

## On the dynamics of exploited populations of *Tisbe holothuriae* (Copepoda, Harpacticoida)

### V. The toxicity of cadmium: Reponse to sub-lethal exposure

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**ABSTRACT:** A total of 30 weekly exploited populations of the harpacticoid copepod *Tisbe holothuriae* Humes were exposed to 148 or 222  $\mu\text{g Cd}^{++} \text{ l}^{-1}$ , combined with exploitation rates of 10, 30, 50, 70 or 90 % under conditions of surplus food supply at 22 °C and 30 ‰ S. During the observation period, most populations exhibited distinct U-shaped density trends. Addition of  $\text{Cd}^{++}$  prolonged and reinforced the downward trends present in the initial periods of the experiments. If population densities, both in control and test populations, fell short of a certain value, the age structures shifted in favour of the nauplii. More pronounced reductions in population densities of the test populations did not result in increased elevations of the nauplius fraction. Within 23 weeks (or 20 generations), the effect of  $\text{Cd}^{++}$  on population density was counteracted by an acclimation process. No relationship could be established between exploitation rate and observed effects. Erroneous assumptions on the adaptability of parametric methods had led to invalid statements on the dispersion of data published in previous papers of this series. These statements have been revised. Possible limitations of the significance of the results obtained are discussed in some detail.

### INTRODUCTION

In recent years attention has repeatedly been called to problems concerning pollution of aquatic environments by cadmium (cf. a recently published paper on economic and social aspects of cadmium pollution by Nobbs & Pearce, 1976, and literature cited by Hoppenheit & Sperling, 1977). Up to now, the majority of papers dealing with effects of cadmium on aquatic organisms have been concerned with acute exposures to the pollutant. However, today one frequently encounters the statement that knowledge of the concentration of a pollutant which kills 50 % of test specimens in a given time is insufficient to assess an acceptable non-toxic concentration (cf. Sprague, 1971; Olla, 1974; Nobbs & Pearce, 1976). Studies on acute toxicity may have serious limitations because, for example, they ignore differences in the sensibility of a test species throughout several consecutive generations (Winner & Farrell, 1976), the possibility of the occurrence of adaptations (Stockner & Antia, 1976) and the impairment of reproduction at concentrations in which there is no effect on survival (Mount, 1968).

Since cadmium has been proven to be highly toxic to aquatic organisms (cf. Anderson, 1950; Kumada et al., 1973; Baudouin & Scoppa, 1974; Vernberg et al., 1974, and literature cited by Hoppenheit & Sperling, 1977) and because of the obviously great need for data on the effects of chronic exposure, it appeared reasonable to conduct experiments with *Tisbe holothuriae* which has previously been shown to be an appropriate organism to study several components of its population dynamics in the laboratory (cf. Hoppenheit, 1975a, b; 1976).

## MATERIAL AND METHODS

All experiments were made in essentially the same manner as those described in previous papers (Hoppenheit, 1975a, b; 1976; Hoppenheit & Sperling, 1977).

The populations of *Tisbe holothuriae* Humes were maintained in 200 ml of non-aerated sea-water in 500-ml, wide-mouth, flat-bottom flasks at  $22 \pm 1^\circ \text{C}$  in a room having 12 h light per day. Fifteen populations were each exposed to 148 and 222  $\mu\text{g Cd}^{++} \text{l}^{-1}$ . Both groups were subdivided into groups of three replicates each, which were exploited weekly at rates of 10, 30, 50, 70 or 90 % according to the table presented by Hoppenheit & Sperling (1977, p. 330). The specimens were fed dried mussel flesh (mantle) once a week following exploitation. At the time of weekly exploitation, 90 % of the contaminated medium was renewed. In samples of 10 ml drawn before the harvests, the numbers of nauplii and adults plus copepodids were determined.

For further details the reader is referred to previous publications of this series.

## RESULTS

In a study on the effects of  $\text{Cd}^{++}$  on weekly exploited populations of *Tisbe holothuriae* (Hoppenheit & Sperling, 1977) it has been shown that concentrations of 222  $\mu\text{g Cd}^{++} \text{l}^{-1}$  or less do not result in extinction of an exploited population.

The characteristics of distributions of population-density data in three populations exploited weekly at rates of 30, 50 or 90 % (cf. Fig. 1) before and after the addition of 148  $\mu\text{g Cd}^{++} \text{l}^{-1}$  are given in Table 1. Density data obtained at the initial phase of population development are not taken into consideration. The distributions were found to be approximately normal and free of trend. Comparisons of the means by use of the t-test yielded significant differences between the time series before and after addition of  $\text{Cd}^{++}$  ( $\alpha < 0.01$ ). No further approximately normal distribution together with independence of density data has been found at the same time in both parts of an experiment in the remaining 12 populations exposed to 148  $\mu\text{g Cd}^{++} \text{l}^{-1}$ .

All populations exposed to 222  $\mu\text{g Cd}^{++} \text{l}^{-1}$  displayed deviations from normality and/or randomness to such an extent that no attempt has been made to test the significance of differences between time series belonging together. The results of experiments carried out at an exploitation rate of 10 % are shown in Table 2.

Six populations exploited at a rate of 10 % served as controls in order to distin-

gish disturbing influences of unknown and uncontrollable factors which possibly would have been able to mask or to simulate an effect in the period following addition of  $\text{Cd}^{++}$ . Five populations exhibited significant trends in population densities. Figure 2 presents the smoothed course of population density of a control experiment over a period of 70 weeks. The curve has been smoothed by moving an average of 3 items. The use of a new sea-water charge in Week 1 is followed by an increase of population density until Week 4. Owing to this effect it is assumed that the new charge of sea-water, recently placed at our disposal by ship, had better properties than the stored

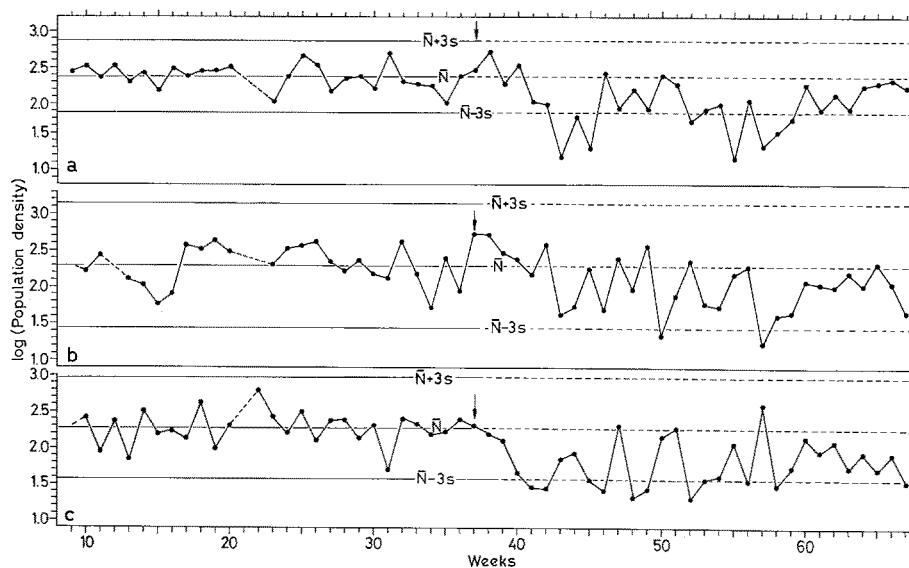


Fig. 1: *Tisbe holothuriae*. Courses of population densities in three populations at weekly removals of 30 (a), 50 (b) or 90% (c) of specimens before and after addition of  $148 \mu\text{g Cd}^{++} \text{ l}^{-1}$  (indicated by an arrow)

water used before. A steady deterioration of "quality" of the water in subsequent weeks and an acclimation process were supposed to interact and to produce the U-shaped trend, which is exhibited more or less distinctly by all 36 populations under consideration. A detailed account of acclimation processes will be given in consecutive papers (Hoppenheit, in preparation). For the present, therefore, only an indication of the existence of such processes will be given.

As test populations were established 10 weeks earlier than controls the reaction to water from the renewed supply can be demonstrated more distinctly in the former. The courses of population densities in two populations exposed to  $148$  and  $222 \mu\text{g Cd}^{++} \text{ l}^{-1}$ , respectively, have been plotted in Figure 3. Again, the curves have been smoothed by moving an average of 3 items. Obviously the use of sea-water newly placed at disposal (Arrow I) resulted in a considerable population growth. In the population exploited weekly at a rate of 90% the increase of population density is retarded.

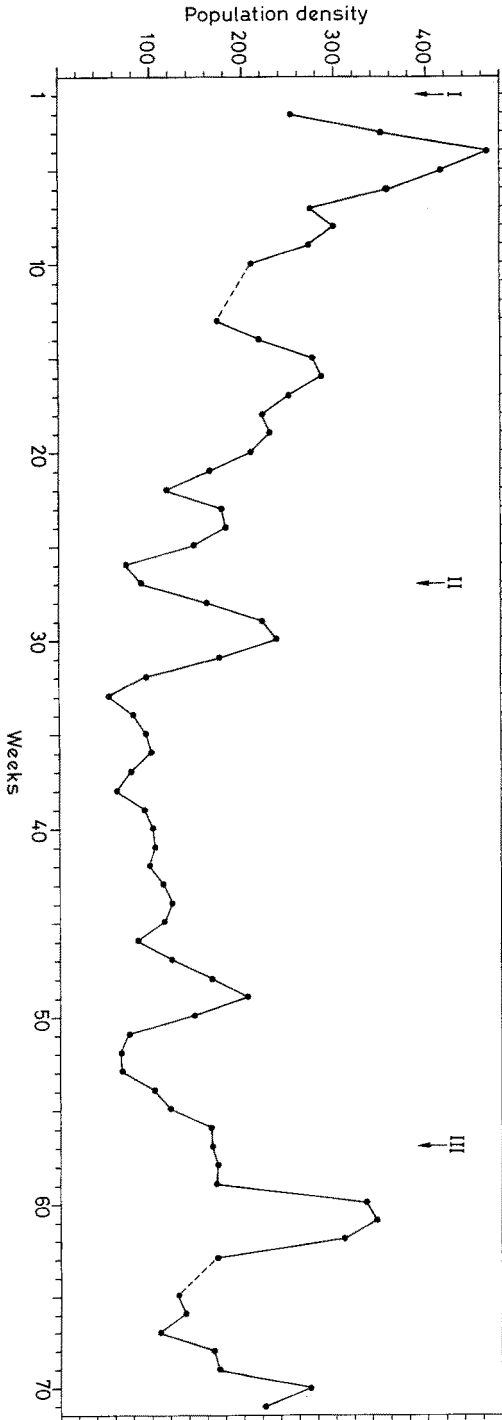


Fig. 2: *Tisbe holothuriae*. Course of population density (moving average of 3 items) in a control population at weekly removal of 10% of specimens. Use of a new sea-water charge at arrow I, addition of Cd<sup>++</sup> to test populations at arrow II, termination of test experiments at arrow III

Table 1

Mean population densities prior to removal of specimens in three exploited populations of *Tisbe holothuriae* exposed to  $148 \mu\text{g Cd}^{++} \text{l}^{-1}$  before (1) and after (2) addition of  $\text{Cd}^{++}$ . Explanation of symbols used in Tables 1 to 9: k number of populations; N population density;  $N_i$  population density at renewal of 90% of water per week;  $N_2$  population density at renewal of 50% of water per week; N median of population density; n size of a sample; p relative frequency; s standard deviation; V coefficient of variation

Characteristics	30 %/o		Exploitation rate 50 %/o		90 %/o	
	(1)	(2)	(1)	(2)	(1)	(2)
$\overline{\log N}$	2.3750	2.0185	2.3046	2.0396	2.2693	1.8003
$S_{\log N}$	0.1646	0.3618	0.2820	0.3747	0.2323	0.3373
n	27	30	25	30	27	30

Table 2

Mean population densities prior to removal of specimens in three populations of *Tisbe holothuriae* exploited at a rate of 10% before (1) and after (2) the addition of  $222 \mu\text{g Cd}^{++} \text{l}^{-1}$ . (For explanation of symbols see Table 1)

Characteristics	Experiment A		Experiment B		Experiment C	
	(1)	(2)	(1)	(2)	(1)	(2)
$\overline{\log N}$	2.3994	1.8732	2.3773	1.7187	2.4207	1.8274
$S_{\log N}$	0.2932	0.6091	0.2324	0.5560	0.2843	0.5416
n	26	30	26	30	26	30

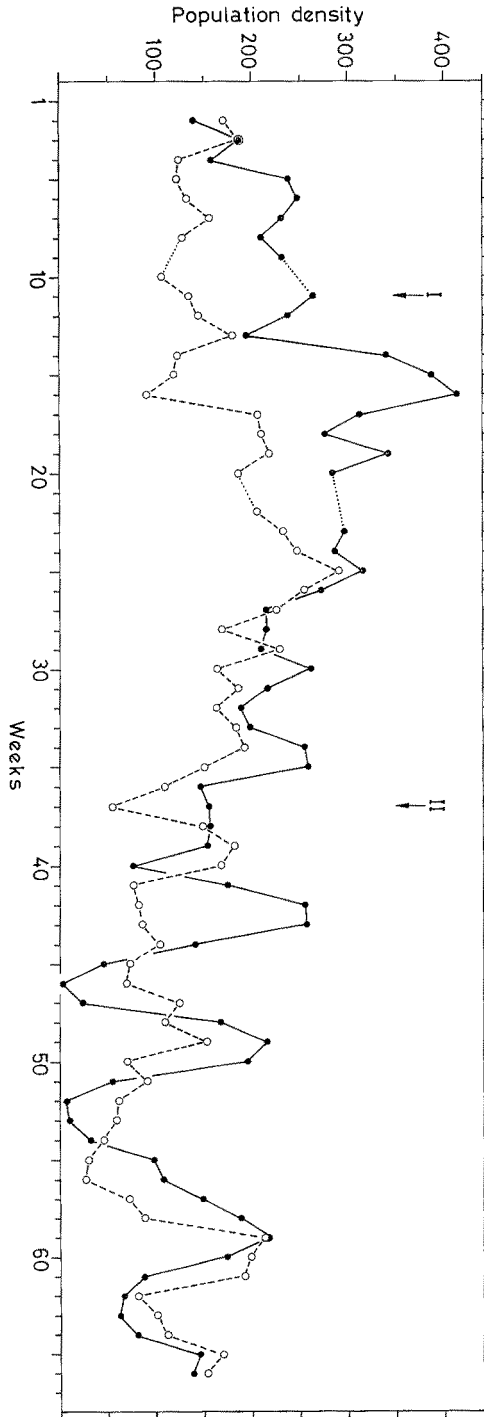


Fig. 3: *Tisbe holothuriae*. Courses of population densities (moving averages of 3 items) in two populations exposed to 148 µg Cd<sup>++</sup> l<sup>-1</sup> and 10 ‰ exploitation (●) or 222 µg Cd<sup>++</sup> l<sup>-1</sup> and 90 ‰ exploitation (○). (For further explanations see Fig. 2).

For comparison of tendencies in control and test populations Figure 4 was prepared. Since the test of Dixon for the analysis of extreme values (cf. Sachs, 1968; p. 278 f.), which is rather insensitive to deviations from normality and homogeneity of variance, showed no significant differences between population densities either in

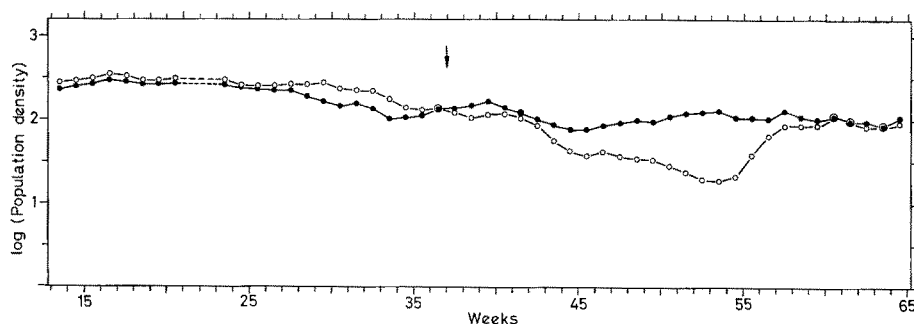


Fig. 4: *Tisbe holothuriae*. Courses of mean population densities (moving averages of 6 items) of pooled control (●) and test populations (○) exploited weekly at a rate of 10% before and after the addition of  $\text{Cd}^{++}$  (indicated by an arrow)

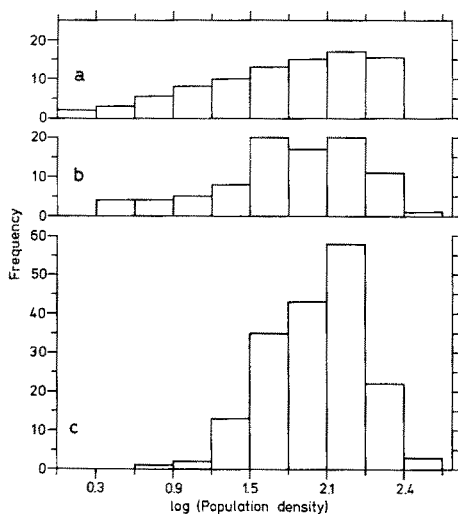


Fig. 5: *Tisbe holothuriae*. Frequency distributions of densities of pooled control populations (c) and populations exposed to 148 (a) 222  $\mu\text{g Cd}^{++} \text{l}^{-1}$  (b). Exploitation rate: 10%

the six control populations or in the six test populations exposed to 148 or 222  $\mu\text{g Cd}^{++} \text{l}^{-1}$  the data of either group were pooled and average-population densities were calculated for every point of time. The resulting curves of means were smoothed by moving an average of 6 items to obtain a distinct picture of the essential events. Figure 4 illustrates that the downward trend was prolonged and reinforced in the test populations after addition of sub-lethal amounts of  $\text{Cd}^{++}$ . While in the controls

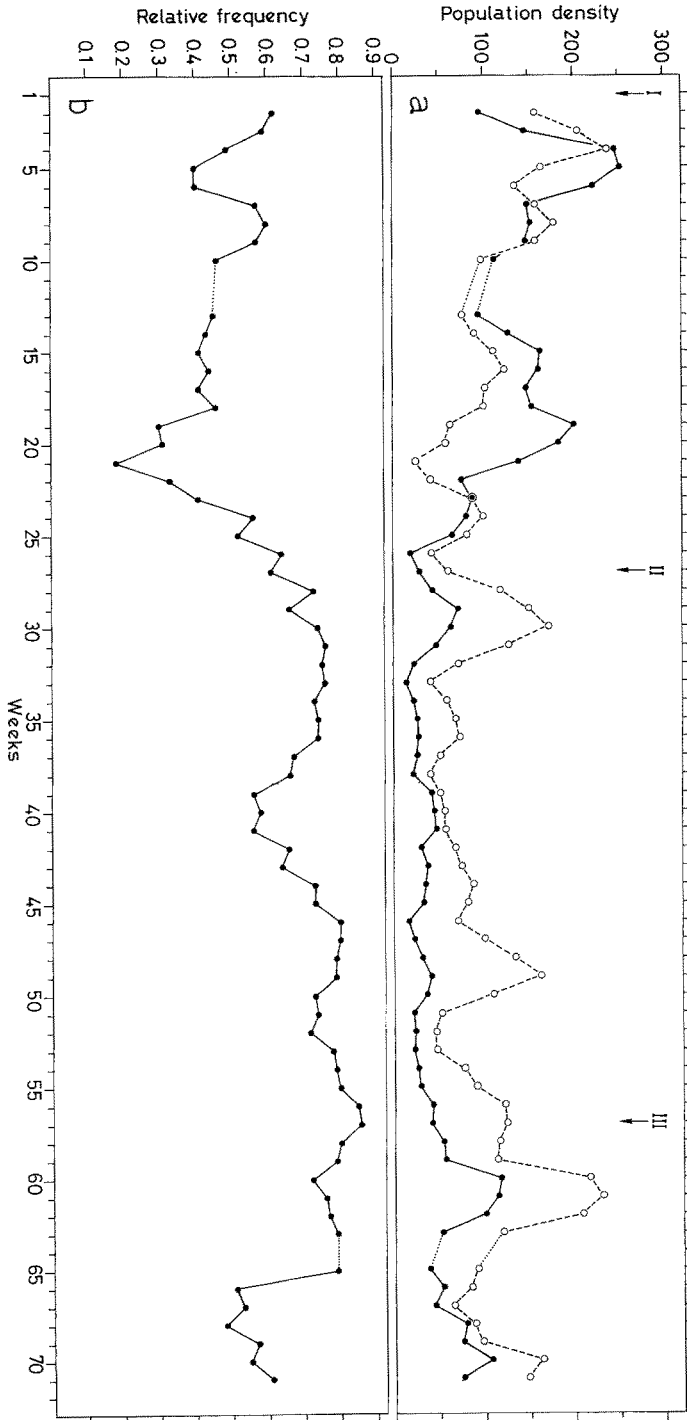


Fig. 6: *Tisbe holothurina*. Courses of population densities of nauplii (○) and adults plus copepodids (●) in a control population at weekly removal of 10% of specimens (a) and course of relative frequency of nauplii (b). Moving averages of 3 items. (For further explanations see Figure 2)



Table 3  
 Mean relative frequencies of nauplii of three exploited populations of *Tisbe holothuriae* exposed to 148  $\mu\text{g Cd}^{++}\text{l}^{-1}$  before (1) and after (2) addition of  $\text{Cd}^{++}$ . (For explanation of symbols see Table 1)

Characteristics	30 %/o			Exploitation rate			
	(1)	(2)	(2)	(1)	(2)	(1)	(2)
$\bar{p}$	0.51	0.68	0.53	0.74	0.59	0.76	
$\frac{\sin^{-1} \sqrt{p}}{s \sin^{-1} \sqrt{P}}$	45.6	56.3	46.7	60.1	50.6	61.8	
$\frac{n}{s}$	8.4	10.1	10.4	8.9	13.1	9.7	
	27	30	25	30	27	30	

Table 4  
 Mean relative frequencies of nauplii in control populations of *Tisbe holothiriae* exploited at a rate of 10% for the periods before and after the addition of Cd<sup>++</sup> to test populations. (For explanation of symbols see Table 1)

Characteristics	Experiment					
	A	B	C	D	E	F
			Period before addition of Cd <sup>++</sup> to test populations			
$\bar{P}$	0.40	0.45	0.41	0.48	0.46	0.49
$\frac{\sin^{-1} \sqrt{p}}{\sin^{-1} \sqrt{P}}$	38.5	41.9	39.5	43.5	42.7	44.3
$\frac{s_{\sin^{-1} \sqrt{p}}}{n}$	13.6	15.0	14.3	11.5	13.9	12.9
	25	25	25	25	25	25
			Period after addition of Cd <sup>++</sup> to test populations			
$\bar{P}$	0.67	0.68	0.71	0.69	0.69	0.68
$\frac{\sin^{-1} \sqrt{p}}{\sin^{-1} \sqrt{P}}$	55.3	55.9	57.6	56.9	56.8	55.9
$\frac{s_{\sin^{-1} \sqrt{p}}}{n}$	8.6	7.7	8.7	8.3	9.7	7.9
	30	30	30	30	30	30

Table 5

Mean relative frequencies of nauplii in populations of *Tisbe holothuriae* exploited at a rate of 10% before (1) and after (2) addition of 148 and 222  $\mu\text{g Cd}^{++} \text{ l}^{-1}$ , respectively. (For explanation of symbols see Table 1)

Characteristics	Experiment A		Experiment B		Experiment C	
	(1)	(2)	(1)	(2)	(1)	(2)
$\bar{P}$	0.50	0.64	0.51	0.73	0.49	0.73
$\frac{\sin^{-1} \sqrt{p}}{s \sin^{-1} \sqrt{p}}$	45.3	53.8	45.4	59.6	44.3	61.0
$\frac{\sin^{-1} \sqrt{p}}{n}$	12.8	16.3	8.7	13.3	11.6	12.6
	26	30	26	30	26	30
			Addition of 148 $\mu\text{g Cd}^{++} \text{ l}^{-1}$			
$\bar{P}$	0.47	0.66	0.49	0.66	0.53	0.69
$\frac{\sin^{-1} \sqrt{p}}{s \sin^{-1} \sqrt{p}}$	43.3	55.4	43.9	55.3	47.0	56.3
$\frac{\sin^{-1} \sqrt{p}}{n}$	11.1	13.1	12.9	11.2	9.8	13.4
	26	30	26	30	26	30
			Addition of 222 $\mu\text{g Cd}^{++} \text{ l}^{-1}$			

an inversion of the trend appears between the 45th and 46th experimental weeks, the inversion is delayed in the test populations and occurs between the 53rd and 54th weeks. After the 60th week mean-population densities are equal: The effect of addition of 148 or 222  $\mu\text{g Cd}^{++} \text{ l}^{-1}$  has evidently been balanced by an acclimation process within the 23 weeks or 20 generations. Generation time has been found to be 7.9 days at 22° C (Hoppenheit, 1976).

The distributions of pooled values of population densities of test and control populations for the period of addition of  $\text{Cd}^{++}$  to test populations are shown in Figure 5. All distributions exhibit negative skewness. As some inhomogeneity by clustering as a consequence of pooling has to be expected, the X-test of van der Waerden & Nievergelt (1956) was applied to prove the differences between the central tendencies. Mager & Theil (1974) showed that the application of this test can be profitable in the case of inhomogeneity of data. The comparisons yielded  $\alpha < 0.001$  (two-tailed) at exposure to 148  $\mu\text{g Cd}^{++} \text{ l}^{-1}$  and  $\alpha < 0.002$  when 222  $\mu\text{g Cd}^{++} \text{ l}^{-1}$  were added.

Previous experiments have yielded a close inverse relationship between population density and relative frequency of nauplii (Hoppenheit, 1976). Therefore, it can be expected to find a downward trend in density linked to an increasing relative frequency of nauplii, and vice versa. From Figure 6a, which presents the course of variation of density both in nauplii and adults plus copepodids of the control population shown in Figure 2, it appears that the ratio of nauplii to adults plus copepodids is altered in favour of the nauplii at low population densities. The changes in age structure can be taken directly from the plot of relative frequencies of nauplii in Figure 6b. The population exhibits a distinct downward trend of density in both the nauplii and the adults plus copepodids in the first phase of the experiment before addition of  $\text{Cd}^{++}$  to the test populations. The downward trend in density is accompanied by a decrease in the relative frequency of nauplii until the 21st experimental week. At this time, density of nauplii reached its lowest value (cf. Fig. 6a). While the entire population displays further decrease of density until the 33rd week (cf. Fig. 2) the relative frequency of nauplii increases to a value of 0.75. The fraction of nauplii remains enlarged almost to the end of the observation period when an increase of population density results in lower values.

A similar course of variation of relative frequency in nauplii has also been observed in the test populations of Figure 1 exhibiting no significant trends in population densities in either part of the experiments. As in the control the relative frequencies of nauplii started to rise some weeks before the beginning of the test period. The inspection of the variation of the population structure seems to provide a more distinct indication of the existence of a trend in population density than the use of statistical tests.

To stabilize the variances all relative frequency data of nauplii of experiments presented in Figure 1 were transformed into  $\sin^{-1} \sqrt{p}$  (Table 3). At weekly exploitation of 90 % of the specimens the transformed data exhibited a significant trend, which could be successfully eliminated. The comparisons of mean relative frequencies of nauplii of the periods before and after addition of 148  $\mu\text{g Cd}^{++} \text{ l}^{-1}$  by the t-test (by the X-test in the case of non-normally distributed data at 30 % weekly exploitation) showed significant differences in each case. Weighted analyses of variance (weighted

Table 6  
 Mean relative frequencies of nauplii in populations of *Tisbe holothuriae* exploited at a rate of 10% before (1) and after (2) addition of 148 and 222 µg Cd<sup>++</sup> l<sup>-1</sup>, respectively. (For explanation of symbols see Table 1)

Characteristics	Control		148 µg Cd <sup>++</sup> l <sup>-1</sup>		222 µg Cd <sup>++</sup> l <sup>-1</sup>	
	(1)	(2)	(1)	(2)	(1)	(2)
k	6	6	3	3	3	3
$\frac{\sin^{-1} V/p}{\sin^{-1} V}$	41.7	56.4	45.0	58.1	44.7	55.7
$\frac{V}{V}$	12.5	8.5	11.0	13.5	10.3	12.4
$\frac{V}{V}$	0.30	0.15	0.24	0.23	0.23	0.22
n	150	180	78	90	78	90

Table 7  
 Mean absolute deviations of population densities from the means and medians in exploited populations of *Tisbe holothuriae* at weekly renewal of 90 or 50% of culture water. (For explanation of symbols see Table 1)

Exploitation rate	k	$\bar{N}_1$	$\bar{N}_1$	Mean deviation (in % of $\bar{N}_1$ and $\bar{N}_1$ )		n	$\bar{N}_2$	Mean deviation (in % of $\bar{N}_2$ and $\bar{N}_2$ )		n
				$\bar{N}_1$	$\bar{N}_1$			$\bar{N}_2$	$\bar{N}_2$	
0.10	6	306	274	29	31	108	189	184	27	72
0.50	3	280	284	27	26	54	151	136	38	36
0.90	6	260	244	32	34	108	114	100	43	72

by sample size), which resulted in the same significance levels, have been performed additionally to check the results obtained by the t-test, which should not be applied if sample size varies widely.

In an earlier paper on the influence of rate of weekly water renewal on population density of exploited populations of *Tisbe holothuriae* (Hoppenheit, 1975a), a reduction both in density and relative frequency of nauplii at reduced water renewal rate was reported. There too the comparisons of mean values of transformed relative frequencies before and after reduction of water-renewal rate were performed by means of the t-test (cf. Hoppenheit, 1975a; Table 4). As in the cases mentioned above weighted analyses of variance yield the same levels of significance. The decrement of the relative frequency of nauplii found at a reduced rate of water renewal is in concordance with present observations on decrease of relative frequency of nauplii in the period up to the 21st week (cf. Fig. 6b), provided that an increasing deterioration of quality of water supply has taken place in this period. Only if – as in the present experiments – the population density falls short of a certain value, the age structure of a population changes in favour of the nauplii. This behaviour may protect a population against extinction and renders possible the acclimation to impaired environmental situations by providing enough material to the selective agent.

Tables 4 and 5 present the mean relative frequencies of nauplii of control and test experiments at 10 % weekly exploitation. About 40 % of the time series of transformed data exhibit trends and/or deviations from normality. Differences between mean values of populations belonging to the same group and the same experimental period are small and no outliers were found by the test of Dixon (cf. Sachs, 1968; p. 278 f.). Therefore, the  $\sin^{-1} \sqrt{p}$  were pooled (Table 6). No significant deviations from normality could be established in the pooled data by the chi-square test. The comparisons of the means by the t-test yielded significant differences between the periods before and after the addition of  $\text{Cd}^{++}$  both in control and test populations ( $\alpha < 0.001$ ). As not all conditions for the use of the t-test were satisfied (variances are not constant) weighted analyses of variance have been computed which provided the same levels of significance.

From Table 6 it appears that the more intense reduction of population density in populations exposed to  $\text{Cd}^{++}$  (cf. Fig. 4) does not result in a larger elevation of the sample fraction of nauplii. But judging by the coefficients of variation there seems to be a higher variability of data in test populations following addition of  $\text{Cd}^{++}$  (0.23 and 0.22, respectively, compared with 0.15).

## DISPERSION OF DATA

### Addendum to previously published papers

Doubts of the correctness of previously made statements on dispersion of data entailed a verification of conclusions drawn on dispersion of population data in foregoing publications (Hoppenheit, 1975a, b; 1976\*). From this checking it followed

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\* Erratum: In this article the  $\gg$  in line 29 of page 119 should read  $\geq$  and not as printed.

Table 8  
 Mean absolute deviations of population densities of adults plus copepods from the means and medians in exploited populations of *Tisbe holothuriae* at weekly renewal of 90 or 50% of culture water. (For explanation of symbols see Table 1)

Exploitation rate	k	$\bar{N}_1$	$\tilde{N}_1$	Mean deviation (in % of $\bar{N}_1$ and $\tilde{N}_1$ )	n	$\bar{N}_2$	$\tilde{N}_2$	Mean deviation (in % of $\bar{N}_2$ and $\tilde{N}_2$ )	n
0.10	6	148	134	34	37	130	119	32	34
0.50	3	136	128	30	31	106	101	33	36
0.90	6	90	77	40	47	54	45	46	72

Table 9  
 Mean absolute deviations of population densities of nauplii from the means and medians in exploited populations of *Tisbe holothuriae* at weekly renewal of 90 or 50% of culture water. (For explanation of symbols see Table 1)

Exploitation rate	k	$\bar{N}_1$	$\tilde{N}_1$	Mean deviation (in % of $\bar{N}_1$ and $\tilde{N}_1$ )	n	$\bar{N}_2$	$\tilde{N}_2$	Mean deviation (in % of $\bar{N}_2$ and $\tilde{N}_2$ )	n
0.10	6	158	136	42	48	59	53	46	51
0.50	3	144	144	43	43	45	39	64	72
0.90	6	170	151	37	40	60	50	50	72

that erroneously-made assumptions on the adaptability of parametric methods have to some extent led to invalid statements. The first paper of this series (Hoppenheit, 1975a) reported some aspects of effects of change in water renewal rate. In that publication a parametric test has been used to prove differences between coefficients of variation of untransformed population density data (cf. Tables 1 to 3 of that paper). It has been concluded that the reduction of the set point of population density by a decrease in rate of water renewal is accompanied by a reduction of

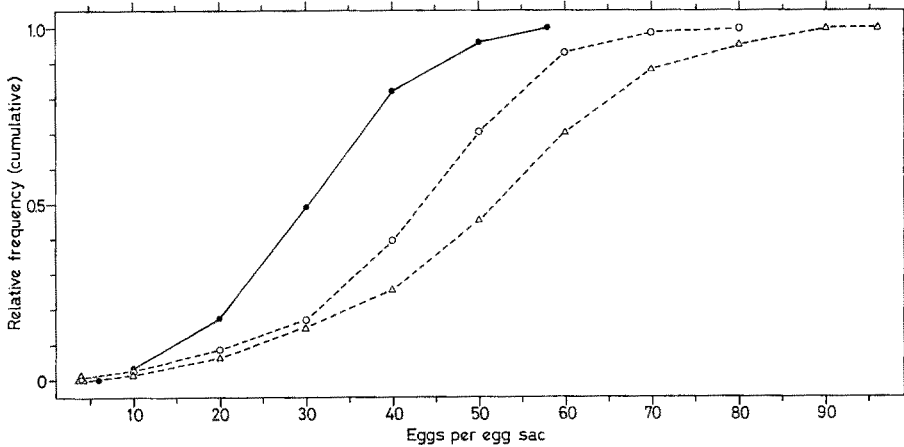


Fig. 7: *Tisbe holothuriae*. Cumulative relative frequencies of the productions of eggs per egg sac in populations exploited at rates of 10% (●), 70% (○) or 90% (△)

the range of fluctuation of the controlled condition, so that the precision of adjustment expressed in percentage remains essentially unchanged. This conservative decision has to be revised. Tables 7 to 9 present an impression of the situation. The mean absolute deviation from the mean and the median expressed as percentage has been used as a measure of the precision of adjustment. As can be taken from the tables the precision of adjustment remains about equal in the case of 10% weekly exploitation. At exploitation rates 50 or 90% it becomes poorer with reduction of population density following a reduction of water renewal from 90 to 50% weekly. A comparison of the mean deviation values contained in Tables 8 and 9 shows that with decreasing population density the precision of adjustment is more reduced in the population of nauplii than in the population of adults plus copepodids.

In the populations of Figure 1 of the present paper calculations of mean deviations have also yielded a distinct reduction of precision of adjustment of population density in the second halves of the experiments. Therefore, except in the case of small exploitation rates a higher variability of data at reduced population density caused by a deterioration of water properties has to be expected.

No evidence has been found of a decreasing variability in the intrinsic rate of natural increase with increasing rate of exploitation as stated previously (Hop-



penheit, 1975b). From  $\ln N_t = \ln N_0 + rt$  where  $N_0$  is the population density following exploitation,  $N_t$  the population density before the next exploitation and  $r$  the intrinsic rate of natural increase, it follows that  $r$  is normally distributed if  $N_t$  or  $N_0$  are log-normally distributed (cf. Koch, 1966). The proof of the  $r$ -values, the means of which are shown in Table 5 in Hoppenheit (1975 b), according to the proposal of

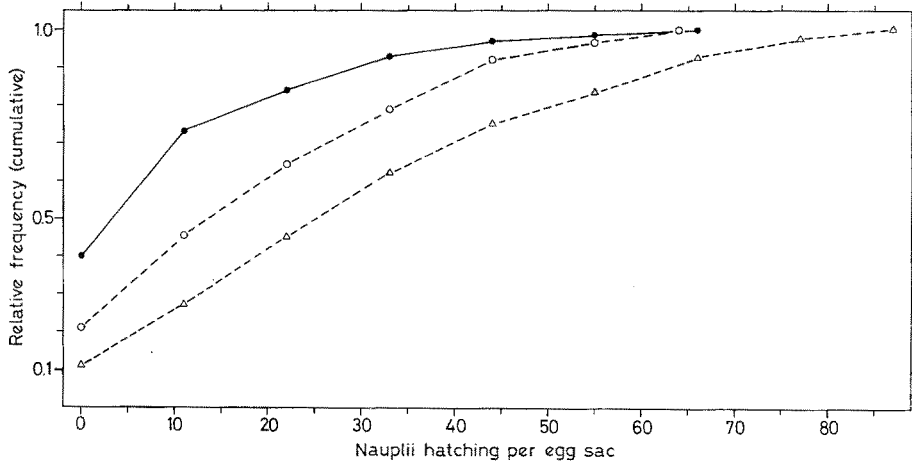


Fig. 8: *Tisbe holothuriae*. Cumulative relative frequencies of nauplii hatching per egg sac in populations exploited at rates of 10 (●), 70 (○) or 90% (△)

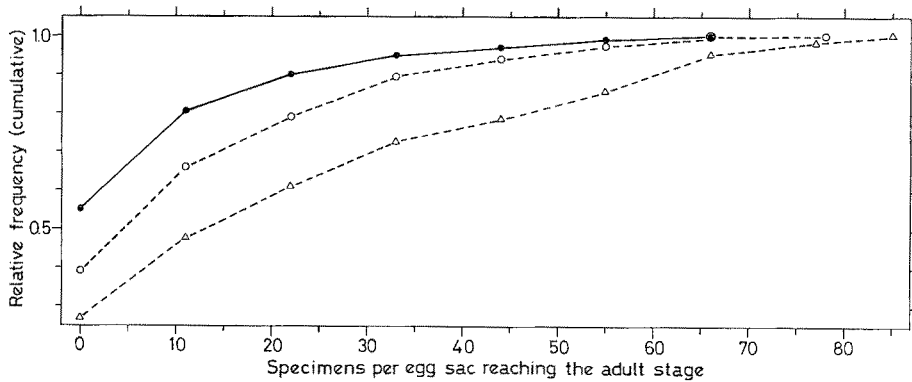


Fig. 9: *Tisbe holothuriae*. Cumulative relative frequencies of specimens per egg sac reaching the adult stage in populations exploited at rates of 10 (●), 70 (○) or 90% (△)

Mager & Mager (1974) by use of probability paper, has yielded approximate normal distributions and no outliers. Thus, a transformation of values (cf. Hoppenheit, 1975b, Table 5) is needless and misleading. As tests for trend have shown no significant deviations from randomness in the time series presented in Figures 3 to 7 in Hoppenheit (1975b), the parametric test provided by Hartley (cf. Sachs, 1968; p. 480 f.) to prove the homogeneity of several variances of samples of equal size has been applied which

resulted in no significant heterogeneity. As no inverse relationship exists between the exploitation rate and variability of intrinsic rate of natural increase, it cannot be stated (cf. Hoppenheit, 1975a) that the relation between birth and death rate ( $r$  equals birth rate minus death rate) and thereby the relation between the regulating variables mortality and fertility are subjected to relatively higher fluctuations at lower exploitation rates. As is to be expected from density data (cf. Hoppenheit, 1975b; Table 1) the variability in the  $r$ -values is slightly less at moderate exploitation rates and it has to be stated that birth and/or death rates are subjected to slightly higher fluctuations at low *and* high exploitation rates.

In Hoppenheit (1976, p. 114) it was stated that the variability of numbers of nauplii and adults produced per egg sac decreases with increasing exploitation rate and that these findings correspond with the formerly found reduction of variability in the rate of increase. As has been demonstrated above, the former assumption of a reduction of variability of the rate of increase with increasing exploitation has to be revised. In Figure 7 the cumulative relative frequencies of the productions of eggs per egg sac are presented for the experiments at an exploitation of 10, 70 or 90 % weekly (cf. Hoppenheit, 1976; Table 4). Curves at the exploitation rates of 10, 30 or 50 % were found to be almost identical. Due to practical difficulties the desirable multiple comparison of the dispersions could not be made. Single comparisons by Hagas' dispersion test (cf. Lienert, 1973; p. 388 f.) showed 7 significant higher dispersions of data at the higher exploitation rate among the 10 possible combinations ( $\alpha < 0.01$ , two-tailed). From inspection and the test results it may be concluded that increasing exploitation rate yields a higher dispersion in numbers of eggs produced per egg sac. In nauplii hatching per egg sac (Fig. 8) single comparisons have shown significant increase in dispersion in 90 % exploitation as compared to the other rates ( $\alpha < 0.01$ ). In numbers of specimens per egg sac reaching the adult stage (Fig. 9) significant differences in dispersion ( $\alpha < 0.01$ ) were only found between 90 % exploitation on the one hand and 10 and 50 % on the other.

The increase of dispersion in the production of eggs per egg sac with increasing exploitation rate is evident in numbers of nauplii hatching per egg sac only at 90 % weekly exploitation. In the numbers of adults produced per egg sac differences in dispersion are minor and hardly detectable.

## DISCUSSION

The results reported in the preceding paper on responses to lethal exposure (Hoppenheit & Sperling, 1977) and those in the present paper indicate that *Tisbe holothuriae* tolerates relatively high concentrations of  $Cd^{++}$  in comparison with other crustaceans such as *Daphnia magna* (Anderson, 1950; Biesinger & Christensen, 1972), *Crangon septempinosus*, *Pagurus longicarpus* and *Palaemonetes vulgaris* (Eisler, 1971), *Tigriopus japonicus* (D'Agostino & Finney, 1974) and larvae of *Uca pugilator* (Vernberg et al., 1974).

With few exceptions, unfortunately, it has not to date been possible to breed sensitive and ecologically important marine species in the laboratory. In the present

case too, an easy-to-breed organism has been studied, which may be less vulnerable to pollution. Moreover, it has to be taken into account that the stock populations were maintained for several years in the laboratory before experiments were started. In the culture water high concentrations of  $\text{NO}_2^-$  have been found (Hoppenheit, 1975a) indicating that the populations are able to tolerate a high degree of pollution from decomposing organic material. This water burden – besides other factors – may act as a selective force contributing to a change of the genetic structure of the populations tested. Hence, their responses may have been modified. Since it has been demonstrated by the present paper that an acclimation process may be terminated in a relatively short period of time, one can scarcely expect to deal with populations comparable to those occurring in their natural habitat.

The experiments were performed at a salinity of 30 ‰ and a temperature of 22° C. Generally, high temperatures seem to increase the amount of  $\text{Cd}^{++}$  taken up by crustaceans whereas increasing salinity reduces the uptake (O'Hara, 1973a, b; Hutcheson, 1974; Vernberg et al., 1974, 1977, Jones, 1975). Dissolved oxygen concentration can be vigorously reduced at high population densities (Hoppenheit, 1975a). The mode of action of dissolved oxygen in experiments on the toxicity of  $\text{Cd}^{++}$  is not unique. In fishes, Middaugh et al. (1975) and Voyer et al. (1975) report an increased sensitivity at lower concentrations of dissolved oxygen. Findings by Clubb et al. (1975) in aquatic insects have shown an increasing toxicity of  $\text{Cd}^{++}$  with increasing concentration of dissolved oxygen due to an increased amount of the metal taken up.

In the preceding paper (Hoppenheit & Sperling, 1977) experiments were reported in which 3 populations each were exposed to 500 and 1125  $\mu\text{g Cd}^{++} \text{ l}^{-1}$  at a removal rate of 5 ‰ of specimens *five* times a week to detect acute mortality. After a reduction of population density to 2 specimens per 10 ml one population exposed to 1125  $\mu\text{g Cd}^{++} \text{ l}^{-1}$  recovered from acute intoxication and reestablished initial population density within 3 days. The possibility, therefore, has to be taken into consideration that the exploitation regime has an influence on the capacity of a population to compensate for deleterious stresses.

As the importance of modifying factors can scarcely be overestimated and may account for much of the variation in toxicity found in the literature (cf. Sprague, 1970), more efforts should be made to assess the possible interaction of environmental factors and poisonings.

In studies on the toxicity of transition metals – especially when performed under static conditions as in the present case – the question arises as to what extent the metal reacts chemically or is adsorbed by particulate matter and to which fraction of the initially added metal the test organisms are actually exposed. Thus the relatively low sensitivity found in *Tisbe holothuriae* could be the consequence of an adulteration by the experimental conditions and may be attributed to a reduced amount of  $\text{Cd}^{++}$  actually available to the test organisms because the metal has partly been captured by compartments of the elected experimental system which are not in interaction with the copepods. Consequences to be drawn from the partitioning of the toxicant in the experimental system will be discussed in some detail in a subsequent paper (Sperling & Hoppenheit, in preparation).

As it has been found that survival time of the populations is related to the initially adjusted concentration of  $Cd^{++}$  (Hoppenheit & Sperling, 1977), the scale given by the different designated concentrations has been used as a reference in describing the obtained results. Since the amount of  $Cd^{++}$  to which the copepods are actually exposed has to be expected to depend on the type of the experimental system elected, it cannot be excluded that deviating results are achieved when the manner of experimentation is changed.

Although the significance of the results obtained may be limited by uncertainties with reference to number and importance of factors determining the experimental conditions, investigations on population dynamics of *Tisbe holothuriae* should be continued because this species complies in an outstanding way with the requirements needed to gain more insight into the regulating mechanisms operating at the population level under the influence of toxicants.

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