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Advances in Geosciences

Disentangling the effects of El Niño on a population of the polychaete *Sigambra bassi* in the Bay of Ancón, Peru

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Abstract. The macrobenthic community in shallow soft-bottom areas in the Bay of Ancón, Peru, is characterized by low biodiversity due to low oxygen concentrations. During El Niño (EN) events, higher water temperature and higher concentrations of dissolved oxygen induce a temporary increase in biodiversity. However, the structure and dynamics of the emerging macrobenthic community and populations, especially the polychaete *Sigambra bassi*, vary strongly among events. The reasons for this variation are poorly understood, in particular the relative influence of abiotic versus biotic factors. To disentangle how abiotic and biotic factors influence the different responses of the population of *S. bassi*, population models were developed based on detailed long-term monitoring data, which include four El Niño events. The results show that *S. bassi* abundances are favored by abiotic environmental conditions during EN, namely high temperature and dissolved oxygen concentration, but these abiotic effects are modulated by different biotic processes. In two EN events with relatively similarly high temperature anomalies (EN 1982–1983 and 1997–1998) different biological interactions (competition, predation, facilitation) and different species composition of the community resulted in different responses of the population of *S. bassi*.

1 Introduction

The Peruvian-Chilean Upwelling Ecosystem in the Southeast Pacific is one of the most productive areas of the world ($\sim$1 kg C m^{-2} y^{-1}) (Zuta and Guillén, 1970), and distribution and diversity of the benthic communities in this region are influenced by the location of the oxygen minimum zone (OMZ $<$0.5 ml O_2 l^{-1}) and the ENSO interannual variability (Levin et al., 2002).

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However, in benthic communities, both abiotic conditions and biotic processes influence the distribution, abundance and biomass of species. Important biotic processes include recruitment, growth, survival and fecundity (Woodin, 1974; Rosenberg et al., 1983; Wu, 2002; Simonini and Prevedelli, 2003a, 2003b). These communities are dominated by macrofaunal ($>$0.5 mm) invertebrates, and in soft sediments the most abundant macrofaunal group is polychaete worms (Fauchald, 1977).

A major ecological factor for benthic communities is oxygen (Díaz and Rosenberg, 1995). High primary productivity can lead to high accumulation of organic matter on the bottoms, especially in enclosed and stratified sea areas, and the oxygen consumption can be higher than the supply, leading to oxygen deficiency and reduction of benthic communities (Rosenberg, 2001). Ambient temperature also has a profound influence on exothermic physiology. Tolerance to temperature of marine invertebrates differs between species and populations, depending on latitude or seasonal temperature acclimatization, and is therefore related to geographical distribution (Pörtner, 2001). At small scales, larval settlement of polychaetes can also be influenced by changes in temperature (Bolton and Havenhand, 1997; Pörtner, 2001; Cotter et al., 2003).

Some species of polychaetes in soft sediments are considered bioindicators of the impact of El Niño (EN) events, because they increase in abundance during EN (Tarazona and Arntz, 2001; Tarazona et al., 2001). Analyses of long-term data from the Bay of Ancón have shown that early and late responses of some of these species are positively correlated with the increase in dissolved oxygen concentration and temperature at the bottom as well as to sea surface temperature anomalies in the eastern Pacific during EN (Tarazona et al., 2001). However, their increase in abundance is not necessarily similar during different EN events. This study focuses on the biological impact of EN on the macrobenthic community

Table 1. Formulas used in the study (Peña et al., 2005).

$s_{O_2}=(1-e^{-1\cdot(O_t-O_i)})^3$	Settlement rate for oxygen
$s_T=(1-e^{-0.3\cdot(T_t-T_i)})^3$	Settlement rate for temperature
$N_{t+1}=N_t\cdot(1-M)+(s_{O_2}\cdot s_T)\cdot N_i$	Model I: Only abiotic factors
$N_{t+1}=N_t\cdot(1-M)+(s_{O_2}\cdot s_T)\cdot(1-\frac{N_t}{K})\cdot N_i$	Model II: Abiotic factors and competition
$N_{t+1}=N_t\cdot(1-M)\cdot(1+\frac{N_t}{F})+(s_{O_2}\cdot s_T)\cdot(1-\frac{N_t}{K})\cdot N_i$	Model III: Abiotic factors, competition and facilitation
	Root mean square deviation

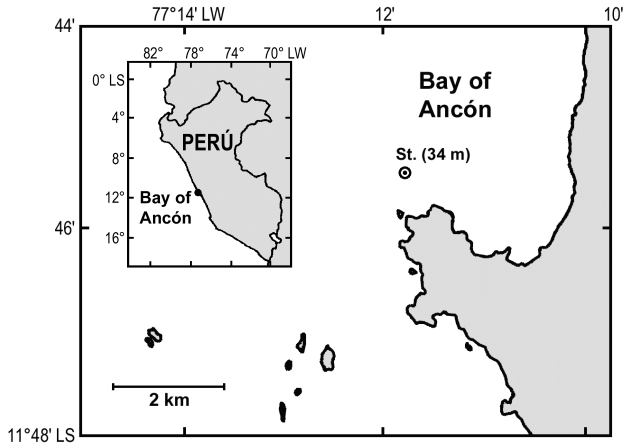

Fig. 1. Study site and location of the sampling station (34 m deep) at the soft bottom of the Bay of Ancón, Peru.

and aims to disentangle how changes in abiotic (environmental) factors such as water temperature and dissolved oxygen concentration, and biotic factors such as competition or facilitation, influence the different responses of a population of the polychaete *Sigambra bassi* (Pilargidae), which has shown different responses to EN (Tarazona et al., 1999).

2 Methods

The observed data for the present study come from a monitoring carried out in the Bay of Ancón, 40 km north of Lima (Fig. 1), since September 1981. The soft-bottom macrobenthos was sampled once a month at a fixed station (34 m deep; 11°45′12″ S, 77°11′50″ W), at monthly intervals. Three replicates of sediment were taken from the bottom of the fixed station each sampling day using a van Veen grab with a sampling area of 0.04 m^2. The samples were sieved over a mesh size of 0.5 mm and fixed immediately in 10% formalin in seawater buffered with borax. All animals retained were sorted, identified and counted in the laboratory. For this study, only the monthly average abundance of *S. bassi* was used (individuals per 0.04 m^2). On each sampling day, a Niskin bottle was also used to sample water at the bottom of the station for the measurement of the dissolved oxygen concentration using the Winkler method (Carpenter, 1965). The Niskin bottle was equipped with an inverted thermometer to measure temperature at the bottom of the station.

During non-El Niño periods, biodiversity in the Bay is very low due to hypoxia or anoxia, but during El Niño periods, increase of temperature and dissolved oxygen of the seawater, change of oceanic currents carrying tropical and oceanic species, and other abiotic and biological changes result in favorable conditions for new species settlement and increase in biodiversity and biological interactions (Arntz and Tarazona, 1999). Thus, the near-bottom temperature and dissolved oxygen concentration can be considered as two of the main abiotic factors influencing population growth in the macrobenthic community.

Three time-discrete population models, including different abiotic and biotic processes, were developed to simulate the density of the polychaete *S. bassi* (Table 1). The models consist of mathematical equations that calculate the variations of the polychaete density in response to environmental data (Table 2). As long-term data are available from the station, these two basic abiotic factors (near-bottom temperature and dissolved oxygen concentration) are included in the first and most simple model. Each subsequent model version considers the additional impact of biotic factors (for more details regarding the models and the parameter values, see Peña et al., 2005).

To compare model output and data for a specific parameter set, the root mean square deviation (RMSD) was used; a low RMSD value corresponds to a good agreement between the predicted and observed time series of the abundance of *S. bassi*. Four events of EN, i.e. 1982–1983, 1986–1987, 1991–1993 and 1997–1998, were analyzed separately, dividing the long-term data in four periods, each containing one EN event (Fig. 2): Sep-1981 to Sep-1984, Nov-1986 to Apr-1988, Mar-1990 to Dec-1994, and Jan-1996 to Dec-2000. As the mean abundance, m, of *S. bassi* differs strongly in the four EN events (m=2.9, 0, 4.4 and 14.1 for the three events, respectively), RMSD has been related to the corresponding mean of an event (RMSD/m=RMSD*). As *S. bassi* in EN 1986–1987 had zero density, only simulations with Models I and II were run, and RMSD* was not applied.

3 Results

During the very strong EN 1982–1983, the observed density of the polychaete *S. bassi* was low, compared with the

Table 2. Parameters and variables used in the models.

Parameter	Description
t	Time step (one month)
s_{O_2}	Larval settlement rate depending on dissolved oxygen concentration
s_T	Larval settlement rates depending on water temperature
O_t	Observed near-bottom dissolved oxygen concentration at time step t in ml O_2 l^{-1}
T_t	Observed near-bottom temperature at time step t in °C
O_i	Minimum threshold of dissolved oxygen concentration allowing for settlement
T_i	Minimum threshold of water temperature allowing for settlement
N_t	Simulated density of the population at time step t in ind. 0.04 m^{-2}
M	Monthly mortality rate of adults
N_i	Monthly number of larvae immigrating
y_t	*S. bassi* observed values in ind. 0.04 m^{-2}
n	Number of months
m	Mean abundance of *S. bassi*
K	Carrying capacity (ind. 0.04 m^{-2})
F	Number of individuals at which the facilitation doubles individual survival (ind. 0.04 m^{-2}).

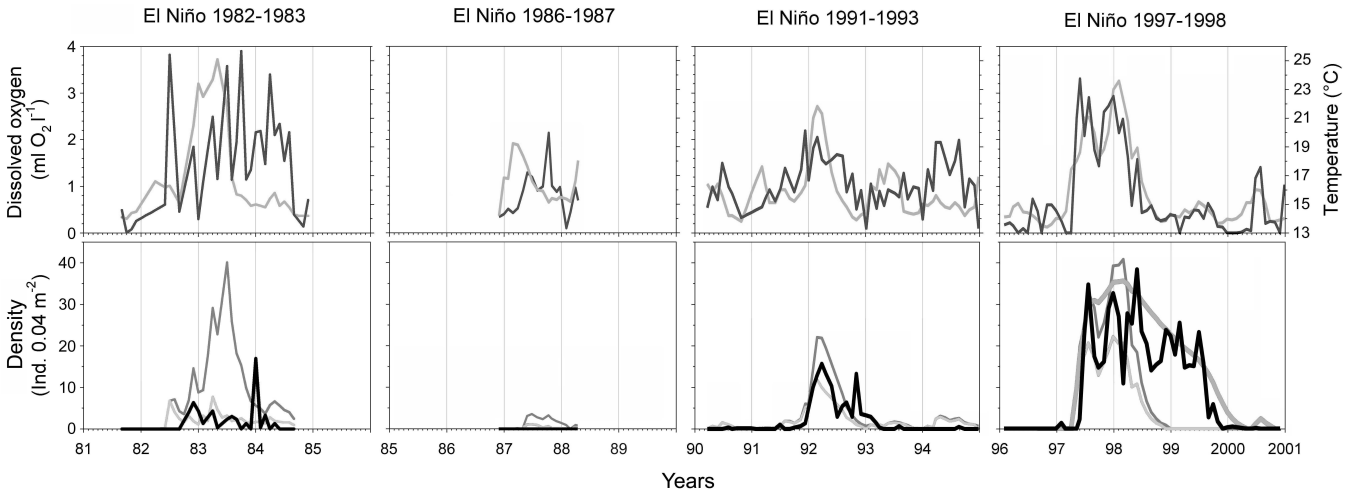

Fig. 2. Observed concentration of dissolved oxygen (dark line) and temperature (grey line) at the 34 m deep during three El Niño (EN) events (upper row) and observed abundance of *Sigambra bassi* (lower row, black line) and output from the Model I (dark grey), Model II (light grey), and Model III (light grey, fat line, only shown in the third EN event). Parameters: M=0.4, N_i=30, K=3 (EN 1982–1983); M=0.4, N_i=10, K=10 (EN 1986–1987); M=0.4, N_i=30, K=18 (EN 1991–1993); M=0.4, N_i=30, K=40, F=20 (EN 1997–1998, M=0.5 in Model III). Years, e.g. ,82, correspond to the January of that year (modified after Peña et al., 2005).

high values registered for the entire macrobenthic community at 34 m depth in the Bay of Ancón (Fig. 2). During the also very strong EN 1997-1998, the total density of the community was low, but *S. bassi* was the most abundant species in the community, with this high abundance continuing past the end of this EN. During the weak EN 1986–1987 there were no records of *S. bassi*, and in the long and moderate EN 1991–1993, there were some peaks of high abundance, which, however, were much lower than in EN 1997–1998 (Fig. 2).

Long-term variation in the polychaete density was simulated using the three models and testing different values for the parameters. Near-bottom temperature and dissolved oxygen concentration influence settlement rate via an exponential relation. The dissolved oxygen concentration threshold was chosen at 0.3 ml O_2 l^{-1} according to field measurements and literature that maintains that soft-bodied infauna can be found above this concentration (Rosenberg et al., 1983). Figure 3 show the ranges of parameter values leading to a good match between model output and observations.

For Model I, T_i=13°C is the most suitable minimum threshold temperature (*S. bassi* is already present with temperatures above 13°C) for the immigrant planktonic larvae to settle down, and lowers RMSD* values. For EN 1982–1983, the lowest deviations are restricted to high mortalities and very low numbers of immigrant larvae in all three models, and a very low carrying capacity (K=3) included in Model II lowers the RMSD* for a wider range of parameter values (Figs. 2–3).

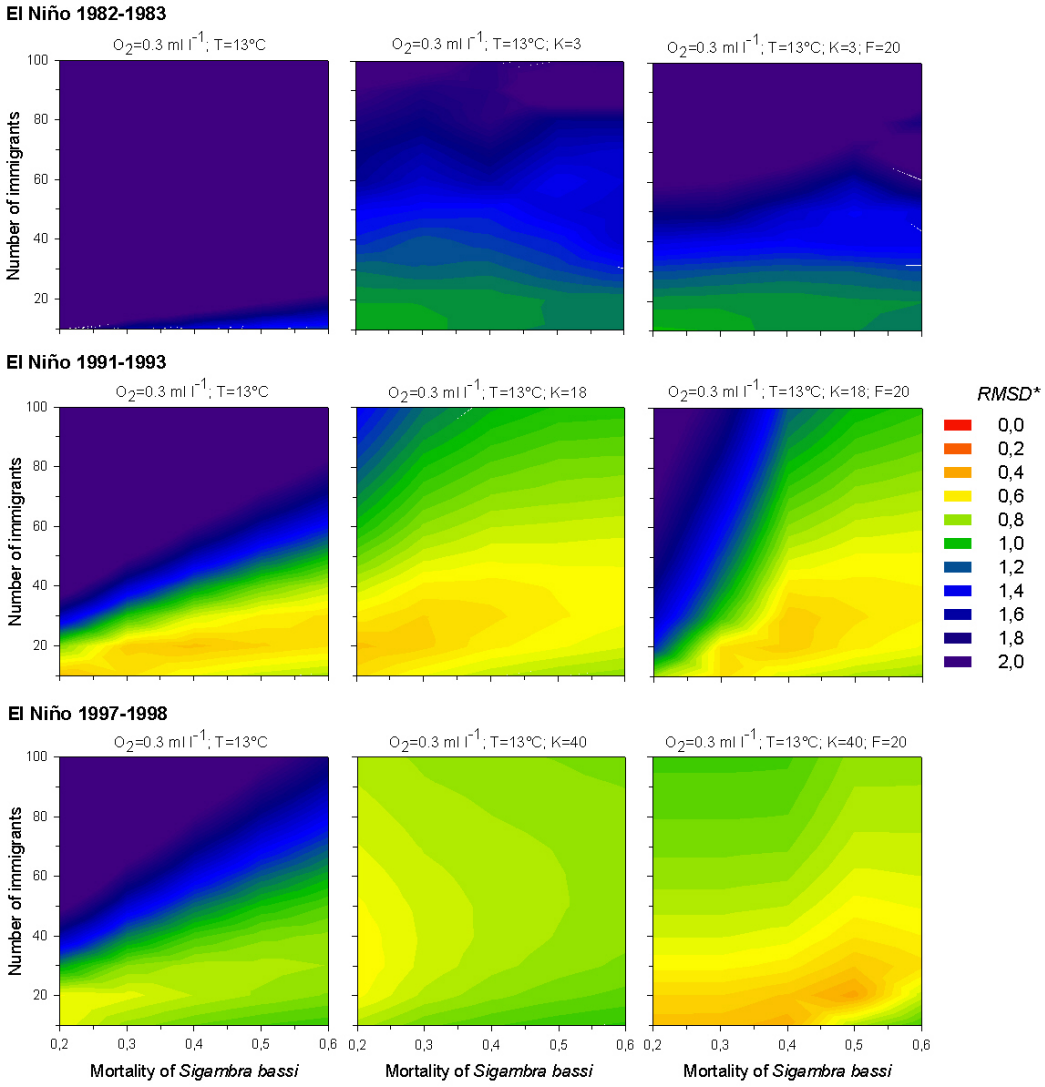

Fig. 3. Deviation between the simulated and observed dynamics of *Sigambra bassi* using RMSD* for different parameter combinations of mortality and number of immigrant larvae. Three models and three El Niño events are considered: Model I (first column), Model II (second column), and Model III (third column) and EN 1982–1983 (first row), EN 1991–1993 (second row) and EN 1997–1998 (third row) (from Peña et al., 2005).

Models I and II were used to explain the absence of *S. bassi* during the weak EN 1986–1987 (Fig. 2). Using Model I, the weak abiotic anomalies during this event do not allow high abundances unless a very high number of immigrant larvae are put into the model. Using Model II, besides a low number of immigrant larvae, a low carrying capacity (e.g. K=10 or K=3), can decrease the abundances (Fig. 2).

EN 1991–1993 shows low deviations in the whole range of mortality, but only for low numbers of immigrant larvae; to increase the range of low RMSD* values, K=18 had to be assumed (Figs. 2–3). Both Models I and II show that the main increase in density is mainly related to the increase of the first peak of temperature and dissolved oxygen concentration.

For EN 1997–1998, RMSD* are also lower in the whole range of mortality and low number of immigrant larvae. Model I shows that the high densities depend in part on the high temperatures reached, and Model II reveals that the system had a higher carrying capacity, that is K=40. Model III explains the remaining high densities of *S. bassi* after oxygen and temperature decrease better than the other models, and RMSD* values are lower for F=20 and low numbers of immigrant larvae (Figs. 2–3).

4 Discussion

The three models and long-term abiotic and biological data not only show the importance of abiotic and biotic factors influencing population dynamics of the polychaete *S. bassi* during four EN events, but also help suggest possible explanations for *S. bassi*'s responses to these events.

According to Model I, abiotic conditions in the Bay of Ancón during EN, i.e. increase of near-bottom temperature and near-bottom dissolved oxygen concentration (no hypoxic conditions), favor larval settlement of *S. bassi*, possibly via physiological effects on the metabolism of the larvae or changes in the viscosity of the water (Bolton and Havenhand, 1997). This can be seen in Fig. 2, where selected simulation runs for the four EN events are shown together with the observed densities. However, the high water temperatures and dissolved oxygen concentrations reached in EN 1982–1983 contradict the low abundances of *S. bassi* in this event.

According to the models, during EN 1982–1983, low numbers of immigrant larvae at which low RMSD* values are obtained (Fig. 3) could have influenced a low recruitment during this event, resulting in lower densities of *S. bassi*. This might also indicate that the time of onset of EN 1982–1983 in southern Spring (October 1982) did not coincide with high densities of available larvae of *S. bassi* to settle, i.e. spawning periods and recruitment patterns for this species during the year, but not when this EN started (Cotter et al., 2003). However, the abundance of larvae in the water column is not necessarily correlated with settlement or recruitment patterns in soft-sediment communities, as the processes influencing post-settlement may have greater repercussions on these communities (Olafsson et al., 1994; Morgan, 2001).

It has been maintained that competition for space is not a determinant process in soft sediments, neither for settlement nor for post-settlement (Morgan, 2001). Despite this, the inclusion of negative density dependence in the recruitment in Model II seems to work well for *S. bassi* in all EN events. Similar results were obtained by Woodin (1974) for the polychaete *Platynereis bicanaliculata*, which presented strong intraspecific competition for space in the tidal flats. This may be due to the small spatial scale of sampling area considered in the present study ($0.04\,m^2$) and Woodin's experiments ($0.05\,m^2$ area of experiment). The different carrying capacities for *S. bassi* in each EN obtained with Model II, especially the low carrying capacity during EN 1982–1983, suggest the influence of other factors. Woodin (1978) and Olafsson et al. (1994) state that in soft-sediment environments, biological intra- and interspecific interactions are important determinants of community patterns, so it is possible that the presence of other species, acting as prey, competitors, inhibitors or predators, modified the carrying capacity for *S. bassi*. The abundances obtained in the present study reflect the complexity in interactions reached by the community during each EN event, and hence, the responses of *S. bassi*.

The absence of *S. bassi* during the weak EN 1986–1987, according to the models, might be in part due to the weak increase of near-bottom temperature and dissolved oxygen as well as the fact that the temperature rise (in December 1986) did not coincide with the increase in dissolved oxygen (in April 1987; Fig. 2). Therefore, high abundances of *S. bassi* in the area could only have been reached with a very high input of larvae. However, the absence of *S. bassi* suggests unsuccessful recruitment due to low larval supply, high mortality of post-settled individuals, or a low carrying capacity due to presence of other species.

During the strong EN 1997–1998, the high abundances reached by *S. bassi* can be explained by the favorable abiotic conditions during this event, high temperature and dissolved oxygen concentration. In this event, *S. bassi* was by far the most dominant species of the system (Fig. 2, Tarazona et al., 1999), and the high carrying capacity (K=40) is likely to be close to the maximal carrying capacity of the system.

The inclusion of intraspecific facilitation in Model III provides a possible explanation of why high densities reached by *S. bassi* in EN 1997–1998 persist even when the favorable abiotic conditions are gone. The very high densities of *S. bassi* during EN 1997–1998 may have a positive effect on the survival of individuals, especially through adult-larval interaction, i.e. intraspecific facilitation. Gregarious larval settlement and metamorphosis in response to conspecific cues lead to patchy distribution of many polychaetes (Qian, 1999). Larval settlement of these polychaetes may be stimulated by conspecific resident individuals that exude chemical attractants or by physical contact between larvae and adults (Minchinton, 1997). Bruno et al. (2003) assume that survival of individuals can also be enhanced by living in aggregations, because this can diminish effects of environmental stress and predation.

This modeling study shows that EN events, through the increase of water temperature and oxygen and likely other factors, has a strong impact on the population dynamics of macrobenthic organisms, and provides possible explanations for the different responses of *S. bassi* population to EN. According to the models, abiotic conditions during EN events, i.e. high near-bottom temperature and dissolved oxygen concentration, are favorable for the settlement of *S. bassi*, but they are not sufficient to explain its differences among EN events. When thermal conditions are similar (EN 1982–1983 and 1997–1998) for the population, the different densities in each EN event are mainly dependent on the different biological interactions (competition, predation, facilitation). That means that after the appearance of new species in the community due to favorable abiotic conditions, biological interactions develop and increase during the process of an EN event. These interactions differ from one EN to another, resulting in the different responses of the populations in the macrobenthic community.

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