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Opportunistic predatory feeding behaviour of *Munida intermedia* A. Milne-Edwards & Bouvier, 1899 targeting juveniles of *Lepidopus caudatus* (Euphrasen, 1788) in the north-western Mediterranean Sea

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Abstract

The genus *Munida*, inhabits various marine habitats and exhibits versatile feeding behaviour. This study explored the behavioural patterns of *Munida intermedia*, shedding light on its opportunistic behaviour and competitive interactions within its ecological niche. In 2018, during an investigation using a remotely operated vehicle (ROV), carried out on the Méjean shoal (north-western Mediterranean Sea), at 397 m depth, specimens were observed engaging in opportunistic predatory feeding, targeting juveniles of the bathypelagic silver scabbardfish *Lepidopus caudatus*. Our findings underscore the dynamic nature of *M. intermedia* feeding habits and the significant role of competitive interactions within its habitat, highlighting the role of video technology in capturing real-time information.

Keywords: decapod crustacean; bathypelagic fish; bathyal habitat; ROV-imaging.

Introduction

Squat lobsters are decapod crustaceans classified under the superfamilies Galatheoidea Samouelle, 1819, and Chirostyloidea Ortmann, 1892. They have been observed in all oceans, at depths varying from shallow subtidal zones to 5330 m, and in habitats spanning from subarctic to Antarctic regions (Lovrich & Thiel, 2011; Schnabel *et al*., 2011). They can thrive in extreme environments such as hydrothermal vents, cold seeps, and oxygen-depleted zones, facing challenging conditions including high pressure, cold temperatures, low food availability, darkness, hypoxia, and exposure to toxic compounds such as sulfides (Lovrich & Thiel, 2011). The squat lobster of the galatheid genus *Munida* Leach, 1820 stands out as the most speciose (~400 species) (Machordom *et al*., 2022) and cosmopolitan (Bailie *et al*., 2011), in the squat lobster family Munididae Ahyong, Baba, Macpherson & Poore, 2010. *Munida* species are commonly found dwelling on sandy and muddy bottoms (Ateş *et al*., 2005), as well as on rocky substrates, ranging from shallow waters at around 50 m depths to approximately 3000 m (Cartes, 1993; Bailie *et al*., 2011; Lovrich & Thiel, 2011; Schnabel *et al*., 2011; Maiorano *et al*., 2013). High population densities often result in the formation of aggregations. The rationale behind such aggregations remains uncertain; however, the consequence is fierce competition between individuals for essential resources such as sustenance, shelter, and mating opportunities within specific habitats (Trenkel *et al*., 2007). Like other decapod crustaceans (e.g., Sneddon *et al*., 1997; Edwards & Herberholz, 2005), competitive interactions between mature *Munida* spp. specimens, particularly males, are mediated through agonistic behaviours using their chelipeds as weapons (e.g., Claverie & Smith, 2007). Regarding the dietary preferences of *Munida* spp., direct analyses of stomach contents have been conducted for only a few species. For instance, the benthic *Grimothea gregaria* (Fabricius, 1793) from the Beagle Channel consumes approximately 30 different types of food, with its diet primarily consisting of particulate organic matter (POM), algae, and crustaceans (Romero *et al*., 2004). In Golfo San Jorge, the benthic *G. gregaria* acts as a scavenger in regions with a high supply of fisheries by-catch, feeding on crustaceans (*G. gregaria* and the shrimp *Pleoticus muelleri* (Spence Bate, 1888)) discarded by hake and shrimp fisheries. In unfished areas, it has a more diverse diet (Varisco & Vinuesa, 2007). On the Mediterranean continental slope, *Munida tenuimana*

Sars, 1872 has a varied diet that includes pelagic material (e.g., marine snow) as well as benthic material, including fish remains (Cartes, 1993). The detritivorous behaviour of *M. tenuimana* is thought to be an adaptation to the resource scarcity typical of deep-sea environments at depths greater than 1000 m (Cartes, 1993). *Munida sarsi* Huus, 1935 is an opportunistic species that feeds on a wide range of food types, including carrion (Brinkmann, 1936; Garm & Hoeg, 2000; Hudson & Wigham, 2003). Moreover, the analysis of 130 stomach contents of *Munida rugosa* (Fabricius, 1775) by Zainal (1990) revealed a predominantly animal-based diet, with polychaetes and crustaceans as the primary sources of food. The presence of varied polychaete setae and jaws suggests consumption of multiple species. Furthermore, two studies found that squat lobsters actively prey on pelagic organisms. In a study by Hudson & Wigham (2003), an individual *M. sarsi* was observed amid a swarm of krill, attempting to catch individual krill swimming just above the seabed. Another study (Nizinski *et al*., 2023) reported that *Eumunida picta* Smith 1883 specimens capture pelagic fish directly from the water column. The prey observed included at least three types of fish: Myctophidae (likely *Ceratoscopelus* sp.), Macrouridae (probably *Nezumia* sp.) and Sternoptychidae (*Polyipnus* sp.). Thus, squat lobsters exhibit versatile feeding behaviours, including suspension feeding, deposit feeding, grazing on algae, scavenging, active predation, and occasional cannibalism (Lovrich & Thiel, 2011). Their inclination toward animal-based food over plant-based fare is apparent, with scavenging and preying on other organisms forming part of their feeding repertoire, especially for specimens living at great depths where plant components are practically absent. Notably, larger individuals have been observed to display cannibalistic tendencies, preying on smaller ones, particularly in crowded aquarium tanks (Zainal, 1990).

During a survey conducted using a remotely operated vehicle (ROV) on the Méjean shoal, in the north-western Mediterranean Sea, *M. interemedia* specimens were observed opportunistically preying on juveniles of the silver scabbardfish *Lepidopus caudatus* (Euphrasen, 1788); a bathypelagic fish distributed worldwide, commonly found at depths ranging from 200 to 400 m, often near seamounts, islands, and sandy bottoms (Mariño-Briceño *et al*., 2022).

Our research aims to further describe the feeding behaviour of *M. intermedia* focusing, in particular, on its active predation of live animals when opportunities arise.

Materials and Methods

In September 2018, as part of the activities of the RAMOGE agreement, signed by France, Monaco, and Italy for the protection of the marine environment, a scientific campaign was conducted on the Méjean shoal, in the north-western Mediterranean Sea, aboard the R/V L'Atalante (Ifremer). The area is located approximately 18 km from the French coast, in front of the city of Cannes (Fig.1A). It is aligned with the canyon of Cannes and lies

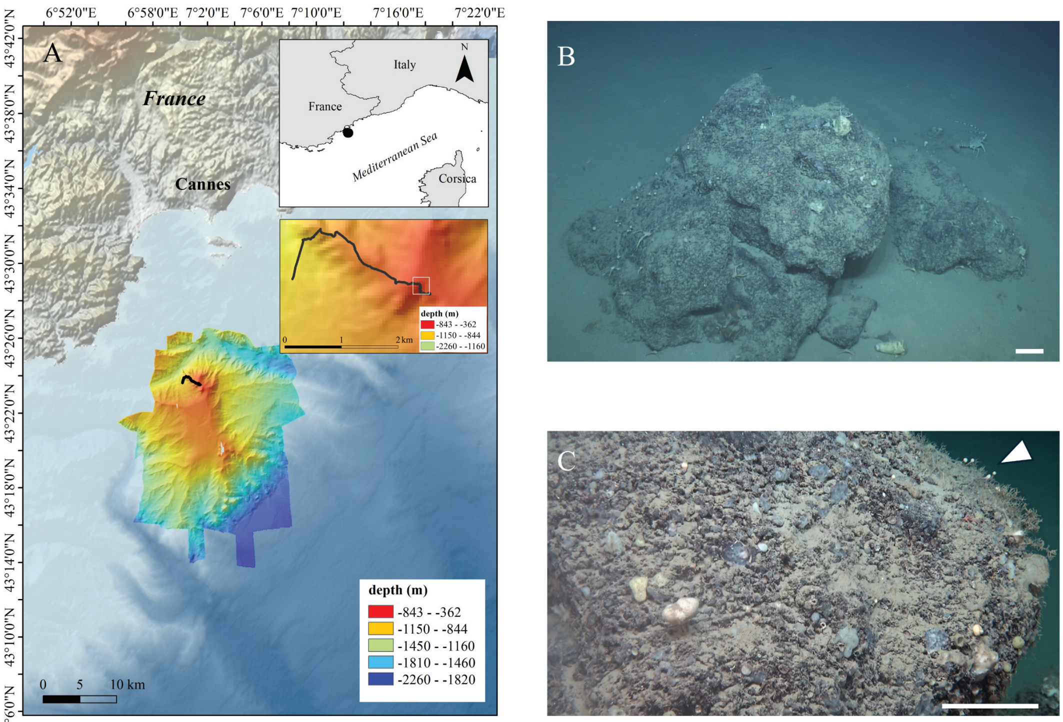

Fig. 1: (A) Multibeam map of the Méjean shoal with depicting the ROV dive location (black line). The inset in the upper right displays the location of the study area (black dot), and the inset below provides a close-up view of the ROV dive. Background bathymetry was obtained from the EMODnet portal (https://emodnet.ec.europa.eu/en/bathymetry). The white square in the close-up view of the ROV dive indicates the location of the rock where *M. intermedia* specimens were observed; (B) rock where feeding behaviour was observed, scale bar = 20 cm; (C) magnification of (B): brachiopods, lollipop (white arrow) and encrusting sponges dwelling on the rock, scale bar = 10 cm.

between 361 and 2255 m depth. The shoal is characterized by a muddy seafloor with scattered rocks covered by sediment.

A comprehensive bathymetric chart of the study area was generated using a Kongsberg EM122 multibeam sonar, with a resolution of 25 m per cell, using the GLOBE© Ifremer software. Subsequently, the area was investigated with a ROV VICTOR 6000, executing one dive. The ROV was equipped with a powerful lighting system, high-resolution cameras (4K and full HD), and two mechanical arms for sample collection. It also features a conductivity, temperature, and pressure probe (SBE 19plus V2 Seacat), a navigation and obstacle detection sonar, an altimeter for measuring the distance to the bottom, an underwater positioning system (USBL), an inertial navigation system, and a Doppler Velocity Log (DVL) for precise positioning. The ROV dive was conducted along a depth gradient, from 357 to 919 m. Special attention was paid to maintain a consistent ROV cruising speed (approximately 1 kn) and altitude (approximately 3 m above the seabed). The ROV track was imported into ArcGIS 10.3 and a cleaning process was performed to remove anomalies.

The ROV video was post-processed using a VLC media player and Free Studio software to document the predatory behaviour of certain *M. intermedia* specimens on juveniles of the silver scabbardfish *L. caudatus* near rocks. Additionally, all specimens of *M. intermedia* were counted. The identification of *M. intermedia* specimens was performed by referencing the morphological diagnostic characteristics outlined in the existing literature (e.g., Zariquiey Alvarez, 1968), and comparing the images with published photographs.

Results

The dive lasted 6 h and 34 min and covered a linear distance of 5 km. The benthic environment featured diverse combinations of muddy bottoms and rocky outcrops. The rocky areas were particularly rich, hosting a high density of sponges (encrusting and massive), hydrozoans, arborescent foraminifera, echinoderm cidarids, several specimens of the green spoonworm *Bonellia viridis* (Rolando, 1821) (Annelida), and of the squat lobster *M. intermedia*. The rocky zones also featured black coral skeletons covered with parasitic Zoantharia, as well as an area characterized by the presence of the white gorgonian *Muriceides lepida* Carpine & Grasshoff, 1975. In addition, a biogenic conglomerate consisting of dead corals and bivalves was observed. Notably, the muddy areas were characterised by a high abundance of burrows and bioturbation.

During the ROV dive, at a depth of 397 m, 54 specimens of *M. intermedia* were observed on a rock measuring approximately 2 m in linear length (Fig. 1B), which was covered with brachiopods, lollipop and encrusting sponges (Fig. 1C). Here, four distinct and successful predatory events were documented, featuring squat lobsters preying on juveniles of the silver scabbardfish *L. caudatus*. The presence of the ROV influenced the behaviour of these fish that, blinded by the lights of the ROV, quickly dived toward the seabed to seek shelter. This behaviour frequently caused the formation of sediment clouds, making fish more vulnerable to capture by squat lobsters. On one occasion, the entire sequence of a capture was observed, involving three specimens of *M. intermedia,* and it lasted about 50 s (Fig. 2, S1). In the initial phase, two of the three specimens (specimens 1 and 2 in Fig. 2A) were engaged in capturing prey. They used their chelipeds, attempting to pilfer the prey from each other. Approximately 10 s later, specimen 3 joined the pursuit, employing its chelipeds to seize the prey (Fig. 2B-C). Specimen 1 used its right cheliped to push specimen 2 away, continuing to hold the prey with the left cheliped, trying to take it away from specimen 3 (Fig. 2C). Subsequently, specimen 2 released its grip, and specimens 1 and 3 continued to compete for prey using their chelipeds (Fig. 2D). After about 15 s from the start of the fight, specimen 3, with its right cheliped, managed to detach a piece of the fish's caudal part and quickly brought it to the maxillipeds while continuing to hold the rest of the fish with the left cheliped (Fig. 2E, S1). At the same time, specimen 3 began to move backward, and approximately 22 s later, specimen 1 initiated a backward movement, attempting to secure sole possession of the fish (Fig. 2E). Finally, specimen 3 let go of the hold, and specimen 1 retreated beneath the rock, successfully carrying the prey along (Fig. 2F). In addition, it was observed that chelipeds, along with maxillipeds, were used by squat lobsters to orient the prey horizontally by placing it on its shorter side, and then transferring it to their mandibles. Concurrently, three other opportunistic predatory events were observed (Fig. 3A). With the exception of one case, in which a specimen was observed alone with a fish not held with chelipeds (Fig. 3C), *M. intermedia* specimens were observed engaging in predatory behaviour, competing for their prey using chelipeds both to seize prey and to keep competitors away (Fig. 3B-D).

Discussion

Squat lobsters exhibit a diverse range of feeding habits, spanning from the consumption of particulate organic matter to cannibalism, with various intermediate scenarios (Lovrich & Thiel, 2011). In the Mediterranean Sea, at >1000 m depth, *Munida* spp. usually adopt a detritivorous feeding strategy as an adaptation to the limited resources that are characteristic of deep environments (Cartes, 1993). Moreover, specimens, can be considered opportunistic as regards their diet, adept at handling and consuming a broad spectrum of animal tissues (Garm & Høeg, 2000, 2001). In a laboratory study on the feeding habits of *Grimothea gregaria* (as *M. subrugosa*), Karas *et al.* (2007) found a preference for meat over macroalgae. The species demonstrated a broad niche width and behaved as a generalist feeder with various feeding habits. Contrary to traditional beliefs about Galatheoidea (Nicol, 1932; Kaestner, 1993), the research of Karas *et al*. em-

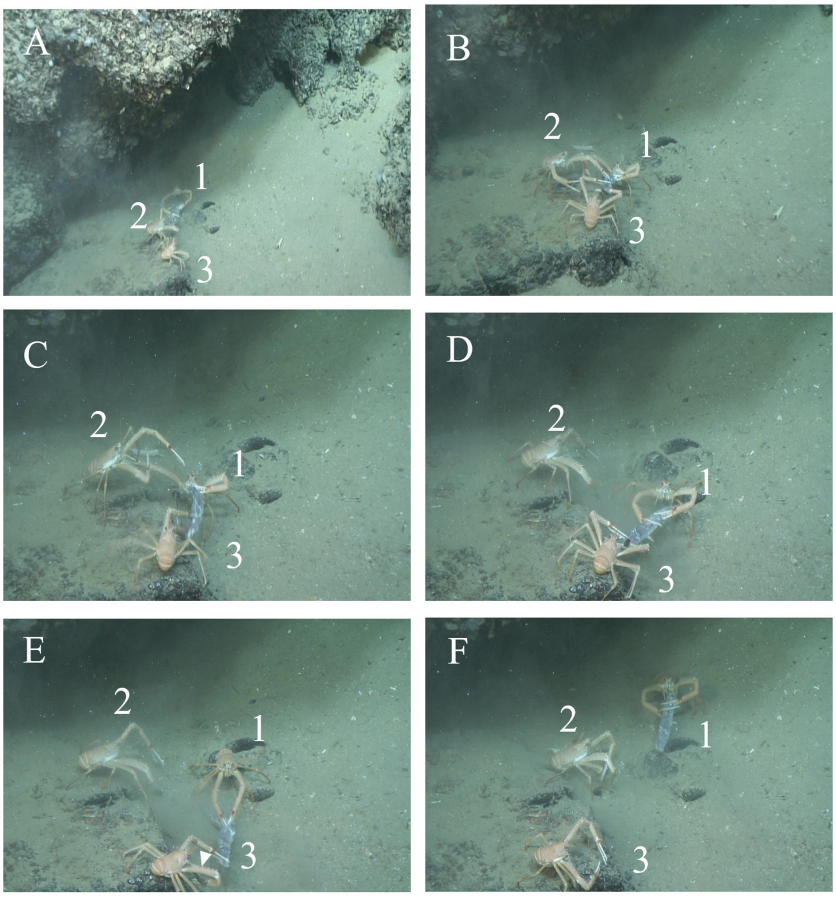

Fig. 2: Representative video frames of *Munida intermedia* specimens (1, 2 and 3) preying on juveniles of the silver scabbardfish *Lepidopus caudatus*; (E) the white arrow points to the caudal part of the fish in the right cheliped of specimen 3. This part was cut off by specimen 3 and is being held in its right cheliped and maxillipeds.

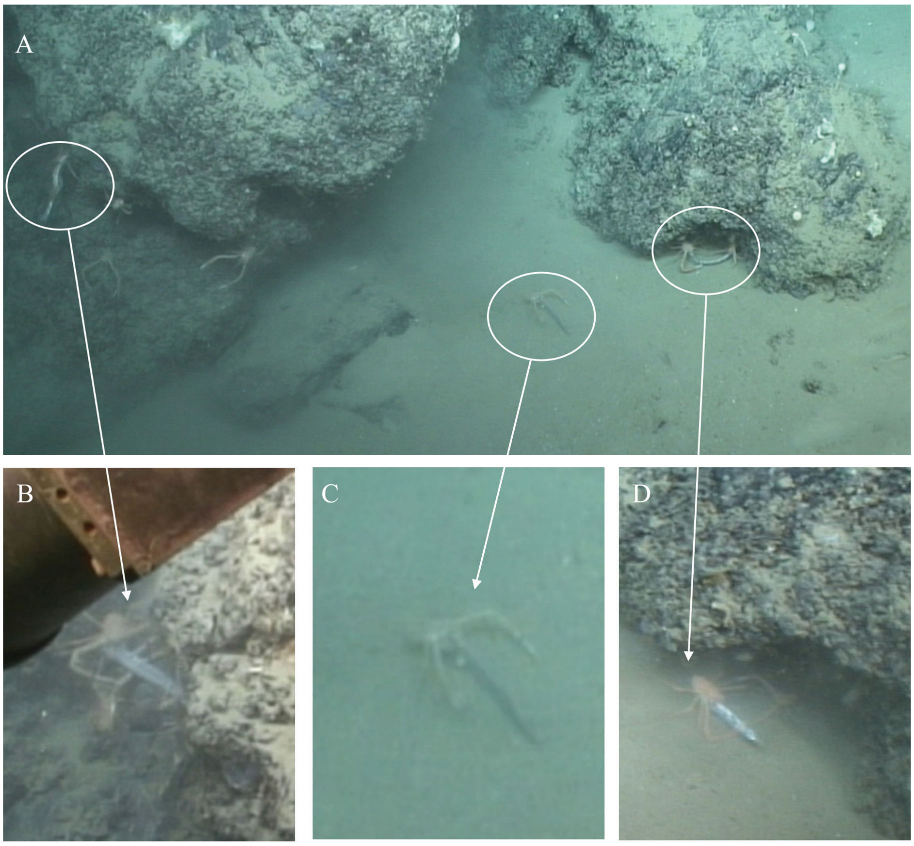

Fig. 3: (A) Squat lobsters preying on juveniles of the silver scabbardfish *Lepidopus caudatus*; (B-D) close-up views of the three predatory events; (C) the only observed case of a specimen alone that does not hold the fish with its chelipeds.

phasizes the importance of scavenging and active preying for *G. gregaria*. As reported by Garm & Høeg (2001) and Lovrich & Thiel (2011), the mouthparts serve various functions, encompassing food manipulation, ingestion, generation of water currents and grooming, and the movement patterns associated with these functions are frequently complex. Generally, Galatheoidea employ two feeding methods: the chelae and maxillipeds size large food pieces, passing them to the mandibles, or the third maxillipeds and pereiopods are utilized to gather finely chopped material from the substrate (Nicol, 1932; Garm & Høeg, 2000; Lovrich & Thiel, 2011). Nevertheless, during our observation, the capability of *M. intermedia* specimens to catch live juveniles of the silver scabbardfish *L. caudatus* was further increased by the active use of the chelipeds. The same behaviour was observed, during an ROV dive, by Hudson & Wigham (2003) in *M. sarsi*, feeding on *Meganyctiphanes norvegica* (M. Sars, 1857), on the UK continental shelf. The authors suggest that this behaviour is likely influenced by specific habitat factors, such as the diurnal migration of large swarms of *M. norvegica*, which may have led some *M. sarsi* individuals to develop a feeding strategy that uses their chelipeds to capture prey swimming very close to the bottom. During our observations, squat lobsters usually competed for access to the prey, displaying aggressive behaviours. Notably, the chelipeds were not only instrumental in gathering food but also played a role in intra-individual conflicts over prey, a behaviour previously documented by Berrill (1970) for *M. sarsi*. In a recent study by Nizinski *et al*. (2023), the researchers note that *E. picta* acts as an active predator, hunting and capturing live prey within their reach swimming close to the bottom They observed that *E. picta* can catch prey items of various sizes, including mid-water fish species of similar size to the predator. Our study on the predatory feeding behaviour of *M. intermedia* specimens highlights a feeding strategy that is influenced by specific habitat factors, including stealing food from conspecifics. During the course of our study, the presence of juveniles of the silver scabbardfish *L. caudatus*, which tends to descend toward the seafloor when stunned by ROV lights, prompted certain squat lobster specimens to display opportunistic feeding behaviours on preys that, normally, do not constitute part of their diet. They actively seize opportunities to capture fish using their chelipeds, thus highlighting their capability to prey actively on live animals when the opportunities arise. Although both *E. picta* and *M. intermedia* capture live pelagic prey, our results highlight that the latter seems to adopt this feeding strategy opportunistically, whereas the former exhibits behaviours that are more characteristic of a sit-and-wait predator (Nizinski *et al*., 2023). It is worth noting that the presence of the ROV resulted in an increased abundance of potential prey for *M. intermedia*, thereby influencing the behaviour of both squat lobsters and fish (e.g., Spanier *et al*., 1994; Ryer *et al*., 2009).

Our research further underscores the importance of video technology in acquiring real-time information about *M. intermedia*. Traditionally, data on this genus in the Mediterranean Sea, have been collected through bycatch, experimental trawl surveys (e.g., Huguet *et al*., 2005; Maiorano *et al*., 2013), or using underwater television (UTV) to estimate specimen density, as demonstrated in a survey carried out in the Adriatic Sea (Gramitto & Froglia, 1998). In our study, for the first time, video technology enabled the documentation of opportunistic active predation by *M. intermedia* on juveniles of the silver scabbardfish, *L. caudatus*. However, more data are needed to gain further understanding of the feeding behaviour of *M. intermedia*.

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Supplementary Material

The following supplementary material is available for this article:

S1: video sequence of *Munida intermedia* specimens preying on a juvenile of *Lepidopus caudatus*.