

Elasmobranch egg capsules associated with modern and ancient cold seeps: a nursery for marine deep-water predators

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ABSTRACT: At 2 modern deep-water cold-seep sites, the North Alex Mud Volcano (eastern Mediterranean Sea, water depth ~500 m) and the Concepción Methane Seep Area (south-east Pacific Ocean, water depth ~700 m), we found abundant catshark (Chondrichthyes: Scyliorhinidae) and skate (Chondrichthyes: Rajidae) egg capsules, respectively, associated with carbonates and tubeworms. Fossilized catshark egg capsules were found at the 35 million year old Bear River Cold-Seep Deposit (Washington State, USA) closely associated with remains of tubeworms and sponges. We suggest that cold-seep ecosystems have served as nurseries for predatory elasmobranch fishes since at least late Eocene time and therewith possibly play an important role for the functioning of deep-water ecosystems.

KEY WORDS: Catshark · Skate · Authigenic carbonate · Tubeworm · Methane · Deep sea · Chemosynthesis

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INTRODUCTION

Cold-seep ecosystems are based on chemosynthetic processes fueled by methane and petroleum discharge (Levin 2005, Suess 2010). Microbial anaerobic oxidation of methane (Treude et al. 2003, Knittel & Boetius 2009) or sulfate reduction coupled to petroleum degradation (Joye et al. 2004, Orcutt et al. 2010) lead to the accumulation of hydrogen sulfide in sediments, which then forms the energy basis for chemosynthetic food chains (Sahling et al. 2002, Cordes et al. 2005, Levin 2005). Organisms that are in many cases endemic and adapted to thrive or survive in this habitat often dominate these extreme environments. The inhabitants depend either directly on chemical energy (e.g. free-living and endosymbiotic

methanotrophic or thiotrophic bacteria; chemosymbiotic clams, mussels, and vestimentiferan tubeworms) or feed on biomass produced by chemosynthesis (e.g. predatory snails and crustaceans, deposit-feeding polychaetes) (see Sibuet & Olu 1998, Levin 2005 and references within both). Especially in the deep sea, cold seeps provide an alternative energy source (Paull et al. 1984) in addition to the sparse rain of organic matter arriving from the euphotic zone (Suess 1980). However, after microbial degradation of methane and petroleum has caused massive precipitation of carbonate in anoxic sediments (Peckmann et al. 2001, Barbieri & Cavalazzi 2005), the resultant seep carbonates are often subsequently exposed by erosion and may become a home for heterotrophic hard-ground settlers (e.g. cnidaria

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and sponges) that feed on photosynthetically produced carbon (Levin 2005, Sellanes et al. 2008). The carbonate landscape also offers a refuge for mobile animals such as fish, echinoderms, crustaceans, gastropods, and annelids (Sellanes et al. 2008). In the present study, we report that numerous shark and skate egg capsules were associated with carbonates and in many cases worm tubes from 2 existing and 1 fossil (35 million yr ago) cold seeps. Oviparous deep-water sharks are reported to preferentially deposit their eggs at well-ventilated and sheltered locations, such as elevated colonies of octocorals and gorgonians, to increase survivorship and decrease predation (Etnoyer & Warrenchuk 2007). Eggs of oviparous deep-water skates are found associated with canyon heads (Hoff 2010) or edges (Love et al. 2008) that may provide optimum current conditions for egg ventilation. Here we demonstrate that cold-seep habitats with exposed carbonate landscapes and tubeworm colonies serve as nurseries for deep-water elasmobranchs, providing further evidence for the importance of these localized environments for the deep-sea community.

MATERIALS AND METHODS

Cold-seep samples and visual data were collected from the active North Alex Mud Volcano (NAMV) in the eastern Mediterranean Sea (31° 57.955' N, 30° 08.239' E; water depth 497 m; Feseker et al. 2010) with the RV 'Pelagia' on 22 November 2008, the active Concepción Methane Seep Area (CMSA) off Central Chile (36° 23.452' S, 73° 42.097' W; water depth 705 m; Sellanes et al. 2008) with the RV 'Sonne' on 02 October 2010, and the late Eocene Bear River Seep Deposit (BRSD) in southwestern Washington State, USA (46° 19.943' N, 123° 55.964' W; Goedert & Squires 1990). At the NAMV, photographs and video footage were acquired with a fully electric driven remotely operated vehicle (ROV) 'Cherokee' (Sub Atlantic) equipped with a forward looking color digital camera and a forward-looking digital color still camera with flashgun. At the CMSA, photographs and video footage were acquired with the Ocean Floor Observation System (OFOS). OFOS consists of a frame equipped with the following instruments: 2 video cameras, a digital still camera system with 2 remote flash heads (Ocean Imaging Systems), 2 Xenon lights (Oktopus), a storage CTD (RBR) and 3 red lasers (Oktopus). The frame was towed behind the vessel at a speed of about 0.5 to 0.8 knots at a distance of about 1.5 m above the seafloor, which is

controlled manually by the winch operator. For this purpose, a ground weight (200 mm wide) was suspended below the sled on a rope of 1.5 m length. Two laser pointers were used to scale the video and the still camera images. The laser pointers were oriented parallel to each other and with beams fixed 500 mm apart, while a third was pointed at an oblique angle, getting in line with the other 2 lasers when the sled was 1.5 m away from the sea floor. The images were taken by remote control. At the BRSD, carbonate samples were taken from an isolated 35 million year old seep deposit that measured ca. 68 × 38 m in width and 15 m in height and was found within uplifted deep-water mudstone of the Cascadia accretionary wedge (Goedert & Squires 1990, Goedert & Benham 2003, Kiel 2010). The BRSD fauna is dominated by the mussel *Bathymodiolus willapaensis*, worm tubes are common, and shells of large solemyid, lucinid, and vesicomid bivalves occur throughout the deposit as well as remains of numerous small gastropods (Goedert & Squires 1990, Squires & Goedert 1991, Goedert et al. 2003, Kiel 2006, 2010). A peculiar feature of this seep deposit is the abundance of fossilized 3-dimensional specimens of the hexactinellid sponge *Aphrocallistes polytretos* (Rigby & Jenkins 1983) intermingled with mussel shells, worm tubes, and the egg capsules reported here.

RESULTS AND DISCUSSION

At the 2 modern cold-seep sites, the NAMV and the CMSA, we found numerous shark and skate egg capsules, respectively, associated with cold-seep carbonates. At the NAMV, possibly hundreds of golden to dark brown colored shark egg capsules (length ca. 50 to 70 mm) were found inside a dense tubeworm field (*Lamellibrachia* spp., Fig. 1A,B), which was rooted in sediments containing carbonate crusts. The capsules, which had no visible tendrils, were either placed between the tubes or lay on the surrounding ground. Yolk was visible through the walls of many capsules (Fig. 1C,D), indicating that the embryos were still developing. Size, shape, and color of the capsules were similar to those reported for the deep-water catsharks *Galeus melastomus* according to Iglésias et al. (2002) — length: 51 to 65 mm; width: 18 to 23 mm; shape: roughly vase-like; surface: smooth and glossy, with keratin-like texture; posterior end oval with 2 very short coiled horns in close contact; anterior end truncate, with a small horn on each corner; color: golden brown when extracted from the oviduct, changing to dark brown after exposure to

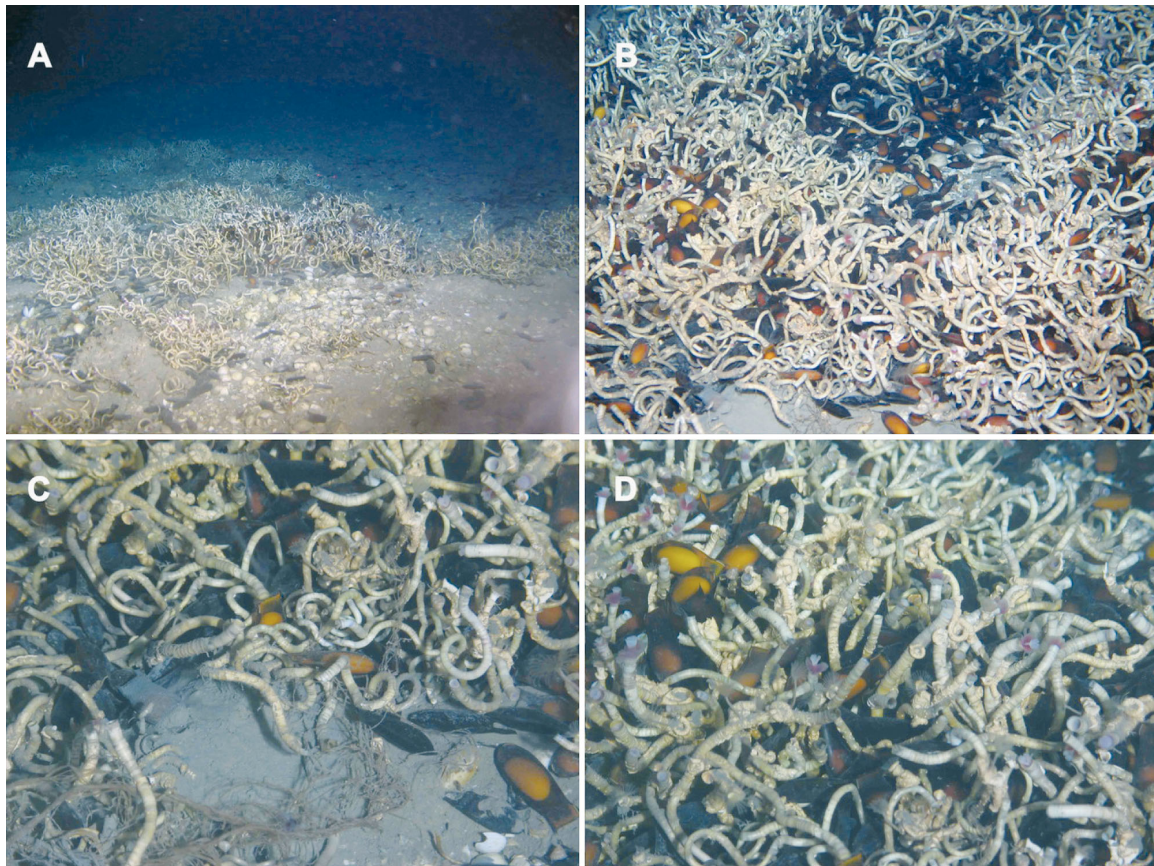


Fig. 1. *Galeus melastomus*. Shark egg capsules of the deep-water catshark in a tubeworm field at the North Alex Mud Volcano, eastern Mediterranean Sea. (A) Overview of the tubeworm field (*Lamellibrachia* spp.), which was rooted in sediments containing carbonate crusts. The shark egg capsules (golden and dark brown) were located either between tubeworms or lying on the nearby ground. Also visible inside the field are white lucinid clams. (B) Tubeworm field center illustrating the density of the egg capsules. (C) Tubeworm field close-up showing the full shape of an egg capsule in the lower right corner. Bright yolk is visible inside. (D) Close-up showing the egg capsules entangled in the 3D tubeworm field structure. The red and white heads of tubeworms are noticeable in some tube openings. For scale, the maximum diameter of the worm tubes was ~10 mm

sea water. *G. melastomus* is a very common deep-water catshark in the Mediterranean Sea at water depths around 500 m. During the video survey (Video clip 1 in the supplement at www.int-res.com/articles/suppl/m437p175_supp/) anemones, shrimps, a squid and juvenile fishes were also found living inside the tubeworm field, indicating that other, non-seep organisms also take advantage of this habitat.

At the CMSA, hundreds to thousands of large black skate egg capsules were found on and in between massive blocks of exposed carbonate (average capsule length 250 to 300 mm including horns; Fig. 2A,B,E), which were part of an extensive carbonate landscape that is raised approximately 200 m (700 m water depth) above the surrounding seafloor (900 m water depth). The eggs were sometimes associated with tubeworms (*Lamellibrachia* spp.;

Fig. 2C,D) adhering to the carbonates. Determining whether embryos were still developing inside the capsules was difficult. Some capsules had a clean surface, whereas others were partially covered by sediment (Fig. 2B). Size, shape, and texture of the capsules were very similar to those reported from species of the genus *Bathyraja* (Ebert 2005, Ebert & Davis 2007, Ebert et al. 2008). This genus is comprised of ~45 described species, which generally occur on continental slopes below 200 m (Compagno 1999). This area has possibly been a nursery for several generations of skates (Hoff 2010). Large (total length ca. 1.50 m) specimens of deep-water skates (*Bathyraja* spp.; e.g. Ruocco et al. 2006, Sellanes et al. 2008), including one possibly gravid female with a swollen abdomen, were discovered in the vicinity of the egg capsules (Fig. 2F). In a video survey with the OFOS, capsules were seen either randomly distrib-

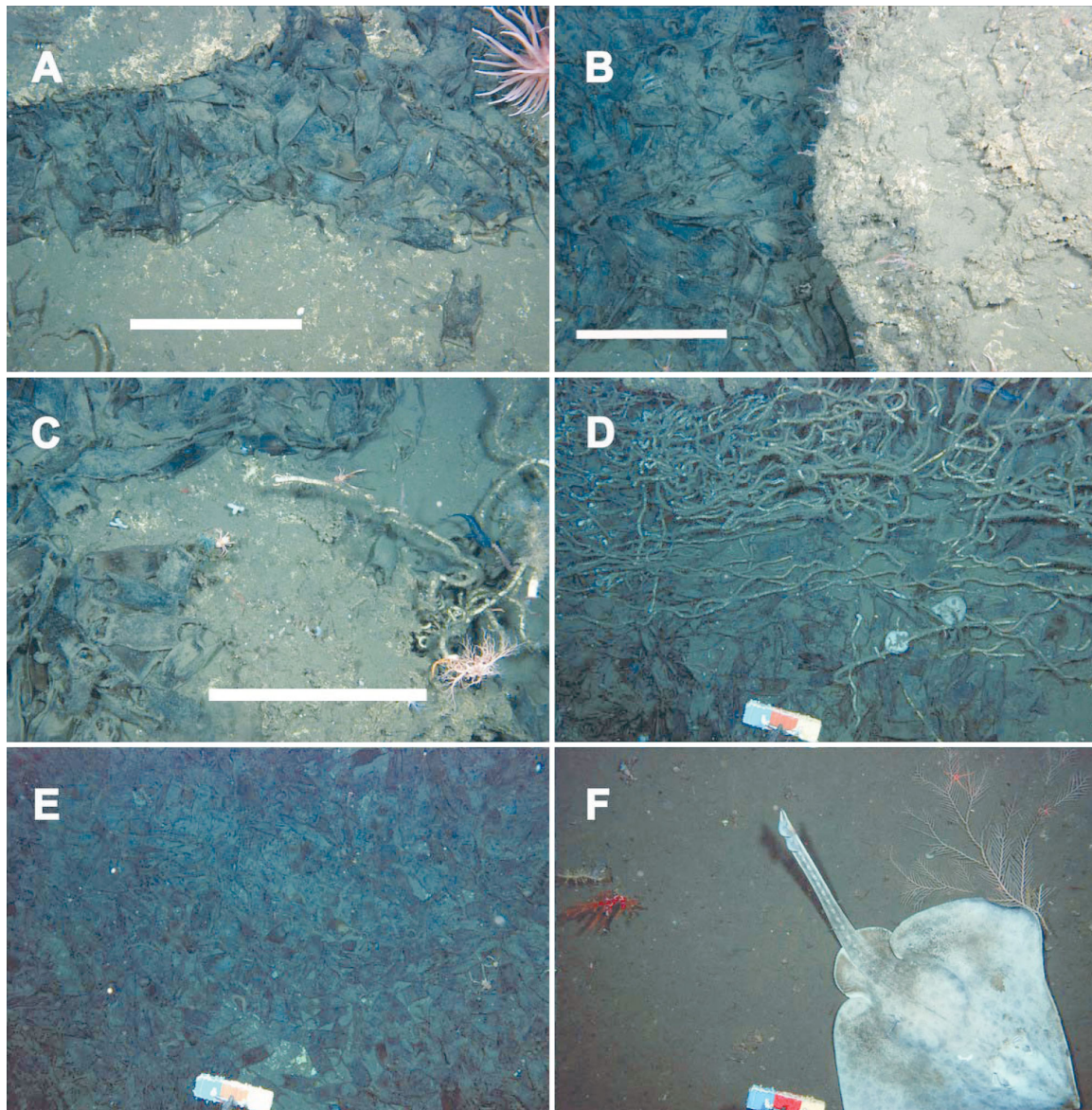


Fig. 2. *Bathyraja* spp. Skate egg capsules on massive blocks of exposed carbonate in the Concepción Methane Seep Area, South-East Pacific Ocean. (A,B) Capsules between large carbonate boulders. (C,D) Capsules associated with tubeworms. (E) Massive accumulation of capsules on a carbonate platform. (F) A large deep-water skate (*Bathyraja* spp.) observed near the egg nursery; the abdomen appears swollen indicating gravidity. Scale bars: 500 mm; ground weight (in D,E,F): 200 mm (not at ground level)

uted on the carbonate platforms or accumulated in niches between boulders (Video clip 2 in the supplement available at www.int-res.com/articles/suppl/m437p175_supp/).

At the BRSD, we collected 30 fossilized shark egg capsules and fragments thereof. All of the capsules were found closely associated with abundant remains of bathymodiolin mussels, hexactinellid sponges, and tubeworms (Fig. 3). The capsules had an inflated fusiform shape, a slightly constricted

waist, and a surface with at least 12 rough longitudinal ridges; we did not see tendrils on either end, but this may be an artifact of preservation. The capsules were up to 50 mm long, 15 mm wide, and 11 mm thick. Most specimens were preserved as internal molds and only some show the actual capsule with the ribbed surface; a few specimens were preserved as external molds. The most similar extant egg capsules to those found at the BRSD are those of the deep-water catshark *Apristurus* spp.; these capsules



Fig. 3. *Apristurus* spp. Remains of shark egg capsules (most similar to the deep-water catshark *Apristurus*, see Results and Discussion) in 35 million yr old cold-seep carbonates from the Bear River Seep Deposit, Washington State, USA. (A) Internal mold of egg capsule embedded in cold-seep carbonate (scale bar: 5 mm [vertically]). (B) External and internal molds of egg capsules (scale bar: 4 mm). The ribbed capsule wall (white arrows) is visible and fossilized worm tubes (black arrows) surround the capsules

commonly have a similarly tapering posterior end and coarse ribs on the surface (Sato et al. 1999, Iglésias et al. 2002). The attribution of the BRSD egg capsules to *Apristurus* is also consistent with the fossil record of teeth of *Apristurus*, which extends into the late Eocene (Adnet et al. 2008). The only other extant scylorhinid with a fossil record extending into the Eocene, including in the Pacific Northwest of the United States, is *Scyliorhinus* (Welton 1972, Adnet et al. 2008); however, the egg capsules of this genus are apparently smooth (Rusaouën et al. 1976, Ebert et al. 2006).

The observations of skate and shark egg capsules in modern seeps from 2 very distant continental margins (Mediterranean Sea and South-East Pacific Ocean) suggest that deep-water elasmobranchs may use cold seeps for nurseries in many parts of the world oceans. Fossilized shark egg capsules from the ancient 35 million year old seep deposit in the North American Cascadia accretionary wedge demonstrate that this association has persisted since at least the late Eocene. Carbonate deposits provide locations for capsule holdfasts, e.g. through tubeworms, gorgonians (Etnoyer & Warrenchuk 2007), and sponges (Hoff 2010); protection (between carbonate boulders or tubeworms), and/or enhanced current conditions (e.g. ventilation) for the egg capsules (Etnoyer & Warrenchuk 2007, Flammang et al. 2007, Love et al. 2008, Hoff 2010) on the otherwise nearly flat deep-sea floor. We do not know if the seep biostrome is still of importance for the neonate and juvenile sharks and skates after hatching because we could not confirm their presence in the vicinity of the egg capsules.

Neonate catsharks (Ebert et al. 2006) and skates (Hoff 2010) are reported to leave their nurseries, probably to escape predation, and to migrate into deeper or shallower depths until they return for mating. However, the seep biostrome could provide ample and localized food sources in the form of small fishes, crustaceans, mollusks, and annelids (Fig. 1, Video clip 1 for NAMV; Sellanes et al. 2008 for CMSA).

The discovery of elasmobranch egg capsules associated with modern and ancient seep deposits adds a new perspective to the significance of the patchily but globally distributed (Suess 2010) chemosynthesis-based cold-seep ecosystems for the vast heterotrophic, photosynthesis-based ecosystems of the continental slopes. Predators play a significant—although not entirely understood—role in the functioning and composition of marine ecosystems (Heithaus et al. 2008, Baum & Worm 2009). By serving as nurseries for deep-water marine predators, cold seeps are important components of deep-sea ecosystems and should not be considered as only extreme and exceptional habitats; their presence or absence is likely to influence faunal diversity along continental margins.

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