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Spatial variability of the decomposition rate of *Schoenoplectus tatora* in a polluted area of Lake Titicaca

Maria Letizia Costantini[1], Letizia Sabetta, Giorgio Mancinelli and Loreto Rossi

Department of Genetics and Molecular Biology – Ecology Area – University of Rome ‘La Sapienza’, Via dei Sardi 70, I-00185 Rome, Italy
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Abstract: Lake Titicaca is the largest freshwater lake in South America and one of the highest and oldest of the world’s large lakes, but very little of its ecology is known. We report results from a study on the spatial variation of decomposition rate of *Schoenoplectus tatora* in Inner Puno Bay affected by direct wastewater discharges. The aims of the research were: (1) to evaluate the effect of benthos exclusion and the influence of other environmental factors on decomposition and (2) to map the decomposition rate in order to describe the spatial heterogeneity in the water body. We carried out the study at 21 sampling points using both fine-meshed and coarse-meshed litterbags to exclude and to allow detritivore action, respectively. Decomposition was on the average faster in the former than in the latter treatment. However, the difference decreased with increasing detritivore abundance, and reversed in the most densely populated waters of the bay. Coupled spatial dependence of the decomposition rate and temperature was observed. Both variables were related with the distance from the wastewater discharges, suggesting that thermal pollution constrains the decomposition rate within the inner bay. Detritivores did not change the general trend imposed by temperature, but their presence increased the spatial heterogeneity of the process.

Key Words: ancient lake, detritivores, detritus, geostatistics, mass loss rate, pollution, spatial pattern, totora

INTRODUCTION

Large lakes have great ecological, economic, social and cultural importance (Borre *et al*. 2001). They provide crucial ecosystem services, such as denitrification, water, food and energy supply. Moreover, because of their high endemic species numbers, ancient large lakes are ideal natural laboratories for evolutionary studies (Martens 1997).

Lake Titicaca is the largest freshwater lake in South America, the highest of the world’s large lakes and one of the oldest. Major threats to the resident organisms are accelerated eutrophication and water diversion (Borre *et al*. 2001, Revollo 2001). Inner Puno Bay, which is about 2.1% of Lake Titicaca, is one of the most vulnerable areas of the entire lake. Enclosed between two promontories and almost completely isolated from the main bay by macrophyte stands, this shallow water body is suffering from organic and bacteriological contamination caused by direct discharges of wastewaters from the urbanized area of Puno City, which is expected to increase its population substantially in the near future.

Schoenoplectus tatora, known locally as totora, is one of the most abundant macrophytes in Inner Puno Bay (Collot *et al*. 1983) but stands are decreasing due to water pollution. Totora contributes enormously to the local economy, being harvested as cattle fodder, for roofing, handicrafts and the construction of rafts (Levieil & Orlove 1990). Moreover, it represents a major source of autochthonous organic matter (Dejoux 1991), largely supporting the aquatic detritus-based food webs and fisheries. In shallow waters decomposition of the macrophytes is fundamental for nutrient cycling. Nutrients are taken up during plant growth and then released as plants decompose. Decomposition is a complex ecosystem-level process, which depends on both biotic and abiotic environmental factors and is therefore sensitive to water pollution (Leland & Carter 1985, Newman *et al*. 1987). Environmental changes that influence decomposition rates also affect the release of nutrients and their availability to primary producers. In the last two decades decomposition studies have clarified

[1]Corresponding author. Email: marialetizia.costantini@uniroma1.it

the crucial role of micro-organisms and detritivores (Fazi & Rossi 2000, Gulis & Suberkropp 2003, Hieber & Gessner 2002, Rossi 1985, Sabetta *et al*. 2000, Suberkropp 1992, Webster & Benfield 1986) and, more recently, have emphasized the importance of the spatial pattern of decomposition rate as a quantitative and qualitative descriptor of ecosystem functioning (Epstein *et al*. 2002, Rossi & Costantini 2000). Spatial pattern and scale of variability can differ markedly from site to site and the difference can be related to disturbance history. Thus, not only the knowledge of the effects of changing environmental factors but also the description of the 'geography' of the process variation can be extremely useful in developing proper managing strategies in areas affected by increasing human impacts.

At present, very little of the ecology of Lake Titicaca is known and no published information is available on the decay rates of *S. tatora*. In the present paper we report results from a short-term study on the mass loss rate of this plant species in Inner Puno Bay, using both fine-meshed and coarse-meshed litterbags to exclude and to allow detritivore action and thus to evaluate the effects of benthic biomass variation. The aims of the research were: (1) to measure the decomposition rate taking into account critical environmental factors such as temperature, dissolved oxygen, pH, wave action, depth and sources of pollution; (2) to map the decomposition rate through geostatistics for evaluating spatial heterogeneity in the water body as a basic cognitive tool for the future management of this unique ecosystem.

METHODS

Study site

Lake Titicaca is the largest freshwater lake in South America. It is a transboundary site between Bolivia and Peru (14°07′–17°08′S, 68°02′–71°06′W) located between the two snowy mountain ranges of East and West Cordillera in the central Andes. With a surface of 8300 km^2, a maximum length of 195 km, 285 m of maximum depth, and an average width of 50 km, it is the highest navigable lake in the world (3808 m asl). Both Peruvian and Bolivian sectors are included in the list of Wetlands of International importance (no. 881 and no. 959), established after the Convention of Wetlands (Ramsar, Iran, 1971). One of the unique characteristics of this lake is the temperature of its waters, being warm for that altitude (from −10 °C to 12 °C), allowing the existence of rich aquatic flora and fauna. There are a number of endemic fish and invertebrate species present (Dejoux & Iltis 1992, Northcote 2000) and the site is extremely important for migratory shorebirds and Andean waterbirds. Algae and submergent and floating vegetation are abundant (Collot *et al*. 1983, Iltis 1991). The dominant emergent species is the totora, *Schoenoplectus tatora*, which extends down to 2–4-m depth in muddy, nutrient-rich substrates. Stands of totora in the Puno Bay are protected by the National Reservation of Lake Titicaca since they host a rich fauna and largely support the local economy. When the totora drifts away from the shore, it forms floating islands where the Uro people live. Most of them are fishermen and use totora to build houses and boats, to make craft items to sell, or as complementary food. Totora is also used for water quality treatment as it can absorb nitrate, phosphate, heavy metals such as manganese, and other chemical compounds.

Lake Titicaca is divided into three main basins (Figure 1). The north-western and south-eastern basins (Puno Bay and Lago Pequeño, respectively) are highly littoral since large areas extend down to the maximum depth of submersed or adnate macrophytes. About 80% of Puno Bay is within the littoral zone, but in some regions high turbidity, in part associated with cultural eutrophication, is restricting the depth to which macrophytes flourish (Levieil *et al*. 1989, Northcote 2000). The Inner Puno Bay is characterized by a surface area of 16.1 km^2 and a mean depth of 2.7 m. Depth is maximum in front of Puno City (7 m) and along a narrow canal stretching southward to the outer bay, while it decreases to the north of the canal at the bay entrance (Figure 1). With a volume of 43.7 million m^3 the bay behaves like a polymictic lake (Vincent *et al*. 1986). The wide stands of *Schoenoplectus tatora*, which cover about 14% of the Inner Bay surface, leave open a 300-m wide canal that represents the only communication with the outer bay. Inner Puno Bay has no tributaries but it is suffering from progressive water pollution and eutrophication caused by sewage and other wastes that are directly discharged from Puno City into the bay without treatment. Besides, there are problems related to inflow of solid wastes into the bay during rainfall because of inadequate waste collection systems. Under these conditions the stands of totora are decreasing.

Sample collection and detritus processing assessment

The study of both the decomposition and macro-invertebrate colonization of *Schoenoplectus tatora* was carried out in 21 sampling sites randomly chosen in a 400-m^2 grid within the Inner Puno Bay (Figure 1). As a crude indicator for the decomposition rate in its early phases, the mass loss of totora was measured at increasing time intervals using the mesh-bag technique (Bocock & Gilbert 1957, Petersen & Cummins 1974). This widely used technique is suitable for field comparative studies when interest lies in separating effects

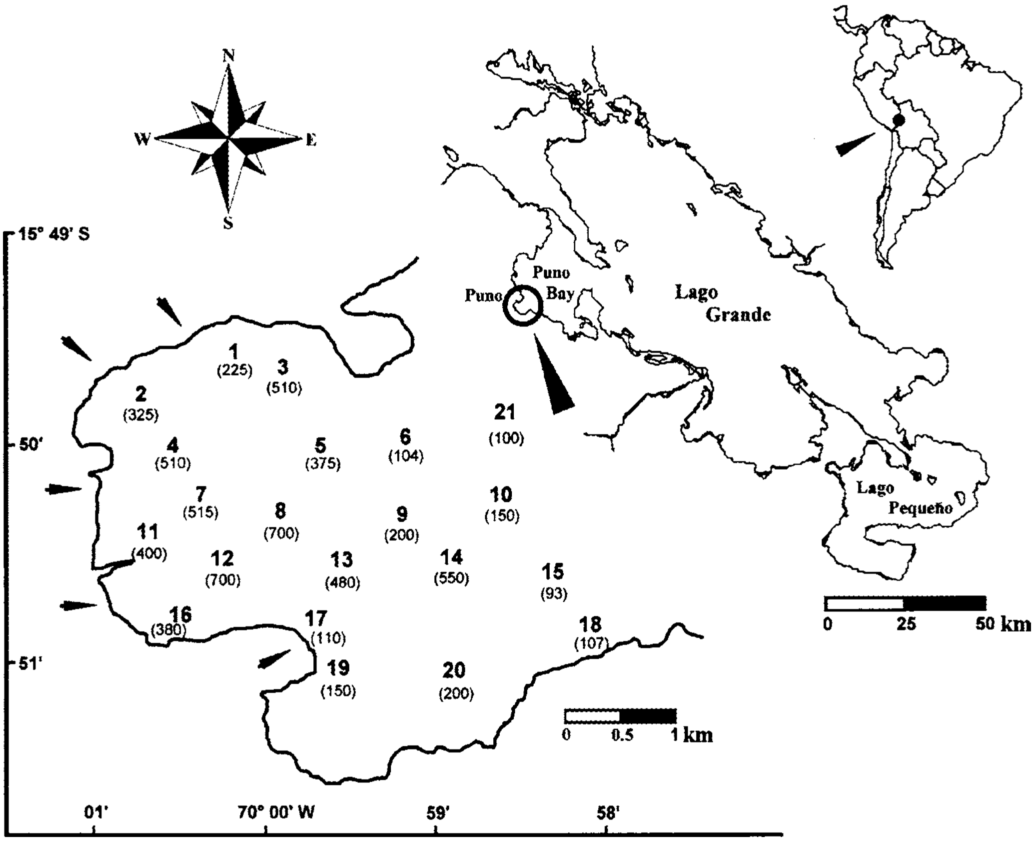

Figure 1. Geographical location of Inner Puno Bay (Lake Titicaca) and spatial distribution of sampling points. Depths (cm) are reported in brackets. The small arrows indicate inflows of wastewaters from Puno City.

of different components of the detritus-associated community (Boulton & Boon 1991). Senescing totora was collected from littoral stands in the bay and stored in an aerated dry room until use. Brown fragments 15 cm long were weighed in 10-g (± 0.005) bundles, which were then tied with a nylon string at half-length and placed in mesh-bags with two different mesh sizes (7- and 0.1-mm mesh; hereafter called unprotected (UP) and protected (P) litterbags, respectively). Mesh-size of 0.1 mm prevented colonization by meio- and macrofauna, while it permitted both entry to bacteria and fungi and gas exchange. P and UP litterbags were randomly anchored to the lake bottom at each sampling site. Additional litterbags were not exposed to water, weighed after oven drying at 60 °C for 72 h and then after ignition in a muffle furnace at 500 °C for 6 h to determine the initial ash-free dry mass (hereafter AFDM). Hot-water-soluble substance, lignin, hemicelluloses and cellulose fractions were determined according to Harper & Lynch (1981).

Six litterbags (three unprotected and three protected) were retrieved by hand from each site after 7, 28 and 56 d of submersion, using scuba when necessary. Samples were carefully and separately placed in polythene boxes containing lake water and carried to the laboratory in an insulated container. In the laboratory, totora litter was removed from the bags, any other adhering debris was cleaned off and the macroinvertebrates associated with each unprotected litterbag were counted. The dry mass after oven drying (at 60 °C for 72 h) and the ash content after ignition (at 500 °C for 6 h) of each litterbag and each animal were determined to assess the ash-free dry mass (AFDM).

Portable field instruments were used at each sampling time to measure physical and chemical parameters at each site close to the litterbags. pH was measured using a Delta OHM pH meter (model HD8705) provided with a temperature probe TP870 for the automatic temperature compensation. Dissolved oxygen was measured using a dissolved oxygen meter (model MO128, Mettler Toledo). Temperature compensation was made with an ATC probe. Values were corrected for the barometric pressure and instruments were calibrated with the respective buffer solutions. Water transparency was measured using the Secchi disk. To obtain a measure of the potential influence of sewage discharge we determined the distance of each sampling site from the nearest ones among all the sewage discharge points using a map with scale 1:100 000. Effective fetch (as a measure of how the wind governs the waves) was computed according to a method introduced by the Beach Erosion Board (Hakanson 1981).

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Data analysis

Regression analysis between remaining totora mass and time was used to determine the fit of two classical decomposition models: (1) the simple exponential model, $M_t = M_0\,e^{-Kt}$ (Olson 1963), and (2) the composite exponential model, $M_t = (M_0 - R)^{-KLt} + e^{-KRt}$ (Lousier & Parkinson 1976), where M_0 is the initial AFDM, M_t is remaining AFDM at time t (in d) and K is the breakdown coefficient expressed in d^{-1}; R is the mass of the refractory part of detritus and L is the labile one. The half-life, that is, the time necessary for the detritus mass to decrease to 50% of its initial AFDM, was expressed as ln(2)/K and used only if the regression was significant.

Before performing statistical analysis the frequency distribution of the data was assessed and the data were log-normal or square-root transformed in order to better normalize the variate's distribution where necessary. An exhaustive exploratory data analysis was performed before computing any of the spatial statistics customarily associated with geostatistics. The stepwise multiple regression procedure applied to log-transformed data was used for examining the relationship between half-life and the environmental factors (temperature, DO, pH, transparency, depth, fetch, animal abundance). In order to reduce the number of variables, principal components analysis (PCA) was performed on the data matrix. The number of extracted factors was determined using the Scree Test and a varimax normalized rotational strategy was adopted to extract factor scores.

To determine quantitatively the spatial variation of the decomposition process and the other environmental parameters we used the semivariogram analysis, a geostatistical procedure that permits evaluation of the degree of spatial autocorrelation among sampling points within the habitat for any given parameter (Matheron 1971, Rossi *et al*. 1992). Semivariograms were obtained by plotting the semivariance (the average similarity between the value occurring in pairs of sample points separated by lag distance) against the geographic distance between sample points, calculated from coordinates of sampling sites expressed in the UTM metric system. The semivariogram function describes the relationship between spatially correlated data. The best-fit model was chosen in order to maximize regression coefficient and minimize residual sums of squares. Three components of the semivariogram were determined: (1) the nugget variance (C_0), (2) the sill or asymptote (C) and (3) the range (Matheron 1963). The nugget exists when $\gamma(0)$ is not equal to zero and the semivariogram function has a positive value of intersection with the γ(h)–axis. This term indicates a non-resolvable variance that characterizes the microheterogeneity at the sampling location and can be attributed to either measurement error or spatial dependence at scales smaller than those measured (Rossi *et al*. 1995). The semivariance increases with increasing distance until the sill, *C*, is reached. Up to this point, the regionalized variables at the sampling locations are correlated. Then they must be considered to be spatially independent. This distance of correlation is called range. The proportion of spatial structure [C/(Co + C)] provides a measure of the proportion of sample variance (Co + C) that is explained by the spatially structured variance C. The semivariogram calculation is followed by the kriging procedure to interpolate the variable at unsampled location and to produce a detailed map (Matheron 1963, Rossi *et al*. 1995). We have also determined the spatial relationship between different pairs of spatially structured variables by cross-variogram analysis as an alternative to conventional correlation analysis that is not applicable to spatially dependent variables (Legendre 1993). The cross-variogram is the plot of cross-semivariance against the distance h (Rossi *et al*. 1995). Two variables are defined as cross-correlated if the value of one at a given location statistically depends on the values of the other at nearby location (Myers 1982, Rossi *et al*. 1992). Fitting theoretical models to cross-variograms is performed following the same procedure used for auto-variograms.

Geostatistical analysis was performed through GS+, version 5.1.1 (Gamma Design Software).

RESULTS

Litter quality and environmental control of totora decomposition

Dry *Schoenoplectus tatora* was composed of 30% hot-water-soluble substances, 8% lignin, 56% cellulose and 5–6% total ash. The ash-free mass loss was rather slow, remaining 86–90% (average 89%) of the initial mass after 1 wk and 69–83% (average 77%) after 8 wk. All data-points (three replicates for three time points + t0) fitted best the simple exponential model of decomposition in each sampling site (Table 1). The half-life time, calculated from the exponential model as days necessary for reducing the initial litter mass to 50%, has been used for comparing the loss rates. Descriptive statistics of this functional measure as well as other major environmental parameters are reported in Table 2.

Differences in the mass loss over time were significant both among sites and between the unprotected and protected litterbags (Table 3). Variation across the lake was higher in the former litterbag treatment than in the latter (CV: 40.3% vs. 29.0%). However, in both cases the totora half-life time decreased with water temperature (Table 4), which rarely exceeded 12 °C throughout the study period (Table 2). As regards the unprotected

Table 1. Half-life time of unprotected (UP) and protected (P) litterbags and invertebrate abundance (number of individuals: mean ± SE with the relative percentages of amphipods) in the 21 sampling sites. Half-life (d) was expressed as ln(2)/K from Olson's simple exponential model. The r^2-values are reported (n = 10).

	Half-life				Animal abundance	
	UP		P			
Site	d	r^2	d	r^2	All invertebrates (Number per litterbag)	Amphipods (%)
1	239	0.41	161	0.50	0.83 ± 0.17	100
2	131	0.77	128	0.85	3.67 ± 1.54	100
3	533	0.41	187	0.66	0.11 ± 0.11	100
4	178	0.59	133	0.77	1.17 ± 0.50	100
5	231	0.61	248	0.59	6.22 ± 3.04	100
6	365	0.44	239	0.72	15.89 ± 12.57	26
7	289	0.49	365	0.46	16.78 ± 7.91	98
8	330	0.44	210	0.59	1.78 ± 0.48	100
9	315	0.46	193	0.81	1.11 ± 0.62	100
10	126	0.86	210	0.41	9.83 ± 5.50	19
11	193	0.77	193	0.76	0.33 ± 0.33	100
12	365	0.41	257	0.50	0.17 ± 0.17	100
13	224	0.71	224	0.67	2.56 ± 1.09	100
14	330	0.48	330	0.48	4.89 ± 0.29	90
15	267	0.72	301	0.55	32.33 ± 8.45	99
16	277	0.58	267	0.67	0.33 ± 0.19	100
17	131	0.94	124	0.85	6.00 ± 0.84	100
18	462	0.18	301	0.58	4.11 ± 1.93	50
19	136	0.92	231	0.67	1.78 ± 1.61	100
20	301	0.69	315	0.44	1.44 ± 1.28	100
21	204	0.49	239	0.41	14.50 ± 0.83	49

litterbags, totora half-life was not significantly related to the whole set of environmental factors considered in this study (temperature, dissolved oxygen, fetch, depth, animal abundance, transparency and pH; multiple $r = 0.78$, $F_{6,14} = 1.87$, $P = 0.16$), but the stepwise multiple regression analysis showed that temperature, dissolved oxygen, fetch and depth (multiple $r = 0.66$, $F_{4,17} = 3.61$, $P = 0.03$) and also temperature and dissolved oxygen (multiple $r = 0.66$, $F_{2,19} = 4.42$, $P = 0.03$) can be good predictors of totora decomposition. A simple negative correlation existed between the unprotected totora half-life and the ratio of effective fetch to depth ($r = -0.62$, $P < 0.01$). The principal components analysis (PCA) indicated three components explaining 86.5% of the total variance in decomposition data (Table 5): the first component, accounting for 46.8% of the variance, included pH, water transparency and fetch, while the second component (24.3% of the total variance) invertebrate abundance and water depth, and the third component (14.9% of the total variance) water temperature and dissolved oxygen. Half-life data and factor 1 scores from PCA were significantly related ($r = 0.50$, $P = 0.02$). No relationships were observed with the other factors ($r = 0.13$ and $r = 0.17$ for factor 2 and 3, respectively; ns).

Table 2. Descriptive statistics of the half-life time (d) of the protected (P) and unprotected (UP) litterbags, animal abundance (number of individuals per litterbag) and chemico-physical parameters measured in Inner Puno Bay. SD = standard deviation, CV = coefficient of variation (%). Skewness and kurtosis for untransformed data are reported.

			Range					
Variate		Mean	min	max	SD	CV%	Skewness	Kurtosis
Half-life (d)	P	231	124	365	67	29.0	0.15	−0.67
	UP	268	126	533	108	40.3	0.66	0.07
Animal abundance (Number of individuals per litterbag)		5.99	0.11	32.33	7.86	131.2	2.05	3.97
Temperature (°C)		11.0	9.6	12.2	0.6	5.8	0.37	0.12
pH		8.65	6.38	9.13	0.74	8.6	−2.3	4.42
Dissolved oxygen (mg l^{-1})		9.15	7.70	10.58	0.78	8.5	0.01	−0.69
Transparency (cm)		58	25	75	12	20.8	−1.27	2.02

Table 3. Two-way ANCOVA of the totora mass remaining in the litterbags (factor 1 = sites; factor 2 = litterbag treatment, P vs. UP; covariable = time).

	df effect	F	P
Sites (1)	21	2.41	6.27×10^{-4}
Treatment (2)	1	5.02	0.03
1 × 2	21	1.33	0.15

Animal effects

The invertebrate community colonizing the unprotected litterbags was low in diversity. We found four species of amphipods belonging to the genus *Hyalella*, and four taxa of molluscs: *Taphius montanus* (Planorbiidae), *Littoridina* spp. (Hydrobiidae), *Anysancylus crequii* (Ancylidae) and bivalves. The amphipods were the dominant group, representing more than 90% of the invertebrate community in most sampling sites with the exception of the outer sites (sites 6, 10, 14 18 and 21; Table 1). Invertebrate abundance was low and highly variable in space (Tables 1 and 2; mean = 5.99 individuals per litterbag corresponding to 3.20 individuals g^{-1}, and range = 0–17.46 individuals g^{-1} including all data-points).

Although the half-lives of the protected and unprotected litterbags were related ($r = 0.44$, $P < 0.05$), they were on average shorter in the former than in the latter (231 d vs. 268 d; Table 2). The difference between the two treatments decreased with the increasing animal abundance, and beyond a certain threshold (*c.* three individuals per litterbag) it increased again due to faster decomposition of the unprotected totora (Figure 2).

Spatial pattern

Significant spatial autocorrelations of totora half-life time, invertebrate abundance and water temperature were found (Table 6, Figure 3). Semivariogram analysis showed that a substantial portion of the variation [C/(Co + C)] in these autocorrelated variates was spatially dependent. The spherical model was the best fit in all the cases.

The semivariance of half-life in the protected litterbags increased regularly with the separation distance, and the nugget variance amounted to 27% of the total variance

Table 5. Summary of principal components analysis performed on the environmental data collected at the 21 sampling sites in Inner Puno Bay.

	Component		
	1	2	3
(A) Principal components			
Eigenvalue	3.28	1.70	1.04
% total variance	46.80	24.35	14.90
(B) Factor loadings			
Temperature	0.41	– 0.13	0.80
pH	0.93	– 0.07	0.20
Dissolved oxygen	0.12	0.12	0.87
Transparency	0.91	0.06	0.24
Invertebrate abundance	0.18	– 0.91	– 0.14
Depth	0.46	0.82	– 0.23
Fetch	0.70	0.50	0.24

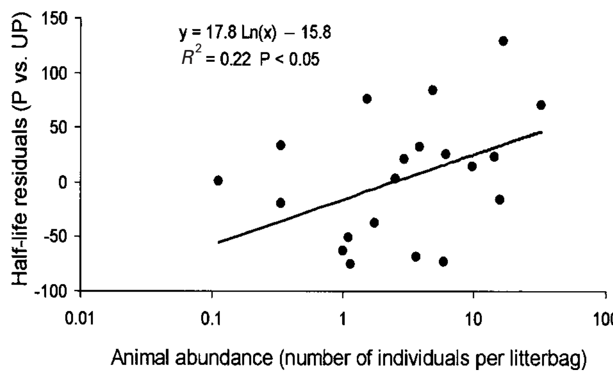

Figure 2. Residuals of the unprotected (UP) vs. protected (P) totora half-life regression as a function of animal density.

(Table 6). The decomposition rate of the unprotected litterbags had an increase of variance up to 1473 m and a negligible nugget variance. The maps indicated faster decomposition spots towards the north-western and south-western coasts, as well as at the bay entrance where unprotected totora detritus decomposed faster than the protected one (Figure 4).

The invertebrate abundance was spatially structured with the semivariogram increasing up to 3983 m (Table 6; Figure 3). The highest abundance was observed at the bay entrance. Temperature semivariogram had a range distance of 2078 m and negligible nugget variance (Table 6, Figure 3). Temperature and the half-life of the unprotected totora were also spatially co-structured,

Table 4. Regression and cross-variogram model parameters between half-life time of both unprotected (UP) and protected (P) litterbags and water temperature.

	Regression parameters			Crossvariogram parameters			
Cross-variate	model	r^2	P	Effective model	Proportion range (m)	$C/(C_0 + C)$	r^2
Half-life UP vs. temperature	Linear	0.29	0.04	Spherical	3457	0.998	0.74
Half-life P vs. temperature	Linear	0.31	0.04	–	–	–	–

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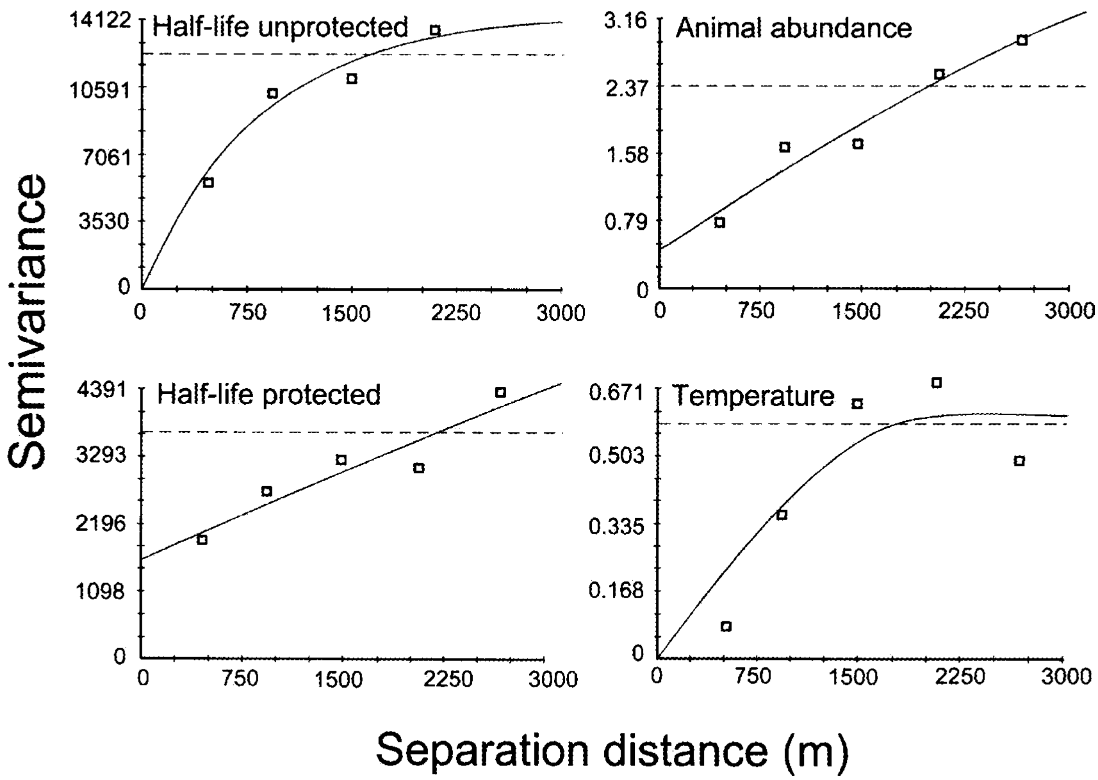

Figure 3. Semivariograms of half-life time of both unprotected and protected litterbags, water temperature and invertebrate abundance. Model parameters are shown in Table 6.

with negative slope of cross-semivariogram and co-regionalization (Table 4, Figure 5).

Invertebrate abundance was the most spatially variable parameter (CV = 131%) among those measured. It increased with the distance from the nearest sources of pollution ($r = 0.55$, $P < 0.01$). Though varying little in space (Table 2), temperature and dissolved oxygen decreased with this distance ($r = -0.56$ and $r = 0.60$ respectively, $P < 0.01$), while the totora half-life time increased (Figure 6).

DISCUSSION

The analysis of our study on *Schoenoplectus tatora* decomposition pointed out two main conclusions: (1) totora decomposed slowly, but the mass loss rate increased with increasing water temperature and at high invertebrate density; (2) mass loss rates were spatially autocorrelated and their spatial distribution showed functionally heterogeneous areas within the Inner Puno Bay.

Table 6. Semivariogram model parameters of half-life time (protected, P, and unprotected, UP, litterbags), animal abundance and temperature in Inner Puno Bay.

Variate		Lag used (m)	Model	Semivariogram model parameters			Effective range (m)	Proportion $C/(C_0 + C)$	r^2	RSS
				nugget (C_0)	sill ($C_0 + C$)	A_0(m)				
Half-life	P	600	Spherical	1560	5707	6036	6036	0.727	0.88	3.92×10^5
	UP	630	Spherical	10	12610	1473	1473	0.999	0.93	2.29×10^6
Animal abundance		600	Spherical	0.36	3.34	3983	3983	0.893	0.95	0.15
Temperature		600	Spherical	10^{-3}	0.59	2078	2078	0.998	0.86	0.05

C_0 = nugget variance; $C_0 + C$ = sill or asymptote; A_0 = range parameter used in the formula that defines the best-fit line; effective range = separation distance over which structural variance is expressed; $C/(C_0 + C)$ = relative structural variance; RSS = residual sums of squares – this provides an exact measure of how well the model fits the variogram data.

(Spherical model: $\gamma(h) = C_0 + C\ [1.5(h/A_0) - 0.5(h/A_0)^3]$ for $h \le A_0$; $\gamma(h) = C_0 + C$ for $h > A_0$; where h = lag class interval, C_0 = nugget variance ≥ 0, C = structural variance $\ge C_0$, and A_0 = range.)

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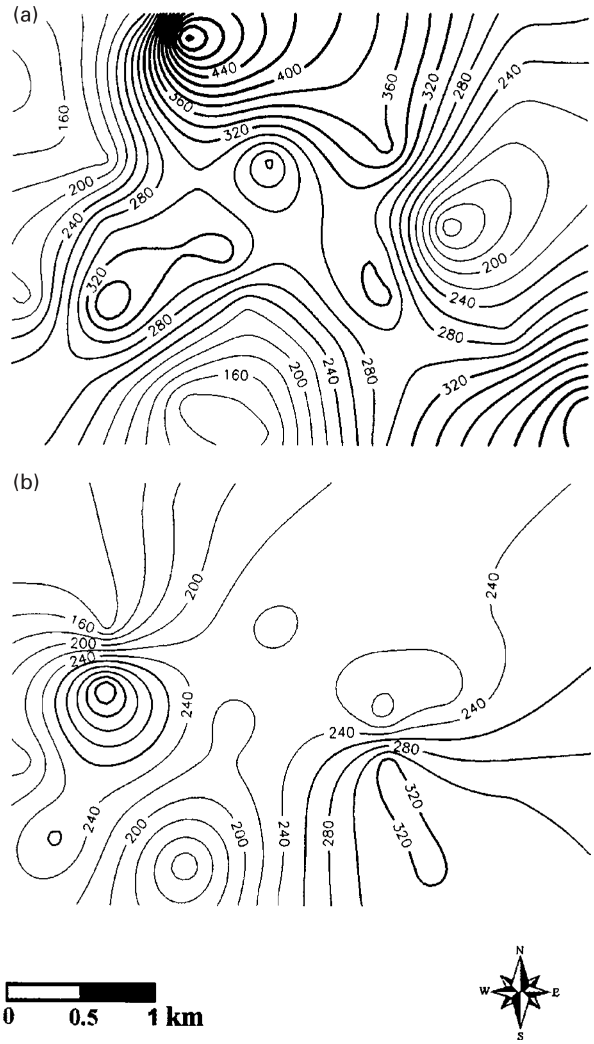

Figure 4. Interpolation map by kriging based on the half-life time (d) of unprotected (a) and protected (b) litterbags of *Schoenoplectus tatora* across the Inner Puno Bay. Values are reported on the map.

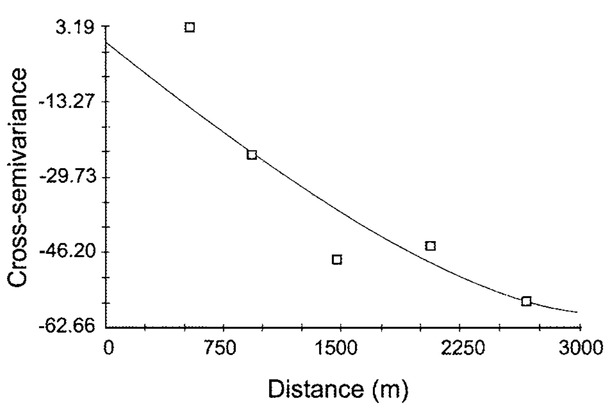

Figure 5. Cross-variogram of unprotected detritus half-life vs. water temperature. Model parameters are shown in Table 4.

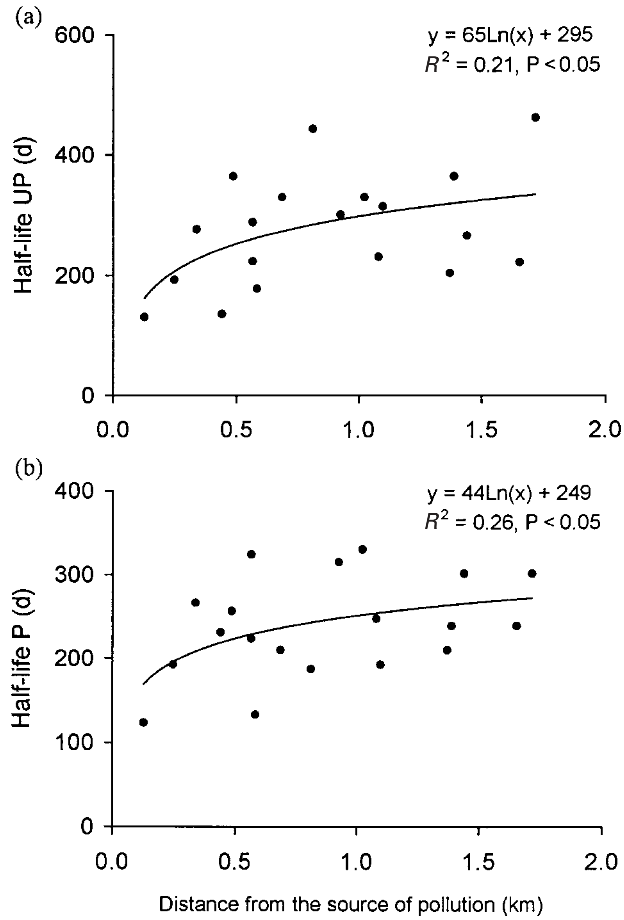

Figure 6. Relationship between the distance from the source of pollution and the half-life of (a) unprotected (UP) and (b) protected (P) litterbags.

As to the first point, *S. tatora* can be considered a slow decomposition resource according to the classification of Petersen & Cummins (1974), which is based on the coefficient rate of selected leaf species ($k < 0.05$ d^{-1} and half-life $t_{\frac{1}{2}} > 138$ d). One major cause of the low breakdown rates may be the low water temperature of Lake Titicaca. Temperature regime is known to influence the breakdown of organic matter (Carpenter & Adams 1979, Irons *et al.* 1994, Webster & Benfield 1986), but no published information is available on this subject for totora. Field studies concerning *Schoenoplectus californicus* reported even lower decomposition rates (half-life $t_{\frac{1}{2}} >$ 500 d) in warmer waters (7–23 °C) than in the bay waters (Villar *et al.* 2001). In laboratory aquaria decomposition of totora was notably faster at higher temperatures (20–25 °C) than those observed in the bay, but refractory structures still persisted after 56 d of incubation. The decomposing totora remained 'spongy' and with its cuticle almost undecomposed (Costantini pers. obs.). Factors other than temperature can also influence decomposition; among them are litter quality characteristics (Aerts 1997, Gallardo & Merino 1993, Meentemeyer 1978, Melillo *et al.* 1982). Senescing totora had relatively low percentage of lignin and ash but high percentage of hot-water-soluble substances, only portions of which were rapidly lost during the first phases of the process at the lake temperature, and cellulose (hemicelluloses and α-cellulose). The lignocellulosic component of detritus is not suitable as food for detritivores and is refractory to decomposition (Benner *et al.* 1984). Most aquatic animals do not possess the enzymes necessary to digest these polymers, but, lignocellulolytic bacteria and fungi can transform them into digestible degradation products and easily assimilable microbial biomass, which are then available to animals (Cummins & Klug 1979). The invertebrates associated with living macrophytes can exceed 100 individuals g^{-1} dry weight in some areas of Lake Titicaca, but the stands of living totora generally are the less suitable biotopes supporting less than 20 individuals g^{-1} (Dejoux 1991). Amphipods and molluscs dominate the benthic fauna and are considered of primary importance for the organic matter decomposition in Lake Titicaca (Dejoux 1991). Our litterbags collected few animals of few species, which fed preferentially on the spongy internal part of the totora where they were found. Abundance of invertebrates associated with the litterbags was spatially dependent, yet none of the measured water parameters were related to it. The high spatial variability observed could depend on the heterogeneous distribution of the aquatic vegetation, but the increase of abundance with the distance from the sources of pollution led us to hypothesize that water pollution, either directly or by changing the vegetation composition, could also play an important role in determining the invertebrate distribution within the bay. Although we have not found a very direct relationship between animal density and decomposition rate, we observed that, when abundance was below a certain threshold, decomposition was slower than in the absence of animals. Rates were faster only at the entrance of the bay in shallow waters, where invertebrate abundance and diversity were the highest in the entire bay. Several studies have demonstrated that detritivores prefer microbial-conditioned detritus rather than the plant substrate alone (Bärlocher 1985, Costantini & Rossi 1995, Rossi & Fano 1979). So at low density they can selectively remove living microbial biomass, slowing down the decomposition (Rossi 1985, Sabetta *et al.* 2000). With the increase of abundance, the plant organic mass can also be ingested and this hastens the plant breakdown (Newell & Bärlocher 1993).

Regarding the second point of discussion, the rate of totora decomposition varied significantly across the bay. Variation was higher when totora was exposed to invertebrate feeding and wave action than when only microorganisms acted. In the first case variograms showed that all apparent variance was explained by the spatial autocorrelation. The spherical model described the spatial structure of the decomposition rate of both exposed and protected totora, but variograms reached very different ranges indicating that the spatial contagiousness of the decomposition data occurred at smaller distances in the former case than in the latter. In particular, the range over which the spatial dependence of the protected totora decomposition occurred, covered the full extent of the inner bay. Furthermore, due to its high nugget variance one quarter of the decomposition variance was not spatially structured. These results let us hypothesize that in the absence of macrobenthic feeding and physical abrasion smaller sampling scales are required to fully describe the spatial structure of the totora decay in the bay. Maps showed that the decomposition rate increased towards the city of Puno in the north-west and the oxidation lagoon in the south-west whether invertebrates were present or not. Yet a steeper gradient occurred when access by invertebrates was permitted. The main explanatory variables of this variation belonged to three principal groups: variables associated with water movement (e.g. fetch, water transparency and pH), animal abundance, and temperature. The last variable turned out to be also spatially autocorrelated. Temperature is considered the main decomposition constraint on a regional scale (Chergui & Pattee 1990, Coûteaux *et al.* 1995), but in Inner Puno bay it was important also at the intra-habitat level. In fact, the half life and temperature were spatially cross-correlated, which means that the value of one at a given location statistically depended on the values of the other at a nearby location (Myers 1982, Rossi *et al.* 1992). The water temperature was also inversely related with the distance from the sewage discharges from Puno City. Consequently, the significant reduction of decomposition rate from this distance makes it difficult to find clear cause–effect relations between the process and wastewaters. However, it is likely that the local distribution of thermal pollution represents a powerful constraint for the decomposition rate as it regulates the microbial decomposer activity (Fuss & Smock 1996, Masseret *et al.* 1998, Paul *et al.* 1978, Webster & Benfield 1986). Detritivores did not change the general trend observed with temperature, but their presence increased the spatial heterogeneity of the process. Functional heterogeneity can be crucial for the bay health since in heterogeneous environments disturbances are likely to act just locally, thus affecting only patches of the entire habitat. In this perspective, gradients of functional variation on the maps (i.e. the isopleth densities) can indicate the probability of stress propagation across disturbance-prone habitat patches (i.e. their intrinsic fragility, *sensu* Ratcliffe 1977), which is expected to be higher in the less isopleth-dense patches.

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