PROC. ENTOMOL. SOC. WASH.
87(1), 1985, pp. 110–115

THE INTERTIDAL ZONATION OF *THALASSOTRECHUS BARBARAE* (HORN) (COLEOPTERA: CARABIDAE)

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Abstract.—In central California, crevices occupied by larvae and pupae of *Thalassotrechus barbarae* were distributed in the upper intertidal zone between Highest Lower High Water (1.53 m) and Lowest Lower High Water (0.87 m). Adults were collected from crevices ranging in height from just below Highest Higher High Water (1.89 m) to just below Mean Lower High Water (1.1 m), but their nightly activities outside the crevices extended from just below the splash zone (2.89 m) down to Mean Higher Low Water (0.72 m).

Carabid beetles are found in a great variety of terrestrial habitats but some are adapted for living in a narrow band or zone within the wider intertidal boundaries on rocky shores, sand beaches or tidal mudflats. Intertidal zonation is characteristic of all life on seacoasts and a vast literature exists on the zones occupied by the more conspicuous sedentary organisms such as barnacles, mussels, limpets and marine algae. However, little is known about zonation of intertidal insects and most of the records are qualitative. Concerning carabid beetles, for instance, Johns (1974) reported finding specimens of *Kenodactylus audouini* (Guérin) ". . . just above the mean tide level" in the Auckland Islands, and Evans (1968) recorded *Tachys* sp. from "crevices at the upper level of the barnacle-algae zone" in western Mexico. Riedl (1963) lists the habitat of *Pogonus luridipennis* Germar and *P. gracilis* DeJean simply as intertidal. In a more quantitative study, Glynne-Williams and Hobart (1952) found individuals of the European intertidal carabid *Aepopsis* (= *Aepus*) *robini* Laboulbène widely distributed at about the mean tide level.

Thalassotrechus barbarae (Horn) is the only pogonine carabid species inhabiting rocky shores on the Pacific coast of North America. Members of this flightless species are distributed from Point St. George near Crescent City in northern California to Bahia Magdalena, Baja California, Mexico (Evans, 1977). This is in a region of mixed tides (Doty, 1957); variations in tidal height take place twice a day, but successive high tides and successive low tides are quite different in height (Fig. 1). Along this coastline beetles live in rocky shore habitats in protected bays such as San Francisco Bay and Bahia Magdalena or on semiprotected exposed coasts such as Carmel Bay and Pismo Beach.

All stages occur in rock crevices in the upper intertidal zone though adults emerge at night when tidal conditions permit and walk over nearby rock and sand surfaces (Evans, 1976). Mating as well as feeding takes place at these times. Rock

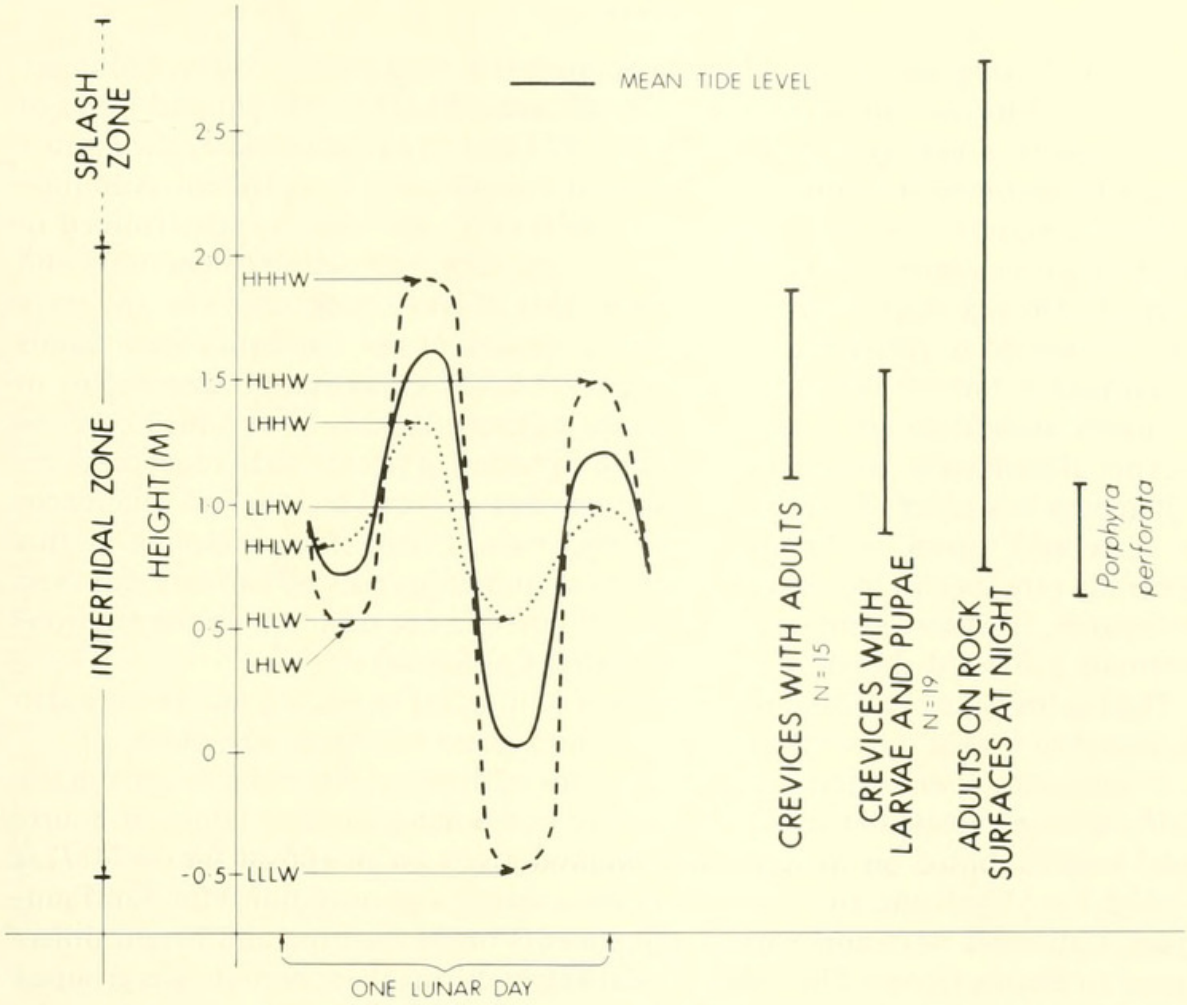

Fig. 1. Ranges of heights of crevices in the intertidal zone at Pacific Grove, California, occupied by adults, larvae and pupae of *Thalassotrechus barbarae*; the range of nocturnally active adults outside crevices; and the range of heights of the alga, *Porphyra perforata*. Algal data from Smith (1969) and tidal diagram modified from Doty (1957). H, L, and W = High, Low and Water with suffixes -est and -er appended to the first two words of each four word set respectively.

crevices form a distinct habitat in the marine littoral (Glynne-Williams and Hobart, 1952; Richoux, 1972) with a characteristic fauna that consists partly of marine and partly of terrestrially-derived constituents, such as insects (Glynne-Williams and Hobart, 1952; Kensler, 1965). Crevices shelter inhabitants from extremes of temperature and humidity and from wave action. Sediments trapped in crevices serve as a substrate for the resident organisms as well as a filter of plankton and organic detritus brought in by tides.

The objectives of this study were twofold. As part of another study on adaptations of *T. barbarae* to the chemical milieu of the crevice habitat the vertical range of heights of crevices occupied by larvae and adults was needed to relate chemical composition of crevice sediments to tidal influences. Secondly, as part of another project on mechanisms of habitat selection in the Carabidae (Evans, 1983) I required information on the vertical distances travelled by adults to help explain how they find their way back to crevices at dawn or at flood tide after their nocturnal perambulations.

Methods

The study area was a rocky shore in Spanish Bay near Pacific Grove, Monterey County, California with a mean tidal amplitude of 1.07 m. Height and times of tides were obtained from the *Tide Tables* 1973 and 1974 published by the United States Department of Commerce, National Oceanic and Atmospheric Administration. Zonation of larvae, pupae and adults of *T. barbarae* was determined in the following manner: during the day rock crevices were selected randomly and opened with a geological hammer. The heights of crevices occupied by any stage were measured in relation to a nearby benchmark of the California State Lands Commission Survey with a Brunton pocket level. Quantitative assessment of numbers of individuals in each crevice or of mean heights of occupied crevices was not attempted because of considerable variation in sizes of individual crevices, differences in degree of exposure of the crevices to wave action, and differences in slope and aspect of the crevice-bearing rock. (Also, since sampling of this generally rare species requires destruction of numerous crevice habitats and their occupants, extensive sampling was neither possible nor desirable in the environmentally protected shoreline areas of central California).

During low tide periods at night, heights of foraging or mating adults were also recorded to obtain the vertical range at which these activities take place.

Frequencies of emersion/immersion cycles of different intertidal heights in the study area were calculated with the use of computer-generated tables of hourly tidal heights, based on the graphical method given on p. 186 of the 1974 *Tide Tables*, for March and July (periods of both spring and neap tides) for San Francisco, California with appropriate adjustments made for time and height differences for Pacific Grove. The range of tidal height during these periods was grouped into 17 classes, each 0.14 m wide and, using the midpoint for each class, the hourly height tables were scanned for the number of times the tide rose above and fell below these midpoints during all the tidal cycles of the two months.

Results and Discussion

As expected, crevices occupied by adults, and by larvae and pupae of *T. barbarae* are distributed in narrow bands on intertidal rocks of central California (Fig. 1). At night, active adults range in a wider band that corresponds roughly to the upper half of the intertidal zone. Also shown in this figure is the zonation of *Porphyra perforata* Agardh (Rhodophyta; Bangiaceae) (Smith, 1969), a red alga that is generally a reliable indicator of *T. barbarae* populations in the region where the distribution of these organisms overlap (essentially the entire Californian coastline); this yellowish-green, leafy alga is also the host plant of *Tethymyia aptena* Wirth (Diptera: Chironomidae) larvae that are eaten by *T. barbarae* adults (Evans, 1980).

Crevices occupied by adults, larvae and pupae were distributed in the upper regions of the intertidal zone corresponding approximately to the mean high tide level. Adults were collected from 15 crevices that ranged in height from 1.10 m (just below Mean Lower High Water) to 1.89 m which is just below Highest Higher High Water. Foraging and mating activities outside the crevices took place over a range extending from 0.72 m (Mean Higher Low Water) to just below the upper limits of the splash zone. Of 19 crevices with larvae and pupae, the highest at 1.53 m (approximately Highest Lower High Water) overlapped part of the

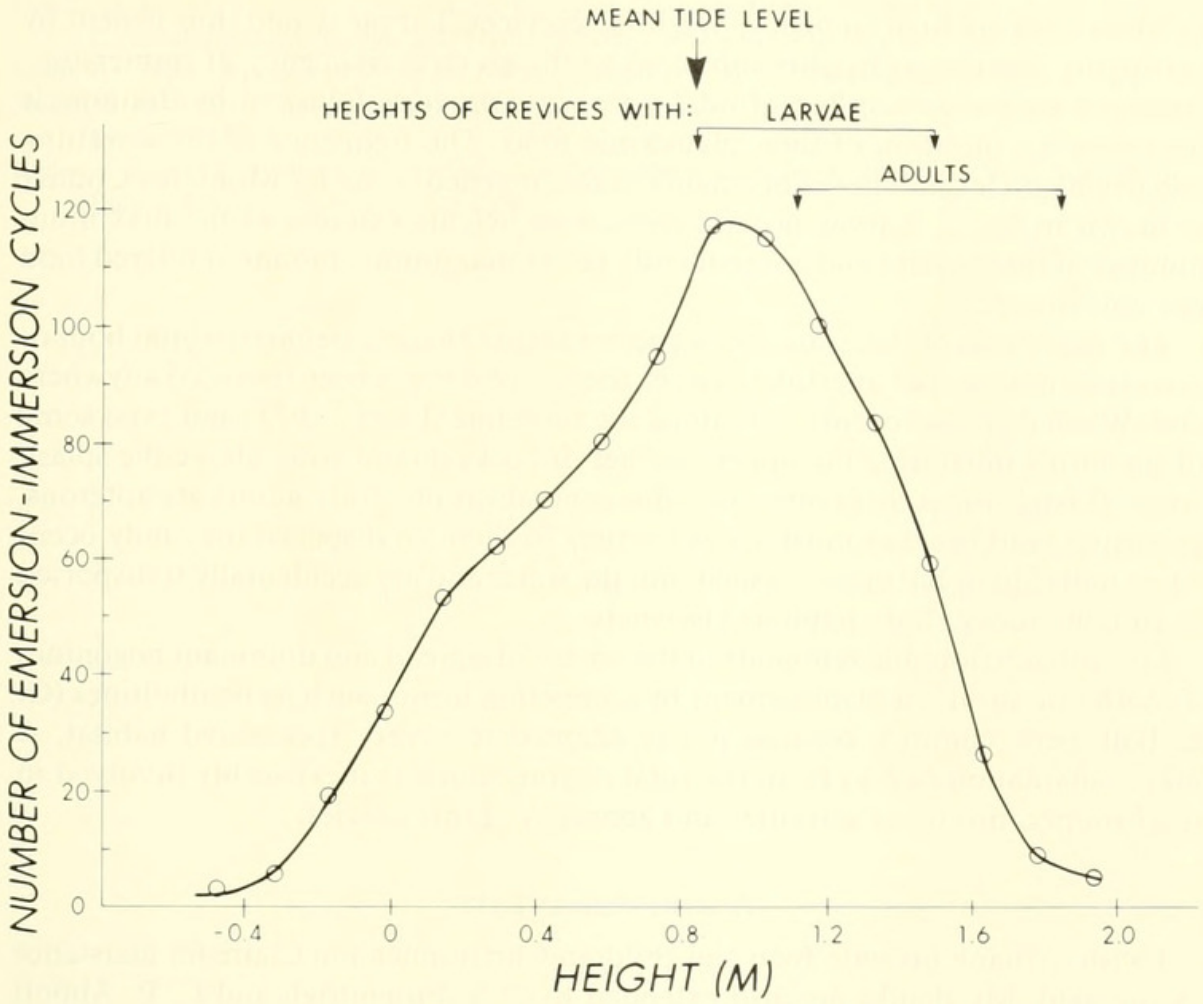

Fig. 2. Number of immersion and emersion cycles for different heights of the intertidal zone at Pacific Grove, California, for March and July, 1974 in relation to intertidal zonation of adults and larvae of *Thalassotrechus barbarae*.

adult range. Larvae and adults were collected together sometimes but since adults were not found in crevices below 1.10 m, females presumably enter such crevices for oviposition as part of their nocturnal activities while higher crevices serve as daytime retreats. Height differences between crevices with larvae and those with adults are probably real because the heavily sclerotized adults appear to be more resistant to water loss and are thus able to tolerate the drier conditions of the higher crevices. However, there is a lower height limit for the larvae below which they would be exposed to excessive periods of immersion. This limit corresponds to 0.87 m (Lowest Lower High Water), a level that is one of several "critical tide levels" (Doty, 1946) in California where changes in dominant species occur due to abrupt differences in duration of immersion or emersion over a period of time. At a level just below 0.87 m the duration of immersion increases two to three times so that crevices in this region are much wetter than those above this limit and are probably unsuitable for an essentially terrestrial insect such as *T. barbarae*.

The difference in ranges of heights of crevices with larvae and those with adults also reflects differences in trophic niches between these stages. Adults are free to scavenge or prey over a height range of more than 1.5 m in the upper intertidal zone whereas larvae are restricted to allochthonous planktonic material brought

in when tides are high enough to wash the crevices. Larvae would thus benefit by occupying crevices at heights subjected to the greatest frequency of immersion/emersion cycles since influx of tidal water into crevices followed by draining is necessary for filtration of their planktonic food. The frequency of these wetting and drying cycles for classes of heights in the intertidal zone for Monterey County is shown in Fig. 2. Larvae occupy crevices at heights exposed to the maximum number of these cycles and consequently to the maximum amount of filtered food per unit time.

The restriction of individuals of a species within sharply-defined habitat boundaries is common to all intertidal insects; they have just not been recorded anywhere else. When dispersal occurs, it is along the shoreline (Leech, 1971) and even some of the forms inhabiting the upper beaches or rocks do not stray above the splash zone. *T. barbarae* is no exception to this generalization. Since adults are apterous, extensive sand beaches must act as barriers to them so dispersal may only occur when individuals fall or get washed into the water and are accidentally transported to suitable rocky shore habitats elsewhere.

Like other halophilic remnants of the once widespread and dominant pogonines *T. barbarae* survived displacement by competing forms, such as bembidiines (G. E. Ball, pers. comm.), because it was adapted to a very specialized habitat. A major adaptation had to be to the tidal regime which is inextricably involved in food supply, timing of activities and zonation of this species.

Acknowledgments

I wish to thank my wife Joan and children Christopher and Claire for assistance in the field. My thanks are also extended to C. S. Pittendrigh and C. P. Abbott for use of the facilities at Hopkins Marine Station of Stanford University and to J. S. Scott for drafting the figures. This research was supported by grant A-1409 from the National Sciences and Engineering Council of Canada.

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