Journal of Coastal Research | 7 | 3 | 853–862 | Fort Lauderdale, Florida | Summer 1991

Disintegration of Holothurian Fecal Pellets in Beds of the Seagrass *Thalassia testudinum*

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ABSTRACT

CONDÉ, J.E., DÍAZ, H., AND SAMBRANO, A., 1991. Disintegration of Holothurian Fecal Pellets in Beds of the Seagrass *Thalassia testudinum*. *Journal of Coastal Research*, 7(3), 853–862. Fort Lauderdale (Florida). ISSN 0749-0208.

Techniques of the lifetime data repertoire are used for detection of the disintegration pattern of fecal pellets of *Holothuria mexicana* **and** *Isostichopus badionotus* (Echinodermata: Holothuroidea), two deposit-feeders that play an important role in the cycling of nutrients in *Thalassia* beds. Pellet mounds could have different composition and be exposed to different disintegrating forces resulting in diverse patterns of disintegration. Traditional methods for lifetime analysis would have resulted in discarding about half of the data. Pellets of *I. badionotus* disintegrate completely in about 8 hours, suggesting a higher probability for being resuspended than those of *H. mexicana* which remain on the substrate after 25 hours. The hazard function of *I. badionotus* suggests a wearing disintegration process, probably due to the internal unconsolidation activity of bacterial and fungal growth. The hazard function found for *H. mexicana* suggests an accidental pattern of disintegration, probably due to the picking inspection of marine motile organisms.

ADDITIONAL INDEX WORDS: *Holothurian, fecal pellets, lifetime data, censured data, Venezuela.*

INTRODUCTION

Holothurians are common inhabitants of sheltered marine shallow-water substrates. The aspidochirote holothurians *Holothuria mexicana* and *Isostichopus badionotus* often coexist in Venezuelan *Thalassia testudinum* beds (SAMBRANO, 1987), where, as deposit feeders, they rework the sediments and due to their deposition of fecal pellets influence nutrient cycling (BAKUS, 1973; YINGST, 1976; WEBB *et al.*, 1977; SLOAN and VON BODUNGEN, 1980; MASSIN, 1982). Holothurian fecal pellets contribute to the detritus pool in coastal ecosystems. Pellets are deposited normally in a random fashion, forming fecal mounds of variable size and organic matter content, often richer than the surrounding sediment (SLOAN and VON BODUNGEN, 1980; SAMBRANO, 1987). Also, the physical instability of the mounds, produces a fecal-rich surface, which eases their resuspension by low velocity currents (RHOADS and YOUNG, 1970). This phenomenon, common amongst feces of other benthic invertebrates (ALLER and DODGE, 1974), would have effects on filter feeding organisms, larval settlement or upon the different levels of colonization processes going on around the deposition area (MASSIN, 1982). As the pellets plunge, fecal matter is transferred to the water column, promoting development and growth of some molluscs (RHOADS, 1973). Organic matter from decaying fecal pellets can be resuspended by waves, currents and biota and will influence the relative amounts of organic carbon (HOPKINSON, 1985). Resuspension seems to favor relocation of particulate material rather than dissolved nutrients (WAINWRIGHT, 1990).

Studies on fecal pellet ingestion suggest coprophagy as an important energy transfer mechanism in marine ecosystems (NEWELL, 1965; JOHANNES and SATOMI, 1966; FRANKEN-

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89018 received 24 March 1989; accepted in revision 2 January 1991.

BERG *et al.*, 1967; FRANKENBERG and SMITH, 1967). Coprophagy is commonly observed amongst deposit-feeders, including holothurians (BAKUS, 1973; HAUKSSON, 1979). *Isostichopus badionotus*, might feed on its own feces (SLOAN and VON BODUNGEN, 1980); the authors associate this fact with the occurrence of *I. badionotus* in sheltered waters. *Stichopus tremulus* selectively feeds on "faecal pellets" and "sediment aggregates" of high organic content (HAUKSSON, 1979). Thus, pellet disintegration time may become an important factor when considerations are made on the nutrient recycling or feces exploitation as nutrient source.

Most of the published work on the microbial colonization and fecal pellets disintegration has been carried out using feces of planktonic crustacea, primarily copepods (HONJO and ROMAN, 1978; TURNER, 1979; BATHELT and SCHELSKE, 1983; GOWING and SILVER, 1983; JACOBSEN and AZAM, 1984; LAMPITT *et al.*, 1990; WAINWRIGHT, 1990). Protozoan and bacteria rapidly colonize copepod fecal pellets, causing their degradation and dispersal in a period of days to weeks (HONJO and ROMAN, 1978; PAFFENHÖFER and KNOWLES, 1979; TURNER, 1979; ALLDREDGE *et al.*, 1987). Feces degradation may also be affected by coprorhexy, as suggested by LAMPITT *et al.*, 1990. Rapid pellet disintegration seems to occur also for small oceanic tunicates (POMEROY and DEIBEL, 1980; POMEROY *et al.*, 1984). The larger and denser fecal pellets of larger salps appear to be less susceptible to microbial colonization and degradation (CARON *et al.*, 1989). SAMBRANO and DIAZ (1986) and SAMBRANO (1987), studied the disintegration time for feces of *Isostichopus badianotus* and *Holothuria mexicana* at Venezuelan coasts. Although time of pellet permanence in the *Thalassia* beds was registered from the instant of deposition until complete dissolution, due to time constraints, observations were not always completed. In those cases, only the lower or upper data on lifetime was available. Using lifetime data analysis the incomplete or censored data could have been analyzed (COHEN, 1965; KALBFLEISCH and PRENTICE, 1980). Suitable techniques to analyze incomplete data have been rarely used (GONZALO *et al.*, 1982; MUENCHOW, 1986; PYKE and THOMPSON, 1986). Traditional life table and survival analysis, as used in ecology, can not use incomplete data. The present paper utilizes these techniques in a study of the dissolution time pattern of fecal pellets of two holothurian species that coexist in *Thalassia* beds at the Morrocoy National Park, Falcón, Venezuela.

MATERIALS AND METHODS

Preliminary experiments were carried out in *Thalassia* beds at Morrocoy National Park, on the Western Venezuelan coasts. Forty pellet mounds of each species, *Isostichopus badionotus* and *Holothuria mexicana*, were periodically observed from the time they were deposited until they disappeared. Their lifetime (permanence) was registered in minutes. After 20 pellets from each species dissolved, the experiment was concluded and the remaining pellets were considered censored (KALBFLEISCH and PRENTICE, 1980).

Although survivorship is not computed for censored times, these do contribute information through the ranking of times. The product-limit estimate (KAPLAN and MEIER, 1958) of the survivorship function, the clinical life table and the survival functions, the MANTEL and HAENSZEL (1959) test, and approximation to model specification survival data are alternative methods considered to process censored observations. The terms survival time, fade-out time, dissolution time, disintegration time and disappearance time, are considered synonymous.

The Kaplan-Meier estimate, while using all collected information, provides a general description of the permanence patterns of the holothuroid's fecal pellets in the environment and their disintegration dynamics. Any other test employed to compare the curves should be less powerful, it would result in discarding much of the collected data.

After the preliminary survey, an extensive field study was undertaken. We observed 244 pellet mounds of *H. mexicana* and 146 of *I. badionotus* from the moment of their deposition at intervals of one hour until they disintegrated or were censored. Observations at night were not possible so some pellets had disintegrated by morning and were treated as censored data at the last time they were observed intact. Experiments were started as pellets were available, so that not all the experiments had concluded after the study; those pellets were also considered as censored observations.

The hazard function reflects the proneness of an individual or component to disappear as a function of time from the beginning of the experiment. For data arranged in intervals, such as those in a life-table, GEHAN and SIDDIQUI (1973) generalized a proposition of KODLIN (1967), suggesting a regression method based on the hazard functions of exponential, linear exponential, Gompertz or Weibull distributions. Each of these hazard functions can be expressed as linear functions of t or ln (t). Therefore, it is possible to make an analysis of regression/correlation and to select the best model using the mean square error of residuals (MSER). Because of its simplicity, we used this method.

A confirmatory analysis of the differences in the survival pattern of both species is obtained using the MANTEL and HAENSZEL (1959) Chi-Square Test allowing comparison of two survival distributions with grouped and censored data. The analysis follows a Chi-Square distribution with one degree of freedom and so can be compared with a tabulated value of Chi-square.

RESULTS

In the preliminary survey a product-limit estimate of survivorship was obtained (Table 1). Pellets of *Isostichopus badionotus* disappear after 375 min, while more than 30% from *Holothuria mexicana* remained on the substrate after 469 min at the end (Figure 1). Median permanence times of 269 min for pellets of the former and 402 min for the latter species were registered. The survivorship curves of pellets of the two species show mixed rates of disintegration. Pellets of *I. badionotus* show three distinct moments of increased loss. *Holothuria mexicana* pellet survival curve is characterized by two different rates, one from 0 to 120 min and the other one up to 469 min.

For the extensive field study, Table 2 shows the complete and censored times of permanence, grouped in 1 min intervals. Columns 2 and 3 include, for each interval, those individuals lost to follow-up and those withdrawn intact or alive (for another study); that is, censored data. Columns 4 to 8 show the variables generated through the lifetime analysis for estimating function values. These functions (Figure 2) are equivalent and closely related, but each of them can be used to analyze and show a particular feature of the data. The variance of the functions (from Columns 9, 10, and 11), allow building the confidence intervals for contrasting statistical hypothesis; *i.e.*: equal disintegration patterns for pellets of both species.

The hazard function detected for each species, expressed as regression formulas are:

I. badionotus: $h(t) = -0.0049 + 0.0544t$

H. mexicana: $h(t) = 0.0422 - 0.0012t$

The slope of the linear exponential equation fitted does not deviate significantly from zero for *H. mexicana* (Table 3); thus, a constant hazard rate can be accepted and, the exponential distribution can be used as a model to describe the pellet disappearance pattern. The linear exponential, allows for an increasing or decreasing hazard function dependent on time or age.

The survival function, shown as a survivorship curve (Figure 1), can be obtained from the clinical life table. This is shown in Figure 2C. The pellets of *Isostichopus badionotus* begin to disintegrate before those of *Holothuria mexicana*. All the pellets of *I. badionotus* disappeared after 8 hours; while those of *H. mexicana* remain in the *Thalassia* beds, many of them remaining on the sediment after 25 hours. Again, these pellets show a mixed pattern of disintegration, one from the start of the experiments up to 8 hours and another with a smaller slope for the remainder of the experiment.

The Mantel-Haenszel Chi-Square test revealed a $\chi^2 = 60.020$, which is larger than the tabulated value, 3.941, for a significance level of 0.05. This result confirms the information from the graphs, the distributions of disintegration times for pellets of both species are significantly different.

DISCUSSION

When compared to the surrounding substrate, the holothuroid fecal mounds, due to their somewhat higher organic matter content (SLOAN and VON BODUNGEN, 1980; SAMBRANO, 1987), could be regarded as high energy spots which, depending on the species and other factors, can exhibit different rates of depletion. As high energy spots, disintegration time of fecal mounds should be an important factor for the nutrient cycle in shallow subtidal sediments. Fecal mounds might contribute to particulate organic matter resuspension and dispersal

Table 1. *Kaplan-Meier estimate (ŝt) of disintegration times (t) in minutes for fecal pellets of two holothurian species.*

	Holothuria mexicana			*Isostichopus badionotus*		
i	t	r	ŝt	t	r	ŝt
1	123	1	0.975	55	1	0.975
2	123	2	0.950	70	2	0.950
3	135 +			85	3	0.925
4	161	4	0.924	85	4	0.900
5	161	5	0.899	86	5	0.875
6	161	6	0.873	87	6	0.850
7	175	7	0.847	90	7	0.825
8	175	8	0.822	105	8	0.800
9	181 +			144 +		
10	181 +			144 +		
11	183	11	0.794	167	11	0.773
12	193	12	0.767	167	12	0.747
13	209	13	0.739	171 +		
14	218	14	0.712	171 +		
15	218	15	0.685	171 +		
16	227	16	0.657	171 +		
17	309 +			171 +		
18	328 +			171 +		
19	328 +			171 +		
20	328 +			176 +		
21	238 +			176 +		
22	345	22	0.623	193 +		
23	345	23	0.588	193 +		
24	354	24	0.554	193 +		
25	371 +			219	25	0.700
26	371 +			232	26	0.653
27	371 +			232	27	0.607
28	371 +			234	28	0.560
29	392	29	0.507	251 +		
30	421	30	0.461	309 +		
31	429	31	0.415	317 +		
32	442 +			317 +		
33	446 +			317 +		
34	446 +			317 +		
35	446 +			322	35	0.467
36	446 +			322	36	0.373
37	469	37	0.311	326	37	0.280
38	526 +			351	38	0.187
39	526 +			351	39	0.093
40	1505 +			375	40	0.000

Symbols +: censored datum; i: rank of observations; r: rank of complete observation.

throughout the water column (*sensu* CARON *et al.*, 1989; WAINWRIGHT, 1990; LAMPITT *et al.*, 1990). Also, for the long-lasting fecal pellets, there is the possibility of becoming a suitable substrate for settlement and growth of other organisms. Due to their high organic matter content, holothurian feces might have, as such, a substantial rate of nutrient return for deposit-feeders (HARGRAVE, 1976; LEVINTON *et al.*, 1984). Fecal pellets of *Isostichopus badionotus* disappear before those of *Holothuria mexicana* and show a linearly increasing hazard rate; that is, as time elapses, the probability of a pellet disappearing increases. This type of hazard function is typical of those processes where wearing down occurs. Pellets of *H. mexicana* remain longer on the substrate and its hazard function suggests a different process of removal. Although the best fit for this species was obtained for a linear exponential model with a slightly decreasing hazard function; the exponential model had a MSER very close to that of the linear exponential model. The exponential distribution shows a constant hazard rate. This is characteristic of processes where wearing is not the main cause of failure and

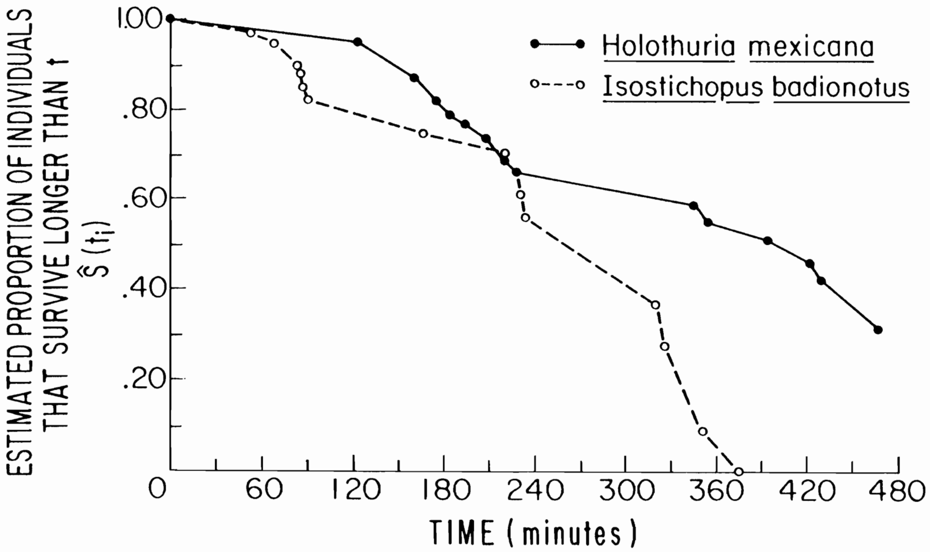

Figure 1. Survival curves for fecal pellets of two holothurian species in *Thalassia* beds of Morrocoy National Park, Venezuela.

this happens accidentally. In these processes the probability of disappearance or death does not depend on the previous history of the individual or component observed (BURY, 1975).

Fecal pellets of *I. badionotus* contain more organic matter than those of *H. mexicana* (SAMBRANO and DIAZ, 1986; SAMBRANO, 1987). Thus, rapid bacterial and fungal growth could be expected; this would facilitate loosening of the pellets, and the destruction of the mucous membrane that surrounds the fecal material (HONJO and ROMAN, 1978), bringing about the wearing process observed. In this case, resuspension of organic matter would be easier. Due to the low content in organic matter of *H. mexicana* pellets, the bacterial or fungal contribution to their break down does not seem as important, at least initially. Thus, pellets remain longer on the substrate and their chance of being exposed to the catastrophic action of picking inspection of crustaceans, fishes, and other organisms is greater than for *I. badionotus*. In addition, pellets of *H. mexicana* seem to attract animals more often than those of *I. badionotus* (SAMBRANO, 1987), a factor that also can contribute to the accidental disappearance pattern. The chance for encounters between pellets mounds and moving disturbers, has a constant hazard rate.

Pellets of *H. mexicana* sustain erosion through time and fuse with the sediment. They become less apparent to the curiosity of benthic organisms; a fact that could explain the slight, although not statistically significant, tendency of its hazard rate to decrease in time.

For field situations such as the one we encountered, where gathering information could be jeopardized by incidents and by time constraints, lifetime data analysis resulted as an appropriate alternative for the fecal mounds disintegration time study. Little work has been done documenting this aspect of the holothurian biology. Holothurian fecal mounds seem to induce bioturbation and organic matter cycle modifications on the water column and on the sediments (RHOADS and YOUNG, 1971; RHOADS, 1973; MOSHER, 1980; MASSIN, 1982). Thus, it seems appropriate to incorporate information such as that presented here in models oriented toward the understanding of benthic community dynamics.

ACKNOWLEDGEMENTS

This work was partially financed by the Consejo Nacional de Investigaciones Científicas y Technológicas (CONICIT), Venezuela, through scholarships to J.E.C. and A.S. From B. Ori-

Table 2. *Life table calculations for fecal pellets of two holothurians.*

1 Time interval $t_i - t_{i+1}$	2 Number lost to followup l_i	3 Number withdrawn alive w_i	4 Number dying d_i	5 Number entering interval n'_i	6 Number exposed to risk n_i	7 Conditional proportion dying $\hat{q}_i$	8 Conditional proportion surviving $\hat{p}_i$	9 Square root of variance of $\hat{S}(ti)$ $\sqrt{VAR[\hat{S}(t_i)]}$	10 Square root of variance of $\hat{f}(t_{mi})$ $\sqrt{VAR[\hat{f}(t_{mi})]}$	11 Square root of variance of $\hat{h}(t_{mi})$ $\sqrt{VAR[\hat{h}(t_{mi})]}$
Holothuria mexicana										
0–1	0	2	0	244	243.0	0.000	1.000	—	0.000	0.000
1–2	0	2	4	242	241.0	0.017	0.983	0.000	0.008	0.008
2–3	15	2	11	236	227.5	0.048	0.952	0.008	0.010	0.015
3–4	30	2	13	208	192.0	0.068	0.932	0.016	0.017	0.019
4–5	0	2	4	163	162.0	0.025	0.872	0.023	0.011	0.013
5–6	40	2	9	157	136.0	0.066	0.934	0.025	0.018	0.023
6–7	12	2	7	106	99.0	0.071	0.929	0.029	0.021	0.028
7–8	20	2	6	85	74.0	0.081	0.919	0.034	0.024	0.035
8–9	6	2	1	57	53.0	0.019	0.981	0.039	0.013	0.019
9–10	0	2	1	48	47.0	0.021	0.979	0.040	0.014	0.022
10–11	0	2	1	45	44.0	0.023	0.977	0.042	0.015	0.023
11–12	0	2	1	42	41.0	0.024	0.976	0.044	0.015	0.025
12–13	0	2	0	39	38.0	0.000	1.000	0.045	0.000	0.000
13–14	0	2	0	37	36.0	0.000	1.000	0.045	0.000	0.000
14–15	0	2	0	35	34.0	0.000	1.000	0.045	0.000	0.000
15–16	0	2	1	33	32.0	0.031	0.969	0.045	0.019	0.032
16–17	0	2	1	30	29.0	0.035	0.066	0.048	0.021	0.035
17–18	0	2	0	27	26.0	0.000	1.000	0.050	0.000	0.000
18–19	0	2	0	25	24.0	0.000	1.000	0.050	0.000	0.000
19–20	0	2	0	23	22.0	0.000	1.000	0.050	0.000	0.000
20–21	0	2	1	21	20.0	0.050	0.950	0.050	0.028	0.051
21–22	0	2	0	18	17.0	0.000	1.000	0.056	0.000	0.000
22–23	0	2	0	16	15.0	0.000	1.000	0.056	0.000	0.000
23–24	0	2	1	14	13.0	0.077	0.923	0.056	0.041	0.080
24–25	0	2	0	11	10.0	0.000	1.000	0.066	0.000	0.000
25	0	0	9	9	9.0	1.000	0.000	0.066	—	—

Isostichopus badionotus										
0–1	0	2	3	146	145.0	0.021	0.979	—	0.012	0.012
1–2	0	2	13	141	140.0	0.093	0.907	0.012	0.024	0.027
2–3	41	2	10	126	104.5	0.096	0.904	0.026	0.026	0.032
3–4	12	2	11	73	66.5	0.165	0.835	0.035	0.037	0.054
4–5	8	2	9	48	43.0	0.209	0.791	0.047	0.043	0.077
5–6	9	2	7	29	23.5	0.298	0.702	0.056	0.053	0.130
6–7	3	2	3	11	8.5	0.273	0.727	0.064	0.060	0.205
7–8	0	0	3	3	3.0	1.000	0.000	0.073	—	—

t_{mi}: midpoint interval; b_i: width of interval, in this case = 1.
$n'_i = n'_{i-1} - w_{i-1} - d_{i-1}$
$n_i = n'_i - (l_i + w_i)/2$. It is assumed that the times of loss and withdrawal are uniformly distributed.
$\hat{q}_i = d_i/n_i$; $\hat{p}_i = 1 - \hat{q}_i$
$\hat{S}(t_i) = \hat{P}_i = \hat{p}_{i-1}\hat{P}_{i-1}$; $i = 2, \ldots, 3$ and $\hat{P}_1 = 1$. Estimate of the survivorship function.
$\hat{f}(t_{mi}) = (\hat{P}_i - \hat{P}_{i+1})/b_i$; $i = 1, \ldots, s - 1$ Estimate of the probability density function.
$\hat{h}(t_{mi}) = 2\hat{q}i/[b_i(1 + \hat{p}_i)]$, $i = 1, \ldots, s - 1$ Hazard function or rate.

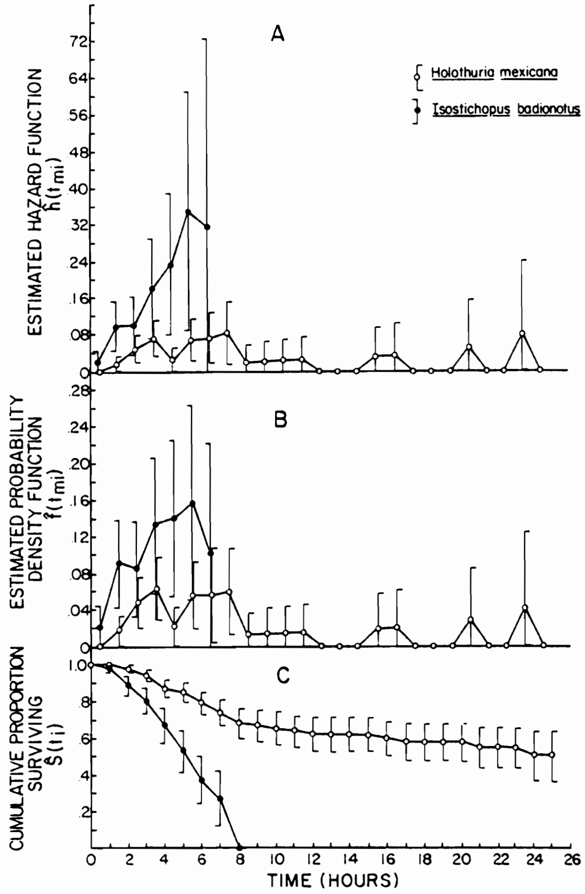

Figure 2. Estimated values for survivorship functions of fecal pellets of two holothurian species: (A) Hazard rate, (B) Probability density function, (C) Survival function. 95% confidence limits are indicated.

Table 3. *Summary of regression/correlation and residual analysis of hazard functions of disappearance times of fecal pellets of* Holothuria mexicana *and* Isostichopus badionotus.

Distribution	Intercept	Slope	Correlation Coefficient	Mean Square Error of Residuals
Holothuria mexicana				
Weibull	− 5.1500	− 2.2799	− 0.2492	0.0012
Gompertz	− 3.6024	− 0.5310	− 0.4468	0.0015
Linear exponential	0.0422	− 0.0012[c]	− 0.2998	0.0008
Exponential	0.0272	0	—	0.0008
Isostichopus badionotus				
Weibull	− 3.0452	1.0706	0.9838[a]	0.0008
Gompertz	− 3.4241	0.4125	0.9135[a]	0.0044
Linear exponential	− 0.0049	0.0544[b]	0.9677[a]	0.0008
Exponential	0.1855	0	—	0.0126

[a] Significant ($p < 0.01$)

[b] Significantly different from 0 ($t = 8.61$; $p < 0.005$, df = 5)

[c] Slope = 0 can be accepted ($t = -0.6990$, $0.095 < p < 0.99$)

huela we received much appreciate assistance. We received valuable suggestions from C.J. Dawes (University of South Florida) and unidentified reviewers.

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□ RÉSUMÉ □

Les techniques répertoriant les temps de vie sont utilisées pour déterminer les modes de désagrégation des pelotes de défécation de *Holothuria mexicana* et *Isostichopus badionotus* (Echinodermata, Holothuroidea), qui sont deux sources de dépôts jouant un rôle important dans le cycle de nourriture des lits à *Thalassia*. Les accumulations de pelotes peuvent avoir différentes compositions et être exposées à différentes forces de désintégration qui donnent divers modes de désagrégation. Les méthodes d'analyse traditionnelle du temps de vie auraient abouti à écarter la moitié des données. Les pelotes de *I. badionotus* se désagrègent complètement au bout de 8 heures, ce qui leur donne une forte probabilité de remise en suspension par rapport à *H. mexicana* qui demeure encore sur le substrat aprés 25 heures. La fonction aléatoire de *I. badionotus* suggère un processus de désintégration par usure pouvant être dû à la non consolidation de l'activité interne de la croissance bactérienne et fongique. La fonction aléatoire trouvée pour *H. mexicana* suggère une désagrégation accidentelle, peut-être provoquée par le grapillage des organismes marins mobiles.—*Catherine Bousquet-Bressolier, Géomorphologie EPHE, Montrouge, France.*

□ ZUSAMMENFASSUNG □

Verschiedene Techniken zur Bestimmung des Lebensalters wurden benutzt zur Auffindung des Zersetzungsmusters von Fäkalkügelchen von *Holothuria mexicana* und *Isostichopus badionotus* (Echinodermata: Holothuroidea), zwei Detritusfresser, die eine wichtige Rolle in dem Nahrungskreislauf in *Thalassia*-Ansammlungen spielen. Die Fäkalkügelchenhügel können eine unterschiedliche Zusammensetzung haben und können unterschiedlichen Zersetzungskräften ausgesetzt sein was unterschiedliche Zersetzungsmuster zur Folge hat. Die Anwendung traditioneller Methoden zur Bestimmung des Lebensalters würde ergeben, daß mehr als die Hälfte der Daten ausgesondert werden müßten. Kügelchen von *I. badionotus* verwittern vollständig in ca. 8 Studen; dieses legt den Schluß nahe, daß sie mit höherer Wahrscheinlichkeit resuspendiert werden als die Kügelchen von *H. mexicana*, welche auf dem Substrat auch noch nach 25 Stunden zu finden sind. Die Zerfallsgeschwindigkeit von *I. badionotus* suggeriert einen Verwitterungsprozeß, der wahrscheinlich auf die innere zersetzende Aktivität von Bakterien- und Pilzwachstum zurückzuführen ist. Die Zerfallsgeschwindigkeit, die bei *H. mexicana* gefunden wurde, macht ein zusätzliches Zersetungsmuster wahrscheinlich, welches seine Ursache wohl in der mechanischen Berührung durch marine freibewegliche Organismen hat.—*Ulrich Radtke, Geographisches Institut, Universität Düsseldorf, F.R.G.*