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The relative role of ecological interactions and environmental variables on the population dynamics of marine benthic polychaetes

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Abstract In order to elucidate how ecological interactions drive the abundances of marine benthic polychaete populations and the role that environmental variables play in their dynamics, we examined long-term dynamics of winter abundance in 13 polychaete species from benthic samples obtained over 15 years (1993 to 2007) at Punta Coloso, northern Chile on the Pacific coast of South America. We examined the relative importance of density dependence, winter sea surface temperature (SSTW) and Southern Oscillation Index (SOI) on polychaete dynamics. All species studied showed conspicuous abundance oscillations, consistent with negative density-dependent population feedbacks. Model selection across a suite of population dynamic models showed that for six species, the best model included the effect of environmental variables, SSTW in the previous year, while the SOI index was the relevant variable in two polychaete species. A pure density-dependent model best explained the population dynamics of the remaining five species. Our results contrast with traditional approaches,

which focus on the importance of abiotic factors in structuring marine benthic systems, and demonstrate the importance of theoretical synthesis and analysis to understand long-term dynamics in these ecosystems.

Keywords Population dynamics · Density dependence · Autoregressive time series models · Polychaeta · Benthic assemblages · Chile

Introduction

The causes of fluctuations in natural populations have been widely discussed for more than six decades (Andrewartha and Birch 1954). In recent years, the two seemingly conflicting views of the population regulation (i.e density-dependence versus density-independence) have been reconciled in a more integrative view that recognizes the importance of both endogenous (density-dependent) and exogenous (density-independent) factors (Lima et al. 2001; Stenseth et al. 2003).

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Traditionally, studies of population regulation in marine species have been addressed from an experimentalist perspective at local scales, emphasizing the role of density dependence (Wilson 1983; Hixon and Carr 1997; Sánchez-Lizaso et al. 2000; Hixon et al. 2012). Conversely, analyses of time series have revealed that temporal variability of exploited stocks can be linked to density-independent climatic and oceanographic variability (Hollowed et al. 2001; Yáñez et al. 2001; Chavez et al. 2003; Lehodey et al. 2006). Nevertheless, in recent years, studies have highlighted the importance of both density-dependent mechanisms and environmental stochasticity, phenomena such as the El Niño Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO), in the regulation of marine populations (Stenseth et al. 2002, 2003).

Polychaete worms are an essential component of benthic marine food webs, playing key roles in the transfer of energy to large organisms (Hutchings 1998; Rouse and Pleijel 2001). Their relatively short life spans and high dispersal ability make these ectotherm organisms sensitive indicators of changes in the physical environment (Rouse and Pleijel 2001), which makes it likely that they should reveal causal associations with environmental fluctuations in temperature or climate. Despite many studies having revealed their dominance in macrobenthic communities along the Humboldt Current System (Gallardo et al. 2004; Palma et al. 2005; Moreno et al. 2008), long-term population dynamics of benthic polychaetes remain poorly studied (Carrasco 1997; Peña et al. 2005; Carrasco and Moreno 2006). These studies have revealed the existence of a strong inter-annual variability in population abundance of polychaete species (Carrasco 1997; Carrasco and Moreno 2006). Peña et al. (2005) used a difference equation modelling approach to evaluate the importance of environmental variability (e.g. ENSO) and density-dependent factors explaining the temporal variability in the abundance of a single polychaete species. Whether these results can be generalized to other species remains unknown. Here, we used long-term data of winter abundance in 13 polychaete species monitored over 15 years in northern Chile to investigate the regulating mechanisms of population dynamics of these organisms. Our goals were: a) to describe the feedback structure that best represents the dominant ecological processes acting on these population of polychaetes; and b) to evaluate the importance of the sea temperature and ENSO fluctuations as environmental drivers of the demographic processes in these populations.

Material and methods

Biological data

The continental shelf off northern Chile, at Punta Coloso, Antofagasta (23°45'S 70°28'W), was surveyed from 1990 to 2007. During this sampling period, 4 stations were

sampled at 50–60 m depth. Sampling (four replicate samples) was carried out by means of a 0.1-m² Petersen grab in two annual cruises (summer and winter). In order to obtain a continuous time series subject to analysis, we examined winter samples from 1993 to 2007, encompassing 15 years of observations. A detailed description of sampling procedures and processing can be found in Carrasco and Moreno (2006). Polychaetes found in the benthic grab samples were sorted into major taxa and then identified according to the species or lowest possible taxonomic level. Thirteen species showed enough data to evaluate their long-term population dynamics: *Magelona phyllisae* Jones, 1963; *Aricidea pigmentata* Carrasco, 1976; *Paraprionospio pinnata* (Ehlers 1901); *Aphelochaeta longisetosa* (Hartmann-Schröder, 1965); *Prionospio peruana* Hartmann-Schröder, 1962; *Nephtys ferruginea* Hartman, 1940; *Leitoscoloplos kerguelensis chilensis* (Hartmann-Schröder, 1965); *Mediomastus branchiferus* Hartmann-Schröder, 1962; *Kinbergonuphis lineata* (Fauchald, 1980); *Nereis dorsolobata* Hartmann-Schröder, 1965; *Megalomma monoculata* Hartmann-Schröder, 1965; *Cossura chilensis* Hartmann-Schröder, 1965 and *Clymenella fauchaldi* Carrasco and Palma, 2003 (All taxonomic details were validated using the available information at the World Register of Marine Species, WoRMS Editorial Board 2016). Data correspond to total catches per winter (abundances). To satisfy the assumptions of stationary standard time series analysis, all time series were previously detrended by adjusting a linear model of the form $X_t = a + b \times t$, where t is time and a and b are the estimated model parameters (Royama 1992; Berryman 1999; Kirchgässner et al. 2012). For each species, we used the residuals of this model plus the mean abundance as the detrended time series to be analyzed.

Climatic data

In order to obtain adequate representations of local climatic data, local sea surface temperature (SST) data were collected from the Extended Reconstructed Sea Surface Temperature analysis (ERSST v3b, Smith et al. 2008), available at <http://nomads.ncdc.noaa.gov/las/getUI.do>. SST records were obtained from 1990 to 2007. Winter and summer (July to September and January to March, respectively) SST averages (SSTW and SSTS, respectively) were used in this study. We also obtained standardized annual data for the Southern Oscillation Index (SOI) for the same time period as the SST data. This index is the standardized difference in the sea level pressure between Tahiti and Darwin (Australia), and provides a quantitative proxy for ENSO. The SOI data series was obtained from <http://www.cpc.ncep.noaa.gov/data/indices/soi>.

Statistical analysis

It has been shown that the patterns of density dependence that a given population experiences will result in the observed dynamical behaviour, with the time series showing characteristic signatures in their autocovariance structure (Royama 1992; Berryman 1999). Thus, it is possible to estimate the strength of density-dependent feedbacks from time series analyses. In this approach, temporal changes in population abundance may be represented by means of stochastic difference equations:

$$N_t = N_{t-1} f(N_{t-1}, N_{t-2}, \dots, N_{t-k}, v_t) \tag{1}$$

Where N_t represents observed abundance at time t , and v_t is a stochastic term affecting the population growth rate. By defining $X_t = \log(N_t)$ and $g(X) = \log(f(N))$, this difference equation may be re-expressed as:

$$R_t = X_t - X_{t-1} = g(X_{t-1}, X_{t-2}, \dots, X_{t-k}, u_t) \tag{2}$$

Where R_t is the population growth rate at time t , and $g()$ is a function that describes how this population growth rate depends on previous population densities. Assuming a linear autoregressive model of order two (AR(2)) for density-dependent feedback, and an additive effect of environmental or climatic variables, a general feedback model for polychaete (X_t) population dynamics may thus be expressed as:

$$R_t = \beta_0 + \beta_1 X_{t-1} + \beta_2 X_{t-2} + cY \tag{3}$$

where β_i ($i=0, 1$ and 2) are the parameters in an ordinary autoregressive model (AR(2), Royama 1992). Parameter c is a scale parameter that weights the additive effect of the climatic or environmental variable Y on R_t (Royama 1992; Berryman 1999; Turchin 2003). Both parameters of the linear autoregressive model are typically referred to as the strength of first- and second-order feedbacks in the ecological literature or direct and delayed density dependence (Royama 1992; Berryman 1999; Turchin 2003). The parameter $(1 + \beta_1)$ provides a measure of the strength of first order or direct density dependence in population dynamics caused by intraspecific interactions (Royama 1992; Berryman 1999). On the other hand, parameter β_2 is essentially a proxy for any second order or delayed density dependence. These delayed population dynamic effects may include disease, parasites, food, or maternal effects (Ginzburg and Taneyhill 1994; Ginzburg 1998; Ginzburg and Colyvan 2004).

Using Eq. (3) as a baseline, and omitting the effect of climatic variables, the relative importance of direct and delayed density dependence may be evaluated by locating the estimated parameters $(1 + \beta_1)$ and β_2 in a Royama's diagram (Fig. 1; Royama 1992; Bierman et al. 2006). Parameter combinations that fall above the semicircle and below the triangle (areas I and II) correspond to dynamics dominated by direct density

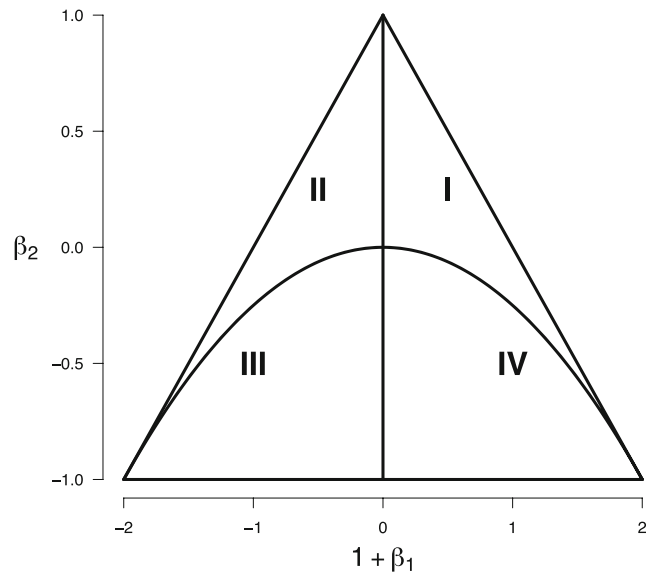


Fig. 1 Autoregressive model dynamics. The figure shows the periodicity of the dynamics of the stochastic second-order autoregressive model shown in Eq. 3. Combination of parameter values outside the triangle lead to extinction. Within the triangle, predicted dynamics will either be stable or show damped fluctuations. If stochastic perturbations are present, observed fluctuations would be persistent. For a full exposition of the model see Royama 1992

dependence. Parameter combinations that fall below the semicircle (areas III and IV) correspond to dynamics dominated by delayed density dependence (cycles; Royama 1992). Thus, the autoregressive model parameters capture both the relative contribution of generic density-dependent processes as well as the diversity of possible population dynamics. It is important to stress that the assumption of linearity provides an approximation to allow easier comparison of the dynamics of populations of different species (Royama 1992; Berryman 1999).

To evaluate the relative influence of climate (represented by SST and ENSO) and density dependence in the dynamics of each species, we tested four hypotheses and their corresponding autoregressive models. In the first hypothesis, we assume that the dynamics of the species depends only on the feedback structure of the population and that environmental variables play no role, thus omitting the effect of climatic variables $Y(t)$. Thus, Eq. (3) is reduced to its first three right-hand terms. In the second hypothesis, we test whether SST is acting on the population by modifying the survival of the previous cohort (X_{t-1}) to winter conditions. To do so, the second model incorporates SSTW as an additive effect on R_t by defining $Y = SSTW$. The third hypothesis assumes that SST is acting on the population by modifying the reproductive capacity of the X_{t-1} cohort, because, as expected for ectotherm organisms, polychaete fecundity is strongly dependent of environmental temperature (Åkesson 1976; Levin and Creed 1986; Angilletta 2006). To do so, the third model incorporates SSTs as an additive effect on R_t , defining $Y = SSTs$.

In the fourth hypothesis, and following previous studies, we evaluate the influence of overall climatic conditions by incorporating the SOI index in an additive fashion (Stenseth et al. 2003). Thus, in this model, we define $Y = SOI$. All four models were fitted using the *stats* library in the R program (R Development Core Team 2014), and ranked according to the Bayesian information criterion (BIC or Schwarz criterion; Schwarz 1978). The model with the minimum BIC was selected as the best model, after due examination of the corresponding BIC weights (BICw) across all the models for a given species.

Results

Polychaete species at Punta Coloso showed a wide richness in types of dynamic behaviors in the study area. Overall, the dominant polychaete species showed significant increases in abundance throughout the 15-year study period (Fig. 2), while subdominant and rare species showed no significant long-term changes in abundance with the exception of *Kinbergonuphis lineata* and *Nereis dorsolobata*, which showed significant decreases (Fig. 3). The estimated parameters $(1 + \beta_1)$ and β_2 indicate that the species *Prionospio peruana*, *Mediomastus branchiferus* and *Nereis dorsolobata*

fell in the area of stable direct density dependence dynamics (Fig. 4). This pattern of population dynamics is characterized by saw-toothed fluctuations in the time series of abundances, and it is the distinct signature of intra-specific competition (Royama 1992; Berryman 1999; Turchin 2003). On the other hand, the estimated parameters of *Magelona phyllisae*, *Aricidea pigmentata*, *Paraprionospio pinnata*, *Aphelochaeta longisetosa*, *Nephtys ferruginea*, *Leitoscoloplos kerguelensis chilensis*, *Kinbergonuphis lineata*, *Megalomma monoculata*, *Cossura chilensis* and *Cllymenella fauchaldi* fell in areas III and IV (Fig. 4), which both are characteristic of delayed density-dependent regulation (Figs. 1 and 4).

The evaluation of the effect of the environmental variables on the dynamics showed that SSTW in the previous year was the most common forcing variable according to our modeling and model selection procedure. Hence, the best model for *Magelona phyllisae*, *Aricidea pigmentata*, *Paraprionospio pinnata*, *Kinbergonuphis lineata*, *Nereis dorsolobata* and *Cllymenella fauchaldi* includes SSTW (Table 1) and gives support to the hypothesis that SST is acting on the population by modifying the survival of the previous cohort (X_{t-1}) to winter conditions. In all these cases, the explained variance (R^2) was higher than 50 % and, in some cases, higher than 60 %, which makes us confident of having captured the essential components of the population dynamics of these

Fig. 2 Time series of polychaete abundance in Punta Coloso, Chile. The figures show natural log (ln)-transformed abundance for **a** *Magelona phyllisae*, **b** *Aricidea pigmentata*, **c** *Paraprionospio pinnata*, **d** *Aphelochaeta longisetosa*, **e** *Prionospio peruana* and **f** *Nephtys ferruginea*. Those species showing significant linear trends are shown with continuous lines

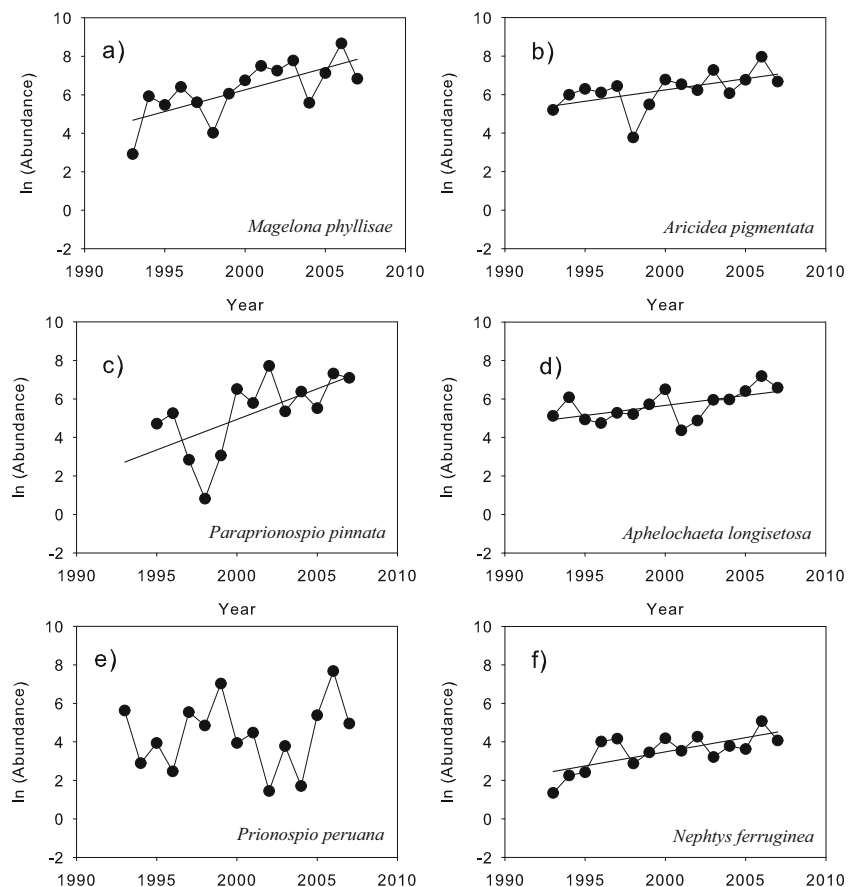
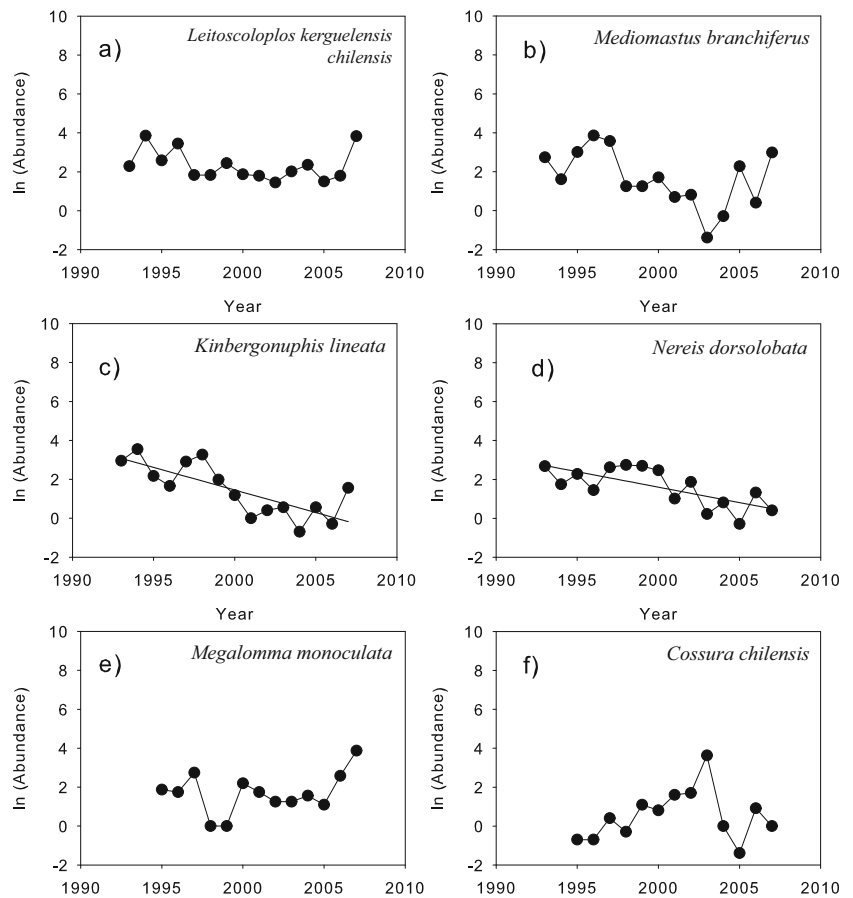


Fig. 3 Time series of polychaete abundance in Punta Coloso, Chile. The figures show natural log (ln)-transformed abundance for **a** *Leitoscoloplos kerguelensis chilensis*, **b** *Mediomastus branchiferus*, **c** *Kinbergonuphis lineata*, **d** *Nereis dorsolobata*, **e** *Megalomma monoculata* and **f** *Cossura chilensis*. Those species showing significant linear trends are shown with continuous lines



species. The second most common selected model was the model with no environmental variables included. The best

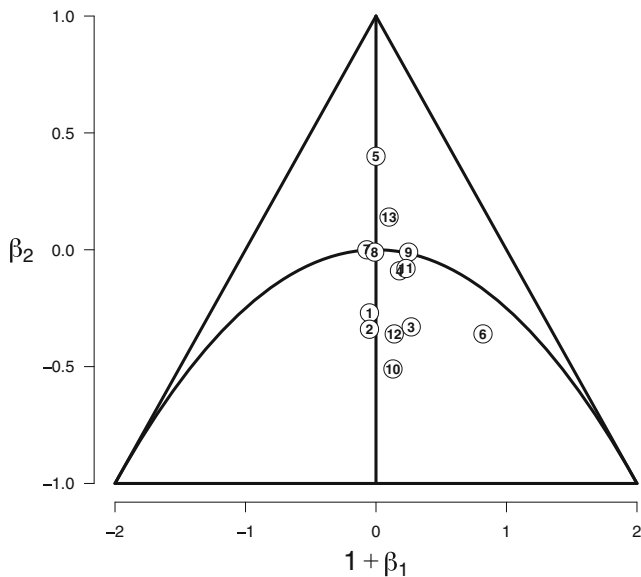


Fig. 4 Fitted autoregressive model coefficients within the same scheme as Fig. 1. The numbers indicate the fitted AR(2) model coefficients ($1 + \beta_1$) and β_2 , which estimate the strength of direct and delayed density dependence, respectively. Numbered circles indicate the fitted coefficient values for each of the species, with numbers corresponding to those for each species in Table 1. See text for details

model for *Nephtys ferruginea*, *Leitoscoloplos kerguelensis chilensis*, *Mediomastus branchiferus*, *Megalomma monoculata* and *Cossura chilensis* did not include environmental variables, but at the same time explained variances were lightly lower than in the previous case (31–53 %, Table 1). Finally, the best models for *Aphelochaeta longisetosa* and *Prionospio peruana* include the SOI index of the previous year, with the percentage of explained variances of 68 % and 56 %, respectively (Table 1). Thus, only the models for hypotheses 1, 2 and 4 were found to account for the observed dynamics. We found no evidence in any of the 13 species for an effect of SST on the reproductive capacity of the X_{t-1} cohort (third hypothesis).

Discussion

In this study, we examine which ecological feedback structure best represents the dominant processes acting on the population dynamics of thirteen benthic polychaetes species at Punta Coloso, northern Chile. Specifically, we examine whether temperature and ENSO fluctuations are the most important environmental drivers of the demographics processes in polychaete populations, as has been suggested in the literature on population biology (Lima et al. 1999a, b, 2001; Estay and

Table 1 Fitted population dynamic models for benthic polychaetes at Punta Coloso, Antofagasta, Chile. The table shows the four models fitted to each species, indicating the parameter values in the equations. The table also shows for each model fitted to each species the determination coefficient (R^2), as well as the Bayesian information criterion (BIC) and the Bayesian information criterion weights (BIC_w). For each species, the best population dynamic models were compared by using the BIC and BIC_w , with the optimal model selected highlighted in bold type

Species	Model	R^2	BIC	BIC_w
Group A: Models which include SSTW				
1) <i>Magelona phyllisae</i>	$R_t = 9.79 - 1.05X_{t-1} - 0.27X_{t-2}$	0.54	44.23	0.53
	$R_t = 17.25 - 1.10X_{t-1} - 0.24X_{t-2} - 0.45SSTW$	0.63	44.16	0.55
	$R_t = 19.21 - 0.99X_{t-1} - 0.2X_{t-2} - 0.48SSTW$	0.58	45.74	0.25
2) <i>Aricidea pigmentata</i>	$R_t = 10.78 - 1.13X_{t-1} - 0.31X_{t-2} + 0.52SOI$	0.57	46.13	0.20
	$R_t = 11.01 - 1.05X_{t-1} - 0.34X_{t-2}$	0.57	40.50	0.10
	$R_t = 20.5 - 1.06X_{t-1} - 0.35X_{t-2} - 0.58SSTW$	0.75	36.24	0.83
3) <i>Paraprionospio pinnata</i>	$R_t = 18.94 - 0.94X_{t-1} - 0.21X_{t-2} - 0.45SSTW$	0.60	42.06	0.05
	$R_t = 11.04 - 1.06X_{t-1} - 0.33X_{t-2} + 0.10SOI$	0.57	43.03	0.03
	$R_t = 6.04 - 0.73X_{t-1} - 0.33X_{t-2}$	0.51	47.50	0.01
4) <i>Kinbergonuphis lineata</i>	$R_t = 27.21 - 0.87X_{t-1} - 0.45X_{t-2} - 1.23SSTW$	0.82	38.79	0.89
	$R_t = 41.26 - 0.61X_{t-1} - 0.12X_{t-2} - 1.71SSTW$	0.73	43.22	0.10
	$R_t = 6.06 - 0.74X_{t-1} - 0.32X_{t-2} + 0.06SOI$	0.51	49.90	0.00
5) <i>Nereis dorsolobata</i>	$R_t = 2.69 - 0.82X_{t-1} - 0.09X_{t-2}$	0.35	43.19	0.05
	$R_t = -8.28 - 1.28X_{t-1} - 0.23X_{t-2} + 0.79SSTW$	0.63	38.53	0.52
	$R_t = -21.02 - 0.84X_{t-1} + 0.18X_{t-2} + 1.06SSTW$	0.61	38.95	0.42
6) <i>Clymenella fauchaldi</i>	$R_t = 2.64 - 0.85X_{t-1} - 0.06X_{t-2} - 0.11SOI$	0.35	45.73	0.01
	$R_t = 2.27 - 1.00X_{t-1} + 0.40X_{t-2}$	0.60	35.17	0.19
	$R_t = -5.66 - 1.39X_{t-1} + 0.6X_{t-2} + 0.54SSTW$	0.71	33.45	0.45
7) <i>Nephtys ferruginea</i>	$R_t = -10.78 - 0.96X_{t-1} + 0.58X_{t-2} + 0.56SSTW$	0.68	34.86	0.22
	$R_t = 1.10 - 0.84X_{t-1} + 0.52X_{t-2} - 0.68SOI$	0.66	35.71	0.14
	$R_t = -8.25 - 0.47X_{t-1} - 0.27X_{t-2} + 0.64SSTW$	0.51	36.86	0.38
8) <i>Leitoscoloplos kerguelensis chilensis</i>	$R_t = -13.56 - 0.15X_{t-1} - 0.32X_{t-2} + 0.68SSTW$	0.47	37.68	0.25
	$R_t = 0.78 - 0.32X_{t-1} - 0.05X_{t-2} - 1.26SOI$	0.42	38.80	0.14
	$R_t = 4.91 - 1.07X_{t-1} - 0.00X_{t-2}$	0.53	34.47	0.45
9) <i>Mediomastus branchiferus</i>	$R_t = 7.93 - 0.83X_{t-1} + 0.05X_{t-2} - 0.27SSTW$	0.57	35.94	0.22
	$R_t = -0.76 - 1.27X_{t-1} + 0.00X_{t-2} + 0.30SSTW$	0.55	36.59	0.16
	$R_t = 5.52 - 1.21X_{t-1} + 0.03X_{t-2} + 0.41SOI$	0.56	36.30	0.18
10) <i>Megalomma monoculata</i>	$R_t = 4.47 - 1.01X_{t-1} - 0.01X_{t-2}$	0.43	37.96	0.50
	$R_t = 3.68 - 1.01X_{t-1} - 0.04X_{t-2} + 0.06SSTW$	0.43	40.47	0.14
	$R_t = 11.58 - 0.94X_{t-1} + 0.16X_{t-2} - 0.38SSTW$	0.46	39.70	0.21
11) <i>Cossura chilensis</i>	$R_t = 4.49 - 1.02X_{t-1} - 0.01X_{t-2} + 0.05SOI$	0.43	40.52	0.14
	$R_t = 2.14 - 0.75X_{t-1} - 0.01X_{t-2}$	0.31	53.95	0.50
	$R_t = 1.16 - 0.76X_{t-1} - 0.04X_{t-2} + 0.07SSTW$	0.32	56.50	0.14
12) <i>Cossura chilensis</i>	$R_t = -13.54 - 0.98X_{t-1} - 0.09X_{t-2} + 0.76SSTW$	0.35	55.88	0.19
	$R_t = 2.29 - 0.74X_{t-1} - 0.03X_{t-2} + 0.57SOI$	0.34	56.08	0.17
	$R_t = 3.58 - 0.87X_{t-1} - 0.51X_{t-2}$	0.49	38.39	0.38
13) <i>Cossura chilensis</i>	$R_t = 7.93 - 0.73X_{t-1} - 0.49X_{t-2} - 0.3SSTW$	0.53	39.95	0.18
	$R_t = -17.57 - 1.45X_{t-1} - 0.69X_{t-2} + 1.06SSTW$	0.56	39.17	0.26
	$R_t = 3.59 - 0.96X_{t-1} - 0.38X_{t-2} + 0.65SOI$	0.53	39.93	0.18
14) <i>Cossura chilensis</i>	$R_t = 2.41 - 0.77X_{t-1} - 0.08X_{t-2}$	0.39	46.11	0.49
	$R_t = 5.07 - 0.77X_{t-1} - 0.12X_{t-2} - 0.16SSTW$	0.40	48.38	0.16
	$R_t = 12.84 - 0.84X_{t-1} - 0.13X_{t-2} - 0.46SSTW$	0.41	48.08	0.18
15) <i>Cossura chilensis</i>	$R_t = 2.57 - 0.82X_{t-1} - 0.07X_{t-2} + 0.4SOI$	0.40	48.32	0.16

Table 1 (continued)

Species	Model	R ²	BIC	BIC _w
Group C: Models which include SOI				
12) <i>Aphelochaeta longisetosa</i>	$R_t = 8.60 - 0.86X_{t-1} - 0.36X_{t-2}$	0.57	32.30	0.29
	$R_t = 10.00 - 0.82X_{t-1} - 0.38X_{t-2} - 0.10SSTW$	0.58	34.62	0.09
	$R_t = 12.43 - 0.85X_{t-1} - 0.36X_{t-2} - 0.18SSTS$	0.58	34.47	0.10
	$R_t = 7.72 - 0.82X_{t-1} - 0.29X_{t-2} - 0.69SOI$	0.68	31.15	0.52
13) <i>Prionospio peruana</i>	$R_t = 4.46 - 0.9X_{t-1} + 0.14X_{t-2}$	0.46	61.46	0.32
	$R_t = -3.42 - 0.99X_{t-1} + 0.04X_{t-2} + 0.56SSTW$	0.49	63.25	0.13
	$R_t = -19.65 - 0.89X_{t-1} + 0.16X_{t-2} + 1.10SSTS$	0.53	62.33	0.21
	$R_t = 2.18 - 0.89X_{t-1} + 0.45X_{t-2} - 2.19SOI$	0.56	61.37	0.34

Lima 2010). In the following, we discuss four aspects of our results: 1) The relative importance (and potential mechanisms) of direct and delayed density dependence, 2) The importance of inter-specific interactions on the observed population dynamics at Punta Coloso, 3) The generality of our findings for polychaete population dynamics, both in the South American Pacific and in other marine regions of the world and 4) The different responses observed across the 13 species.

The first aspect of our results (relative importance of direct and delayed density dependence) shows that observed population fluctuations in all 13 polychaete species studied are consistent with density-dependent feedback structures, in agreement with population dynamics theory (Royama 1992; Berryman 1999; Turchin 2003; Ginzburg and Colyvan 2004). In particular, observed oscillations in abundance of many of these species suggest they could be expected to be the result of negative density-dependent population feedbacks (Figs. 2 and 3; Berryman 1999). Analysis of the linear autoregressive model indicates that with the exception of *Prionospio peruana*, *Mediomastus branchiferus* and *Nereis dorsolobata*, population dynamics of all remaining 10 polychaete species are best described by delayed, second-order density-dependent population processes. These dynamics are characterized by a pattern of cycles in the time series and have been associated either with strong inter-population processes governing the dynamics like predation, parasitism or herbivory (Berryman 1999; Turchin 2003), or to delayed intra-population processes like maternal effects (Ginzburg and Colyvan 2004). On the other hand, the fact that only these three species show direct density dependence, which is often ascribed to the dominance of competitive interactions, suggests most of these polychaete species are likely to be embedded in a complex web of interactions. This may seem counterintuitive, given the low species richness and seemingly “simple” community structure of this group of species. Indeed, the presence of significant delayed density-dependent feedback structure in these species, which follow mainly scavenging or deposit-feeder habits, poses interesting research questions, particularly as regards the

potential mechanism behind these population process delays or lags. Likely candidates may be any of the following: predator-prey lags, or other lagged density-dependent interactions such as parasitism or cannibalistic interactions between different stages of the species' complex life cycle (Ginzburg and Colyvan 2004). This leads to the second aspect of the results that we find interesting to discuss: the importance of inter-specific interactions on the observed population dynamics at Coloso.

Previous work on population dynamics modelling of a predator-prey pair of polychaete species in the Dutch Wadden Sea, *Scoloplos (Scoloplos) armiger* (Müller, 1776) and *Nephtys hombergii* Savigny in Lamarck, 1818, has provided evidence for a weak feedback mechanism between these two species, despite the fact that both species exhibit direct density dependence (Van der Meer et al. 2000). Interestingly, only the log reproductive rate of the predator (*Nephtys hombergii*) was determined by winter temperature, while the prey (*Scoloplos (Scoloplos) armiger*) presented a simpler, first-order autoregressive model. In the case of the polychaete species studied here, more natural history information is required in order to allow accurate identification of predator-prey interactions between the species. Otherwise, any attempts to model an unknown number of predator-prey pairs across all 13 species may lead to a phenomenological model without direct relation to actual biological interactions. More importantly, such a model may incorrectly capture effects such as cannibalistic interactions between different life stages of any given species. To adequately test this potential mechanism for delayed density dependence, either experimental or field studies may be carried out. From an experimental perspective, carefully controlled micro- or mesocosm experiments would be suitable strategies, so as to collect an abundance time series of the different life cycle stages present for a given polychaete species. Such time series, along with stage-structured population models, would

allow inference of any cannibalistic interaction and its relative importance with respect to interspecific competition within each life cycle stage (e.g. Bjørnstad and Grenfell 2001). However, further work is needed to provide specific evidence as to the likelihood of these alternative explanations in the polychaete species at Punta Coloso, as there is currently no detailed information regarding the incidence of cannibalism in these species, or possible parasitic or predation interaction with other species. In light of our results, one possible avenue of research could be to test whether *Prionospio peruana*, *Mediomastus branchiferus* and *Nereis dorsolobata* are preyed upon by the remaining species with second-order or delayed density dependence.

The third aspect to be discussed is the generality of our results for the South American Pacific Ocean or any other marine region. To our knowledge, the only other available study on polychaete population dynamics in the Pacific coast of South America focuses on analysis of monthly monitoring data for population dynamics of the polychaete *Sigambra bassi* (Hartman, 1945) at Bay of Ancón, Perú (Peña et al. 2005). This study attempts to disentangle the relative importance of abiotic and biotic factors in determining the abundance of *Sigambra bassi*, comparing different ENSO events. To do so, it models the lagged monthly abundance as a difference equation model, rather than studying the yearly population growth rate as we have done in the present study (Royama 1992; Berryman 1999). It is interesting to note that the best models selected for different ENSO events required a set of different un-validated assumptions, such as low immigration rate, and differential mortality rates and carrying capacities. Also, selection of these models was based on the root-mean squared deviation, which does not take into consideration the degree of model complexity and number of parameters, thus being prone to over-fitting. Furthermore, although Peña et al. (2005) examined a suite of models, they did not carry out a model selection procedure, and each model they fitted was examined for each individual El Niño event, rather than examining the whole time series. As a result, the modelling and sampling strategy reported by these authors does not allow ready comparison with the results reported in this study. However, what can be compared are the conclusions drawn by these two contrasting approaches. An important point to bear in mind is that our results show that, while six species showed delayed effects of SST, local variables are not the only way to evaluate climatic effects on population dynamics, especially in this region where ENSO events are strong. Climate indices, as SOI (ENSO) are proxies of overall climate conditions and represent “packages of weather” *sensu* (Stenseth et al. 2003). In some cases, this allows a better approximation for studying the influence of climate on population dynamics than the use of local variables (Stenseth et al. 2003). However, while their use in ecological research has increased in the last

10 years, in our study only 2 species show clear effects of SOI: *Aphelochaeta longisetosa* and *Prionospio peruana*, both relatively dominant and abundant species. This leads to the final point of our discussion which is the differential response of the species we studied.

The most abundant polychaete species in Punta Coloso reported by Carrasco and Moreno (2006) are *Aricidea pigmentata*, *Magelona phyllisae*, *Prionospio peruana*, *Aphelochaeta longisetosa* and *Paraprionospio pinnata*. Interestingly, for many of these dominant species, the inclusion of environmental explanatory variables in the population dynamic models resulted in a much higher percentage of explained variance for eight species. In eight species, the best model included an environmental forcing variable. For the species *Magelona phyllisae*, *Aricidea pigmentata*, *Paraprionospio pinnata*, *Kinbergonuphis lineata*, *Nereis dorsolobata* and *Clymenella fauchaldi*, the best model included SSTW in the previous year as a forcing variable, whereas for *Aphelochaeta longisetosa* and *Prionospio peruana*, SOI emerged as the only important forcing variable. Thus, population dynamics of the dominant, most abundant species tend to be explained by hypotheses that consider an interaction between density-independent abiotic factors and density-dependent regulation feedbacks. In contrast, for all the five remaining species (*Nephtys ferruginea*, *Leitoscoloplos kerguelensis chilensis*, *Mediomastus branchiferus*, *Megalomma monoculata* and *Cossura chilensis*), the best model did not include any environmental variable, with pure density-dependent regulation being the supported mechanism. Interestingly, these are mostly subdominant species, with lower abundances. It is important to note that for these five species, the percentage of explained variance tended to be lower (31–53 %). This relatively high residual variance suggests that other environmental variables, different from those linked to temperature like SST or ENSO, could be important in determining the abundances of these species. An alternative may be that these species are immersed in more complex food webs than what is described by a simple AR(2) model, be it as a result of oxygen dynamics (Peña et al. 2005), or as a result of the variability of primary productivity. In this regard, it must be noted that empirical observations show that SST is negatively correlated to primary production in the study area (Daneri et al. 2000). If SST provides an adequate proxy for primary production, and primary production has a relevant role, then models testing the direct effects of summer temperature (hypothesis 3) would have provided a better fit to the observed time series, which was not the case. A conclusive test would require the use of a more direct proxy or measurement of primary production at the study area. Hence, future work may include efforts to obtain adequate time series estimates for primary production, such as remote sensing estimates of chlorophyll-a concentration. This would allow the examination of relative importance of local climate (SST and

productivity), regional climate (ENSO) and density dependence on polychaete population dynamics. Finally, we would like to highlight that our work shows how basic population dynamic theoretical models (Royama 1992; Berryman 1999; Turchin 2003) allow interesting insights to be gained on benthic population dynamics. Although this approach contrasts with traditional approaches, which focus on the importance of abiotic factors in structuring marine benthic systems, the results obtained demonstrate the importance of theoretical synthesis and time series analysis to understand long-term dynamics in benthic ecosystems.

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