

NOTES

LABORATORY STUDIES OF THE PATTERN OF REPRODUCTION OF THE ISOPOD CRUSTACEAN *IDOTEA BALTICA*

The isopod *Idotea baltica* is a cosmopolitan species that can be an important component of fishes' diets in the field (summarized in Sywula 1964 and Strong and Daborn 1979). Tinturier-Hamelin (1963) reported that *I. baltica* extends along all European coasts, from Finland to Gibraltar, including Great Britain; it is present in the Baltic, the Mediterranean, and the Black and Caspian Seas. In North America it is present from Nova Scotia to North Carolina. In addition, Sywula (1964) reported that it is also found in South America, Bermuda and Barbados, the Red Sea, Australia, New Zealand, and Java.

Investigators who have observed *I. baltica* in the field have reported the species' association with the dominant plants of the community. Interestingly, the type of associated plant varies with geographic locality. In Nova Scotia it is found on *Ascophyllum nodosum* (Strong 1978), in the Baltic on *Fucus vesiculosus* (Salemaa 1979), in Poland on *Zostera* (Mobius 1873, as reported in Sywula 1964), and on *Ulva lactuca* in Jamaica Bay, NY (present study). Generally, the animals' principal food is the plant on which they are found, and this species is often the principal primary consumer of its community (Strong and Daborn 1979), occupying a critical link in local fish food chains.

The present study was undertaken to provide information about *I. baltica*'s reproductive behavior and physiology under laboratory conditions in order to determine the feasibility of developing it as a fish food for mariculture systems.

Materials and Methods

All animals were collected in July and August 1985, by removing attached *Ulva lactuca* thalli from the fouling community attached to submerged piers at the Barrrens Island Marina, Jamaica Bay. The animals were sorted from these collections in the laboratory, and placed in individual 22.5 cm diameter glass culture dishes of ambient seawater (29 ppt) either in heterosexual pairs (30 pairs), or in isosexual pairs (20 male and 20 female isosexual pairs). The pairs were maintained at room temperature (\bar{x} = 24.3 \pm 2°C SD), with a light cycle of 15:9 L:D. They

were fed *Ulva lactuca* thalli ad libitum. These pairs were observed 2 times a day, 12 hours apart, in the light, and maintained until one of the members of the pair died. Observations consisted of noting the occurrence of molts and ovulations, as well as any reproductive behaviors exhibited.

Intermolt periods were calculated by counting the number of days between the first and second molts only of animals maintained in heterosexual pairs. This was done to minimize any artifacts of culture conditions.

In addition to the pairs, 60 females were isolated in individual 10 cm diameter culture dishes. These females were used to determine the variability in timing of molts, ovulations, and expression of reproductive behavior. Females were observed at 12-h intervals, and the dates and times of their molts noted. Males were introduced either on the day the females molted, on day 1 or day 2 after the molts, or no males were introduced at all (12, 19, 13, and 16 different females observed, respectively). The occurrence and timing of copulations, ovulations, and subsequent brood developments were noted for all four groups of females.

Finally, to determine the timing of copulation with respect to the sequence of the shedding of the two parts (see following section) of the female's exoskeleton, males were introduced to five females between the first and second partial molts and the males' responses noted.

Results

Molts

Intermolt periods.—Individuals of both sexes molted repeatedly until they died. Some females molted four times in succession. The average intermolt period of the females was 13.4 \pm 0.8 SD days (n = 17, range = 12-15 days); for the males it was 13.0 \pm 4.4 days (n = 15, range = 7.5-23.0 days). There was no significant difference between the sexes (Student's t -test; t = 0.24, df = 30, P > 0.05).

Nature of the molts.—The exoskeleta of both sexes were cast off the same way. First the posterior half of the exoskeleton (from the fifth segment back) was shed, then the remaining anterior portion was cast off. The anterior part included the first four pairs

of oostegites of the female's brood pouch; the posterior part included the fifth and last pair. There was an interval between the shedding of the two parts (females: $\bar{x} = 6.5 \pm 6.1$ SD hours, $n = 35$, range = 0-12 hours; males: $\bar{x} = 8.3 \pm 6.9$ SD hours, $n = 36$, range = 0-24 hours). There was no significant difference between the intervals of the two sexes (Student's t -test: $t = 1.41$, $df = 69$, $P < 0.05$). Finally, the observations suggest that there is no terminal molt in either sex, because all individuals molted until they died.

Amplexus

Males picked up and held onto females until the females molted. During amplexus, females were held ventral to the male, and only the males' movements resulted in locomotion. There was no specialized point of attachment on the female. The male inserted the angle formed by the dactyl held slightly extended from the palm of its second gnathopod into the space between the curved, lateral edges of the female's first and second pereopod segments. Sometimes males held onto females with posterior pereopods as well, but this was only for brief periods of time.

The occurrence of amplexus was correlated principally with female intermolt stage. Amplexus began about $\bar{x} = 1.9 \pm 1.4$ SD days before the female molt ($n = 15$, range = 0.0-4.5 days) and all couples separated within 12 hours after the female discarded its anterior cast. Thus, females were in amplexus for approximately the latter 14.2% of their intermolt periods.

Most females were in amplexus 24 hours before their posterior molts and separated from the males 24 hours after their anterior molts (Table 1; Fisher's exact probability test, $P < 0.001$). In contrast, most males were not in amplexus either before or after their molts (Table 1; 83.3% and 64.3% not in amplexus before and after the molt, respectively). However, there was a significantly greater proportion of males in amplexus after than before their molts ($\chi^2_1 = 3.94$, $P < 0.05$). Thus, amplexus was

TABLE 1.—Frequencies of occurrences of amplexus 12 hours before the posterior molt and 12 hours after the anterior molt in *Idotea baltica* maintained in heterosexual pairs.

Sex	Number of molts	Before		After	
		Number in amplexus	Number apart	Number in amplexus	Number apart
Females	33	31	2	1	32
Males	42	7	35	15	27

principally correlated with female intermolt stage, but male intermolt stage had an affect as well.

Finally, amplexus was never observed in either male or female isosexual pairs.

Copulations

During copulation the male held the female's body in a perpendicular, ventral position, and inserted its pleopods into the posterior part of the female's brood pouch about five times in rapid succession. This was followed by a rest period of about 5 seconds during which the male retained its hold on the female. Then the sequence was repeated two or three more times.

Copulations occurred within minutes after males were introduced to females that had shed both parts of their exoskeleta, regardless of how many days ago the molt had occurred. In contrast, no copulations occurred in the five females that had just molted the posterior portions. Amplexus was initiated with these females instead, and copulation occurred only after the anterior portion of the exoskeleton was shed.

Ovulations

Isolated females ovulated about 2.9 ± 0.5 SD days after their molts ($n = 14$, range = 2-3.5 days). In contrast, females maintained with males in heterosexual pairs ovulated $\bar{x} = 0.12 \pm 0.2$ SD days after their anterior molts ($n = 26$, range = 0-0.5 days). The difference was significant (Student's t -test: $t = 25.92$, $df = 38$, $P < 0.001$). Another difference between isolated females and females maintained in heterosexual pairs was that none of the broods of the former group developed, while most of the latter broods did (Table 2: 0 of 14 vs. 24 of 26 broods, respectively; Fisher's exact probability test: $P < 0.001$). Eggs ovulated by isolated females were no longer observed in the brood pouches about 5.0 ± 1.8 SD days after the females' molt ($n = 12$, range = 3-6 days) or about 2.0 ± 1.5 SD days after ovula-

TABLE 2.—Frequencies of ovulations and viable broods of isolated females and females paired with males.

	No. of females	Number of		Number of ovulated broods that	
		ovulations	no ovulations	develop	do not develop
Isolated females	16	14	2	0	14
Paired females	26	26	0	24	2

tion ($n = 12$, range = 0.5-5.0 days). These observations show 1) that females ovulate in the absence of a male, but 2) delay their ovulations under those conditions; and 3) such eggs disappear from the brood pouches a few days after ovulation.

The introduction of a male to a female any time during the approximately 3-d period that females could delay their ovulations stimulated ovulation. Copulations generally occurred within 5 minutes after males were introduced to females 0, 1, or 2 days past their molts, and all ovulations occurred within 3 hours of copulation. There was no significant difference in the frequencies of copulations and ovulations among females isolated for different lengths of time (Table 3; $\chi^2_2 = 0.008$, $P > 0.05$ and $\chi^2_2 = 0.712$, $P > 0.05$ for copulations and ovulations, respectively).

In contrast, the broods of females who copulated and ovulated 0 and 1 day after their molts developed significantly more often than did the broods of 2-d postmolt females (Table 3; $\chi^2_1 = 3.61$, $P < 0.05$). This suggests that unfertilized eggs aged past 2 days have reduced viability.

TABLE 3.—Frequencies of copulations, ovulations, and viable broods of isolated females introduced to males 0, 1, and 2 days past the females' molts.

Days after molt	No. of females	Number of				Broods that develop	
		Copulations		Ovulations		Yes	No
		Yes	No	Yes	No		
0	12	10	2	10	2	10	2
1	19	16	3	14	5	12	7
2	13	11	2	11	2	5	8

Discussion

The present study has shown that males and females remain apart until towards the end of the female intermolt period, when amplexus is begun. This continues until the female molts, when copulation, followed by ovulation occurs. Females repeated this cycle in the laboratory until they died. Some females produced three broods in succession, without a rest period. In contrast, females in the field in Nova Scotia produce only one brood (Strong 1978), and in the northern Baltic most have one brood (although some may have two (Salemaa 1979)).

It is impossible to say whether the difference in the number of broods produced in the field and in the laboratory is caused by environmental and/or genetic differences. In support of the first explanation, a recent symposium has demonstrated the im-

portance of photoperiod in regulating the timing of reproductive activities of marine animals (Marcus 1986), and, specifically, in the number of broods of some peracarids (Steele and Steele 1986). The photoperiod of Nova Scotia may limit the number of broods there. In support of the second explanation, Healy and O'Neill (1984) noted that two populations of *I. granulorum* produced different numbers of broods in Ireland and in Britain, although there was no significant difference in temperature or latitude at the two locations. Further, while Tinturier-Hamelin (1963) found no reproductive barriers among *I. baltica* from different parts of Europe that were hybridized in the laboratory, she did conclude that the subspecies were genetically distinct. Only laboratory culture, under identical conditions, of representatives from different geographic localities will reveal whether the difference in the number of broods is genetic.

The present observations also reveal that *I. baltica* females spend relatively little of their intermolt periods in heterosexual pairs (14%) compared with other peracarids (the mean of seven other peracarids was 32% (Borowsky 1986)). Strong (1978) reported that a short amplexus period was correlated with a high risk of fish predation in the amphipod *Hyallela azteca* and suggested that couples are more visible than single individuals. This may be the case here as well. Fish and predaceous shrimp are abundant in the community from which individuals for the present study were collected (D. Franz pers. commun.¹).

Both sexes cast off the posterior parts of their exoskeleton before the anterior parts. Since the female's anterior portion includes most of the brood pouch, the new marsupium is not completely exposed until both parts are shed. Males did not copulate with females that had not molted the anterior cast. The sequence of molts and copulation makes sense, because the present study shows that copulations stimulate ovulations. If copulation occurred before the anterior portion of the pouch were shed, the new eggs might be secreted into the old brood pouch, and then discarded along with the anterior molt.

The present study reveals some flexibility in the timing of key reproductive events. Females could copulate until about 36 hours after they cast off their anterior molts without incurring a significant reduction in fecundity. However, if copulation did not occur by about 3 days after their molts, females

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ovulated spontaneously. These eggs did not develop and disappeared from the brood pouches after a few days. Thus, there appears to be no sperm storage in *I. baltica*, and females must be accompanied by a male at the time of their molts to ensure the development of their broods.

One interesting observation was that males engage in amplexus significantly more often after than before their molts. This may be explained by the observation that neurons become detached from the exoskeleton a few days before the molt (Guse 1983). Thus, if contact and/or water-borne pheromones are secreted by receptive female *I. baltica* as they are in some other peracarid females (Borowsky 1984, 1985, 1986), it is possible that the males cannot sense the stimuli produced by females shortly before their own molts, and therefore are less likely to engage in amplexus at that time.

Conclusion

The results of the present study show that *I. baltica* adults can be maintained in the laboratory, and will reproduce freely with minimal effort and at minimal cost. Females fed exclusively on *Ulva lactuca* produced many broods in succession in non-aerated, uncycled water. While further study is necessary to determine whether juveniles will develop under these conditions, and, if so, what the yield will be, the observations reported here suggest the feasibility of culturing this species for fish mariculture systems.

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OCCURRENCE OF THE FIRST FRESHWATER MIGRATION OF THE GIZZARD SHAD, *DOROSOMA CEPEDIANUM*, IN THE CONNECTICUT RIVER, MASSACHUSETTS¹

Occurrence of a freshwater migration of the gizzard shad, *Dorosoma cepedianum* (Lesuer) (Clupeidae), is documented for the first time in a New England river system. Adult gizzard shad were observed and collected at the Connecticut River fishlift facility in Holyoke and upstream in Massachusetts during 1985 and 1986. It is believed that the Connecticut River migrants are derived from a population recently observed in Long Island Sound and already occurring in the Hudson and Connecticut River estuaries and Nantic Bay.

The gizzard shad is a widely distributed species occurring in marine and tidal freshwaters along the

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