982–83. Under “normal,” non-Niño conditions, the station at 15 m depth which lies within the zone of nearshore turbulence and resuspension of particles suffers from hypoxia frequently but not permanently. The 34 m station is physically more stable and influenced by permanent hypoxic, at times anoxic, conditions (Tarazona, 1984). During and after EN, oxygen saturation improved considerably at both stations and allowed colonization by species which were either present in the bay but unable to survive at the two localities under normal conditions, or were introduced by other features of EN like the inflow of warm water masses of subtropical or oceanic origin. The respective events are analyzed both at the community and species level.

Table 1. Conversion factors (wet weight to ash free dry weight) obtained for some principal species and groups in Ancón Bay.

Species or taxonomic group	Conversion factors
MOLLUSKS	
<i>Nassarius dentifer</i>	0.0520
<i>Nassarius gayi</i>	0.0523
Miscellaneous mollusks	0.0531
CRUSTACEANS	
<i>Pinnixa transversalis</i>	0.1302
<i>Pinnixa valdiviensis</i>	0.1305
Miscellaneous crustaceans	0.1408
POLYCHAETES	
<i>Parandalia fauveli</i>	0.1518
<i>Sigambra bassi</i>	0.1335
<i>Owenia collaris</i>	0.1333
<i>Magelona phyllisae</i>	0.1343
<i>Chaetopterus</i> sp.	0.2062
<i>Spiochaetopterus</i> sp.	0.2062
Miscellaneous polychaetes	0.1386
OTHERS	
<i>Thioploca</i> spp.	0.0298
Anthozoa	0.1496
Nematoda	0.1179
Nemertea	0.1357
Miscellaneous others	0.1375

2. Material and methods

Macrobenthos was sampled monthly at 15 m (January 1982–October 1984) and 34 m depth (September 1981–September 1984) in Ancón Bay, Peru, lat. 11°45'S, long. 77°11'W (Fig. 1).

At each date, three samples were taken by means of a van Veen grab of 0.04 m². Samples were sieved over a mesh size of 0.5 mm, and fixed immediately in 7% formalin in seawater buffered with borax. All animals retained, including large nematodes and filamentous bacteria, were sorted.

All ash free dry weight (AFDW) biomass figures presented in this paper were calculated using conversion factors (Table 1). These are mean values derived from preserved material corresponding to the summer and fall samples. A Mettler micro balance was used to determine the dry weight (after drying in an oven at 90°C for 24–36 h), and the AFDW (after drying for 24 h at 450°C).

Water samples for temperature, salinity and oxygen saturation measurements were collected on each of the sampling days from ca. 0.5 m above the bottom, using a Niskin

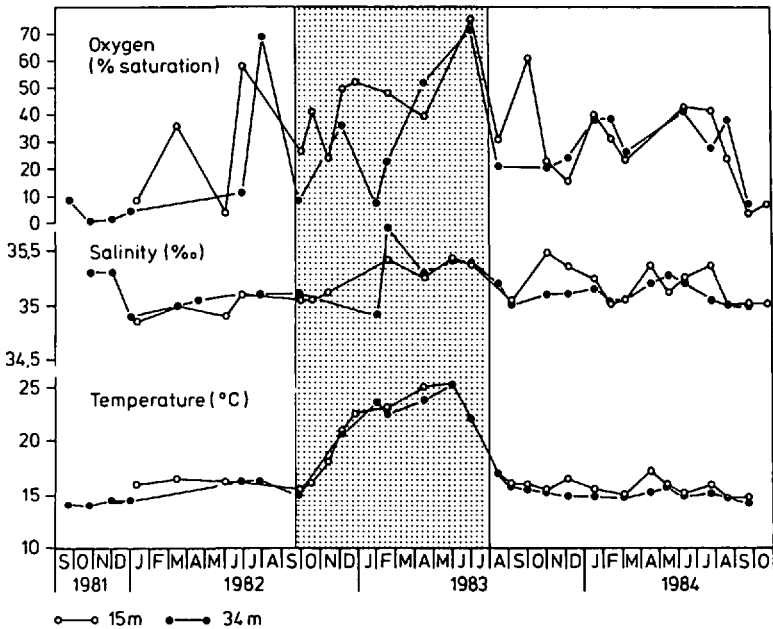


Figure 2. Near-bottom oscillations of abiotic parameters at the 15 and 34 m depth stations. Shaded area: EN 1982–83.

bottle. An inductive salinometer was used for measuring salinity, and Winkler's method was used for estimating the oxygen saturation of the water.

Benthic organisms were sorted, identified and counted in the laboratory. Density and biomass values were extrapolated to one m^2 . Diversity of the community was measured using the Shannon-Wiener information function (Shannon and Weaver, 1949), and evenness according to the J' index proposed by Heip (1974). Finally, $\log(n + 1)$ transformed abundances (using the abundances per $0.04 m^2$) were used in the representations of oscillation patterns for some of the numerically dominant species.

3. Results

The overall changes of abiotic parameters with the onset of the 1982–83 EN have been described in detail by Zuta and Farfan, 1983 and Barber and Chavez, 1983.

a. Changes of the oceanographic and sedimentological conditions. In the Bay of Ancón near-bottom values for temperature and salinity showed similar fluctuations at both stations during the period of investigation: temperature varied between 14 and 17°C before and after EN and increased to 25.1°C during EN (Fig. 2). Salinity was less than 35.3‰ before EN, varied between 35.1 and 35.7‰ during the event, and remained high until July 1984.

Hypoxic conditions were typical of the 15 m station before EN. The O_2 saturation

values increased to 75% prior to the observed temperature increase and remained relatively high throughout the event and until July 1984. At the 34 m station the near-bottom waters were at times even anoxic before EN. During EN oxygen saturation increased to 71.5% and remained at a relatively high level (above 25%) up to one year after EN (Fig. 2).

The content of organic matter was $4.41\% \pm 0.63$ (SD) viz. $4.50\% \pm 0.46$ (SD) before EN and $4.62\% \pm 2.00$ (SD) viz. $9.12\% \pm 4.43$ (SD) after EN at the 15 m and 34 m stations, respectively (G. Carbajal, pers. comm.)

b. Oscillations of macrozoobenthos at the community level. A list of macrozoobenthic species collected from each of the two stations during the study period is given in Table 2. Before EN the species number fluctuated between 3 and 17 at 15 m and between 0 and 6 at 34 m. During and after EN, the number of species increased to 45 and 24 at 15 and 34 m, respectively. The maximum value was reached in December 1982, about two months after the onset of EN, at 34 m depth, whereas at 15 m it was observed in February 1983. However, at this station too the highest number of new species was registered in December. The species numbers remained high until nearly one year after EN. Therefore, they declined to levels similar to those before the event, i.e. <16 at 15 m and <6 at 34 m depth. During EN the cumulative number of species showed a strong increase at both stations (Figs. 3 and 4).

The diversity (H') values both at 15 and 34 m began to increase before EN and remained high—apart from certain oscillations—until May (34 m) viz. September 1984 (15 m). At the 15 m station the sudden decline during the later phase of EN and the strong increase after the event mark the change from *Owenia collaris* to *Phoronis* sp., after a short period when most species declined strongly in abundance and some species disappeared (Fig. 5). The course of the evenness curves (same figures) is not quite the same for the two stations; it is somewhat irregular at 15 m and high during and after EN at 34 m.

Macrozoobenthos densities were considerably higher at 15 m than at 34 m depth. The EN-induced increase also occurred earlier and lasted longer at the shallower station. Densities during normal (hypoxic) conditions did not exceed 4000 and 425 Ind. per m^2 at 15 and 34 m, respectively (Fig. 6), whereas maxima of 43100 and 13550 Ind. per m^2 were registered during EN.

Significant changes in species dominance also occurred during EN. At both stations the dominance values were much higher before and after EN than during the event. At 15 m depth the dominant species were the polychaetes *Owenia collaris*, *Magelona phyllisae*, *Chaetozone* sp. and the phoronid *Phoronis* sp. Of these species, *O. collaris* was most abundant during EN whereas *Phoronis* took over after EN until hypoxic conditions returned. At 34 m the polychaetes *Paraprionospio pinnata*, *M. phyllisae*, *Chaetozone* sp. and *Leitoscoloplos chilensis* were dominant. The dominance of *P. pinnata* was always of short duration.

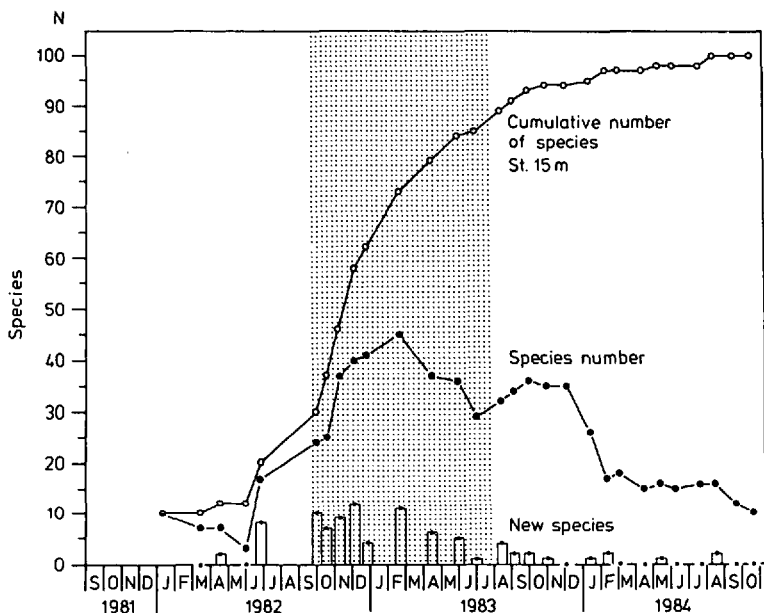


Figure 3. Species number, number of "new" species joining the community, and accumulated number of species at the 15 m station. Shaded area: EN 1982-83.

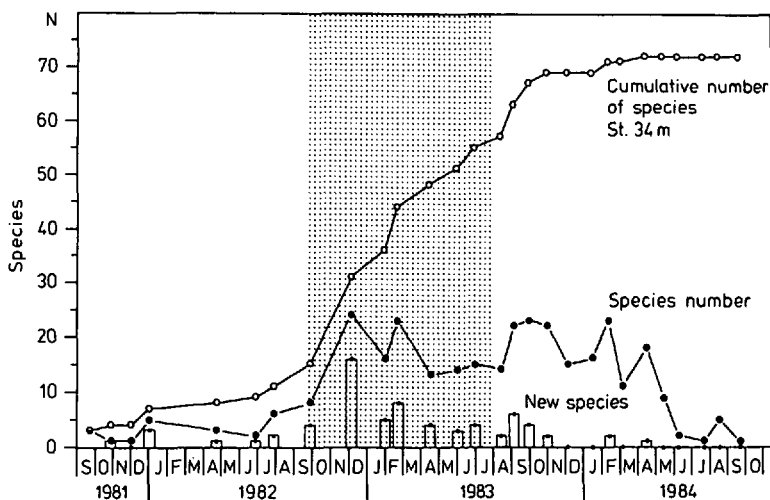


Figure 4. Species number, number of "new" species joining the community, and accumulated number of species at the 34 m station. Shaded area: EN 1982-83.

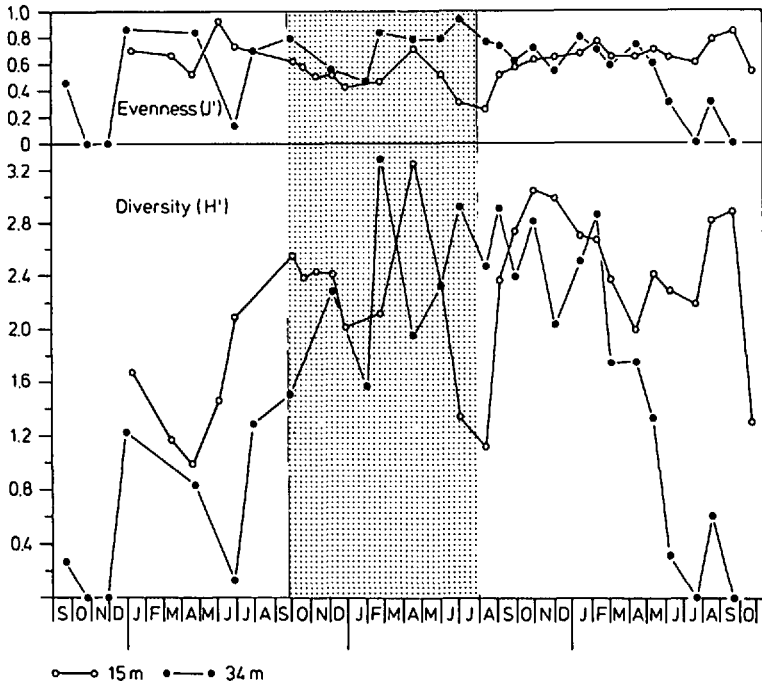


Figure 5. Diversity (H') and evenness (J') of macrobenthos (\pm SE) at the 15 and 34 m stations. Shaded area: EN 1982-83.

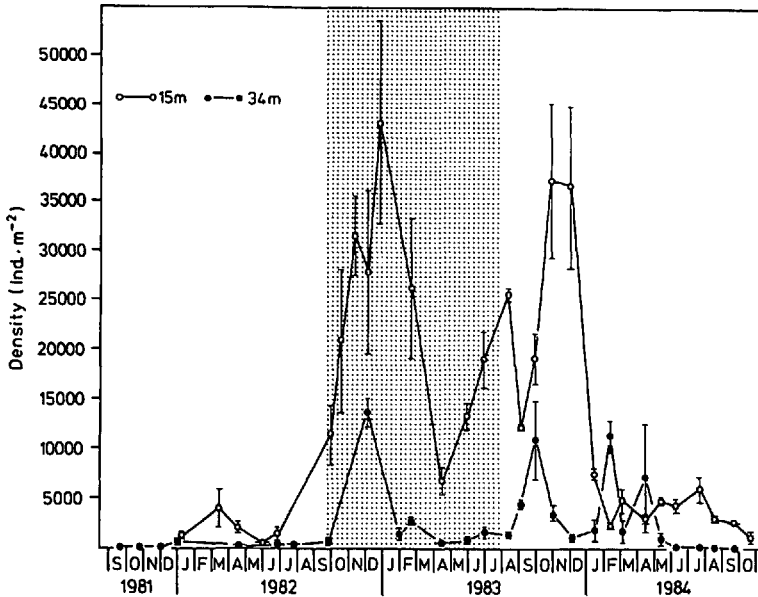


Figure 6. Density of macrobenthos (\pm SE) at the 15 and 34 m stations. Shaded area: EN 1982-83.

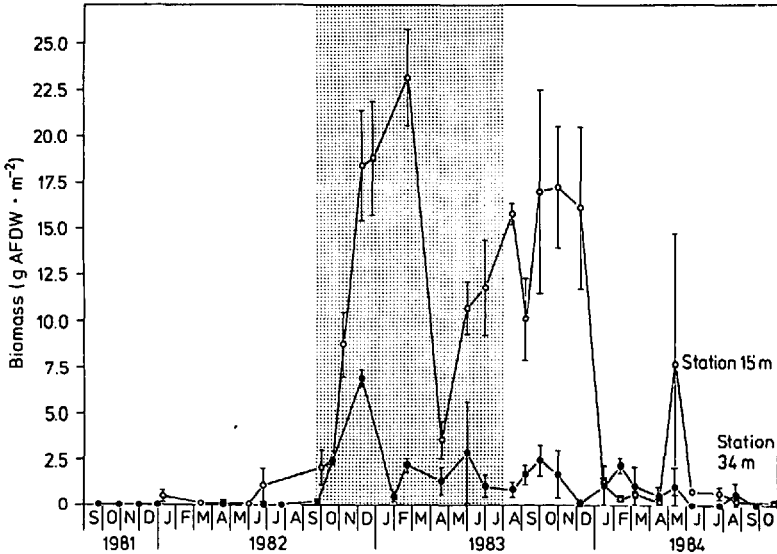


Figure 7. Biomass (ash free dry weight) of macrobenthos (\pm SE) at the 15 and 34 m stations. Shaded area: EN 1982–83.

At both depths, biomass oscillation patterns were similar to the density changes. Increases occurred without any obvious time delay with respect to density increases for our sampling intervals of time (Fig. 7). The maximum values observed during EN (December 1982) were 18.41 g AFDW per m^2 at 15 m and 6.89 g AFDW per m^2 at 34 m. Biomass values under hypoxic conditions never exceeded 1.08 g AFDW per m^2 at 15 m and 0.02 g AFDW per m^2 at 34 m. At 15 m depth the numerically dominant species also had the highest biomass. Both numbers and biomass varied similarly. This was not always the case at 34 m depth where different species alternated as dominants by weight, among them the polychaetes *Chaetozone* sp., *P. pinnata*, *Diopatra rhizoicola* and *Notomastus magnus*, the crustacean *Pinnixa valdiviensis*, nemerteans and hemichordates.

c. Specific oscillations of important species. The patterns of oscillation observed varied among the different species, and in some cases with depth for the same species (Figs. 8 and 9). Three main groups can be distinguished: those abundant under hypoxic conditions (“tolerant residents”), those absent under hypoxic conditions but which invade the area during EN (“immigrants”), and those that live at the stations or in the surroundings in low numbers under hypoxic conditions and proliferate strongly when the environment improves (“opportunists”).

Tolerant residents like the polychaetes *Parandalia fauveli*, *M. phyllisae* and *Chaetozone* fluctuated indifferently to the oceanographic perturbations brought about

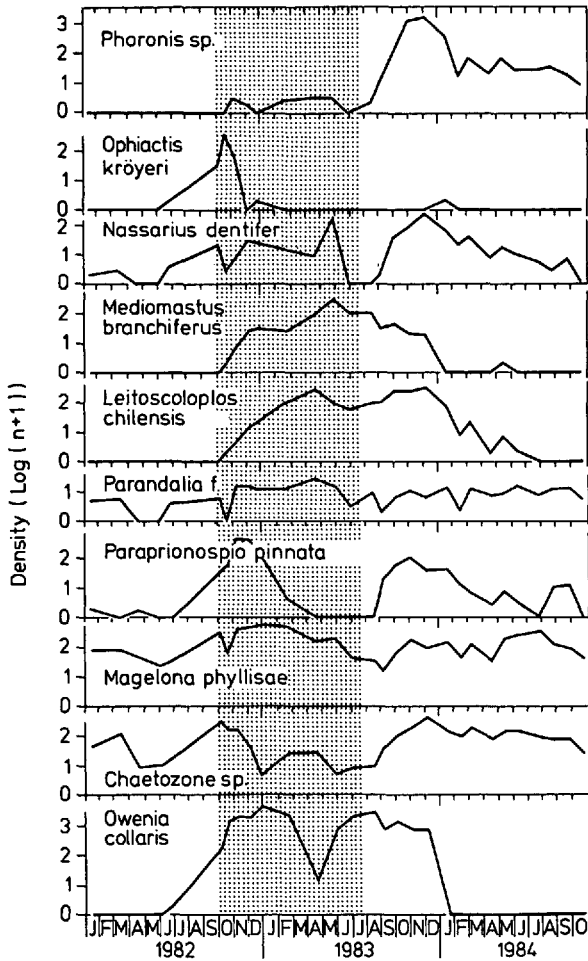


Figure 8. Oscillations of dominant species at the 15 m depth station (log (n + 1) transformed densities using n per 0.04 m²). Shaded area: EN 1982–83.

by EN. The immigrant polychaete *L. chilensis* increased strongly at the onset of EN and maintained high densities into 1984, whereas *Phoronis* increased only slightly during the event, but strongly afterwards. Among the opportunists, the polychaete *P. pinnata* revealed a seasonal pattern, with EN increasing the amplitude of the oscillation, and the ophiurid *Ophiactis kröyeri* had a single prominent peak shortly before and at the beginning of EN. The gastropod *Nassarius dentifer* increased in a similar way maintaining higher densities than normal throughout the event, and showed another positive development after EN which lasted into the second half of 1984.

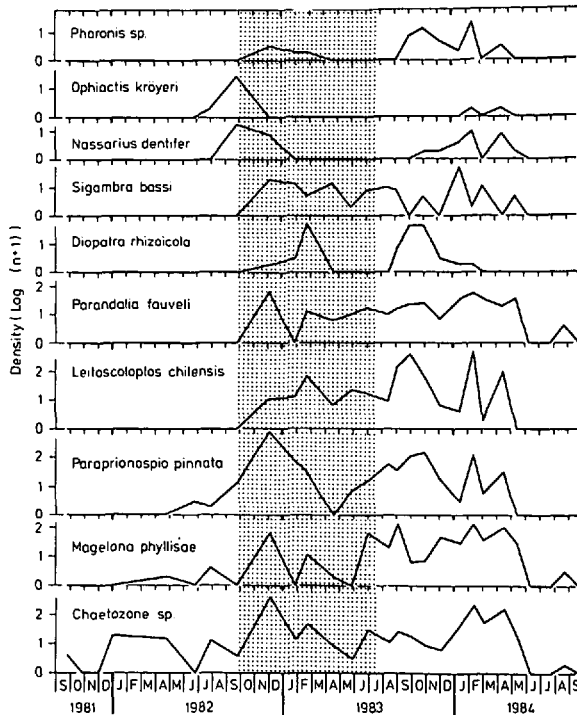


Figure 9. Oscillations of dominant species at the 34 m depth station ($\log(n + 1)$ transformed densities using n per 0.04 m^2). Shaded area: EN 1982–83.

4. Discussion

Among the three abiotic factors studied in the Bay of Ancón during this investigation, near-bottom water temperature showed the clearest variation. There were no differences between the two stations in time and width of the oscillations caused by EN. Both at 15 and 34 m depth, the temperature increase began at approximately 16°C in October 1982, which is consistent with the appearance of the first Kelvin wave off Peru (Smith, 1983), reached a peak of 26°C in May–June 1983 and returned to the pre-Niño level in August–September 1983. This short-term increase viz. decline of 10°C at 15 and 34 m depth was much higher than the normal seasonal range of increase of sea surface temperatures on the central Peruvian coast (Zuta and Guillén, 1970). Also the maximum temperature exceeded the peak summer value of EN-free years by far. Clearly, this kind of drastic change is restricted to very strong EN events which occur only once or twice a century (Quinn *et al.*, 1986). In moderate or weak events they may be within a $1\text{--}4^\circ\text{C}$ range. The effect of such severe positive temperature anomalies is poorly documented; for an exception see Ankar and Jansson (1973). Temperate latitudes may experience higher seasonal temperature variations (Arntz and Rumohr, 1982, 1986), but then they are part of the normal summer-winter

oscillation to which the fauna in those areas is adapted. Negative temperature anomalies ("ice winters") occur fairly frequently (Smidt, 1944; Ziegelmeier, 1964; Crisp, 1964; Cushing and Dickson, 1976; Laevastu, 1984; Beukema, 1985; Rumohr *et al.*, in prep.) but never differ from the normal temperature range to such an extent.

Little can be said with regard to the variations in salinity. From a biologist's point of view the changes were not remarkable although the generally high concentrations were surprising, revealing the existence of oceanic waters nearshore. Salinity was somewhat higher at both stations during and after EN, and the curves coincide for the period February 1982–May 1984.

Dissolved oxygen near the seafloor increased at both stations before there was a change in temperature, and obviously before the Kelvin wave could have reached Peru. At 15 m depth the O₂ increase began in June and at 34 m in September. Both stations had their highest oxygen saturation in July 1983, and the duration of positive O₂ anomalies lasted longer than that of temperatures, up to July 1984. A positive effect of EN on O₂ saturation, far beyond the duration of the event proper, was noted in deeper waters off Peru, too (Arntz *et al.*, 1985; Salzwedel *et al.*, 1986) and is consistent with post-hypoxic developments in other marine areas where reoxygenation usually has a longer-lasting effect (Rosenberg, 1980; Jørgensen, 1980; Harper *et al.*, 1981; Dethlefsen and v. Westernhagen, 1983; Imabayashi, 1983; Tsutsumi and Kikuchi, 1983; Gaston *et al.*, 1985; Imabayashi and Endo, 1985; v. Westernhagen *et al.*, 1986).

The responses of the fauna to the changes brought about by EN 1982–83 were dramatic both on the community and species level. On the community level, direct changes were documented in the strong increase of species present, and in the sudden rise of the total density and biomass at both stations. The increase in species number at 15 and 34 m began as early as June and July 1982, respectively. Even when the total number of species declined, new species continually joined the community until May (34 m) or September 1984 (15 m). It is surprising that the increase in density and biomass started in October 1982 simultaneously at both stations; consistent with what we know about the arrival of the first Kelvin wave, but without the typical time delay between the density and biomass peaks which have been reported from other areas (Pearson and Rosenberg, 1978; Arntz and Rumohr, 1982). At 15 m depth there are at least 3, at 34 m several small peaks in the density and biomass curves. This may have been due, in part, to immigration; but the non-existence of a time delay between the onset of changes in both parameters also reveals the highly opportunistic nature of most colonizers. The strong decline in diversity and evenness observed at the 15 m station between April and August 1983 reflects structural changes within the community during the later phase of EN connected with an increasing dominance of *Owenia collaris*. From August 1983, *Phoronis* becomes the first dominant, but several other species increase as well (cf. Fig. 8) and cause another ascent of the diversity and evenness curves.

Whereas the community parameters species number, total density, total biomass

and diversity oscillate similarly at both stations, a breakdown into species reveals a number of differences. These differences are due, on the one hand, to the nature of the colonizers (residents, opportunists, immigrants, cf. Section 3c), on the other hand to changes in the trophic structure. Before EN both communities were dominated by deposit feeders. However, at 15 m these were replaced by tube-building organisms such as the polychaete *Owenia collaris* and the phoronid *Phoronis* sp. which are primarily suspension feeders (Dales, 1957; Fauchald and Jumars, 1979; Emig, 1982). These worms, in high densities similar to those found at the shallower station during EN, stabilize the sediment (Fager, 1964; Yingst and Rhoads, 1978; Eckman *et al.*, 1981) but can inhibit further colonization of other larval settlers (Woodin, 1976). At 34 m, the deposit feeders dominant at this station before the event were replaced by other deposit feeders. One reason for this may have been the higher content of organic matter at the deeper station where normally there is less turbulence, and hardly any fauna existent to use the available matter. During EN there is a submergence in Ancon Bay of the populations of suspension feeders maintaining, however, the zonation pattern described by Rhoads and Young (1970). Apparently more use is made during EN of the deeper soft bottoms, as has been reported by Arntz *et al.* (1985) for several stations at 50 and 100 m depth off Peru.

It seems very likely that a combination of an increase in oxygen and high temperatures is responsible for the direct impact on the benthic fauna in Peruvian shallow water. The oxygen increase prepares the normally inhospitable grounds for colonization, and the continuation of higher O₂ values after the event permits a certain persistence of the newly formed communities before the environment returns to normal, hypoxic or anoxic, conditions. The increase of bottom water temperatures favors the immigration of a large number of organisms from (sub)tropical areas and enhances growth and production of the new settlers. The role of salinity is not clear although it may be a useful indicator for oceanic inflow (Ochoa *et al.*, 1985; Rojas de Mendiola *et al.*, 1985; Tsukayama and Santander, 1988). Other abiotic factors are also likely to exert a direct impact on colonization during EN, for example the currents, some of which are enhanced and may change direction (Tarazona, 1984; Tarazona *et al.*, 1985b; Arntz, 1986). In addition, there are indirect effects by biotic factors which themselves have changed under the impact of an altered abiotic milieu: an altered nutrient regime with consequences for the various food chains in the upwelling ecosystem, but with nutrients in sufficient quantities nearshore to allow even for an increase in phytoplanktonic and benthic production (Tarazona *et al.*, 1985b; Barber and Chavez, 1986). Increased predation by invertebrate and fish invaders from the tropics may be important (Del Solar, 1983; Tarazona, 1984; Tarazona *et al.*, 1985b; Arntz and Valdivia, 1985; Arntz *et al.*, 1985; Kong *et al.*, 1985; Vélez and Zeballos, 1985; Arntz, 1986); increased competition (by immigrants) in some cases and reduced competition (by mortality of competitors) in others, as discussed by Arntz (1986). Some of these factors are identical with those that reshape marine benthos communities under post-hypoxic conditions, but others are characteristic of EN.

The upwelling ecosystem off Peru has evolved a remarkable capability of reacting fast and efficiently to positive changes induced by EN. Population proliferations and rapid changes in dominance occur once the normal main stressor—low O₂—becomes inefficient and biological interactions are activated. What is most striking, however, is the fact that both the O₂ increase and the increase in species number at 15 m started several months before the first Kelvin wave reached the South American continent (Smith, 1983; Chavez *et al.*, 1984). Similar premature responses have been reported for shallow water surf clam populations (Arntz *et al.*, 1987), some North Chilean benthic organisms such as sea urchins (Tomicic and Soto, pers. comm.), and for the seabirds of Christmas Island (Schreiber and Schreiber, 1983). As yet we do not have an idea as to the mechanisms involved in these events.

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