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NOTE

Shifting feeding behaviour of deep-sea buccinid gastropods at natural and simulated food falls

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ABSTRACT: The deep sea is a low food input environment, hence large food falls from the surface waters are important in supporting a wealth of scavenging deep-sea fauna. The probability of observing such events is very low, due to their unpredictable and short-lived nature. The video system of a cabled observatory installed within a cold seep clam field in Sagami Bay (1100 m depth; Central Japan) recorded a rare event. We observed a fish dying directly in front of the camera and being immediately perceived and preyed upon by *Buccinum yoroianum* (Neogastropoda: Buccinidae), while still alive. Up to 76 large snails responded to the fish and consumed the carcass within ~8 h, with no intervention by decapod crustaceans. There was only small participation of eelpouts (Zoarcidae). For comparison, we report on supplementary findings from a different area and depth of the Pacific Ocean. These observations were recorded by a baited camera lander which simulated a food fall. Within 6 h, the buccinid *Tacita zenkevitchi* aggregated on the bait, competing with fishes. These observations confirm that deep-sea buccinids can shift their feeding behaviour between active predation and scavenging. Our perception, however, seems conditioned by the observational methodology we use: buccinids may appear as scavengers when using photography (e.g. by baited landers) producing single snapshots in time, or as predators when observed in a natural setting and video-taped continuously with a cabled observatory.

KEY WORDS: *Buccinum yoroianum* · *Tacita zenkevitchi* · Zoarcids · Cabled observatories · Landers · Baited cameras · Scavenging behaviour · Natural food falls

INTRODUCTION

The deep-sea is the largest biome on earth. The seafloor at depths >1000 m constitutes ~65 % of the earth's surface, hosting a collection of ecosystems with communities that are still largely unknown (Ramirez-Llodra et al. 2010, Snelgrove 2010). Compiling an adequate understanding of deep-sea animals' life habits such as distribution, diet, behaviour or reproduction, has been hampered by technical difficulties in sampling at extreme depths (Gage & Bett 2005). As a result, there is a major gap in knowledge on deep-sea ecosystems (Aguzzi et al. 2012).

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In the deep sea beyond the reach of sunlight (reviewed by Childress 1995) there are 2 major sources of energy provision: (1) autochthonous, derived from chemosynthetic communities, found e.g. at cold seeps or hydrothermal vents (Paull et al. 1985, Lutz & Kennish 1993, Fujikura et al. 1999); and (2) allochthonous, delivered as particulate organic matter originating from the surface waters or large food falls (carrion carcasses; Stockton & DeLaca 1982, Britton & Morton 1994, Bailey et al. 2007). An undetermined fraction of food supply is consumed by scavengers which feed upon dead biota, the sinking carcasses of which reach the seafloor with high energy contents (Klages et al. 2001). Carrion food falls may consistently support populations of scavengers from coastal environments to hadal depths (Jamieson et al. 2009a,b). Generally, a succession of bait-attending fauna appears rapidly at food falls. Typically, the dominant species are amphipods and demersal fish (Collins et al. 1999, Jones et al. 2003, Yeh & Drazen 2009, Jamieson et al. 2011a, Yeh & Drazen 2011). Amphipods are highly efficient in removing the external tissues of carrion falls, exposing the underlying mass, where fishes usually begin their feeding (Jones et al. 1998, Kemp et al. 2006, Jamieson et al. 2010, 2011b).

These observations are generally based on simulated carrion falls when bait is delivered to seafloor on landers (Bagley et al. 2004), or by Remotely Operated Vehicles (ROV; Humphris 2009). Natural food falls are extremely rarely observed with these *in situ* imaging-technologies as they are infrequent and unpredictable in space and time, making the probability of their detection extraordinarily low (Klages et al. 2001, Soltwedel et al. 2003, Yamamoto et al. 2009). However, the increasing number of permanent video-observatories on the deep seafloor is providing new possibilities of ecological monitoring at longer timescales than ever before (Aguzzi et al. 2010, 2011a,b, 2012, Matabos et al. 2011, Ruhl et al. 2011).

We document an extraordinary rare event which was recorded by a video system installed on a deep-sea cabled video-observatory: a dying fish, while still alive, was intercepted by the scavenging gastropod *Buccinum yoroianum* Ozaki, 1958 (Neogasteropoda: Buccinidae; synonym: *Buccinum soyomaruae* Okutani, 1977). In order to provide an overview of the feeding behaviour of buccinids and their ecological relevance within deep-sea trophic food webs, we report on supplementary observations from a different area of the Pacific Ocean (the Peru-Chile Trench) using a baited camera lander to simulate food falls.

MATERIALS AND METHODS

Cabled observatory video-annotations (natural food fall)

The video ascertaining the natural food fall (an unknown macrourid fish) was captured by an infrared Panasonic CAM-92, 3CCD camera, mounted on the Real-Time Deep-Sea Floor Permanent Observatory of Sagami Bay. The observatory is located in a hydrocarbon cold seep field of clams (*Calyptogena soyoae* Okutani, 1957) at a depth of 1100 m, off the Hatsushima Island, central Japan (NW Pacific Ocean; 34°59.97'N, 139°13.69'E; Kasaya et al. 2009, Momma et al. 1998). The video spans 12 h (17:00 to 5:00 h, 24 June 1999), starting 1 h prior to the fish falling and ending a few hours after. The camera recorded in a time-lapse mode (1 frame every 5 s), illuminated by a permanent source of white light, which does not perturb natural behaviour (Aguzzi et al. 2010b). The video film can be viewed at www.int-res.com/articles/suppl/m458p247_supp/.

A 4-quadrant grid was superimposed on each frame in order to precisely count gastropods within the different portions of the camera's field of view (FOV). Only large gastropods were counted whose body was fully included in 1 of the 4 quadrants. The temporal development of the scavenging activity was described by representing the sum of individuals per minute for each quadrant and for all quadrants together.

Lander observations (simulated food falls)

Buccinidae in the Peru-Chile Trench were observed using the Hadal-Lander B (Jamieson et al. 2009c). Between 1 and 5 September 2010, the lander was deployed in the trench at 6 different depths: 1037, 4602, 5329, 6173, 7050 and 8074 m. The lander recorded 5-megapixel digital still images (1 min^{-1}) at an elevation of 1 m above seafloor. The FOV was 62 × 46.5 cm (0.29 m^{-2}) and baited with ~1 kg tuna (*Thunnus* spp.). To recover samples of photographed species for taxonomic identification, the 3 lander legs were fitted with small invertebrate funnel traps, also baited with tuna (~200 g). The traps were positioned to rest directly on the seafloor when *in situ*.

In the acquired images, the shell lengths were measured using proprietary image analysis software Image J (NIH, USA), calibrated against a scale bar present in the FOV. Likewise, Image J was used to mark the position of individuals in subsequent images using the X-Y tool. The distance travelled between each image was then used to determine overground locomotion speed. The absolute speed (cm min^{-1}) was divided by shell length (SL) to provide a size-specific speed (SL min^{-1}).

RESULTS

Natural food fall event in Sagami Bay, Japan

When the dying fish reached the seafloor in the FOV at Min 58 (video start t_0 = 17:56 h) the number of visible *Buccinum yoroianum* was low in all quadrants. The fish was still alive and visibly quivering for 75 min during the observation period. After the fish had reached the seafloor, the number of *B. yoroianum* increased from a minimum of 2 at Min 58 to a maximum of 76 at Min 205. They rapidly approached from the left upper quadrant and moved with their probosces protruded forward in an undulatory fashion. At the peak activity, 30 ind. (39 %) were on the carcass, 40 (53 %) remained in close proximity and only 6 (8 %) stayed away. By Min 482, the number of individuals had decreased to 2. The carcass was completely consumed in ~8 h. The temporal response of *Buccinum yoroianum* to the natural food fall is quantitatively described in Fig. 1.

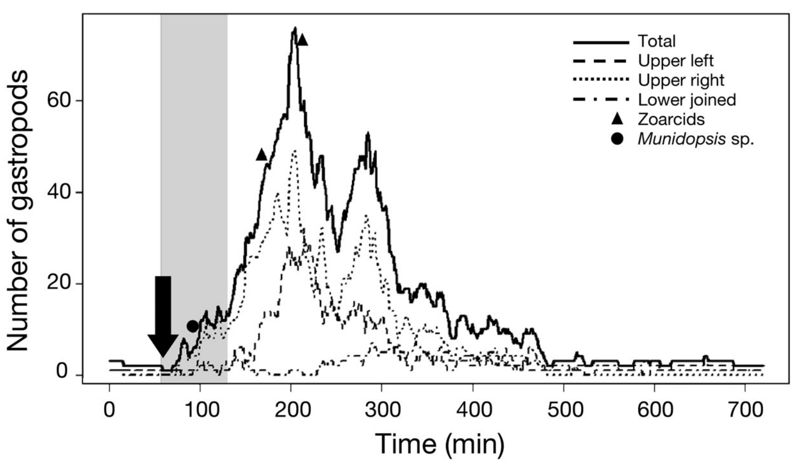

Fig. 1. *Buccinum yoroianum*. Time series of visual counts describing the mixed predatory-scavenging behaviour of this buccinid in Sagami Bay, Japan. Individuals were counted separately in the 4 quadrants of the camera's field of view, but counts from the lower quadrants were pooled. Numbers are presented along with the total. After fish–seabed contact (Min 75; arrow), the fish remained moribund for 75 min (shaded area). The number of gastropods increased rapidly, as individuals were probably attracted by the movements of the fish. The interaction of 2 zoarcids and 1 *Munidopsis* sp. is indicated

Buccinum yoroianum in the upper right quadrant also seemed to perceive the arrival of the fish and its twitching movements. However, their ability to locate the exact position of the fish was apparently delayed in comparison to the individuals approaching from the opposite side, presumably as they were located upstream in the current flow. The movements of the dying fish produced sediment plumes, which drifted in the ambient current leftward relative to the FOV.

Other species participating in this scavenging event appeared only occasionally (see Fig. 1). A white squat lobster (*Munidopsis* sp.) was present for a very short time, without approaching the carcass. Zoarcid fishes interacted twice in this event at Min 173 and 207. The zoarcids were observed removing strips of tissue by twisting and rotating their body. The first zoarcid was present in close proximity for 9 min while the second and smaller individual was sighted for only 2 min. Drifting sediment, resuspended by the first zoarcid feeding event at Min 173, confirmed the previously described direction of the currents.

Simulated food fall event in the Peru-Chile Trench

The buccinid *Tacita zenkevitchi* Lus, 1975 was observed at 2 sites in the Peru-Chile Trench (4° 27.016' S, 81° 54.719' W, 5329 m deep; and 7° 48.042' S, 81° 17.011' W, 6173 m deep) over periods of 11 h 9 min and 18 h 40 min, respectively (Fig. 2). At 5329 m, 6 h 3 min after the lander touchdown, individuals aggregated on the bait, increasing to a maximum of 5 individuals just prior the end of recording (9 h, 46 min; Fig. 3). Each gastropod entered the FOV, travelled directly to the bait and positioned itsself on top of it. There they stayed until being forcibly removed by a macrourid fish *Coryphaenoides yaquinae*. At 6173 m, the buccinid behaviour appeared similar to that at 5329 m in the early stages (Fig. 3), but then was increasingly disturbed by an unidentified ophidiid fish: some gastropods were repeatedly knocked over, driven into the sediment, or removed from the FOV.

At 5329 m, *Tacita zenkevitchi* individuals had a SL of 5.33 ± 0.7 (mean ± SD), and 4.7 ± 1.1 cm at 6173 m. From the baited traps at 6173 m, 3 specimens

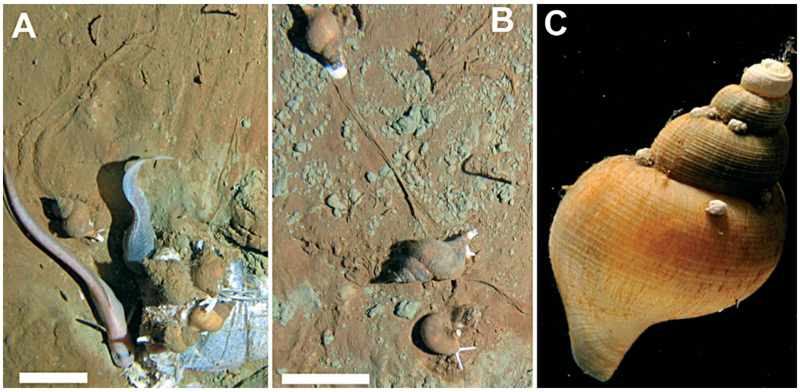

Fig. 2. *Tacita zenkevitchi*. Aggregation individuals at 5329 m depth in the Peru-Chile Trench. (A) Four individuals are sitting on the bait, a fifth is approaching (between the zoarcid and liparid fishes). (B) Mucus trail left in the gastropod's track. (C) *T. zenkevitchi* recovered from the baited trap at 6173 m (shell height = 45 mm). Scale bar in A and B: 5 cm

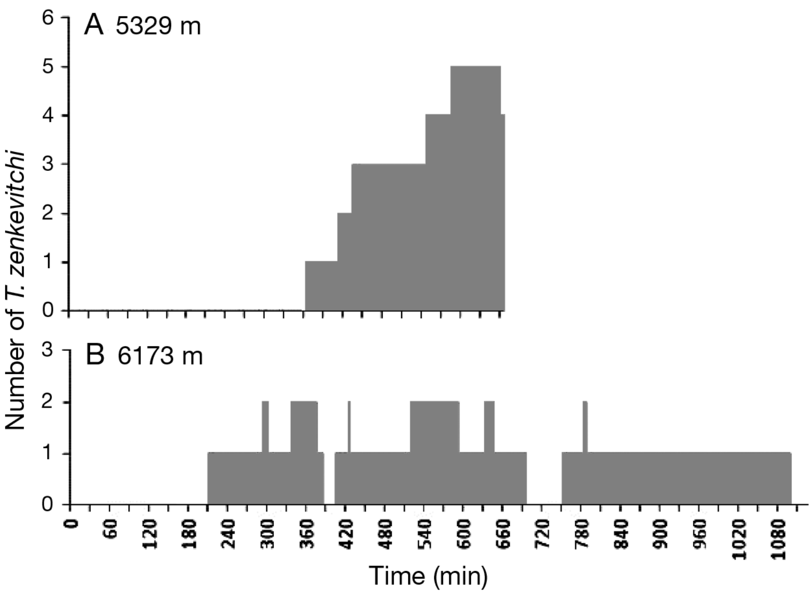

Fig. 3. *Tacita zenkevitchi*. The arrival rate of individuals at the bait at (A) 5329 m depth, showing a linear increase in numbers over time ($y = 0.0144x - 4.1729$; $R^2 = 0.89$) until the end of picture-taking, and at (B) 6173 m depth, where the arrival rate is perturbed by an unidentified ophidiid fish

Table 1. *Tacita zenkevitchi*. Morphometric data from 3 specimens of the buccinid gastropod recovered from 6173 m in the Peru-Chile Trench

Specimen	Shell (mm)		Aperture (mm)		No. of
	Height	Width	Height	Width	whorls
1	45	26	25	15	4
2	23	13	13	7	4
3	25	13	14	9	4

were recovered (see Table 1 for morphometric data), while none were recovered from 5329 m.

Tacita zenkevitchi travelled towards the bait at an absolute speed of 3.2 ± 1.5 cm min^{-1} (mean ± SD; specific speed = 0.6 ± 0.3 SL min^{-1}) at 5329 m, and 2.3 ± 1.2 cm min^{-1} (0.6 ± 0.2 SL min^{-1}) at 6173 m. *T. zenkevitchi* left clearly visible tracks of depressed sediment with a mucus lining. This lining was observed to peel off the seafloor when another individual traversed through it. The width of the tracks was 1.7 ± 0.3 cm. Together with the mean locomotion speed of *T. zenkevitchi* this results in an average area coverage of 0.03 ± 0.02 m^{-2} h^{-1} per individual.

DISCUSSION

We observed how *Buccinum yoroianum* rapidly aggregated on and consumed a naturally moribund fish in the cold seep clam field of Sagami Bay while the dying fish was still moving. Thus, the buccinids revealed a mixed predatory and scavenging feeding activity. We also reported on the purely scavenging behaviour of another buccinid species, *Tacita zenkevitchi*, from a different oceanic area, the Peru-Chile Trench. These observations can be ecologically generalized to confirm the opportunistic mixed predatory and scavenging behavioural guild for deep-sea buccinids. This is the first time that a natural food fall has been witnessed in the deep sea both prior to, and after, an animal has actually died (Yamamoto et al. 2009).

Our findings from simulated food-fall experiments with a lander were also surprising. From previous baited camera literature (Jones et al. 1998, 2003, Jamieson et al. 2009c, 2011a), it appears that buccinid gastropods were only marginally detected and their ecological role in food-fall consumption was apparently negligible. Landers similar to the one used in the present study have been used hundreds of times at many depths in many geographic locations and gastropods were seldom reported. The presence of buccinids in the Peru-Chile Trench and in Sagami Bay can possibly be explained by the chemosynthetic typology of the surveyed habitats. The Peru-Chile Trench is a seismically active subduction zone with associated hydrothermal vents and cold seeps (Torres et al. 1996, Fujikura et al. 1999). We hypothesize that the increased presence of Buccinidae at these sites and not in the wider deep sea, may be an effect of these geological features, in the proximity of which gastropods are known to aggregate (Warèn & Bouchet 1993, Bates et al. 2005).

Although foraging methods of deep-sea scavengers are still somewhat speculative, odour plume detection within downstream currents may occur by actively searching (Rochette et al. 1994) or by a sit-and-wait strategy (Bailey & Priede 2002). In Sagami Bay, buccinids rapidly located the dying fish within the ambient current regime which, however, could not be quantified in the absence of current meters at the observatory. Nevertheless, the direction of the current was inferred indirectly by video inspection of resuspended sediment. The approach to the event from down current suggests that buccinids utilize their olfactory senses to detect prey or carrion odours carried by currents. The detection of noise associated with carrion falls reaching the seabed as well as the associated noise and vibrations of scavenging activity may contribute to locating a food fall via mechanoreception (Klages et al. 2002, Premke et al. 2003).

Although zoarcids and galatheid squat lobsters were occasionally present, the overwhelming dominance of the buccinid gastropods and absence of any large scavenging fish was surprising in the Sagami Bay observations. The reason for the absence of other major fauna is presently unknown as no other studies of this kind have focused on the behaviour of macrofauna in the Sagami Bay cold seep area. Unexpectedly, no red crabs *Paralomis multispina* were observed despite this species' known abundance in the area (Aguzzi et al. 2010b). Also, only a single white galatheid species (*Munidopsis* sp.; Cubelio et al. 2008), known to be endemic in cold seep areas including Sagami Bay, was observed. Most baited camera studies indicate a prominent role of scavenging amphipods (e.g. Hessler et al. 1978, Blankenship & Levin 2007, Jamieson et al. 2009b). However, their role in the portrayed scavenging event could not be assessed due to the relatively large distance from the camera to the carcass and the low resolution of the video system, probably insufficient to detect such small organisms. Scavenging amphipods are likely the dominant group in Sagami, making buccinids only the second most important one (Nishida et al. 1999). The absence of scavenging fishes was also conspicuous, as they are dominant at similar depths in other locations (e.g. King et al. 2006, 2008, Yeh & Drazen 2009, 2011).

Deep-sea Buccinidae may include species with an obligate scavenging life-style (Britton &Morton 1994, Martell et al. 2002, Ilano et al. 2005). Nevertheless, the unpredictable source of food in the form of sparse carrion falls suggests taxa are unlikely to favour such a specialization towards obligate scavenging (Kaiser & Moore 1999). According to our observations, buccinids can be broadly considered as both opportunistic scavengers and predators (Nickell & Moore 1992, Naganuma et al. 1996).

The speed at which buccinids can traverse the seafloor is also important in terms of bioturbation of surface sediments. The results from the Peru-Chile Trench showed a (size-specific) locomotion speed of 0.6 SL min^{-1} and a track width of 1.7 cm. This provided an area of coverage (mean ± SD) of 0.03 ± 0.02 m^2 h^{-1} per gastropod. Assuming the size and speed of the Sagami Bay population is similar, then just 33 of these individuals would have covered ~1 m^2 of seafloor in 1 h. Therefore the mass aggregations of facultative scavenging gastropods is not only important to the dispersal of surface-derived organic matter in the form of food falls, but also to rapid bioturbation within the vicinity of the food fall and in the wider catchment area of the odour plume.

In conclusion, our perception of deep-sea buccinid feeding habits seems to be conditioned by our sampling method. They appear as scavengers when using baited cameras, and conversely as predators, when using prolonged video recording as by fixed cameras in cabled video-observatories.

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