PRELIMINARY OBSERVATIONS ON THE SALINITY AND TEMPERATURE TOLERANCES AND SALINITY PREFERENCES OF *DEROCHEILOCARIS TYPICA* PENNAK AND ZINN 1943.

by

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Résumé

Des expériences préliminaires ont été réalisées sur des spécimens de *Derocheilocaris typica*, Pennak et Zinn, 1943, adultes et juvéniles de grande taille, récoltés dans la plage de Nobska, Massachusetts, Etats-Unis, dans le but de déterminer le niveau général de tolérance de cette espèce aux actions conjuguées de températures (7, 22 et 29 °C) et de salinités (15, 31 et 47 g/1) existant dans la zone intercotidale d'une plage tempérée. Les valeurs de t-50 (taux de mortalité de 50 p. 100 après 24 h) ont été analysées et comparées avec des valeurs semblables obtenues chez *D. remanei*. En plus, une chambre à salinité fluctuante a été construite et les préférences pour une salinité donnée ont été déterminées. Il apparaît que *D. typica* supporte mieux une salinité de 31 g/1 à 7 et 22 °C, alors que des salinités extrêmes de 15 à 47 g/1 lui sont létales. Bien que *D. typica* semble très peu actif en comparaison avec les autres Crustacés du thalassopsammon, il montre une aversion très nette pour des salinités de 9 g/1 d'un côté de l'échelle et de 62 g/1 de l'autre côté, et une préférence pour des salinités comprises entre 20 g/1 et 50 g/1.

Ces résultats, basés sur un petit nombre de données, semblent montrer que *D. typica* pourrait supporter des écarts de température légèrement plus grands et des écarts de salinité plus petits que les populations européennes de *D. remanei* de Canet-Plage et Mimizan (France). Une tolérance plus grande aux écarts de température que chez *D. remanei* semble en accord avec la répartition géographique plus vaste constatée chez *D. typica.*

La répartition de *D. typica* dans la plage de Nobska pourrait être en partie le résultat d'une sélection ou d'un refus de certains facteurs tels que des températures et des salinités extrêmes. Ceci contribuerait à expliquer l'absence de D. *typica* du sable de surface à Nobska.

Introduction

The extended geographic range and very contagious local distribution of mystacocarid crustaceans have been observed by Pennak and Zinn (1943), Blackwelder (1965), Hessler and Sanders (1966) and Hall (1972) for *Derocheilocaris typica,* and by Delamare-Deboutteville (1960), Jansson (1966) and others for *Derocheilocaris remanei.*

Explanations for this distribution have been based on physical and chemical factors, singly or in combination (grain size, sorting, turbulance, temperature, salinity, oxygen availability), or on biotic factors (especially feeding habits). Jansson (1966) used salinity tolerance and preference data to support his belief that the landward limit of distribution for *Derocheilocaris remanei* in non-tidal Canet Plage can be attributed, at least

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partially, to excessively low salinities in the landward portions of the beach.

Delamare Deboutteville (1960) maintained that salinity has a minimal effect on the distribution of *Derocheilocaris remanei,* since he found large numbers of this species in interstitial water whose salinity ranged from 5.4 to 40.8 p. 1000. He considered that availability of food was the most important factor affecting the landward distribution of this animal.

Hessler and Sanders (1966), and Hall (1972) cited the occurrence of *Derocheilocaris typica* in interstitial water with temperatures ranging from —1.5°C (Nobska Beach, Cape Cod, Massachusetts) to 28°C in Miami, Florida. Hall (1972), Zinn (personal communication) and the field observations of Found indicate that *D. typica* occurs naturally in salinities of 11 to 36 p. 1000. It would appear then that *D. typica,* like *D. remanei,* is both eurythermal and euryhaline, capable of surviving the fluctuating and often extreme conditions of a high-energy beach of the temperature zone.

Kinne (1957), Boaden (1963), Gray (1965, 1966a, 1966b) and Jansson (1967) stressed the importance of studying the effects of specific factors by means of laboratory experiments in addition to field work in order to understand more completely the causes of the microdistribution of meiofaunal organisms in an interstitial habitat. In this way, tolerance tests may be used to determine the range of values for a particular factor under which an organism may survive, while preference experiments would indicate the ability of test organisms to sense and respond to various levels of a specific factor.

In this investigation, we determined the tolerances of *Derocheilocaris typica* toward various combinations of lemperature and salinity and designed a salinity preference apparatus suitable for this animal whose normal behavior appears to be quite sluggish compared with that of many other members of the meiofauna (Hall, 1972). It was hoped that information from the preference experiments might help to explain whether the distribution of this species is the result of active selection for a specific level of one or more factors or if it is the result of passive movement caused by the hydrodynamic factors of the beach, as suggested by Hall (1972). The results of these preliminary experiments would, at least, indicate the appropriate conditions of temperature and salinity at which to conduct subsequent laboratory studies with this species, including respiratory, feeding or culturing investigations. In addition, it might aid in further understanding the usual contagious microdistribution of *D. typica* in intertidal beaches.

Materials and methods

Sampling.

One sample (± 20,000 cm^3) was collected during low tide, between the mid and high tide levels at 20 to 40 cm depth on Nobska Beach, Woods Hole, Massachusetts, U.S.A. The entire sample was then placed at a mean temperature of approximately 7°C, since previous attemps by the authors and by Zinn (personal communication) to keep *Derocheilocaris typica* alive for extended periods of time had shown this method to be the most successful. By taking one large field sample and maintaining it in the laboratory rather than periodically taking several small samples when the animals were needed, we could be relatively confident that all of the experimental animals belonged to a single population subjected to nearly identical conditions.

Tolerance Experiments.

Tolerance experiments were performed to determine the ability of *Derocheilocaris typica* to survive over a range of temperatures and salinities encountered in temperate, marine, intertidal beaches. For this reason, low, intermediate and high levels of salinity and temperature were chosen for study.

For the tolerance tests, a sample of sand which had been kept at a mean temperature of 7°C for 6 days, was placed at room temperature (25°C) for 8 days, to allow the animals to acclimate to this temperature. Extraction was made by gently agitating a small amount of sand (± 30 cm^3) and seawater (± 20 cm^3) in a glass dish for one minute and decanting into a Petri dish. This process was repeated three times with each subsample of sand. Adult and large juvenile animals were removed by pipette and placed in holding dishes at ambient room temperature until the number of animals required for the tests was obtained.

TABLE 1.
Definitions of terms used to describe the conditions of animals in the tolerance tests.

Term	Description
Active	« normal » behavior, that is, rapid and relatively constant movements of appendages, flexing of body and crawling.
Sluggish	types of movement are « normal » but slower, as if in slow motion.
Moribund	long pauses between movement, occasional flexing of body and weak movements of appendages.
Dead	no movement when touched with a probe.

Approximately 10 randomly selected animals were then pipetted into 35 mm plastic Petri dishes, each of which contained 4 ml of one of the salinity test solutions at room temperature. The dishes were then covered and placed in the dark at 7°C, 22°C or 29°C. The three salinities used at each temperature were 15, 31 and 47 p. 1,000. The two extreme salinities were obtained by diluting (with atmospheric water) or evaporating 31 p. 1,000 seawater, respectively. Two dishes each containing approximately ten animals were subjected to each of the nine conditions.

Observations were made approximately every 7 hours with more frequent readings at critical periods. At each reading, the condition of each animal was recorded as active, sluggish, moribund or dead (Table 1). The salinity in each dish was taken with an American Optics salinity refractometer at least once every 2 days and adjusted when necessary to the original concentration. The amount of time necessary for the 50 p. 100 level of mortality—or t-50—to be reached was estimated for each dish from graphs of percent mortality against time.

An additional tolerance experiment was made under similar conditions except the animals were acclimated to a cooler temperature (7°C) for 6 days and then allowed to slowly warm to room temperature. Ten animals were then tested under each condition. The same general trends were found for both the "high temperature" and "low temperature" acclimated animals. Although unmatched t-tests indicated no significant difference between the mean t-50-values of the two groups, the authors felt that complex displacements of the mortality curves indicated that more animals should be tested.

Preference Experiments.

A plexiglass tray 75 mm long X 25 mm wide X 11 mm deep (internal dimensions) was divided into two chambers (36 mm X 25 mm) by a permanent glass partition. Each of these chambers was fitted with a movable glass divider (Figs. 1 and 2). Cryolite grains with a diameter of .250 mm to .500 mm were soaked in the test salinities for at least 30 minutes. Then, a thin, continuous layer (2 to 3 mm thick) of saturated grains was arranged on each side of the movable divider. Thus, any two salinities could be placed in the chamber, one on each side of the barrier. The excess water, that amount which collects along the sides when the tray is tilted, was withdrawn by pipette from each half of the chamber. After several trials, a layer of water just covering the cryolite grains, that point at which the grains appear almost invisible in seawater, was found to satisfy the three important criteria: 1) minimum diffusion between the two salinities once the divider is removed, 2) sufficient water for three salinity readings at the end of the experiment, about .5 cm^3 per reading, and 3) enough to allow *Derocheilocaris typica* to move easily between the grains and yet not so much that the animals float. With the

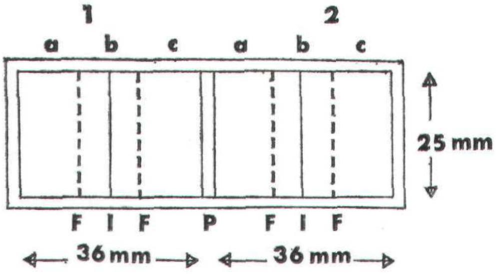


FIG. 1.

Two chambered tray (1,2) for testing salinity preference in *Derocheilocaris tgpica.*

P: permanent partition between 2 chambers; I: initial position of movable dividers; F: final position of movable dividers; a, b and c: divisions of each chamber formed when the final dividers (F) are inserted for salinity readings.

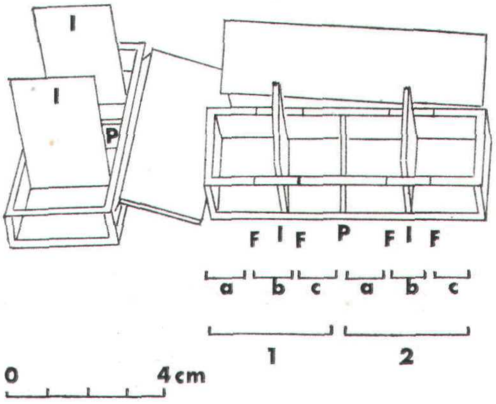


FIG. 2.

Side and frontal views of the preference tray, showing movable dividers in the initial position (I) ready for loading the two halves of each chamber with cryolite grains saturated with seawater of the desired salinity. Etchings on the tray indicate the final position (F) of the movable dividers, partitioning each chamber into three divisions, a, b and c. P is the permanent partition between chambers 1 and 2.

grains arranged in each half of the chamber, the divider was removed and five animals, which had just been extracted, were pipetted with no more than .25 cm^3 of water into the center of the dish. The dish was covered with a glass slide and observations were made every 5 to 10 minutes through the cover in order to keep evaporation to a minimum. At each observation, when the positions of the animals were recorded diagramatically, the degree of activity of each animal was noted. Since preliminary work with this apparatus indicated that *Derocheilocaris typica* was capable of moving over half the length of the chamber in 5 minutes, each test was run for 30 to 35 minutes. Diffusion of the two test salinities in the chamber provided the animals with a gradient with extreme salinities at each end of the chamber. For this reason, at the end of the experiment, after the positions of the animals were carefully recorded, the chambers were divided into thirds by glass partitions. The grains of cryolite were clumped in each 1/3 of the dish so that a drop of water could be withdrawn by pipette for salinity determination with a salinometer. The two outer thirds of the chamber (areas a and c, Fig. 1) were always found to have nearly the original salinity while the middle third (area b, Fig. 1) had an intermediate value. Thus preference or avoidance between three levels of salinity could be determined in one test.

RESULTS

Tolerance Experiments

The t-50-values for the nine combinations of salinity and temperature, presented in Table 2, were statistically treated by a two-way analysis of variance. The null hypothesis stated that temperature and salinity, singly and/or in combination, were not responsible for the differences in the t-50-values, but that these values were likely to occur by chance alone. However, the F ratios for the effect of salinity (10.80 with 2 and 9 d.f.) and the effect of temperature

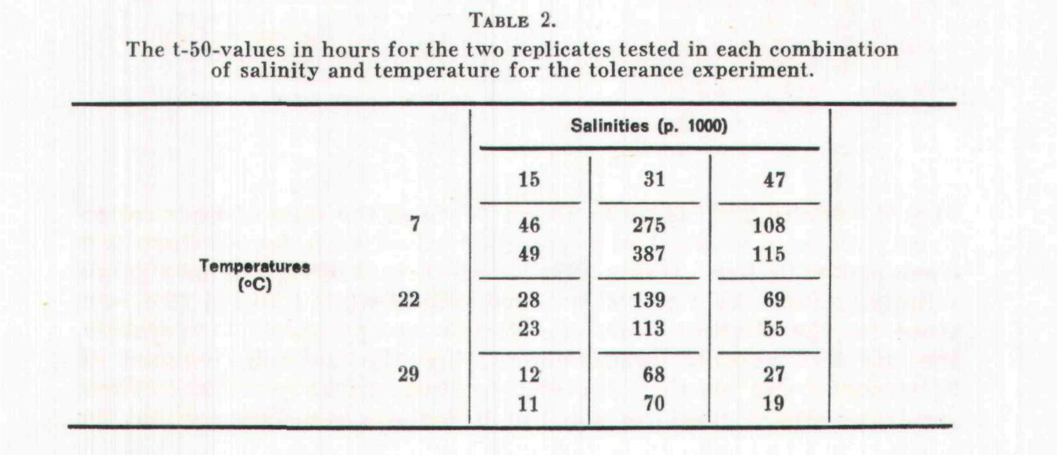


TABLE 2.

The t-50-values in hours for the two replicates tested in each combination of salinity and temperature for the tolerance experiment.

		Salinities (p. 1000)		
		15	31	47
Temperatures (°C)	7	46	275	108
		49	387	115
	22	28	139	69
		23	113	55
	29	12	68	27
		11	70	19

(8.13 with 2 and 9 d.f.) demonstrated that these values would occur by chance alone, less than 1 and 5 p. 100 of the time, respectively. The F ratio of the interaction of these two factors (9.92 with 4 and 9 d.f.) would also occur less than 1 p. 100 of the time. Therefore, the null hypothesis was rejected; various levels of salinity and temperature separately have a significant effect on the survival of *Derocheilocaris typica* and the combined effect is significantly greater at some levels of these factors than at other levels.

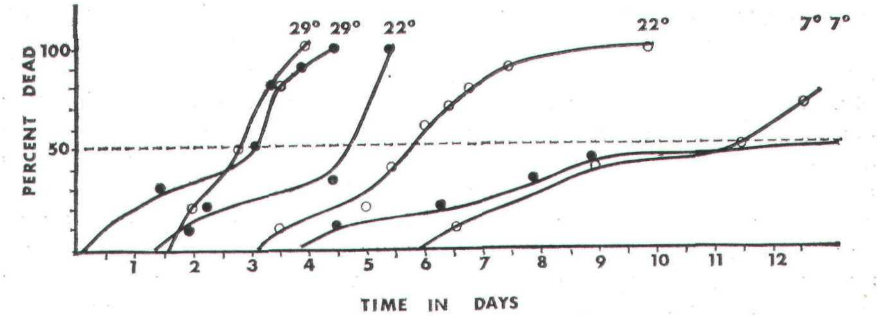


FIG. 3.

t-50-curves showing the influence of three temperatures (°C) on the death rate of *Derocheilocaris typica* in seawater of 31 p. 1000. The curves for two replicates at each temperature are shown. Approximately ten animals were used in each replicate. The t-50-value for the second replicate (•) at 7°C was 16 days and 100 p. 100 dead at 25 days.

Specifically, greatest survival was obtained in 31 p. 1,000 at 7°C with a t-50-value equal to 387 hours (16.1 days). Two of the animals under these conditions lived 25 days. Second best survival occurred when the salinity was 31 p. 1,000 and the temperature was 22 °C (t-50 140 hours or 5.8 days). These results might be expected since similar conditions are encountered in their natural habitat (approximately 31 p. 1,000 and 23°C at 20 to 40 cm depth at the time of their collection). Poorest survival was recorded when high temperature was combined with low salinity (29°C and 15 p. 1,000). At any single salinity, animals kept at 7°C survived longest while those at 29°C survived for the shortest time. Conversely at any single temperature, the greatest survival Was obtained by the animals exposed to 31 p. 1,000 and shortest survival by those in 15 p. 1,000. These results presented graphically in Fig. 3, 4 and 5, clearly show that the

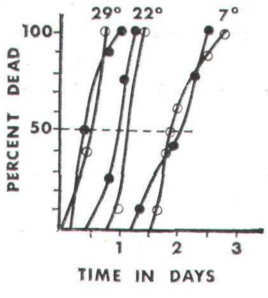


FIG. 4.

t-50-curves showing the influence of three temperatures (°C) on the death rate of *Delocheilocaris typica* in seawater of 15 p. 1000. The curves for two replicates at each temperature are shown. Approximately ten animals were used in each replicate.

differences in time survived between the replicates are small compared with the differences between the three temperatures.

The results of the temperature and salinity tolerance tests using low temperature acclimated animals support these conclusions statistically, showing significance for the effect of both salinity and temperature at the .01 and .05 levels of probability respectively.

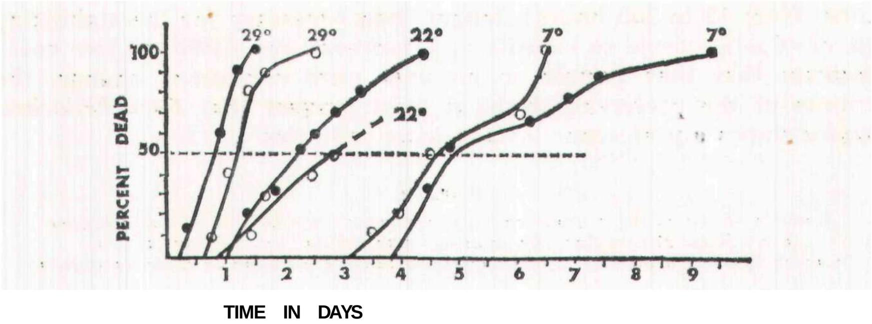


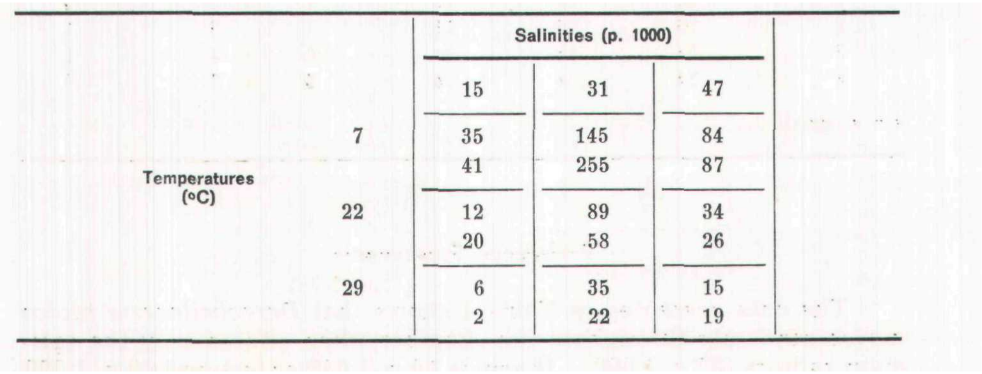
FIG. 5.

t-50-curves showing the influence of three temperatures (°C) on the death rate of *Derocheilocaris typica* in sea water of 47 p. 1000. Two replicates of approximately ten animals each are shown for each temperature. The first replicate (O) at 22°C was accidently discontinued shortly after to 50 p. 100 mortality level was reached.

The degree of activity shown by specimens of *Derocheilocaris typica* during the tolerance tests provides information concerning their ability to select or avoid specific areas of a beach. If it is assumed that only active and sluggish animals (as defined in Table 1) are capable of selective or avoidance behavior, a "50 p. 100 activity level" can be calculated that is the time at which 50 p. 100 of the animals are active or sluggish and 50 p. 100 of them are moribund or dead. At this point a comparison of the "50 p. 100 activity level" (Table 3) with the t-50-values (Table 2) indicates that in slightly less than 2/3 of the time taken to reach the t-50-values in any of the test conditions, 50 p. 100 of the animals would no longer be likely to show any pre-

TABLE 3.

« 50 p. 100 activity levels » in hours, of specimens of *Derocheilocaris typica* in the salinity and temperature tolerance experiment.

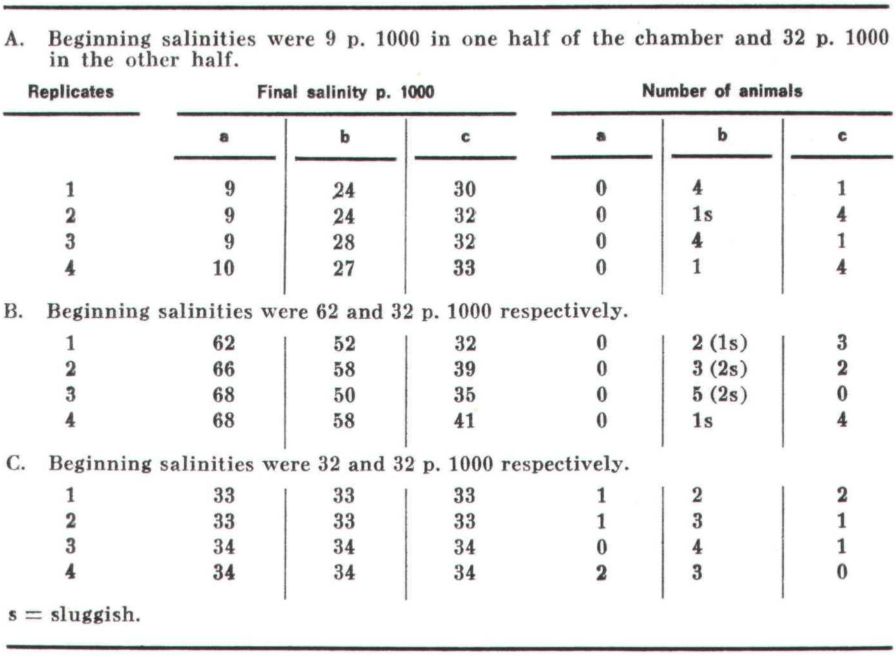


		Salinities (p. 1000)		
		15	31	47
Temperatures (°C)	7	35	145	84
		41	255	87
	22	12	89	34
		20	58	26
	29	6	35	15
		2	22	19

ference behavior. However, even under the most extreme conditions tested (29°C and 15 p. 1,000), the "50 p. 100 activity level" is not reached for 2 to 6 hours, which might be sufficient for the majority of the mystacocarid population to avoid even this extreme condition should it occur. In the other combinations of salinity and temperature tested, the "50 p. 100 activity levels" clearly showed that *Derocheilocaris typica* is able to remain relatively active for long periods of time (from 12 to 255 hours), longer than necessary for the stabilizing effect of a tide cycle on salinity and temperature. Although this could indicate that they remain in an area until conditions change, the results of the preference tests at least suggest that *Derocheilocaris typica* shows a preference toward some salinities.

TABLE 4.

Results of the salinity preference experiments with *Derocheilocaris typica*.
After 30 to 35 minutes, the chamber was divided into thirds (a, b, c).
In earch third, the salinity was determined and the number of animals counted.



A. Beginning salinities were 9 p. 1000 in one half of the chamber and 32 p. 1000 in the other half.

Replicates	Final salinity p. 1000			Number of animals		
	a	b	c	a	b	c
1	9	24	30	0	4	1
2	9	24	32	0	1s	4
3	9	28	32	0	4	1
4	10	27	33	0	1	4
B. Beginning salinities were 62 and 32 p. 1000 respectively.						
1	62	52	32	0	2 (1s)	3
2	66	58	39	0	3 (2s)	2
3	68	50	35	0	5 (2s)	0
4	68	58	41	0	1s	4
C. Beginning salinities were 32 and 32 p. 1000 respectively.						
1	33	33	33	1	2	2
2	33	33	33	1	3	1
3	34	34	34	0	4	1
4	34	34	34	2	3	0

s = sluggish.

Preference Experiments

The data presented in Table 4 shows that *Derocheilocaris typica* moves randomly throughout the chamber when offered only the optimum salinity (32 p. 1,000). It avoids 10 p. 1,000 or less and 60 p. 1,000 or more. *D. typica* prefers salinities between approximately 24 and 50 p. 1,000. However, from the large number of sluggish animals found in the highler salinity, it appears that salinities of about 50 p. 1,000 or more may stress the animals particularly at a room temperature of about 28°C. This is substantiated by the results of one test using 55 and 32 p. 1,000 as original salinities. After 35 minutes, four animals were in 35 p. **1,000,** one animal in 42 and none in 55 **p. 1,000.** Further testings, would probably indicate a preferred range of salinities from ± **24** to ± **40 p. 1,000.**

DISCUSSION

Following the criteria of lethality, resistance and tolerance expressed by Lasserre and Renaud-Mornant **(1971), where** the zone of lethality equals t-50-valves equal to or less than 24 hours, the zone of resistance equals t-50-values greater than 24 hours but equal to or less than 48 hours, and the zone of tolerance equals t-50-values greater than 48 hours, it is possible to compare the data of the present investigation for *Derocheilocaris typica* with the results of Jansson (1966) and Lasserre and Renaud-Mornant (1971) for *Derocheilocaris remanei* (Table 5). Although the higher resistance and lethal temperatures were not determined for *D. typica,* it is apparent that these temperatures are higher than those for both the Canet and Mimizan populations of *D. remanei* tested under their respective optimal salinities. The higher lethal temperature for *D. typica* may well reflect its geographic distribution into lower latitudes than the presently known distribution of *D. remanei.* On the other hand, the range of tolerance to salinity appears to be considerably narrower in *D. typica* as compared with *D. remanei.* Further experiments with *D. typica* are required in the range of 15 to 31 p. 1,000 to determine a more precise lower boundary of tolerance and at salinities in excess of 47 p. 1,000 to determine a more accurate upper boundary of tolerance.

TABLE 5.

A comparison of the levels of physiological tolerance at various temperatures and salinities for *Derocheilocaris typica* and *Derocheilocaris remanei,* each tested at near optimal salinities and temperatures.

Derocheilocaris typica	***Derocheilocaris remanei***	
Atlant. (Woods Hole) 31 p. 1000	**Mediter. (Canet)* 20 p. 1000**	**Atlant. (Mimizan)** 20 p. 1000**
T 7°, 22°, 29°C.	T 9-20°C.	T 5-23°C.
	R 28°C.	R 28°C.
	L 30°C.	L 30°C.
22°C	**15°C**	**15°C**
T 31, 47 p. 1000	T 15-40 p. 1000	T 10-40 p. 1000
L 15 p. 1000	R 10, 50 p. 1000	R 7, 50 p. 1000
	L 0-5 p. 1000, 60 p. 1000	L 0-5 p. 1000, 60 p. 1000

L = Zone of Lethality = t-50 $\leqslant$ 24 hours.
R = Zone of Resistance = t-50 $>$ 24 hours and $\leqslant$ 48 hours.
T = Zone of Tolerance = t-50 $>$ 48 hours.

* Data from Jansson (1966).
** Data from Lasserre and Renaud-Mornant (1971).

Analysis of data for survival at various temperatures under conditions of non-optimal salinity in *Derocheilocaris typica* indicates that a temperature of 29 °C is lethal for this organism at 15 and 47 p. 1,000. Test specimens of *D. typica* were quite tolerant to a salinity of 47 p. 1,000 at 7°C and only slightly tolerant to 15 p. 1,000 at 7°C. This survival data at salinity conditions considered non-optimal by the present investigators is valuable in that it shows that *D. typica* becomes much less tolerant to fluctuations in temperature when it finds itself in salinities varying 50 p. 100 from 31 p. 1,000. This data supports the suggestion of Hall (1972) that both contagious distribution and seasonal migration in the intertidal beach may reflect the attempt by *D. typica* "to reach an area of maximum stability" in regard to salinity. If it wanders from this zone of salinity tolerance, *D. typica* may begin to experience severe metabolic stress, Lasserre and Renaud-Mornant (1971) demonstrated such metabolic stress in *D. remanei* by measuring the respiratory rate under either very hypotonic or very hypertonic conditions. Such respiratory studies with *D. typica* should help to define further its zone of salinity tolerance. In addition, an investigation of the metabolic rate of *D. typica* at 7°C might help explain their long survival rates at this temperature.

A comparison of the results of salinity preference tests, with *D. remanei* determined by Jansson (1966) and with *D. typica,* indicates that both species display roughly the same range of salinity preferences. *D. remanei,* collected at 12 p. 1000, showed a preference for 20 to 40 p. 1000, even when offered 10 p. 1000, and an aversion to 60 p. 1000 and lethality at 5 p. 1000. Whereas *D. typica,* collected at approximately 31 p. 1000, preferred about 24 to less than 50 p. 1000, and clearly avoided 9-10 and 62-68 p. 1000.

The results of the tolerance and preference tests indicate that *Derocheilocaris typica* is able to tolerate a slightly higher but narrower range of salinities and a wider range of temperatures than *D. remanei.* If this is true, it would be expected that *D. typica* could inhabit beaches with a wider range of temperatures and higher salinities and to be found over a wider range of geographic conditions. Whether for these reasons or because of the possible influence of other factors, *D. typica* does have a wider geographic range with its northern limit further North (with respect to temperature) than that of *D. remanei* (Hessler and Sanders, 1966).

Probably, many factors interact to cause the microdistribution within a beach. Jansson (1966), from his tolerance and preference work with *Derocheilocaris remanei,* suggested that low salinities might be an important factor in controlling the landward distribution of Û. *remanei* on the tideless beaches at Canet Plage, while turbulence probably is the limiting factor in the seaward distribution of this species.

The distribution of *Derocheilocaris typica* has been studied in detail at Woods Hole by Hall (1972). The center of the population occurs in the high beach at 20-45 cm depth. From the present investigation, it seems reasonable to suggest that the depth at which the mystacocarid population is found may well reflect an avoidance to extremes of temperature and salinity as well as other factors such as the amount of pore water which may be encountered in the surface layers of the beach. In addition, there is a fresh water pond on the landward side of the beach, subsurface outflow from which might limit the landward distribution of *D. typica.* Hall (1972) further reports both seasonal and tidal fluctuations in the pattern of distribution. For instance, in the winter although the center of abundance of the population moves landward and deeper into the beach as though seeking the most stable conditions, Hall suggests that this distribution may merely be the result of hydrodynamic factors in the beach passively moving the animals into aggregations rather as berms are formed.

This investigation shows that *D. typica* has a range of preferred salinities and is capable or near normal movement, even at extreme temperatures and salinities, for a number of hours to several days. The animal can tolerate a wide range of salinities and temperatures. Therefore, it appears possible that the distribution of *D. typica* is, at least in part, the result of avoidance and/or selective behavior for one or more factors, of which salinity and temperature may be of great importance.

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Summary

The general limits of salinity and temperature tolerance and a range of preferred salinities were determined for *Derocheilocaris typica. D. typica* survives longest at near normal ambient salinity 31 p. 1000 and temperatures 7° and 22°C. The combination of low salinity 15 p. 1000 and high temperature 29°C is most rapidly lethal. Its range of temperature tolerance (approximately 7-29°C) at optimal salinity is greater than that for *D. remanei,* while the salinity tolerance range (between 15 and 31 to 47 p. 1000) at or near optimal temperature for *D. typica* is smaller is shifted to higher salinities.

Preference tests show a slightly broader range of preferred salinities (24-50 p. 1000 or less) for *D. typica* with many of the animals becoming sluggish at 50 p. 1000 or higher. *D. typica* exhibits a clear aversion to salinities of 60 p. 1000 or more and to 10 p. 1000 or less.

In addition to reaffirming the results of previous investigations that species of *Derocheilocaris* are euryhaline and eurythermal, this investigation has shown that, at least under some conditions, *D. typica* can exhibit definite salinity preferences. Even though this animal is sluggish compared to some other meiofaunal species, it can remain nearly normally active for relatively long periods of time at extreme temperatures and salinities giving it ample time to display preference behavior. The distribution of *D. typica* at Nobska Beach may in part result from an active selection-avoidance behaviour to one or more factors among which salinity and temperature may be of first importance.

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