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Reproduction of the Continuously Breeding Tropical Hermit Crab *Clibanarius clibanarius*

Sudha Varadarajan* and T. Subramoniam

Department of Zoology, University of Madras, Madras 600005, India

ABSTRACT: On the Indian east coast, the hermit crab *Clibanarius clibanarius* breeds continuously with peak activity from September to January, corresponding to the onset of the retreating monsoon. Individuals within the population breed asynchronously and vary widely in their carapace lengths, probably because of steady, year-round recruitment. Our data on reproduction emphasize the flexible use of an apparently stable, tropical environment by these crabs.

INTRODUCTION

In tropical marine waters, where sea temperatures fluctuate little seasonally, many invertebrates are known to reproduce throughout the year (Giese and Pearse, 1974). In Indian waters a major factor that influences intertidal as well as offshore forms is the monsoon rain that differs in time and intensity on the east and west coasts (Panikkar and Jayaraman, 1966). Semiannual breeding patterns have been reported for a number of species on the east coast of India (Giese and Pearse, 1974), where little rain falls during the South-west monsoon and heavier rain falls during the retreating monsoon (Hu-Cheng, 1967). However, other species along this coast have annual breeding periods or breed throughout the year (e.g. Kemp, 1915; Panikkar and Aiyar, 1939; Paul, 1942; Nagabhushanam, 1962; Antony Raja, 1963; Giese et al., 1964; Nagabhushanam and Dhamne, 1977; Subramoniam, 1977); hence generalization is difficult.

The present study deals with the reproductive activity of the anomuran crab *Clibanarius clibanarius* Dana and compares it with that of other species. It provides a better understanding of the factors regulating reproductive patterns along the Indian coast.

MATERIAL AND METHODS

Specimens of *Clibanarius clibanarius* Dana, an offshore hermit crab, were collected monthly from launches plying off the coast of Madras at depths of 9 to 18 m. In January and February, 1976 and January, 1977 all crabs were scarce and few could be collected. Females, smaller in size than males, often occupied smaller gastropod shells of different species of *Murex, Bursa, Babylonia* or *Turitella*. After removal from the shell, the length from the tip of the rostrum to the posterior indentation on the mid-dorsal line of the cephalothorax was taken as carapace length. The soft abdomen was opened, the ovaries were separated from the hepatic tissue and gonad-indexes and hepatic indexes (Giese, 1967) and egg mass indexes (Subramoniam, 1979) were calculated**.

The ovaries were classified into stages according to colour changes and oocyte diameters (Varadarajan and Subramoniam, 1980), where Stage 1 ovaries are the least mature and Stage 3 ovaries contain oocytes ready to be spawned.

RESULTS

Fluctuations of mean gonad indexes of *Clibanarius clibanarius* witness almost uninterrupted breeding for the population in the coastal waters off Madras (Fig. 1). Mean gonad indexes suggest 2 peaks annually: One centering around September to October, the other

* Present address: Marine Biological Station, Zoological Survey of India, 12, Leith Castle Street, Santhome, Madras 600 028, India

** $\frac{\text{Wet wt. of egg mass}}{\text{Wet wt. of animal}} \times 100 = \text{Egg mass index}$

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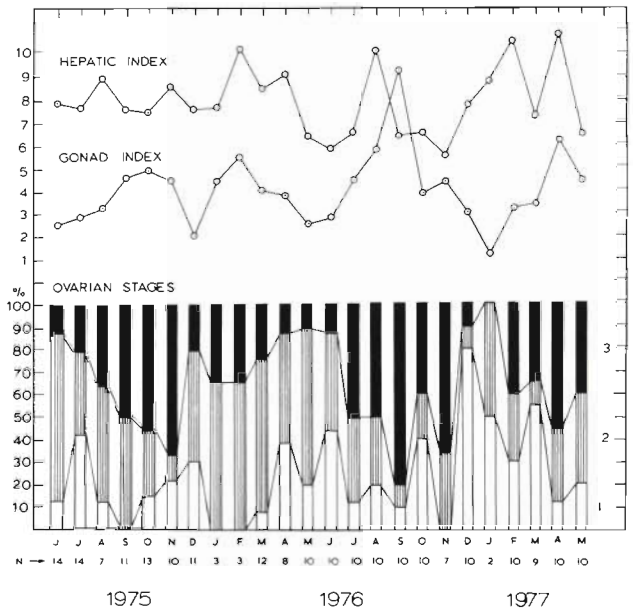

Fig. 1. *Clibanarius clibanarius.* Mean gonad indexes, hepatic indexes and percentage of ovarian stages of females off Madras plotted against time (June 1975 to May 1977). Solid bars: Stage 3; striped bars: Stage 2; empty bars: Stage 1. N = sample size

around February to April. This semi-annual pattern has been recognised in many invertebrates of the tropics influenced by monsoons (Giese and Pearse, 1974). However, there was considerable variation between years. The very high mean gonad index in September 1976, for example, was not seen in September, 1975.

The reproductive activity of *Clibanarius clibanarius*, estimated by the gonad indexes, was complemented by the analysis of ovarian stages, with high gonad indexes corresponding to a high percentage of crabs with Stage 3 oocytes (Fig. 1). This correspondence suggests that increase in weight of the ovary reflects the increase in oocyte-diameter.

Hepatic indexes were nearly always higher than gonad indexes (Fig. 1). They were also relatively more stable and there was little or no relationship between gonad indexes and hepatic indexes.

Egg-mass index is the ratio of the weight of the egg mass carried by a female to body weight; it represents 'the realised reproductive potential' (Eickstaedt, 1969) in a given population (Fig. 2). Except for February, July and November 1976, when no egg-bearing females were recorded, the egg-mass index shows that females brood embryos equivalent to about 16% of their body weight throughout the year.

Over 25% of the females were ovigerous in all samples except those of June and July 1975, February, July and November 1976, and February 1977 (Fig. 2). Maximum percentages of ovigerous females occurred between August and January. There was little relationship, however, between the percentage of ovigerous females in a sample and either the mean gonad index or ovarian stage of that sample. Lack of such a relationship indicates that brooding females were in varying stages of oogenesis, and reflects the absence of reproductive synchrony within the population.

DISCUSSION

The population of *Clibanarius clibanarius* off Madras exhibits continuous breeding with scattered peaks, particularly between August and May. Continuous reproduction with breeding peaks is well known in

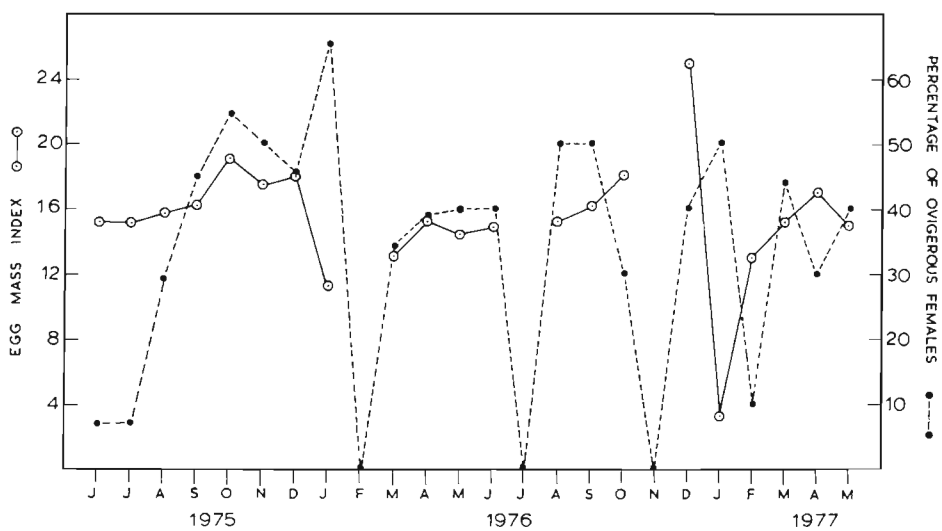

Fig. 2. *Clibanarius clibanarius.* Egg-mass indexes and percentage of ovigerous females off Madras, plotted against time (June 1975 to May 1977). Sample sizes given in Fig. 1

many other tropical, marine crustaceans (e.g. George, 1962; Antony Raja, 1963; Goodbody, 1965; Reese, 1968). *Clibanarius chapini* and *C. senegalensis* of Ghana (Ameyaw-Akumfi, 1975)) and *C. olivaceous* of Madras (Kamalaveni, 1947) also all breed throughout the year. In the offshore waters of the Madras coast, there is little or no seasonal variation in sea water temperature; the mean monthly range during the entire study was only 4.7 C° (25.5° to 30.2 °C). The variation noted in reproductive activity of *C. clibanarius* showed no relationship to temperature fluctuations; it can be concluded that temperature fluctuations have little or no influence on the reproductive activity of this species in Madras waters.

Species on the west coast of India (Cochin) tend to have peak reproductive activities in November and December, while on the east coast peaks are more spread out and scattered, as with *Clibanarius clibanarius*. This difference may be illustrated by comparing the breeding peaks of the same species on the 2 coasts of India. The shrimp *Penaeus indicus* and crabs *Uca annulipes* and *Portunus pelagicus* all have breeding peaks between October and January at Cochin (Prasad and Tampi, 1953; George, 1962; Pillay and Nair, 1971), but on the east coast they have much more extended peak activities, including all the warmer months (Pannikkar and Aiyar, 1939; Subrahamanyam, 1963; Rahaman, 1967). Such intraspecific variability shows both how sensitive reproduction is to environmental conditions and how generally favourable the east coast is for year-round reproduction. We have compiled breeding records for a total of 63 species of marine invertebrates on the east coast of India, mainly at Madras and Vishakapatnam, and of 15 species on the west coast mainly at Cochin. Each month between 60 and 80% of the east coast species are breeding and there is no seasonal pattern of peak activity (Fig. 3). In contrast, most breeding activity on the west coast occurs between September and March.

Not only are peak breeding activities more restricted in continuously breeding species on the west coast of India than those on the east coast, but restricted breeding seasons are more frequently found in species on the west coast.

The South-west monsoon brings abundant rain to the west coast of India from May to August. Hence the salinity of estuarine, shallow, brackish-water lagoons which receive freshwater from many large rivers diminishes considerably. At the peak of the monsoon there is barely any reproductive activity (Nair, 1965). Postmonsoon rise in salinity restores breeding and, although a second season of light rainfall occurs from October to December, it does not affect breeding of west coast invertebrates to any large extent.

On the east coast of India, the slow, retreating monsoon normally brings rain around October in places 19°–15° N and those south of 15° N, in November (Hu-Cheng, 1967). The discontinuously breeding brackish-water forms of Madras concentrate reproductive activities mainly during the rainy season (Panikkar and Aiyar, 1939). While the deterrent action of the heavy summer rain checks reproduction on the west coast, its milder intensity than the retreating monsoon on the east coast, especially near Madras without any large rivers, may enhance reproduction in, e.g. *Clibanarius clibanarius*.

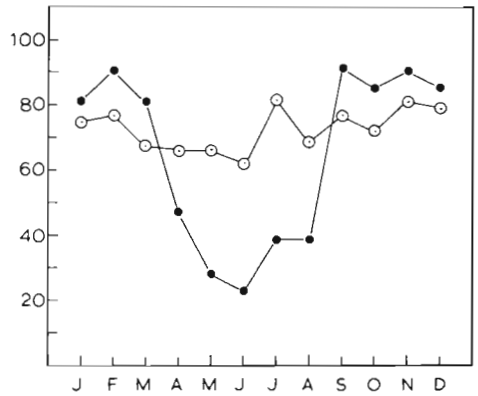

Fig. 3. Percentage of marine invertebrate species breeding each month on the east and west coasts of India. Solid circles: percentages on west coast (N = 15); open circles with dots: those on east coast (N = 63). From an unpublished compilation of breeding records by S. Varadarajan

The salinity of the sea near Madras is not affected to any great extent by the 2 rivers here as even during November to December they are open to the sea only for a few weeks. Monsoon-driven currents flowing from the head of the Bay carry fresh waters discharged by the great northern rivers, diluting the coastal waters almost up to March when the currents are reversed. Thus the monsoon may be the only factor for lowering the salinity of the Madras coast. Yet, these low saline periods have been found to be months of high nutrient content also, due to upwelling (Muthu, 1956). Hence, the rather stable environmental temperature throughout the year and moderate changes in salinity may well be conducive to continuous reproduction in *Clibanarius clibanarius* while the peaks correspond to monsoon and post-monsoon months when nutrients and plankton occur in plenty. Stephenson (1934) observed that most tropical species on the great Barrier Reef breed during warmer months. In the case of Indian coastal invertebrates, however, monsoon rather than temperature is the major factor that influences their reproductive activities.

Ovigerous females never exceeded 66% of the females of *Clibanarius clibanarius* sampled. In con-

trast, breeding frequency was as high as 98% in *Pagurus samuelis* (Coffin, 1960) and over 80% in *Calcinus laevimanus* (Reese, 1968) both of which are more restricted in their breeding seasons. Such restricted breeding may be highly synchronised so that most individuals brood at about the same time while continuous breeders are less synchronised among different individuals. An interesting exception to the above is *Emerita asiatica,* which, although a continuous breeder, touches brooding frequencies as high as 90% in certain months (Subramoniam, 1977).

The presence of ovigerous females with maturing ovaries suggests reproduction right after the release of larvae. When broodless females with maturing ovaries are encountered, they may be either maturing for the first time or after an interbrood period. In *Clibanarius clibanarius* berried females with maturing ovaries were repeatedly found in nearly all individuals between 13 and 20 mm carapace length. Evidence of brooded eggs occurring simultaneously with ripening ovaries have been reported for cirripedes with a more restricted breeding period (Crisp, 1954; Hilgard, 1960), decapods (Pillay and Nair, 1971; Ameyaw-Akumfi, 1975) and isopods (Jones, 1974). When advanced pleopodal eggs occurred together with advanced stages of oocytes, a second brood invariably ensued. This happened continuously in *Emerita asiatica,* breeding being kept at a high level (Subramoniam, 1977). In *C. clibanarius* even at the height of breeding, only 55 to 60% are berried. Brooding individuals with high gonad indexes due to ripe oocytes would undoubtedly reberry without delay. Others with earlier oocyte stages in their ovaries would take a longer time to reberry. Since both types are found at any given time in a population there was pronounced asynchronous breeding.

The wide range in carapace length found in reproducing *Clibanarius clibanarius* in most months is similar to that in *Pandalina brevirostrosis* (Allen, 1965). This is probably because, in *C. clibanarius* at least, new recruits enter the population continuously at different rates throughout the year. Every collection contained, therefore, breeding individuals of varying size classes.

Hepatic and gonad indexes rose and fell synchronously in *Portunus pelagicus* (Rahaman, 1967), suggesting no direct transfer of materials from the former to the latter. However, in *Clibanarius clibanarius* an inverse relationship was found between gonad and hepatic indexes in certain months (Dec. 1976, Jan. 1977) after high reproductive activities, and the hepatopancreas may contribute materials to the gonad at some time. Even when the hepatic index is stable, there may be a quick digestion and a rapid mobilization to the ovary from the hepatopancreas as has been suggested for similar, stable hepatic indexes in *Emerita analoga* (Eickstaedt, 1969).

During our investigation there was a dearth of these crustaceans from January to February, yet among the few females collected, berried forms were present. De Figueiredo and Thomas (1967) attributed the disappearance of berried females of *Nephrops norvegicus* from catches to behavioural changes by the females. But in the present study males also were scarce and factors responsible probably affected males and females equally. Migration of males and females of *Cancer productus* into deeper waters for breeding was noted by Knudsen (1964). Rebach (1974) suggested that some hermit crabs resorted to burying themselves temporarily during reproductive processes, often migrating to a sandy substratum. Although further investigations are necessary, it is obvious from our collections that reproductive activities are not withheld in *Clibanarius clibanarius* from January to February when they were difficult to collect.

Many continuous breeders are relatively unspecialised in their food habits, being either filter feeders or browsers (e.g. Goodbody, 1965; Subramoniam, 1977). *Clibanarius clibanarius,* when maintained in the laboratory, fed on ovarian or hepatic tissues of *Emerita asiatica* or *Uca annulipes* or, more often, scraped algal films off each others' shells. When water was replenished every day, many of them – especially ovigerous females – retreated to the deeper parts of the tilted tank and fed by filtering water, as was seen by the position and working of the antennules. Gerlach et al. (1976) have also reported filter feeding in *Pagurus bernhardus.* Such diverse mechanisms of feeding on all kinds of available food materials might have provided abundant nutrition to support reproductive activities throughout the year.

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