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THE "IDIOSYNCRATIC" EFFECT OF A "SENTINEL" SPECIES ON CONTAMINATED ROCKY INTERTIDAL COMMUNITIES

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Abstract. Depending on their biological characteristics, some species can exert strong (idiosyncratic) effects on ecosystem process. Human impacts on biological communities are related to biodiversity declines but also with species shifts and replacements. In northern Chile, the occurrence of copper mine tailings in seawater is associated with a decrease in the number of sessile species and with rocky intertidal substrate monopolization by one sentinel species, the green ephemeral-opportunistic algae *Entermorpha compressa*. In spite of these changes, several consumer species persist on the contaminated sites. In this study, we test the hypothesis that changes in benthic species dominance and composition is associated with an increase in productivity, which affects intertidal consumer abundance, biomass, and/or diversity. We compare benthic species richness, composition, and productivity as well as the abundance, diversity, and diet of consumer species on contaminated and noncontaminated sites. Our results show that changes in community structure at contaminated sites are related to increased primary productivity, the absence of birds, increased abundance of reptiles and crustaceans, and larger body sizes and biomass of some intertidal fishes. The simplified organization of contaminated communities allowed us to demonstrate the importance of species composition in determining the relationship between species richness and productivity in marine systems. The special characteristics of dominance, persistence, and productivity of *Enteromorpha compressa* (the sentinel species on the contaminated sites) are a clear example of the idiosyncratic effect that some species could have in biological communities.

Key words: Chile; copper mine tailings; diversity; Enteromorpha compressa; *ephemeral algae; form–function models;* Microlophus atacamensis; *rocky intertidal; "sentinel" species; trophic webs.*

Introduction

The analysis of the relationship between species richness and productivity is a key topic of contemporary community ecology (Grace 1999, Waide et al. 1999, Loreau et al. 2001). Changes in species richness may produce increases and/or decreases in productivity (Abrams 1995, Rosenzweig 1995), but a considerable controversy concerning the general form of the relationship between both variables remains (Mittelbach et al. 2001). Three recent reviews (Grace 1999, Waide et al. 1999, Mittelbach et al. 2001) indicate that the topic has been addressed mainly in terrestrial and freshwater systems, neglecting marine ecosystems.

An important component of the controversy (Loreau et al. 2001) is the relative importance of community species composition for the maintenance of some ecosystem processes like productivity (Huston 1997). Several studies show that productivity changes rapidly as species representing new functional groups are added, but less rapidly when new species are redundant of existing functional groups (Walker 1992). In this context, Lawton (1994) proposed a model in which depending on their particular properties or functional traits, some species per se could have a strong "idiosyncratic" effect on ecosystem processes.

For the marine environment, functional-form models are important because they can serve as a background for the study of the productivity–diversity relationship. Based on the idea that the overall form and mineralization of algae could predict many aspects of its physiology and ecology, Littler and Littler (1980) proposed the first functional-form model. They categorized algae into form groups representing ranking for a wide variety of traits including photosynthetic rates, nutrient uptake rates, susceptibility to herbivores, physiological stress, and increasing competitive ability and succession stage. Later, Steneck and Watling (1982) and Steneck and Dethier (1994) defined different form groups, but maintained the characterization of functional physiological and ecological differences proposed by Littler and Littler (1980). In general, the models agree on two clearly defined and extreme groups. One group includes algae that have a relatively simple thallus form and a filamentous body, are opportunistic, rapid colonizers, ephemerals in time, with high calorific tissues, and with high rates of productivity, growth, and reproduction. The species in this group can escape predation through their temporal and spatial unpredictability (ephemer-

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als) or by means of rapid growth. The second group includes algae with structurally and functionally differentiated thallus form, are slow colonizers (usually late succession stages) with seasonal reproductive periods and low productivity. These species can reduce their palatability to predators by complex structural and chemical defenses. Padilla and Allen (2000) criticize these functional form models and showed that only the relationship between primary productivity and algal form has received support.

Based on the model of Lawton (1994), and functional-form models (Littler and Littler 1980, Steneck and Watling 1982), it is expected that productivity levels of benthic marine communities relate to their species composition and dominance but not solely to their species richness. For example, two benthic communities with similar species richness could differ greatly in primary productivity if they are composed of different functional groups. Specifically, a community dominated by ephemeral or opportunistic algae (referred as the first group above) will have a higher productivity than another dominated by kelps or crustose algae (referred as the second group above).

On the other hand, it is recognized that productivity at one trophic level (e.g., primary productivity) may affect the species richness and abundance of higher trophic levels (e.g., herbivores, carnivores) in the community (Mittelbach et al. 2001). Therefore, any change in the productivity of the primary producers, regardless of changes in species composition, will translate to an increase in the abundance and/or diversity of higher trophic levels (Yodzis 1984, Currie 1991). Until now, studies on the relationship between species richness and productivity have mostly focused on basal or primary producers species (Loreau et al. 2001), neglecting a more comprehensive analysis (i.e., multiple trophic level approach).

Human impacts on the environment often cause not only a general decline in diversity, but also predictable functional shifts as sets of species with particular traits are replaced by other sets with different traits (Grime et al. 2000, McCollin et al. 2000). Copper mining has historically been the most important economic activity in northern Chile. The major copper mines and deposits in this region are found on the western slopes of the Andes Mountains, but minor mines and some processing plants are located on the coast (Castilla 1983). As a consequence, several sites along the coast have been affected by the discharges of copper mine tailings for several (>40) years (Castilla and Nealler 1978, Castilla 1996, Correa et al. 1999, 2000, Fariña and Castilla 2001, Miethke et al 1992, Paskoff and Petiot 1990).

The occurrence of copper mine tailings in seawater may drastically change the composition and spatial distributions of rocky intertidal communities (Castilla and Correa 1997, Fariña 2000). One of the most dramatic changes reported has been a decrease in the number of sessile species and monopolization of the rocky substrate by the green ephemeral alga *Enteromorpha compressa* (Castilla and Nealler 1978). This observation motivated Castilla (1996) to propose that *E. compressa* could be considered a "sentinel" species for rocky intertidal communities affected by copper wastes. Recently, Fariña and Castilla (2001) demonstrated that the decrease in diversity is due to the loss of important groups of species like filter feeders (i.e., barnacles and bivalves) and red algae (both foliose and calcareous) and that these changes are permanent features of Chilean rocky shores impacted by copper pollution. Until now, no studies have analyzed how these changes in community structure could affect productivity of the benthic system.

Despite drastic changes in the rocky intertidal landscape, consumers, like birds, (*Cinclodes nigrofumosus*, Aves: Furnaridae), reptiles (*Microlophus atacamensis*, Reptilia: Iguanidae), crabs (*Leptograpsus variegattus*, Arthropoda: Grapsidae) and fishes (*Girella laevifrons*, Pisces: Girelidae) persist at the contaminated sites (Fariña 2000, Fariña et al. 2000). These are species with a wide representation in the coastal desert ecosystems of northern Chile (Mann 1960). The only available studies of these species are restricted to taxonomic discussions (Nuñez and Jaksic 1992, Ortiz 1980*a*, *b*) or to basic autoecological descriptions based on the central Chilean Coast (Muñoz and Ojeda 1998, Varas and Ojeda 1990).

Considering all the above-mentioned antecedents, we hypothesized that, in the copper-affected communities, the reduction of species richness and the substrate dominance by the ephemeral algae *E. compressa* must be associated with an increase in benthic primary production. This increase must translate to an increase on the intertidal consumer abundance and/or diversity. We tested this hypothesis by comparing species richness, species composition, and productivity rates of sites impacted and nonimpacted by copper mine wastes and by comparing the patterns of abundance, diversity, and diet of consumers in these communities.

Methods

Study sites

The study was carried out on the rocky intertidal shores of four sites located close to Taltal city (25°25′45″ S, 70°34′25″ W) on the northern Chilean coast: Enami, Las Conchas, Bandurrias, and Santo Domingo (Fig. 1). Since the 1960s, both Enami and Santo Domingo sites have been affected by discharges of copper mine tailings derived from processing plants located next to the shore. At Enami, the effluents are discharged southward and have formed a tailing bed of ~2 km in length, along the southern side of the sampling site. At Santo Domingo, the waste discharges move northward and have formed a tailing bed of ~10 km in length on the northern side of the sampling site. Las Conchas and Bandurrias, located about 15 km north

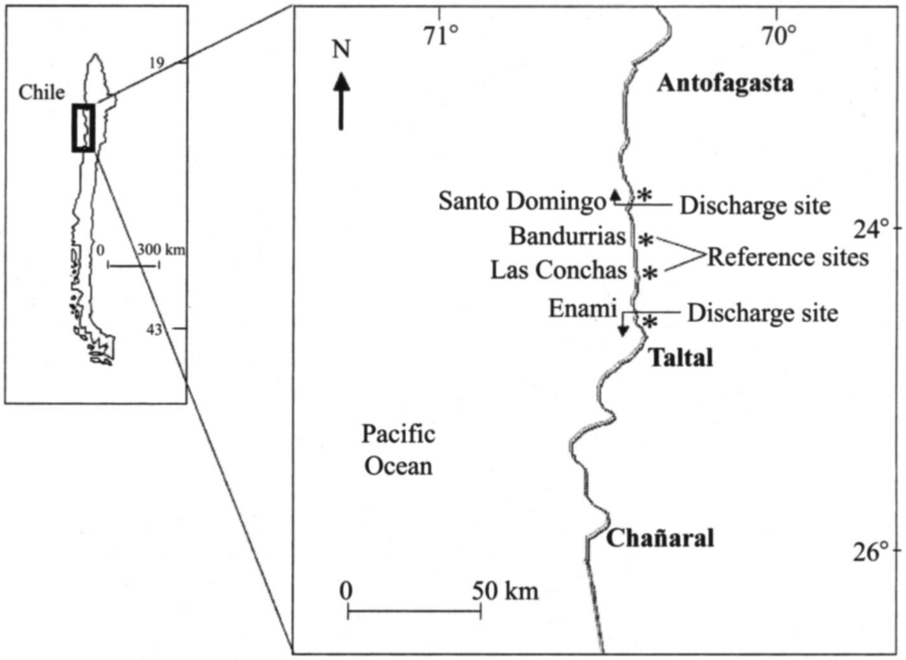

FIG. 1. Location of the discharge, reference sampled (*), and previously studied (Fariña and Castilla 2001) sites.

of Enami and 19 km south of Santo Domingo, respectively, were considered to be noncontaminated sites, and used as control sites.

During 1997 and 1998, Fariña and Castilla (2001) analyzed the levels of trace metals (Cu, Zn, and Cd), and fine-ground wastes (measured as particulate inorganic matter, PIM) in the seawater of the four study sites. Their results showed that copper and fine-ground wastes were the most important contaminants in the seawater of the contaminated sites. These two pollutants were practically absent in the nonaffected sites and this pattern did not change during the study period.

Benthic organisms

Sampling design.—Two benches at each of the four study sites were sampled every two months (i.e., six times) between July of 1997 and May of 1998. The benches were composed of a continuous rocky surface similar in size (±10 m wide × 10 m along the coastline), slope (±0.5 m/m), and exposure to wave action (exposed). Hereafter, each bench is named in relation to its site: Enami (E1 and E2), Las Conchas (LC1 and LC2), Bandurrias (B1 and B2), and Santo Domingo (SD1 and SD2). On each sampling date, 10 fixed plots (0.25 × 0.25 m) were placed along each of three lines between the high and low intertidal levels (parallel to the shore). All the plots along the transects were separated by 75 cm and the lines were separated by ~2 m. The high intertidal level was determined considering the distance between the water level at low tide and the zone in which the surface stand dry, under low and high tides. This level only receives water during the highest tides of the year. The low intertidal level was determined by considering the distance between the water level during low tide conditions and the belt of the intertidal kelp *Lessonia nigrescens* living at the noncontaminated sites (Santelices 1991). This same distance was considered to determine the low intertidal level at the contaminated sites.

Each plot was divided into a grid of 100 equally spaced intersection points. Sessile algae or filter feeding species occurring underneath each point were identified to the lowest possible taxonomic level. Total cover of each species in the plot was obtained directly by the sum of their intersection points (Castilla 1988). Small mobile invertebrates (i.e., <2 cm) occurring in each plot were also identified to the lowest possible taxonomic level.

Previous studies indicated little temporal variation in species richness and abundance of intertidal species at these sites (Fariña and Castilla 2001). Therefore, in this study, the data were averaged over the six sampling dates.

Diversity patterns of mobile invertebrate assemblages occurring on each bench were analyzed for species richness (S) and abundance (number of individuals per plot).

Species representation.—In biological communities, high-represented species show two main characteristics: an important spatial representation and a high persistence or temporal representation. In this study, we define representation as a function of cover (in the case of sessile species) or abundance (in the case of mobile species) and temporal incidence. This strategy allows us to recognize four different categories of species:

1) Highly represented species with high (statistically significant) cover or abundance and temporal incidence;

2) Dominant but ephemeral species with a high (statistically significant) cover or abundance, but reduced (not statistically significant) temporal incidence;

3) Persistent but rare species with a high (statistically significant) temporal incidence, but at reduced (not statistically significant) cover or abundance; and

4) Ephemeral and rare species with a low temporal incidence and with reduced cover or abundance (not statistically significant for both variables).

To recognize these groups, the mean percent cover (or mean abundance) and the incidence (mean number of plots in which each species occurred during the different sampling dates) were calculated. The significance limits (at $\alpha < 0.05$) for each variable (i.e., cover and incidence) were calculated from the frequency distribution of the means generated using a bootstrap procedure, in which the matrix containing the original values of both variables was randomly re-sampled 1000 times, without replacement (Manly 1991).

Productivity and production levels

The levels of productivity and production were studied on the rocky intertidal shores of a representative contaminated site (Santo Domingo) and noncontaminated site (Bandurrias).

Following the methods of Bustamante (Bustamante et al. 1995, Bustamante and Branch 1996), the epilithic algal productivity was measured through the assessment of the chlorophyll *a* concentrations on experimental plates maintained for different periods of time on the rocky intertidal substrates of Bandurrias and Santo Domingo.

During June of 1999, 48 acrylic sanded plates of 10 × 10 cm were randomly installed on the midintertidal levels of each site. The plates were anchored to the substrate by stainless steel screws and surrounded with a fence painted with anti-fouling to exclude trailing grazers (Robles and Cubit 1981). Every month, from July to December, eight plates were retrieved from each site. In this way, six sets with a permanence time of 1, 2, 3, 4, 5, and 6 mo were completed. Collected plates were maintained in dark conditions, frozen, and transported to the laboratory. Under dark conditions, in the laboratory, each plate was submerged for 3 min in 40 mL of methanol at 65°C. The solvent was cooled and centrifuged for 7 min at 98.97 m/s, and an aliquot of 1 mL was taken. The absorbance associated with the concentration of chlorophyll *a* in each aliquot was measured in a spectrophotometer (Shimadzu UV-1201vm, Shimadzu, Kyoto, Japan), recording the values in each case at 665 and 750 nm. Chlorophyll contents are presented as concentration per surface area ($\mu g/cm^2$). Productivity was calculated as the concentration of chlorophyll by surface area and duration of the plates in the intertidal (μg chlorophyll$\cdot cm^{-2}\cdot mo^{-1}$).

The levels of production (biomass) of the organisms occurring on the midintertidal level of each site were also assessed. To accomplish this, eight permanent plots of 20 × 25 cm were randomly selected on the rocky substrate during July 1999. Each plot was completely cleared, with steel brushes and gas torches, and surrounded with a fence painted with antifouling to exclude the trailing grazers. Every month, from August to December of 1999, newly settled sessile and mobile organisms were collected from the plots and identified to the lowest possible taxonomic unit. The biomass of each taxon occurring in the plots was also determined (dry mass).

Consumer species

Patterns of abundance, activity, and diet of intertidal consumers were studied on the rocky intertidal shores of Santo Domingo (contaminated site) and Bandurrias (noncontaminated site). Consumers comprised four major groups (birds, reptiles, crustaceans, and fishes).

Birds.—

1. *Species richness and abundance.*—Species richness (S) and abundance (number of individuals) of bird species occurring along the intertidal shores of both sites were recorded by visual surveys conducted during diurnal low tides. To accomplish this, an area of 5000 m^2 (±50 m wide × 100 m along the coastline), consisting of zones of continuous (benches) and discontinuous (boulders) substrate was visually inspected from 0900 to 1800 hours for seven days in February, April, June, August, October, and December of 1998. Bird observations were done from a fixed and elevated point (i.e., 10 m above the sea level) using binoculars (12 × 50 mm). The observation point at each site was 100 m landward of the highest tidal level.

In order to identify the most representative bird species in the assemblage, the abundance and temporal incidence of each species were analyzed. To do this, the mean percent abundance was plotted against the mean number of dates in which each species was registered, during the 84 days of observations. The species with significantly highest abundance and/or temporal incidence were characterized as representatives following the same criteria used for the sessile and mobile intertidal species. The significance level ($\alpha < 0.05$) was calculated from the frequency distributions of the means generated by the use of "bootstrap" techniques, in which the matrix containing the original data of both variables was resampled 1000 times.

2. *Activity patterns and diet.*—For each surveyed day, in the period of 2 h before and 2 h after the lowest tide level, the activity and foraging times of birds occurring on the rocky shores of each site were recorded. The permanence time of each species on the intertidal rocky shore was considered for activity patterns while for foraging patterns, both prey manipulation and consumption times were considered.

Bird diets were determined qualitatively, by direct observation of prey consumption (i.e., echinoderms, gastropods, and crustaceans) or by recording the movements associated with the consumption of particular small prey (e.g., frontal or lateral pecking for amphipods and barnacles respectively; M. C. Espoz, *personal observation*). This kind of analysis allowed us to differentiate how the birds used the intertidal zone, either as a resting place or for foraging activities (Cornelius et al. 2001).

Reptiles.—

1. *Abundance and activity patterns.*—The patterns of abundance and activity of lizards (*Microlophus atacamensis*) occurring in the intertidal zone of each site were assessed by visual censuses conducted every four months during 1999. Considering the ectothermic nature of *M. atacamensis*, the survey schedule included months with mid (April), low (August), and high (December) environmental temperatures. Each month, four days with diurnal low tides occurring close to noon were selected. For each day, walking surveys of 1 h were done at 0900, 1100, 1300, 1500, and 1700 hours. For each survey, a different area of ~100 m^2 (±4 m wide × 25 m along the coastline) between the high and low intertidal levels was covered, recording in each case the number of individuals on the rocks and their position in the intertidal (i.e., the levels at which the individuals were observed). At the beginning of each survey, the temperature and solar radiation incidence on the rocky surface were recorded, using an infrared radiometer (with a resolution of 2 cm/m between the target and the observer).

In order to accurately characterize lizard abundance patterns at both sites, it was necessary to consider the hours of daylight and temperatures in which individuals are active in the intertidal areas. Daily activity patterns were assessed by determining the relationship between the number of lizards and substrate temperature registered on each survey (i.e., each hour).

2. *Body sizes and diet.*—After each survey at both sites, individuals of *M. atacamensis* in intertidal areas were caught using air-compressed guns. The captured individuals were sexed, weighed (TW = total weight of the individual in grams), measured (SVL = snout–vent length in centimeters), and their digestive tracts were extracted.

Dietary composition was characterized by analyzing the contents of the digestive tracts. Prey taxa were identified to the lowest possible taxonomic unit. The minimum number of digestive tracts needed for a reliable analysis was calculated using the rarefaction curve of the taxa occurring in each analyzed tract. The curve was drawn following the agglomeration of taxa generated by resampling the original data matrix randomized 1000 times (using EstimateS, Colwell and Coddington 1994). This analysis showed that the minimum number of tracts was 10 for Santo Domingo and 18 for Bandurrias, so it was necessary to pool all the individuals captured during the entire study period at each site.

Crustaceans.—

1. *Abundance and activity.*—Abundance and activity patterns of the crab *Leptograpsus variegattus* occurring in Bandurrias and Santo Domingo were studied during January, April, and December of 1999. Considering the nocturnal activity of many land crabs species, visual censuses were conducted at diurnal and nocturnal low tides during two days in each month. Due to this, the survey schedule was restricted to the occurrence of both nocturnal and diurnal low tides on the same day. Six randomly chosen areas of 500 m^2 (±5 m wide × 100 m along the coastline) located between high and low intertidal levels were covered walking for 5 min. In these areas, the number of active individuals was recorded. Walking surveys tend to underestimate crustacean abundances because some individuals will not be exposed at low tide. The number of unexposed individuals also varies depending on intersite differences in substrates, therefore further biasing counts. In our case, the substrate characteristics of the surveyed sites were similar so we assumed the same level of underestimation for both.

2. *Body sizes and diet.*—After each visual survey, individuals of *L. variegattus* were caught on each site. The captured individuals were sexed, weighed (TW = total weight of the individual), measured (TCTL = total cephalothorax length in centimeters), and their digestive tracts, from the cardial stomach to the final telson segment, were extracted.

Body size–biomass relationship and dietary compositions were analyzed and compared by the same procedures explained in the reptile's body sizes and diet section. In this case, the minimum number of digestive tracts was 18 and 24 for Santo Domingo and Bandurrias, respectively. Therefore, the data for the dietary analysis was pooled between the different study dates.

Fishes.—

1. *Abundance.*—Several censuses of the fishes occurring in 24 intertidal pools, of similar volume (5 ± 0.5 m^3) and situated in high, mid, and low intertidal levels (six pools on each level) at each site, were made during September, October, and December of 1998. For each pool census, we used video cameras (to minimize interference by observers). The maximum number of individuals recorded in 60 min was assessed. These censuses were done during low daily tides and only one fish species, *Girella laevifrons*, was observed in the pools.

2. *Body sizes and diet.*—All fish occurring in three low intertidal pools at each site were collected in September, October, and December of 1998. During those months, the recruitment of *G. laevifrons* occurs, so it

is possible to observe higher abundance and wider body-size ranges for this species (Varas and Ojeda 1990). Fish were captured using the ichthyocide rotenone on pools of similar volume (5 ± 0.5 m^2) and location (low intertidal levels).

Because the sample was taken within the same season (summer), the captured individuals during the three dates of sampling were pooled. In this case, the minimum number of digestive tracts defined by rarefaction curves was 29 and 30 for Santo Domingo and Bandurrias respectively, so data for the dietary analysis was also pooled.

Statistical analysis

The spatial pattern of sessile species richness was analyzed using a geostatistical approach (Rossi et al. 1992, Rodriguez and Fariña 2001). As in Smith and Witman (1999), contour maps were plotted by kriging interpolation techniques (Spyglass Transform, version 3.0, Spyglass, Savoy, Illinois, USA), using the mean values for richness from the 30 fixed plots distributed a the grid of 10 × 10 m covering the study area of each bench. Kriging is a geostatistical tool in which, from a defined spatial grid with observed values, it is possible to predict (interpolate) nonobserved values for a determined variable (Cressie 1991). The interpolation function was checked by analyzing the variance homogeneity of the data in the interpolated matrix (Robertson 1987). To do this, the spatial pattern of variances was also plotted on a contour map. For each case (i.e., bench) there were no significant differences in the spatial dispersion of interpolated variance.

The mean species richness and percent cover of sessile and mobile species were compared using two-way analysis of variance (ANOVA) models (Winer 1971). The factors were, site (four levels) and bench (two levels nested within sites). Site and benches were considered random factors because no a priori hypotheses about them were stated and their levels represented one of the several potential combinations over which the study could be done (Underwood 1997). After each ANOVA, a Tukey (hsd) multiple-comparisons test (for single factors) and paired comparisons (for interactions) were performed to determine which means were significantly different (Day and Quinn 1989). Normality of the data was checked by graphical procedures, and when appropriate (i.e., for cover or abundance), the data were transformed (i.e., arcsine square root and $\log(x + 1)$, for cover and abundance, respectively). Results are reported using the original (i.e., nontransformed) variable. Homogeneity of variances and independence of the data were verified using Levenes and Durbing-Watson tests, respectively (Wilkinson et al. 1996). The same criteria for factor categorization, assumptions checking, data transformations, and post hoc tests were used in all the ANOVA models referred to hereafter.

The rate of chlorophyll accumulation was compared by analysis of covariance (ANCOVA) with site (categorical with two levels) and time (continuous) as factors. The model was applied to the relationship between permanence time vs. chlorophyll concentration of the plates. In the model, the interaction between both factors was used to check the assumption of homogeneity of slopes. Prior to the analysis, the covariate (time) was standardized by it own mean to preserve the Fisher squares ratio of the main effect in the model (Huitema 1980).

Productivity rates were contrasted using a two-way mixed ANOVA model, with the factors of site (fixed with two levels) and permanence time (random with six levels). Site was considered fixed because it also represents the situation of contamination to be contrasted. Bandurrias is a noncontaminated site and Santo Domingo is contaminated. Permanence time was considered random because the levels of this factor corresponded to one of the multiple possible arrangements we could use.

The pattern of differences in the collected biomass was also analyzed using a random two-way mixed ANOVA model, considering site (two levels) and date (five levels) as main factors.

One-way random ANOVA models were used to analyze patterns of bird species richness and abundance. The same models were used to analyze the abundance patterns of reptiles, crustaceans, and fishes.

Body sizes and biomass patterns of the captured reptiles, crustaceans, and fishes were analyzed using random one-way ANOVA models, with site as a fixed factor. To preserve the assumption of this kind of model, both variables were transformed ($\log[x + 1]$). The relationship between body sizes and biomass of these consumers was analyzed applying a Pearson parametric correlation test (Zar 1997) on the transformed data ($\ln[x]$). The differences in the slopes of the relationship observed for the individuals from both sites were analyzed using an analysis of covariance model (ANCOVA).

The dietary composition of reptiles, crustaceans, and fishes captured on each site were compared applying the Kendall nonparametric coefficient of concordance (τ) on the values of their prey taxa frequency of occurrences. This coefficient indicates the level of association between the rankings of two or more variables, with a null hypothesis of no association (Siegel and Castellan 1988).

RESULTS

Benthic organisms

A total of 32 taxa were identified in the 1440 sampled plots (Table 1). Fewer taxa occurred in the contaminated sites (10 and eight species for Enami and Santo Domingo, respectively) than on the noncontaminated ones (26 and 29 for Las Conchas and Bandurrias, respectively). In the case of algae, only eight and six species occurred in Enami and Santo Domingo, respectively, while in Las Conchas and Bandurrias, 18 species were recorded. Differences in the number of species between contaminated and noncontaminated sites were most evident for filter feeder species. In both Enami and Santo Domingo, only two species were recorded with a cover of <1%, while in Las Conchas and Bandurrias, this group was composed of eight and 11 species, respectively. In terms of cover, in the contaminated sites the substrate was dominated by the green ephemeral alga *Enteromorpha compressa*, with mean cover around 55–65%. In the noncontaminated sites, several species of green and red algae (e.g., *Ulva lactuca*, *Ectocarpus confervoides*, *Gelidium chilense*, *Hildenbrandtia lecannellieri*) and barnacles (*Jehlius cirratus* and *Notochatamalus scabrosus*) shared the substrate with mean species cover around 10–30%.

Different levels of mean species richness were observed on the benches of the contaminated and noncontaminated sites (Fig. 2). The lowest values occurred in Enami (S = 1.41 ± 0.08 [mean ± 1 SE] and S =1.15 ± 0.02 for E1 and E2, respectively) and in Santo Domingo (S = 1.85 ± 0.12 [mean ± 1 SE] and S = 2.37 ± 0.12 for SD1 and SD2, respectively). Similar high values were observed in Las Conchas (S = 5.49 ± 0.37 [mean ± 1 SE] and S = 6.32 ± 0.28 for LC1 and LC2, respectively) and Bandurrias (S = 6.28 ± 0.45 [mean ± 1 SE] and S = 6.37 ± 0.35 for B1 and B2, respectively). Sessile species richness patterns (S) showed significant differences between sites but not between benches (Table 2). Between sites, the order of significant differences (all Tukey hsd, $P < 0.001$) was Bandurrias (6.32 ± 0.28 [mean ± 1 SE]) and Las Conchas (5.91 ± 0.24 [mean ± 1 SE]) > Santo Domingo (2.11 ± 0.08 [mean ± 1 SD]) and Enami (1.29 ± 0.04 [mean ± 1 SD]).

Cover of sessile species showed differences between sites and between benches (Table 2). Between sites, the order of significant differences was Las Conchas (85.06 ± 2.5 [mean ± 1 SE]) and Bandurrias (84.13 ± 2.2 [mean ± 1 SE]) > Santo Domingo (75.18 ± 1.8 [mean ± 1 SE]) and Enami (69.62 ± 1.61 [mean ± 1 SD]). For Benches, there were significant differences within Las Conchas (LC2 > LC1) and Santo Domingo (SD2 > SD1).

A total of 29 taxa of small mobile organisms were recorded at the study sites. Similar to the case of sessile species, the lowest numbers of mobile species occurred on the benches of Enami (3 and 1 for E1 and E2, respectively) and Santo Domingo (8 and 7 for SD1 and SD2, respectively). Similar and highest values were observed in Las Conchas (19 and 20 for LC1 and LC2, respectively) and Bandurrias (20 and 18 for B1 and B2, respectively).

Mobile species richness showed significant differences between sites and benches (Table 2). Between sites, the sequence of significant differences was Bandurrias (1.98 ± 0.06 [mean ± 1 SE]) and Las Conchas (1.79 ± 0.09 [mean ± 1 SE]) > Santo Domingo (0.75 ± 0.05 [mean ± 1 SE]) and Enami (0.5 ± 0.03). For benches, there were significant differences only within the noncontaminated sites (LC2 > LC1 and B2 > B1).

The abundance of mobile species showed differences between sites and benches (Table 2). At the level of sites, there were differences between the contaminated and noncontaminated sites, but not within them. There were no significant differences between Enami and Santo Domingo (3.35 ± 0.46 [mean ± 1 SE] and 5.02 ± 1.5 for Enami and Santo Domingo, respectively), as well as between Las Conchas and Bandurrias (30.17 ± 4.42 [mean ± 1 SE] and 27.90 ± 3.81 for Las Conchas and Bandurrias, respectively). At the level of benches, only Bandurrias showed significant differences (B1 > B2).

Species representation

Important differences in the patterns of sessile species composition were observed between the contaminated and noncontaminated sites. In the contaminated sites (Enami and Santo Domingo), *Enteromorpha compressa* and bare rock had the highest significant representation, occurring in almost all plots (i.e., mean incidence around 30 plots) and at high cover. In all the benches, the mean cover of this alga was always higher than 55%, whereas bare rock ranged around 25%. In Santo Domingo, two other algae were persistent but rare: *Hildenbrandtia lecannellieri* and *Ralfsia expansa*. In the case of noncontaminated sites, in Las Conchas, *Ulva lactuca* was the species with highest representation, with covers around 25–30% and a mean incidence of 25–27 plots. At this site, bare rock and two alga species (*Hildenbrandtia lecannellieri* and *Ectocarpus confervoides*) were persistent (with incidences around 25 plots) but rare (with covers <20%).

In Bandurrias, *Ulva lactuca*, *Gelidium chilense*, *Hildenbrandtia lecannellieri*, and bare rock were the most common, with mean cover around 25% and mean incidences between 20 and 25 plots. At this site, the alga *Ectocarpus confervoides* and the barnacle *Jehlius cirratus* were dominant but ephemeral (with a mean incidence around 15 plots) but had significantly high covers (with mean cover above 25%).

In the case of mobile species, there were also important differences on their representation at contaminated and noncontaminated sites. In both Enami and Santo Domingo (contaminated sites) the taxa with higher abundance (around five individuals per plot) and incidence (around 15 to 20 plots) was Diptera (flies). At these sites there were no other mobile species with high incidence or abundance.

In Las Conchas and Bandurrias (noncontaminated sites), the gastropod *Nodilittorina peruviana* showed the highest representation with mean abundance ∼20–25 individuals per plot and incidences ∼5–10 plots. At both sites, amphipods were persistent but rare, with

TABLE 1. Percent cover of sessile species occurring on each bench of the contaminated (Enami [E1 and E2] and Santo Domingo [SD1 and SD2]) and noncontaminated (Las Conchas [LC1 and LC2] and Bandurrias [B1 and B2]) sites.

Species	E1	E2	LC1	LC2	B1
Bare rock	30.3 (13.3)	31.4 (11.8)	37.5 (21.5)	12.7 (3.3)	18.6 (8.1)
Algae					
Enteromorpha compressa	63.4 (21.4)	68.3 (11.7)		6.9 (15.4)	
Enteromorpha prolifera	11.4 (28.0)			0.3 (0.8)	
Ulva lactuca			25.2 (4.4)	34.6 (10.8)	17.4 (8.0)
Chaetomorpha linum				0.9 (1.6)	1.9 (1.2)
Ectocarpus confervoides	19.2 (29.9)	0.2 (0.4)	21.0 (5.3)	14.9 (5.6)	25.3 (10.3)
Ralfsia expansa	2.2 (2.7)	0.5 (1.2)	3.4 (2.8)	0.5 (0.9)	1.8 (2.2)
Colpomenia phaeodactyla	0.2 (0.4)		4.4 (1.3)	2.1 (0.7)	2.8 (1.6)
Colpomenia sinuosa			2.3 (1.9)	2.5 (1.0)	2.5 (1.1)
Petalonia fascia			6.2 (5.0)	6.3 (4.8)	7.3 (2.2)
Scytosiphon lomentaria	0.4 (0.7)				0.3 (0.8)
Glosophora kunthii			2.1 (1.5)	0.2 (0.4)	9.9 (2.9)
Polysiphonia paniculata	0.5 (1.1)				
Porphyra columbina			2.3 (4.3)	0.2 (0.4)	6.0 (8.2)
Gelidium chilense			15.9 (3.3)	9.2 (3.1)	30.6 (8.2)
Gelidium lingulatum			1.1 (2.7)	2.1 (3.5)	2.5 (3.3)
Corallina officinalis			17.5 (3.3)	8.8 (2.8)	6.5 (2.8)
Ceramium rubrum			3.5 (4.8)	16.4 (15.6)	3.6 (3.2)
Hildenbrandtia lecannellieri	2.4 (4.9)	0.5 (1.3)	13.2 (3.3)	9.4 (2.2)	10.1 (2.6)
Crustosa–Calcarea			8.8 (4.7)	15.6 (6.1)	2.1 (2.1)
Diatoms			11.3 (7.4)	29.0 (8.1)	12.1 (5.3)
Filter feeders					
Anthothoe chilensis			0.2 (0.4)		0.8 (1.4)
Phymactis clematis			1.1 (0.9)	2.0 (1.0)	1.9 (2.7)
Ascidia, colonial				3.2 (2.3)	
Sabellaridae					2.7 (1.6)
Nothochatamalus scabrosus			3.0 (1.9)	9.2 (3.2)	8.0 (2.4)
Jehlius cirratus			8.3 (3.0)	9.2 (4.3)	32.2 (19.7)
Balanus laevis					0.6 (0.7)
Austromegabalanus psittacus	0.6 (0.9)	0.5 (1.1)	0.3 (0.5)		
Semimytilus algosus			0.2 (0.4)		2.2 (4.3)
Perumytilus purpuratus	0.5 (0.8)	0.5 (0.8)		0.2 (0.4)	1.1 (0.2)
Pyura chilensis					

Note: Values are mean percent cover, with 1 SD in parentheses.

significantly high incidences (with means ~10–20 plots) but nonsignificant abundance (with means around three to four individuals per plot). In Bandurrias, other persistent but rare species were the gastropod *Prisogaster niger* and the starfish *Heliaster helianthus*.

Productivity and production levels

In Bandurrias (noncontaminated) and Santo Domingo (contaminated), chlorophyll *a* concentrations increased in relation to the amount of time that the plates remained in the intertidal (Fig. 3A). As the nonsignificant interaction between site and time factors of the ANCOVA model show (Table 2), the slope of the regression lines was the same for both sites. However, as the main significant effect of the model show, the concentrations of chlorophyll *a* were always higher at Santo Domingo (5.36 ± 0.35 [mean ± 1 SE] $\mu g/cm^2$) than at Bandurrias (4.2 ± 0.32 $\mu g/cm^2$).

In terms of productivity (Fig. 3B), there were marginal differences between sites, but significant differences in time and in the interaction between these two factors. For this interaction the rates, except for the period of 120 d, were higher at Santo Domingo (~1.66 ± 0.05 [mean ± 1 SE] μg chlorophyll$\cdot cm^{-2}\cdot mo^{-1}$) than Bandurrias (around 1.16 ± 0.07 SE μg chlorophyll$\cdot cm^{-2}\cdot mo^{-1}$). These differences in productivity are in concordance with the levels of production (biomass) of the experimental plots.

The mean biomass of the community removed from the experimental plots (Fig. 3C) showed significant differences (Table 2) between sites and dates, but not for the interaction between both factors. At the level of sites, mean biomass was significantly higher at the contaminated site (S. Domingo, with a mean of 16.1 ± 0.8 [1 SE] g/mo) than the noncontaminated site (Bandurrias, with a mean of 9.22 ± 0.6 g/mo). At the level of dates, the highest levels occurred during August (15.06 ± 1.7 g/mo) and October (14.21 ± 1.5 g/mo). These values were significantly higher than the ones for September (11.26 ± 1.2 g/mo) and December (10.78 ± 0.9 g/mo). In terms of species composition, six algae and one barnacle species were recorded in the Bandurrias plots, whereas only *Enteromorpha compressa* occurred in the Santo Domingo plots. The most important species occurring in Bandurrias were the green algae *Ulva lactuca* (73% of the total removed biomass) and the barnacle *Jehlius cirratus* (18% of the total removed biomass). Other species occurring in this site

TABLE 1. Extended.

B2	SD1	SD2
26.3 (9.3)	31.9 (11.2)	23.1 (4.9)
0.4 (1.0)	54.5 (11.2)	58.2 (8.8)
15.0 (7.3)	0.2 (0.4)	0.2 (0.4)
2.8 (3.0)		
23.7 (11.6)		7.9 (8.3)
1.3 (3.1)	5.3 (6.9)	19.9 (17.7)
2.2 (2.0)		
2.8 (1.8)		
10.9 (3.5)		
		1.5 (2.0)
3.5 (1.6)		
5.2 (6.4)		
30.6 (21.1)		
1.1 (1.7)		
3.5 (1.1)		
9.7 (9.7)		
16.9 (5.9)	22.4 (12.1)	15.0 (6.3)
7.5 (3.6)		
21.7 (11.6)		
0.2 (0.4)		
1.8 (0.5)	0.8 (0.8)	
0.6 (1.0)		
0.2 (0.4)		
8.8 (2.6)		
29.7 (19.3)		
1.3 (1.2)		
1.2 (1.1)		
0.6 (1.5)		0.2 (0.4)
0.2 (0.4)		

in the range of 10% of the removed biomass were *Ectocarpus confervoides*, *Porphyra columbina*, *Colpomenia sinuosa*, and *Petalonia fascia*.

In summary, contaminated sites had a significantly lower richness of sessile and mobile species than did the noncontaminated sites. The contaminated sites were dominated almost entirely by the opportunistic-ephemeral alga *Enteromorpha compressa* and Dipteran flies. In the noncontaminated sites, the substrate is shared by several species of green and red algae and by some filter feeders such as barnacles. At these sites several species of small mollusks (gastropods) and small crustaceans (amphipods) occurred at high abundance and/or had high temporal incidence. A detailed analysis of a representative contaminated and a non-contaminated site showed that the differences in species richness and composition were related to productivity levels. These levels were always higher on the contaminated sites.

Consumer species

Birds.—

1. *Diversity and dominance.*—During the 35 days of observations, a total of 20 bird species were identified in the intertidal shores of both sites (Table 3). More species were observed at Bandurrias (20 species) than at Santo Domingo (seven species).

The mean number and abundance of bird species showed significant differences between sites ($F_{1,82}$ = 178.88, $P < 0.0001$ and $F_{1,82}$ = 187.62, $P < 0.0001$ for species number and abundance, respectively). Throughout the study, Bandurrias showed a significantly higher mean number of species and abundance (11.66 ± 0.5 [mean ± 1 SE] species per day and 33.91 ± 2.8 individuals per day) than Santo Domingo (4.0 ± 0.18 species per day and 10.72 ± 0.35 SE individuals per day).

The species with highest representation (i.e., with significant high abundance and temporal incidences) at both sites were *Cinclodes nigrofumosus* (Seaside Cinclodes) and *Cathartes aura* (Turkey Vulture). At both sites, two species were persistent but rare: *Phalacrocorax olivaceus* (Olivaceous Cormorant) and *Larus dominicanus* (Kelp Gull). In this last category, there were differences between both sites. At Bandurrias it was also comprised by *Pelacanus thagus* (Peruvian Pelican), *Nycticorax nycticorax* (Black-Crowned Night-Heron), *Haematopus ater* (Blackish Oystercatcher), and *Numenius phaeophus* (Whimbrel), whereas in Santo Domingo, it was comprised of *Larus modestus* (Garuma Gull) and *Muscisaxicola macloviana* (Dark-Faced Ground-Tyrant).

2. *Activity pattern and diets.*—Not all the bird species recorded at both sites consumed intertidal prey. Only five species at Bandurrias and two species at Santo Domingo were observed feeding in the intertidal. Of these, *Haematopus ater* and *Numenius phaeophus* were the ones with the widest diet (six and five prey taxa, respectively) and they only occurred at Bandurrias. *Nycticorax nycticorax* was observed at both sites but only consumed intertidal prey at Bandurrias. *Larus dominicanus*, *Cinclodes nigrofumosus*, and *Muscisaxicola macloviana* were observed consuming intertidal prey at both sites. Of this group, only *L. dominicanus* showed important differences in dietary composition between the two sites. At Bandurrias, this species consumed echinoderms, gastropods, and fishes, whereas in Santo Domingo, it only consumed fishes (Table 4).

Reptiles.—

1. *Abundance and activity patterns.*—During April and December at both sites, maximum substrate temperatures were ~40°C while in August, they barely exceeded 25°C. Daily substrate temperature reached maximum values between 1300 and 1400 hours. The temporal window of temperatures above 25°C was wider during April and December (around 6 h between 1000 and 1600 hours) than during August (just 1 h around noon).

Lizard activity patterns were tightly associated with variation in substrate temperatures. More active individuals were observed during April and December and during the hours with highest substrate temperatures

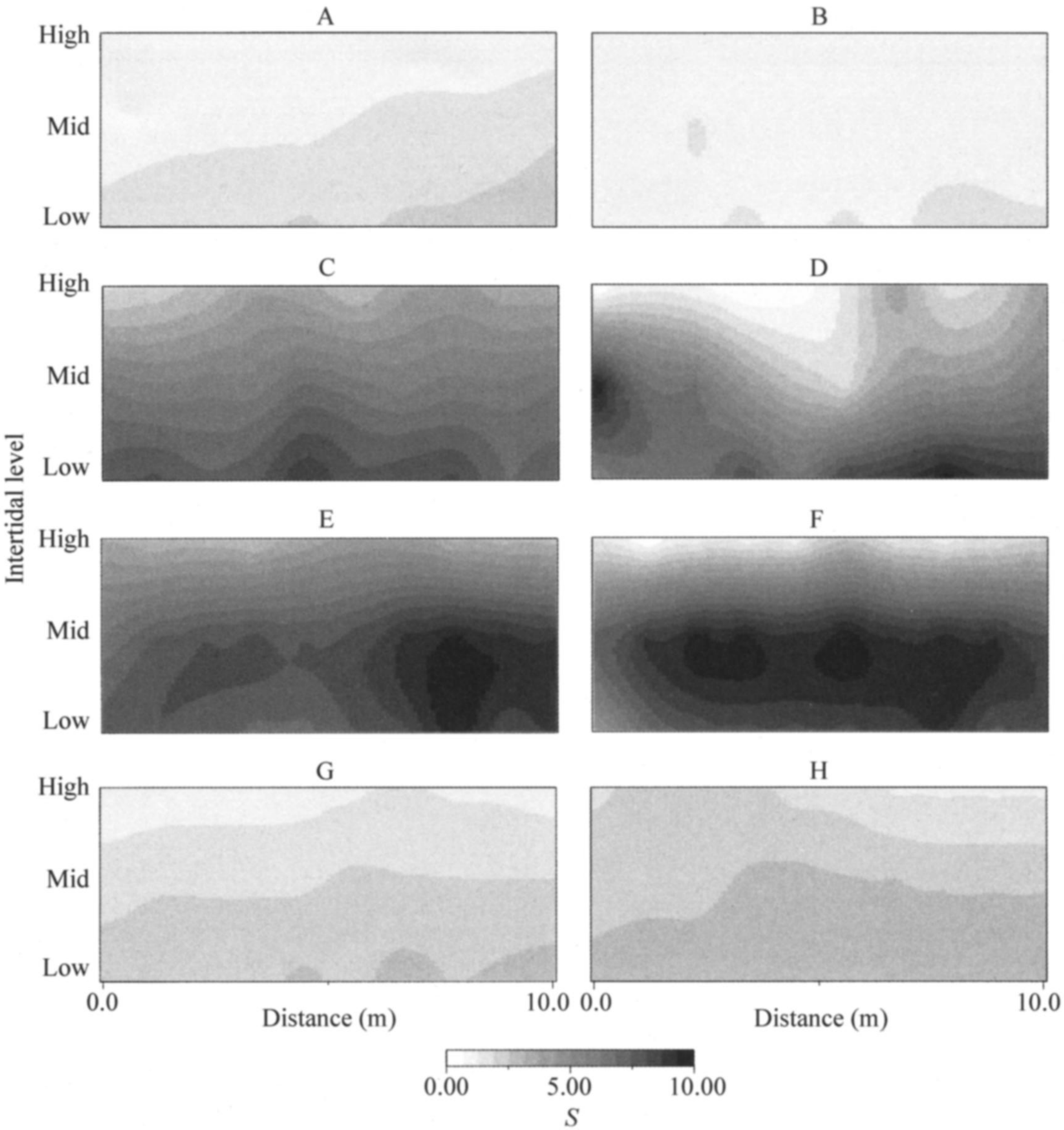

FIG. 2. Contour maps showing the spatial distribution of the sessile species richness (S) on the benches: (A) Enami (E1), (B) Enami (E2), (C) Las Conchas (LC1), (D) Las Conchas (LC2), (E) Bandurrias (B1), (F) Bandurrias (B2), (G) Santo Domingo (SD1), (H) Santo Domingo (SD2).

each month. No individuals were observed during hours at which surface temperatures were below 25°C.

Abundance patterns recorded when substrate temperature was above 25°C showed differences between sites ($F_{1,340}$ = 104.19, $P < 0.0001$). The number of individuals observed in Santo Domingo (3.6 individuals/10 min ± 0.1 [mean ± 1 SE]) was significantly major ($P_{HSD} < 0.0001$) than the one observed in Bandurrias (1.9 individuals/10 min ± 0.1).

2. *Body sizes and diet*.—A total of 53 individuals of *M. atacamensis* were caught at both sites (22 in Bandurrias and 31 in Santo Domingo). The mean body sizes and biomass of lizards showed nonsignificant differences between sites ($F_{1,53} = 0.02$, $P = 0.90$ and $F_{1,53} = 0.59$, $P = 0.46$ for body sizes and biomass, respectively). The slopes of the relationship between these variables (a = 3.29 and a = 3.05 for Bandurrias and Santo Domingo, respectively) did not differ (ANCOVA, $F_{1,51} = 0.41$, $P = 0.53$).

The dietary composition of captured individuals showed no significant associations between sites (τ = 0.23, P = 0.18). The three most important dietary items in Bandurrias were the algae *Ulva lactuca* (23.6% occurrence) and *Porphyra columbina* (14.6% occurrence) and the mobile gastropod species *Nodilittorina araucana* (10.1% occurrence), Amphipoda–Gamaridae (10.1% occurrence), and Diptera (15.7% occurrence). In Santo Domingo, the most important dietary items

TABLE 2. Summary of the different ANOVA models applied on the sessile and mobile species and on the productivity and production variables.

Source of variation	df	MS	F	P
Sessile species				
Species richness (S)				
Site	3	398.71	102.1	0.0003
Bench (site)	4	3.91	1.81	0.1271
Error	232	2.16		
Species cover (%)				
Site	3	1.79	7.33	0.0041
Bench (site)	4	0.25	3.02	0.0186
Error	232	0.08		
Mobile species				
Species richness (S)				
Site	3	32.99	40.94	0.0018
Bench (site)	4	0.81	3.36	0.0108
Error	232	0.24		
Abundance (no. individuals)				
Site	3	9.82	16.45	0.0100
Bench (site)	4	0.60	3.45	0.0092
Error	232	0.17		
Chlorophyll *a* ($\mu g/cm^2$)†				
Site	1	2.86	41.50	0.0010
Time	1	432.88	646.07	0.0010
Site × time	1	0.68	1.29	0.2579
Error	92	0.67		
Productivity ($\mu g \cdot cm^{-2} \cdot mo^{-1}$)				
Site	1	6.02	4.67	0.0800
Time	5	1.09	15.97	0.0001
Site × time	5	1.28	18.83	0.0001
Error	84	0.06		
Production (g/mo)				
Site	1	1891.17	34.81	0.0041
Time	4	112.99	2.68	0.0341
Site × time	4	54.32	1.29	0.2780
Error	150	42.24		

† ANCOVA.

were *Enteromorpha compressa* (23.7% occurrence), Diptera (23.7% occurrence), Amphipoda–Gamaridae (9.3% occurrence), and *Nodilittorina araucana* (10.1% occurrence).

Crustaceans.—

1. *Abundance and activity.—Leptograpsus variegattus* occurred solely at the midintertidal levels. The abundance patterns assessed on 54 visual censuses showed significant differences between sites ($F_{1,62}$ = 74.53, P = 0.0001). Throughout the study period and both during night and day, Santo Domingo showed significantly higher levels of abundance (21.4 ± 1.1 individuals/10 min [mean ± 1 SE]) than Bandurrias (=13.2 ± 0.8 individuals/10 min).

2. *Body sizes and dietary composition.*—There were no significant differences in body size and biomass of the individuals captured at both sites ($F_{1,58}$ = 0.015, P = 0.90 and $F_{1,58}$ = 0.589, P = 0.45 for body sizes and biomass, respectively). The slope of the relationship between these variables (a = 2.38 and a = 2.79, for Bandurrias and Santo Domingo, respectively) showed no significant differences between sites (ANCOVA, $F_{1,56}$ = 1.6, P = 0.21).

The dietary composition of the *L. variegattus* captured at both sites did not show a significant association (τ = 0.26, P = 0.29). In Bandurrias, the most frequent dietary items were diatoms (28.1% occurrence), the algae *Ulva lactuca* (21.8% occurrence), and *Ectocarpus confervoides* (12.5% occurrence), whereas in Santo Domingo, they were diatoms (41.7% occurrence), *Enteromorpha compressa* (33.3% occurrence), and Diptera (13.3% occurrence).

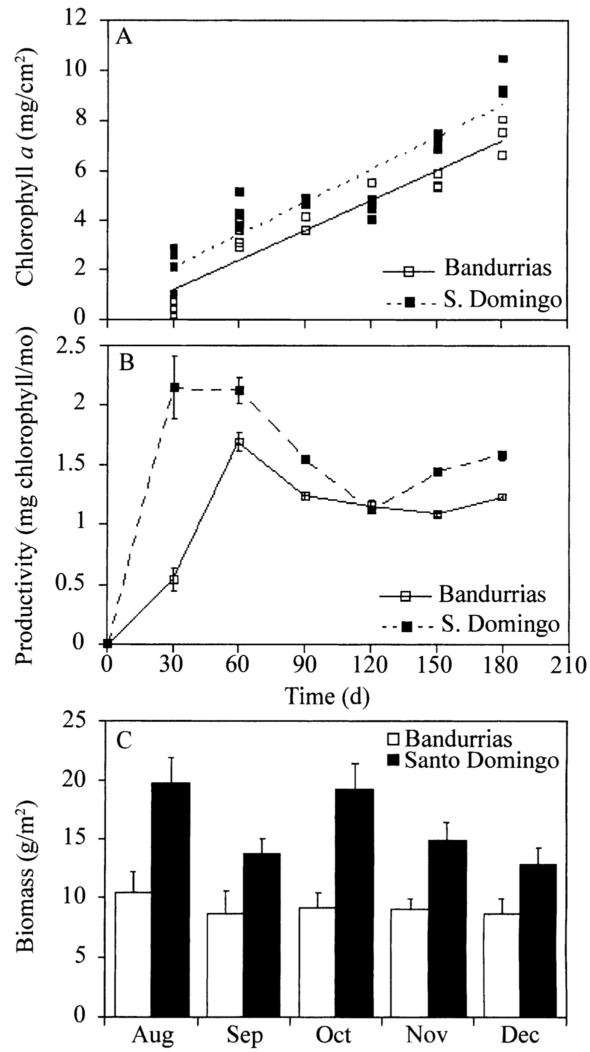

FIG. 3. (A) Changes in chlorophyll *a* concentration and (B) productivity from the plates disposed on the intertidal rocky shores of Bandurrias and Santo Domingo. (C) Production levels (biomass/m²) recorded from the experimental plots disposed in each study site. The adjusted curve for Bandurrias in panel A corresponds to $y = 0.8 + 0.04x$, $r^2 = 0.85$, while that for Santo Domingo corresponds to $y = 0.04 + 0.04x$, $r^2 = 0.90$. Productivity (panel B) was calculated using the relation between chlorophyll concentration and the permanence time of each experimental plate on each site. Error bars represent 1 SE.

TABLE 3. Bird species observed (X) on the benches of Bandurrias and Santo Domingo during the study period: February, April, June, August, October, and December.

	Bandurrias						Santo Domingo					
Species	Feb	Apr	Jun	Aug	Oct	Dec	Feb	Apr	Jun	Aug	Oct	Dec
Sulidae												
Sula variegata	X					X						
Pelecanidae												
Pelecanus thagus	X	X	X	X	X	X						
Phalacrocoracidae						X						
Phalacrocorax gaimardi	X					X						
Phalacrocorax bouganivilli	X					X						
Phlacrocorax olivaceus	X	X	X	X	X	X	X		X	X	X	X
Sternidae												
Larosterna inca	X											
Larinae												
Larus modestus	X	X	X	X	X	X	X	X	X	X	X	X
Larus belcheri	X	X	X	X	X	X						
Larus dominicanus	X	X	X	X	X	X	X	X	X	X	X	X
Ardeidae												
Nycticorax nycticorax	X	X	X	X	X	X	X					X
Haematopodidae												
Haematopus palliates	X			X	X	X						
Haematopus ater	X	X	X	X	X	X						
Scolopacidae												
Arenaria interpes	X				X	X						
Aphriza virgata	X	X			X	X						
Calidris alba	X				X	X						
Numenius phaeophus	X	X	X	X	X	X						
Furnaridae												
Cinclodes nigrofumosus	X	X	X	X	X	X	X	X	X	X	X	X
Tyraninidae												
Muscisaxicola macloviana	X	X	X	X	X	X	X	X	X	X	X	X
Cathartidae												
Cathartes aura	X	X	X	X	X	X	X	X	X	X	X	X
Falconidae												
Polyborus plancus	X		X	X	X	X						

Fishes.—

1. *Abundance.*—The abundance of *G. laevifrons* did not differ between sites ($F_{1,142}$ = 1.0, P = 0.2). In Bandurrias, a mean of 10.3 ± 0.2 individuals/5 min (mean ± 1 SE) was recorded while in Santo Domingo a mean of 10.6 ± 0.2 individuals/5 min was recorded.

2. *Body sizes and diet.*—The body sizes and biomass of individuals captured at Bandurrias were significantly smaller than the ones captured at Santo Domingo ($F_{1,65}$ = 37.60, P = 0.0001 and $F_{1,65}$ = 38.64, P = 0.0001, respectively). In the noncontaminated site, the mean body size of individuals was 8.72 ± 0.12 cm (mean ± 1 SE) and their mean biomass was of 12.98 ± 1.57 g (mean ± 1 SE), whereas in the contaminated site the mean body size was 11.37 ± 0.34 cm and mean biomass was 23.86 ± 2.45 g. In spite of this, the slopes of the relation between these two variables (a = 3.4 and a = 3.0, for Bandurrias and Santo Domingo, respectively) did differ significantly (ANCOVA, $F_{1,63}$ = 6.6, P = 0.1).

The dietary composition of the captured fish did not presented significant associations between both sites (τ = 0.21, P = 0.36). A total of 30 dietary items were identified. The number of these items was higher at Bandurrias (n = 19) than Santo Domingo (n = 7). At a high taxonomic level, the green algae and arthropods were the most important dietary items at both sites. However, within each of these groups, there were differences in prey species number and composition recorded at each site. In Santo Domingo, *E. compressa* and Diptera were the most important items with 87.1 % and 12.4% of the total diet biomass. In Bandurrias, *U. lactuca* and Amphipods accounted for 91% and 4.5% of the diet biomass, respectively.

In summary, in comparison to the noncontaminated, the major differences in species richness and composition of the contaminated benthic communities are related to the absence of species (i.e., birds), changes in abundance (i.e., *Microlophus atacamensis* and *Leptograpsus variegattus*), or to differences on body sizes

TABLE 4. Qualitative dietary composition of the birds observed (X) on the intertidal benches of Bandurrias (BAN) and Santo Domingo (SD).

	Larus dominicanus		*Nycticorax nycticorax*		*Haematopus ater*		*Numenius phaeophus*		*Cinclodes nigrofumosus*		*Muscisaxicola macloviana*	
Variable or prey species	BAN	SD	BAN	SD	BAN	SD	BAN	SD	BAN	SD	BAN	SD
Observation time (min)	342	210	605	22	653	0	451	0	812	755	350	432
Feeding time (min)	36	14	42	0	562	0	230	0	743	700	212	425
Echinodermata												
Tetrapygus niger	X				X							
Mollusks												
Tegula atra	X				X							
Colisella araucana					X		X					
Scurria parasitica					X		X					
Fissurella crassa	X				X							
Enoplochiton niger					X							
Nodilittorina peruviana							X					
Crustaceans												
Cirripedia							X		X			
Amphipoda									X	X	X	X
Leptograpsus variegattus			X	X			X					
Insecta												
Diptera									X	X	X	X
Vertebrata												
Girella laevifrons	X	X	X									

and biomass of intertidal consumers (i.e., *Girella laevifrons*).

Discussion

Benthic organisms

Low species richness and dominance by *E. compressa* are a general feature of intertidal benthic communities affected by copper mine tailings along the northern Chilean coast. Our results are consistent with previous studies conducted at other sites (Castilla and Nealler 1978, Castilla 1996, Castilla and Correa 1997, Correa et al. 2000, Fariña and Castilla 2001), but they also provide new information in some particular and general topics.

Strong, but different, relationships in abundance, species richness, and composition between the sessile and mobile species (of small size) were observed in contaminated and noncontaminated sites. The high cover of *E. compressa* on the contaminated sites was correlated with the high abundance of Diptera. This association has been reported on the temperate coast of California by Robles (Robles and Cubit 1981, Robles 1982). They found that ephemeral algal blooms (composed of *E. compressa* and other algae) occurring after storms are related to explosive increases in abundance of Diptera. These consumers are the primary colonizers after perturbations and reduce the existing high cover of ephemeral algae. On the California coast, this situation persists for two or three weeks after storms. In our study, the high abundance of *E. compressa* was permanent at the contaminated sites (Fariña and Castilla 2001) lasting for at least two years in cases where tailing waste disposal has stopped (Correa et al 1999).

At noncontaminated sites, the high incidence of amphipods may be due to the high cover of red filamentous and green foliose algae such as *Ulva lactuca*, *Ectocarpus confervoides*, and *Ceramiun rubrum*. Hacker and Steneck (1990) showed that algal architecture is a major factor determining amphipod habitat preference and that they prefer foliose and filamentous algal forms.

Productivity and production

Our results indicate that levels of primary productivity were higher at contaminated sites compared to noncontaminated site. However, given that after two months the accumulated chlorophyll and productivity levels at both sites were similar, it is possible that differences in production (accumulated biomass) of both sites reflect high differences in productivity in the first months. Both the dominant algae in the contaminated site (*E. compressa*) and in the noncontaminated site (*U. lactuca*) are early colonizers of intertidal rocky shores (Santelices 1991). In a detailed study of the multiple variables involved in algal photosynthetic processes, Enriquez et al. (1995) demonstrated that photosynthetic efficiency scales positively with the maximum photosynthetic rate, positively with the concentration of chlorophyll *a,* and negatively with tissue thickness. These authors reported that both *E. compressa* and *U. lactuca* have similar maximum photosynthetic rates (26.85 and 26.43 mg $O_2 \cdot [\text{g dry mass}]^{-1} \cdot h^{-1}$, for *E. compressa* and *U. lactuca*, respectively), that *E. compressa* have almost two times more chlorophyll *a* (0.571% dry mass) than *U. lactuca* (0.324% dry mass) and that, in spite of this important difference, both algae present a similar photosynthetic efficiency (0.0866 and 0.0833 mg O_2·[g dry mass]$^{-1}$·h^{-1}, for *E. compressa* and *U. lactuca*, respectively). An explanation for this situation resides in the fact that *E. compressa* shows higher values of tissue thickness (0.171 mm) than *U. lactuca* (0.113 mm). Enriquez et al. (1995) developed their study with adult plants. For our study, and considering the results of Enriquez et al. (1995), it is possible to relate the decrease in productivity of *E. compressa* observed after the second month of monitoring, with changes in any of the variables above mentioned. For example, it is recognized that, during juvenile states, both *E. compressa* and *U. lactuca* present similar body forms and that, during the growing process, *E. compressa* usually develops into a more filamentous body form (Santelices 1989). If these changes in architecture are related to an increase in tissue thickness, it is possible to predict whether *E. compressa* will show a decrease in productivity similar to the one observed in our study. This is a possibility that could be analyzed in future comparative studies.

In regard to our methodologies, it could be argued that the use of productivity plates exerted some bias toward the settlement and colonization of particular groups of organisms. In our case, the plates were colonized mostly by algae, and within this group, by green algae. This kind of plate was originally designed to assess the productivity of epilithic algae (see Bustamante et al. 1995) and it allowed us to assess and compare the productivity of the most widely represented algae in both the contaminated (*E. compressa*) and noncontaminated sites (*U. lactuca*). It could be argued that both the plates and the experimental plots biased the results toward early colonists and ephemeral species (and against sporadic recruiters). However, in our case, the species compositions in both the plates and experimental plots resemble the one observed in the benches of the contaminated and noncontaminated sites (Table 1). More important yet, the species occurring in both plates and plots were the ones preferred by most consumers, relating directly to the objective of our work.

From another perspective, it could be argued that the small spatial scale used in our evaluation of productivity could influence the results obtained. Specifically, for the case of the experimental plots, some studies (Petraitis and Latham 1999, Dudgeon and Petraitis 2001), developed in the area of succession and alternative states of intertidal communities, show clear differences in the possible outcomes for large- vs. small-scale plot clearings. In the case of large-scale experiments (substrate denudations), it is more probable that a state different than the original one will be reached. In contrast, small-scale experiments usually fail to show a switch in community state. In our case, our objective was not to test the possible establishment of alternative states in our communities. Instead, our experimental objective was to analyze the pattern of productivity of the prevailing state of both contaminated and noncontaminated communities. Because of this, the use of a small-scale approach, where the influence of the surrounding community is maintained, was in complete agreement with our goals.

Consumer species

Birds.—Differences in the composition, abundance, and richness of the bird species observed at both sites corresponded to differences in the benthic communities. Bandurrias, the noncontaminated site with a high diversity of benthic organisms, showed a greater bird abundance and species richness than Santo Domingo (contaminated and with a less diverse benthic community).

It is widely recognized that the abundance and species composition of bird assemblages depends on the abundance and diversity of their prey. In this way, the spatial and temporal variations in the bird assemblages are good indicators of changes occurring primary trophic levels. Schnaub and Jenni (2000) demonstrated that residence time in migratory birds highly depends on the prey availability of the visited place. In a 21-year study of diversity and reproductive patterns of six Californian coastal bird species, Ainley et al. (1995) showed that, independent of their magnitude, any change on the oceanographic regime associated with changes on prey diversity and abundance, is reflected in the structure of the bird assemblages.

Within the 20 bird species recognized in our study, eight have been reported as subtidal predators, 10 as intertidal predators, and two as terrestrial or carrion consumers (Araya et al. 1986). The low number of species observed at Santo Domingo was reflected in these three groups. Only four, two, and one intertidal, subtidal, and carrion consumer species, respectively, were observed at this site. Considering the relationship between diversity of primary trophic levels and the structure of the bird assemblages, it is probable that the subtidal benthic communities on the contaminated sites also suffered important changes. In this regard, associated with the increase of diversity observed during summer (October through December) in both localities, there was a peak of abundance and species richness in February. This peak occurred only in the noncontaminated site (Bandurrias) and was composed mainly by subtidal consumer species associated with the Peruvian coast (i.e., *Sula variegata*, *Larosterna inca*, and *Phalacrocorax gaimardi*; Fuentes 1984). Important changes in marine bird populations have been reported for ENSO (El Niño) years. During these years and in response to changes in abundance and spatial distribution of prey, several marine bird species migrate from northern Peru to northern Chile (Alvial 1985, Arntz 1986, Glynn 1988). It is possible that, because of ENSO conditions in summer 1998 (Camus and Andrade 1999), the subtidal birds migrating from Peru to northern Chile increased the diversity of the noncontaminated site. It is important to note that this migration was observed at the noncontaminated site and not the contaminated one, reinforcing the idea that birds respond to prey availability.

On the other hand, the general increase in the bird abundance and species richness could be related to the arrival of migratory species (de Boer and Longaname 1996). In Chile, there are no studies analyzing temporal variation in species composition of birds in coastal areas. However, it is widely recognized that during the summer several migratory species (e.g., *Aphriza virgata*, *Calidris alba*, and *Numenius phaeophus*) come from the northern hemisphere to the coast and that other resident species (e.g., *Phalacrocorax gaimardi*, *Phalacrocorax bouganvilli*, and *Sula variegata*) expand their ranges to the south (Araya et al. 1986).

In relation to intertidal consumer species, *Cinclodes nigrofumosus* was the one with the highest representation at both sites. This species was observed feeding mainly in midintertidal levels dominated by green algae, and a high abundance of small arthropods (like amphipods and Diptera). The high abundance and incidence of *C. nigrofumosus* could be related with their reproductive behavior. The individuals in this species have a high fidelity for their feeding grounds and to build their nest on the high intertidal rocky crevices, usually use several juvenile individuals as helpers during the breeding season (P. Sabat, *personal communication*). Another small arthropod consumer was *Muscisaxicola macloviana*. This is a terrestrial bird and its high abundance at Santo Domingo could be related with the high incidence of prey (Diptera) occurring on the rocky shores of this site. On the another hand, *Haematopus ater* and *Numenius phaeophus* presented the wider dietary spectra and only occurred in Bandurrias. The individuals of *H. ater* were observed feeding on the low intertidal levels and their diets were composed mainly by mollusks (e.g., *Tegula atra*, *Enoplochiton niger*, and *Fissurella crassa*). The individuals of *Numenius phaeophus* were observed mainly on the midintertidal level, searching and eating crustaceans (e.g., *Leptograpsus variegattus*). The dietary composition of both species was in concordance with the mobile benthic species abundance observed in the intertidal. Although there is no published information for *N. phaeophus* on the relation between their abundance and prey availability, the presence and abundance of congeneric species of *H. ater* in both South Africa and California are highly dependent of the prey availability on intertidal shores. These species have been reported as indicators (for their absence) of anthropogenic perturbations (Ainley and Lewis 1974, Hockey 1983).

Reptiles.—All the census data showed that the presence of *Microlophus atacamensis* in rocky intertidal areas of both sites depends on the substrate temperatures. Other studies in terrestrial habitats in Chile and in the Galapagos archipelago (Ecuador) show that atmospheric and substrate temperatures restrict the activities of some con-generic species of *M. atacamensis* (Stebbins et al. 1967, Baez and Cortez 1990).

M. atacamensis occurred solely on the high intertidal levels during morning and evening hours and the major abundances were observed on the hours of highest substrate temperatures on the midintertidal levels. During these hours, more individuals of *M. atacamensis* were observed on the midintertidal levels of Santo Domingo than Bandurrias. The most important dietary items of *M. atacamensis* at both sites were the green algae and small arthropods associated with those algae. It is interesting to note that, as shown in the analysis of benthic organisms, Bandurrias has minor abundance of these prey compared to Santo Domingo.

The differences in prey availability could be related to the observed minor abundance of *M. atacamensis* occurring in Bandurrias. Some studies in the Galapagos Islands with species of the same family of *M. atacamensis* (Iguanidae) show that the abundance of these reptiles depends on the abundance of prey in the intertidal zones. Wikelski et al. (1997) showed that abundance and body size of the marine iguana, *Amblyrynchus cristatus*, depends on the biomass of green and red algae occurring on the rocky intertidal benches of some Galapagos Islands. Copper and Laurie (1987) showed that changes in the distribution and abundance of algal species occurring during ENSO affect in a significant way the abundance and distribution of *A. cristatus* on the mentioned archipelago.

Crustaceans.—Considering that *Leptograpsus variegattus* was active and fed on the same intertidal levels of *M. atacamensis* it is possible that diet composition of the two species is similar. The nonparametric test of concordance showed that for Bandurrias there was a nonsignificant, but spurious, relationship between the dietary composition of both species ($\tau = 0.56$, $P = 0.07$) whereas for Santo Domingo this relationship was significant ($\tau = 0.66$, $P = 0.02$). Considering this, the minor abundance of *L. variegattus* on Bandurrias could be related, as well as in the case of *M. atacamensis*, with differences of prey availability between the two sites. Similar to the case of *M. atacamensis*, some studies show that the abundance of species in the same family of *L. variegattus* depends on the availability of prey. Kenish et al. 1996 demonstrated that seasonal variation in the abundance of macroalgae in intertidal rocky shores of Hong Kong were responsible for temporal variation in abundance of *Grapsus albolineatus* (Grapsidae). McDermott (1998) proposed that the successful invasion of *Hemigrapsus sanguineus* on the Atlantic coast of USA has been related with the high availability of food and with the absence of natural predators for this species.

Fishes.—At both sites, individuals of *G. laevifrons* occurred exclusively in the low intertidal pools. No other species of intertidal fish occurred in these pools

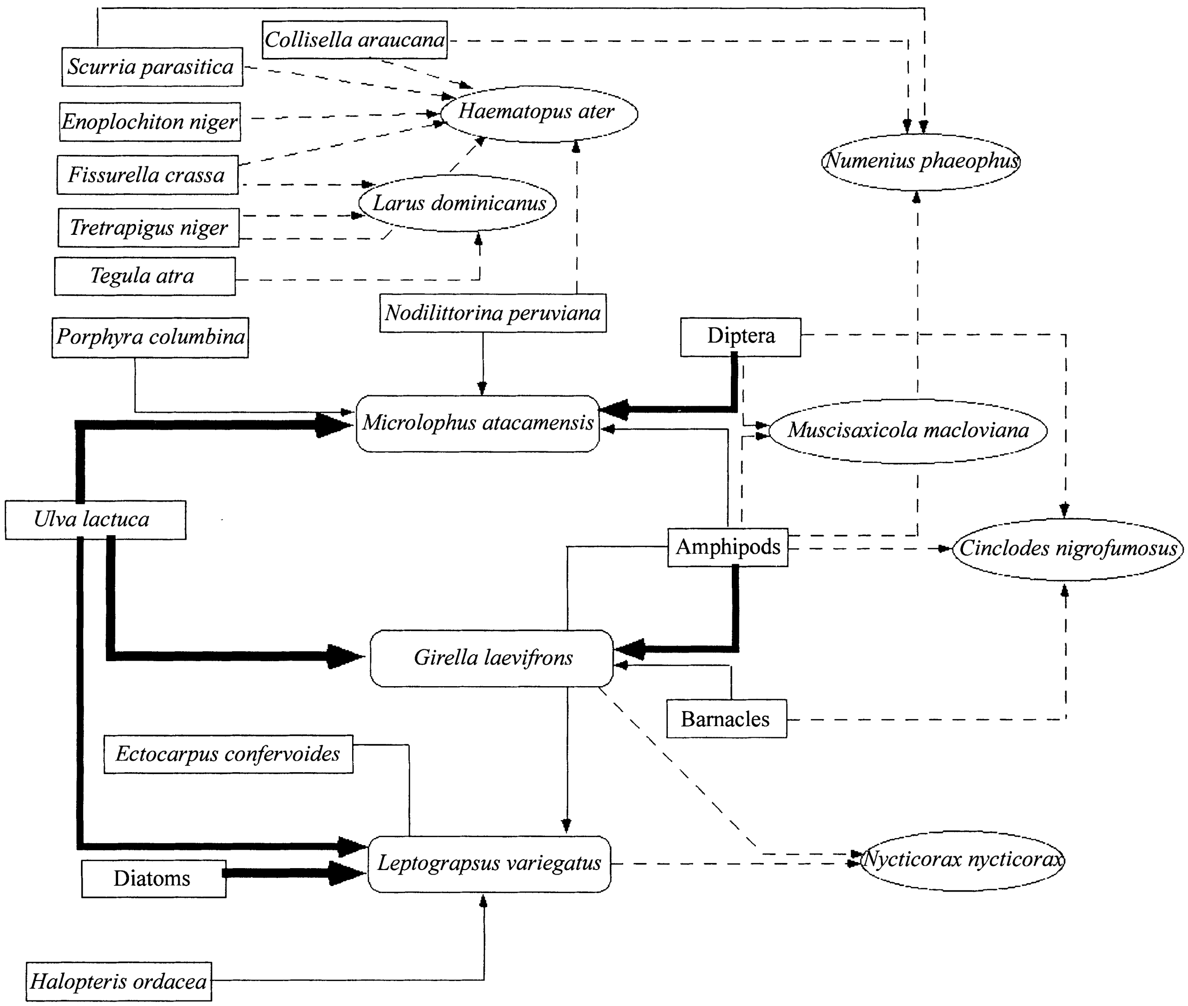

FIG. 4. Trophic web summarizing the results of the dietary analysis of the consumers studied in Bandurrias. Rectangles with sharp corners represent intertidal prey, rounded-corner rectangles represent herbivorous–omnivorous species, and ovals represent the bird species. In the case of *M. atacamensis*, *L. variegatus*, and *G. laevifrons*, the line thickness represents the frequency of occurrence of each item in their digestive tracts. In the case of bird species, dashed lines represent a trophic link registered qualitatively. In each case, the arrow goes from the prey to the consumers.

or in the high and mid intertidal rock pools. These patterns contrast with the situation of *G. laevifrons* in central Chile were it occurs as a transient species in high and mid intertidal levels (Stepien 1990, Muñoz and Ojeda 1998, Pulgar et al. 1999). The geographic differences on the distribution of *G. laevifrons* in the intertidal pools of northern and central Chile could be related with the thermal characteristics and with the presence of other fish species. During diurnal low tides, high-intertidal pools of central Chile can reach temperatures around 36°C, and in northern Chile, above 50°C. Therefore, low intertidal pools in northern Chile have a similar temperature regime as high intertidal pools of central Chile (J. M. Fariña, *personal observation*). In terms of other fish species, it has been proposed that the transient occurrence of *G. laevifrons* in high intertidal pools in central Chile could be a response to the presence of and dominance of other fishes with antagonist and aggressive behavior (such as large-sized *Graus nigra* and *Scartichthys viridis*). These fishes are dominant in the low and mid intertidal pools and displace *G. laevifrons* to high intertidal pools (Hernández et al. 2002).

Similar abundances of *G. laevifrons* were observed in both sites. However, the individuals captured in the contaminated site (Santo Domingo) had larger body sizes and biomass than the ones captured in the non-contaminated site (Bandurrias). In intertidal pools, it is possible to find fish species that spend all their life in this habitat (residents) and species that only occur in this habitat during their juvenile stages (transients), migrating lately to the subtidal (Varas and Ojeda 1992, Muñoz and Ojeda 1998). For the last group, it is widely accepted that the residence time in intertidal pools depends on primary productivity at each site (Horn et al. 1999). In intertidal pools with high prey abundance and

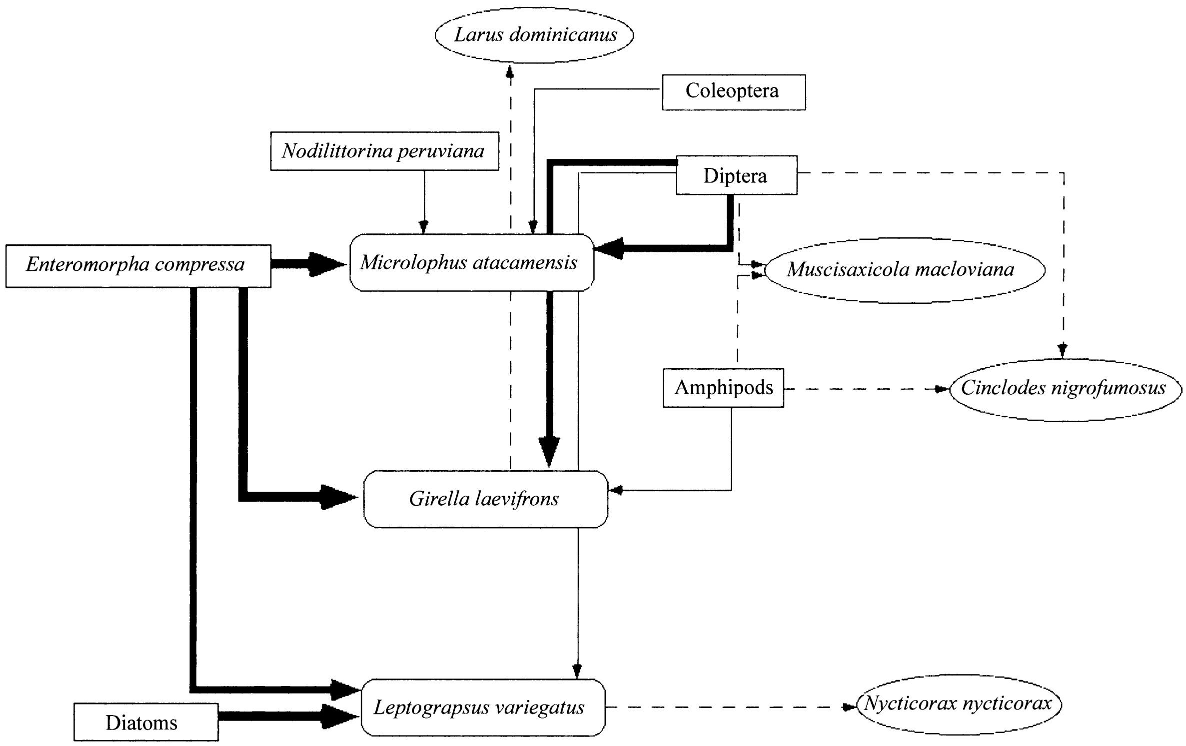

FIG. 5. Trophic web summarizing the results of the dietary analysis of the consumers studied in Santo Domingo. Rectangles with sharp corners represent intertidal prey, rounded-corner rectangles represent herbivorous–omnivorous species, and ovals represent the bird species. In the case of *M. atacamensis*, *L. variegatus*, and *G. laevifrons*, the line thickness represent the frequency of occurrence of each item on their digestive tracts. In the case of bird species, dashed lines represent a trophic link registered qualitatively. In each case, the arrow goes from the prey to the consumers.

availability, the intertidal fishes will have longer residence times and will have larger body sizes. Considering the diet of *G. laevifrons* and the relative cover of their main prey, it could be hypothesized that the food availability observed in Santo Domingo could be responsible for the larger body sizes and biomass of the individuals at this site.

The results of this study highlight some natural history characteristics of the consumer species occurring in both contaminated and noncontaminated sites. Temperature is a key factor determining the activity and feeding behavior of *M. atacamensis* and could be an important factor in the distribution of *G. laevifrons*. Green algae and small arthropods occurring in the mid intertidal levels are the main prey of reptiles, crustaceans and birds.

The food web diagrams summarizing the results of the classic dietary analysis (Figs. 4 and 5), showed a similar number of trophic levels for both sites but a reduced dietary spectra for consumers at the contaminated site. Comparing the diagrams it is evident that the changes on diversity and particularly the loss of small invertebrates is related with the lower diversity of bird species. A good example of this is the change in dietary composition of *Larus dominicanus*, from invertebrates (in the contaminated site) to fishes (in the noncontaminated site). On the other hand, the associations of *U. lactuca*–amphipods and *E. compressa*–Diptera, appear to be the key for maintenance of herbivores and omnivores species in the noncontaminated and contaminated sites, respectively. Because those consumers are more abundant and have larger biomass and/or body sizes, it is likely that major primary productivity of the contaminated sites plays an important role for the maintenance of the trophic web organization.

With regards to considering *E. compressa* as a "sentinel" species (Castilla 1996), the term is applied to species that can be used as indicators of pollution and toxicity and that enable us to judge the potential effects of a contaminant on human health and/or the environment (Jamil 2001). This definition is carried over into two concepts of sentinel species as organisms and sentinel bioassays, both of particular relevance as biological indicators of environmental contamination (Lower and Kendall 1990). As organisms, sentinels correspond to the species that under the occurrence of a specific kind of contamination show significant changes in abundance or distribution (Beeby 2001). As bioassays, the term is more related to organism physiology and is applied to species that show specific changes in their excretory function, mutagenesis, biomass, behavior, enzyme induction, and etc. (Garte 1994). Four limitations have been recognized for the use of sentinel species as organisms (Soule 1988): (1) there is a gap between indicating something (as a sentinel) and showing cause or between cause and effect and remedy, (2) the use of a single specie is not a substitute for a broad-spectrum research program, (3) the deep knowledge of a single species does not automatically convey information about other taxonomically related species, nor about their reactions to environmental variables or stress, and (4) the knowledge of one or a few species does not convey information about the interaction among those species and others in the community.

The situation of *E. compressa* in rocky intertidal communities affected by copper mine tailings in the northern Chilean coast fits the definition of sentinel species as organisms (Castilla 1978, 1983, Fariña and Castilla 2001) and as bioassays (Correa et al. 1999, 2000, Fariña et al. 2000). Considering the recognized limitations of the concept, in our work we utilized a broad perspective to analyze the influence of this "sentinel" species on the entire intertidal community, dealing specifically with limitations 2 and 4 mentioned above.

In conclusion, our results show that, in the benthic communities of contaminated sites, the lower levels of species richness are associated with an increase in productivity. This pattern has two major and contrasting consequences on trophic organization. The decrease of benthic diversity is related to a decrease in carnivorous species richness and increase on productivity is associated with a greater biomass and/or abundance of herbivores-omnivorous species. Some scenarios resulting from the direct and/or indirect effect of human activities are a good candidate to explore theoretical concepts in ecology. In our case, the simplified organization of contaminated communities allowed us to demonstrate the importance of the functional form or species composition for the study of the relationship between species richness and productivity in marine systems. More importantly, it allowed us to demonstrate that, to understand the species richness–productivity relationship, it is crucial to know the trophic relations of the considered species. The special characteristics of dominance, persistence and productivity of *Enteromorpha compressa* (the sentinel species on the contaminated sites) are a clear example of the idiosyncratic effect that some species can have on biological communities.

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