Palaeogeography, Palaeoclimatology, Palaeoecology 374 (2013) 187–196

Contents lists available at SciVerse ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Prey selection by drilling predators: A case study from Miocene of Kutch, India

Devapriya Chattopadhyay *, Saurav Dutta

Department of Earth Sciences, Indian Institute of Science Education & Research, Kolkata, Mohanpur Campus, WB-741252, India

ARTICLE INFO

Article history:
Received 4 September 2012
Received in revised form 4 January 2013
Accepted 22 January 2013
Available online 28 January 2013

Keywords:
Drilling predation
Bivalve prey
Miocene
Prey selection
Naticidae

ABSTRACT

The fossil record of predatory drill holes in shelled invertebrates provides valuable evidence to understand the evolutionary role of biotic interactions in deep time. It is hypothesized from modern studies that predatory gastropods do not randomly attack molluscan prey; rather they select their prey in order to maximize the energy gain. We have tested this hypothesis using bivalves from Miocene marine deposits of Kutch, India. The prey group consists of *Chlamys* sp., *Placuna lamellata* and four species of oyster bivalve namely *Ostrea latimarginata*, *Ostrea angulata*, *Crassostrea gigensis*, and *Hyotissa hyotis.* The overall drilling frequency is 20% and the species level frequency is as high as 35%. There is quite a high incidence of incomplete drill holes; while the assemblage level frequency is 41%, the species level frequency is as high as 57%. Our assemblage demonstrates preferred selection of prey in terms of taxonomy, size, site and valve by the predatory gastropod. Such selections are guided by the energy maximization strategy of the predator. Moreover, the high incidence of incomplete drill hole makes the dynamics even more intriguing since it shows a different pattern of selectivity compared to that of successful attacks. The success rate of an attack differs with size of the predators, hence indicative of an ontogenetic improvement in predatory skills. The overall predation intensity, although comparable to a few reports from other continents, is largely different from the global average of drilling frequency of Miocene.

1. Introduction

Predation plays a major role in natural selection. It has contributed significantly in shaping the global biodiversity of the marine fauna (Carriker and Yochelson, 1968; Vermeij, 1987; Huntley and Kowalewski, 2007; Stanley, 2008). Although the importance of predation has been recognized, it is often difficult to study the effect in deep time due to the lack of preservable traces of such interactions. Predation by drilling gastropods creates a unique scenario where it produces a readily preservable signature of the predatory event in the victim itself. Drilling predation, therefore, has been extensively studied to evaluate hypotheses on evolutionary significance of biotic interaction, such as coevolution (e.g., De Angelis et al., 1985; Kitchell, 1986, 1990) and escalation (e.g., Vermeij, 1987; Kelley and Hansen, 1993, 1996; Dietl and Alexander, 2000). The borehole produced by a muricid or naticid gastropod on prey provides evidence of the success or failure of predation, a measure of the size of the predator and a simultaneous measure of relevant characteristics of the prey (Kitchell et al., 1981; Chattopadhyay and Baumiller, 2007). Moreover, the presence of drilling behavior in Recent molluscan assemblages allows us to conduct actualistic studies and use the results to decipher the biotic interaction in deep time.

Extensive studies have been conducted worldwide to understand the details of drilling predation on bivalves in Recent (reviewed by Kitchell et al., 1981; Kelley and Hansen, 2003; Sawyer and Zuschin, 2010) and ancient ecosystems (reviewed by Kelley and Hansen, 2003; Harper 2003, 2006; Huntley and Kowalewski, 2007). Most of such studies have been conducted on Cenozoic assemblages. There have been reports on Miocene bivalves showing predatory drill holes from all over the globe (Hoffman et al., 1974; Dudley and Dudley, 1980; Colbath, 1985; Kelley, 1988; Kowalewski, 1990; Anderson, 1992; Hoffmeister and Kowalewski, 2001; Zlotnik, 2001; Amano, 2003, 2006; Kelley and Hansen, 2006; Sawyer and Zuschin, 2011) except from the Indian subcontinent. The only study on drilling predation from this area focuses on Mesozoic assemblage (Bardhan et al., 2012).

In the global reports on Cenozoic drilling predation on molluscs, only a very few studies established the nature and cause of selectivity of such attacks. Some approaches tried to explain the selectivity from ecological preference (Hoffmeister and Kowalewski, 2001; Sawyer and Zuschin, 2010) by showing difference in predation intensity in different ecological guilds. Others studied it using energy maximization model to demonstrate the difference in net energy gain by selecting a specific prey (Kitchell et al., 1981; Kelley, 1988).

This study presents the first report of extensive drilling predation from Miocene strata of Kutch, India. We have further investigated the nature of drilling behavior from ecological as well as energy-maximization strategy.

* Corresponding author. Tel.: +91 9874155997.
E-mail address: devapriya@iiserkol.ac.in (D. Chattopadhyay).

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http://dx.doi.org/10.1016/j.palaeo.2013.01.016

2. Materials and methods

2.1. Geologic and paleontological settings

All the samples used for the study were collected from an exposure near Rampar village (N 23°20.110′, E 68°48.735′) located in Kutch region of Western India (Fig. 1) during a field trip in December, 2011. The beds belong to the lower Chhasra Formation of Early Miocene age. The thickness of the beds varied from 30 cm to 200 cm in this region. Chhasra Formation is comprised of two members: lower Claystone and upper Siltstone member (Kumar et al., 2009). The specimens belong to the biostromal composite concentration (also known as community shell concentration, Norris, 1986; Meldahl, 1993; Cantalamessa et al., 2005) of the lower claystone member of the Chhasra Formation, mainly characterized by matrix-supported fabric, randomly oriented shells, low to moderate fragmentation and dissolution of shells (Fig. 2).

Molluscan specimens were collected from the vertical face of the exposure by surface sampling; the heavy rainfall during 2011 considerably loosened the claystone yielding intact fossil specimens. Where the hard rock prohibited the safe recovery of the specimen, we took detailed field photographs for documentation. The Cenozoic molluscan assemblages from Kutch region have been studied and described in detail (Kachhara et al., 2012; Borkar et al., 2004; Chattopadhyay, 2004; Kulkarni et al., 2007, 2009). The present locality represents many of the typical taxa. The faunal assemblage of this locality consists of bivalves (dominantly oysters), gastropods, echinoids and bryozoans.

2.2. Data collection and analysis

Specimens were brought back to the laboratory for detailed study. All the specimens were photographed and examined for evidence of drill holes. The photographs were later analyzed for maximum size, shape and size of the drill holes using digitization software (ImageJ). Dimensions of some fragmented specimens were reconstructed using the relationship between anterior-posterior and dorsal-ventral length of intact specimens of the same species. The size of a drill hole was measured by measuring the maximum outer diameter of the hole (outer borehole diameter or OBD). The valves were recognized as right or left in order to check selectivity of valve by the predator. The collected samples were housed in the paleontology laboratory of Department of Earth Sciences, IISER Kolkata (IISER-K/Ku/Mio/1-319).

All the specimens in our collection were disarticulated valves. Hence, the frequency of drilling predation was calculated by dividing the number of bored valves by the half of total number of valves in the collection (Kowalewski, 2002).

$$\text{Drilling Frequency(DF)} = N_D/(N * 0.5)$$

where

N_D Number of valves with complete drill hole
N Total number of valves.

The incomplete drilling frequency however was calculated by dividing the total number of incompletely drilled valves by the total number of drilled valves present in the collection.

$$\text{Incomplete Drilling Frequency (IDF)} = N_{ID}/(N_{ID} + N_D)$$

where

N_{ID} Number of valves with incomplete drill hole
N_D Number of valves with complete drill hole.

Previous workers have used a similar index called “prey effectiveness (PE),” defined by Vermeij as the number of incomplete drill holes divided by the total number of attempted drillholes (complete and incomplete). Our metric would be comparable to PE if there is no incidence of multiple drill holes. Both DF and IDF were calculated for assemblage level as well as for species level. Assemblage Frequency

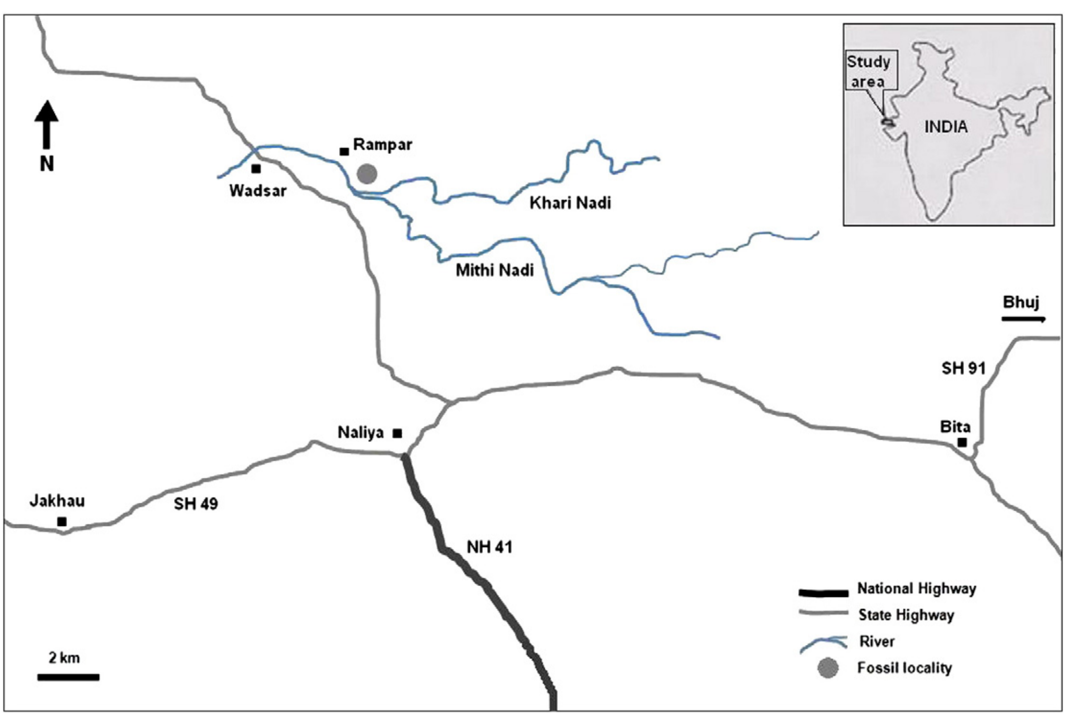

Fig. 1. Detailed map of the locality.