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Author for correspondence:

H. J. T. Hoving

e-mail: hoving@geomar.de

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Bathyal feasting: post-spawning squid as a source of carbon for deep-sea benthic communities

H. J. T. Hoving¹, S. L. Bush^{2,3}, S. H. D. Haddock² and B. H. Robison²

¹GEOMAR, Helmholtz Centre for Ocean Research Kiel, Düsternbrooker Weg 20, 24105 Kiel, Germany

²Monterey Bay Aquarium Research Institute, Moss Landing, CA 95039, USA

³Monterey Bay Aquarium, 886 Cannery Row, Monterey, CA 93940, USA

HJTH, 0000-0002-4330-6507; SLB, 0000-0001-5169-7686

In many oceanic carbon budgets there is a discrepancy between the energetic requirements of deep-sea benthic communities and the supply of organic matter. This suggests that there are unidentified and unmeasured food sources reaching the seafloor. During 11 deep-sea remotely operated vehicle (ROV) surveys in the Gulf of California, the remains (squid carcasses and hatched-out egg sheets) of 64 post-brooding squid were encountered. As many as 36 remains were encountered during a single dive. To our knowledge this is one of the largest numbers of natural food falls of medium-size deep-sea nekton described to date. Various deep-sea scavengers (Ophiuroidea, Holothuroidea, Decapoda, Asteroidea, Enteropneusta) were associated with the remains. Although many of the 80 examined ROV dives did not encounter dead squids or egg sheets ($n = 69$), and the phenomenon may be geographically and temporally restricted, our results show that dead, sinking squid transport carbon from the water column to the seafloor in the Gulf of California. Based on food fall observations from individual dives, we estimate that annual squid carcass depositions may regionally contribute from 0.05 to 12.07 mg C m⁻² d⁻¹ to the seafloor in the areas where we observed the remains. The sinking of squid carcasses may constitute a significant but underestimated carbon vector between the water column and the seafloor worldwide, because squid populations are enormous and are regionally expanding as a result of climate change and pressure on fish stocks. In the future, standardized methods and surveys in geographical regions that have large squid populations will be important for investigating the overall contribution of squid falls to regional carbon budgets.

1. Introduction

Most deep-sea benthic communities depend on particulate organic carbon (POC) that is synthesized in surface waters and eventually settles upon the seabed. Sediment traps have been used for decades to collect and measure this sinking material, allowing insight into local carbon budgets [1]. Deep-sea carbon budgets are often not closed; discrepancies exist between the amount of POC that is captured in sediment traps and the carbon required to sustain the measured biomass and respiration of deep-benthic communities [2,3]. However, *in situ* observations suggest that the remains of various megafaunal organisms and gelatinous plankton, which are excluded from sediment trap analysis, may locally constitute significant sources of carbon [4–9]. The role of medium-sized nektonic carrion (here defined as the remains of squids, chondrichthyans and teleost fishes of 1–100 cm in length) in carbon budgets is largely unknown. Natural observations of such carrion are so rare that typically only individual observations are published [5,10–12]. The paucity of observations stems from limited access to the deep-sea habitat with the imaging tools required to observe and quantify naturally deposited, rapidly consumed carcasses.

Squids are opportunistic, typically fast-growing carnivores that constitute a pivotal link between zooplankton, micronekton and top predators [13]. They appear to be proliferating in the ocean as a result of teleost overexploitation, warming waters and deoxygenation [14–17]. Squids have one reproductive cycle after which they die (semelparity) [18]. Many shallow-water squid species aggregate to mate and to spawn, which may locally result in high biomasses. Post-spawning mortality, after securing egg cases to the seafloor in shallow water, results in the deposition of squid carcasses—a phenomenon that has been documented for neritic squid in the family Loliginidae [19]. Squids are abundant in the open ocean and deep sea, and carcass deposition should thus also occur in oceanic regions where large squid populations exist. This is supported by the fact that squid flesh can be found in the stomachs of abundant deep-sea scavengers [20–22]. Although the reproductive behaviour of oceanic squid is poorly known, some species (e.g. ommastrephids) aggregate for reproduction [23,24]. Nevertheless, observations of squid carrion on the deep seafloor (greater than 200 m) are very rare; the only published account involves carcasses of *Brachyoteuthis*, observed off Cape Hatteras, NC, USA, which were consumed by brittle stars and a type of crab [23]. Scattered remotely operated vehicle (ROV) observations of post-spawning ommastrephids on the seafloor have also occurred (M. Vecchione 2017, personal communication). Accounts of squid carcasses at the sea surface involve spent individuals of squid species that experience ‘gelatinous degeneration’ [25]. The females of these species undergo mantle tissue breakdown as a result of maturation and spawning, then float to the surface after release of the eggs [25]. There they are consumed by seabirds and other epipelagic oceanic scavengers [25]. Various lines of evidence suggest that postspawning dead squid also transport carbon to seafloor communities in the deep sea, but in the absence of direct observations and measurements, the role of squid carrion in the carbon cycle remains unknown. Here we report on squid food falls on the deep seafloor of the Gulf of California, Mexico.

2. Results

Between February and April of 2012 and 2015, the Monterey Bay Aquarium Research Institute conducted surveys in the deep basins of the Gulf of California using their ROV *Doc Ricketts*. Squid carcasses and the remains of squid egg sheets were observed on the seafloor during the course of 11 ROV dives (of a total of 80 dives that reached the bottom) (see: <http://mbari.org/squid-carrion-images>). Nine squid carcasses were encountered, at depths from 1246 to 1698 m, during six of the 11 dives (figure 1; electronic supplementary material, table S1). Recent carcass deposition was indicated by the fact that the mantles of several individuals were still purple due to expanded chromatophores, while the arms were white (figure 1; <http://mbari.org/squid-carrion-images>). Average mantle length of squid carcasses was 351 ± 57 mm (range 281–452 mm: $n = 7$) (for measurements and estimations, see electronic supplementary material, SM1). A black, elongated mass was in close proximity to six of the observed squid. Close-up imagery and sample collection showed that these masses were hatched-out egg sheets (figure 1). Gonatid squids brood their young by holding darkened sheets with embedded developing embryos in their arms [26]. Fragments of egg sheets (without squid) of up to 540 mm in length were observed between

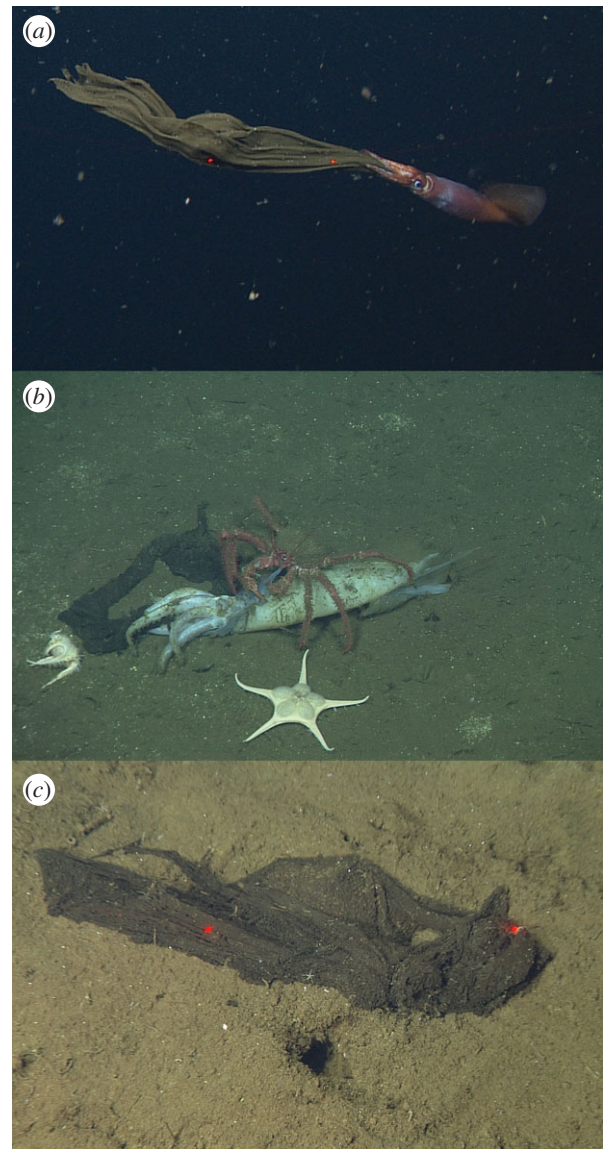


Figure 1. *In situ* ROV observations of living squid and squid carrion in the Gulf of California. (a) Brooding gonatid squid (mantle length approx. 25 cm, 1100 m, dive 344; 24.4° N–109.9° W). (b) Dead squid with hatched-out egg mass with seastars (*Nymphaster diomedae*) and lithodid crab *Paralomis multispina* (1246 m, dive 344; 24.4° N–109.9° W). (c) an isolated empty squid egg sheet (length 50 cm, 1615 m, dive 368, 26.6° N–111° W). The laser dots in (a) and (c) are 29 cm apart.

1072 and 3016 m depth (electronic supplementary material, table S1). Some locations had multiple fragments, and we suspect that some of these fragments came from the same egg sheet (as indicated in electronic supplementary material, table S1). Overall, we examined 55 individual squid food fall locations based on the observed egg sheet fragments (see: <http://mbari.org/squid-carrion-images>). Some of the food fall locations were more than 450 km apart (electronic supplementary material, table S1). While ROV bottom surveys were performed in relatively shallow (less than 1000 m), intermediate (1000–2000 m) and deep (greater than 3000 m) regions, most squid remains (62 remains) were found during nine dives in waters between 1072 and 1698 m. The maximum number of observed squid remains encountered during a single dive included five squid carcasses and 31 egg sheet remains (electronic supplementary material, tables S1 and S2). The two dives that encountered the highest numbers and densities of squid remains were at the same location (latitude

24.40° N, longitude 109.88° W, in the Cerralvo Trough) in 2012 and in 2015. During ROV dives in the water column, brooding squid (figure 1) were observed and three collected specimens of younger ontogenetic stages were identified as *Gonatopsis octopedatus* or a closely related species (R. E. Young 2012, personal communication), suggesting that the dead squid on the seafloor could belong to this species. Fauna observed in the vicinity of, or scavenging on, these food falls included Enteropneusta, Ophiuroidea, Holothuroidea, Decapoda and Asteroidea (figure 1; electronic supplementary material, table S1). A ratfish, *Hydrolagus melanophasma*, was observed with a roughly 150 × 50 mm piece of carrion in its mouth just 150 m from a squid carcass.

3. Discussion

The animal groups that were associated with the squid carcasses have been observed at other natural food falls [27]. Conversely, we did not observe grenadier fishes, isopods, zoarcids, liparids or hagfish—scavengers that are reported to be abundant at artificial and natural food falls [5,11,27]. While all observed squid carcasses and the remains of some hatched-out egg sheets had scavenging fauna associated with them, the majority of the latter did not, suggesting that this material is less palatable. Gonatid squid appear to incorporate ink in the egg sheets [28], which may act as a deterrent to some organisms, including microbiota [29], thus increasing the time it takes to be consumed. The longer residence time of egg sheet remnants allowed us to trace back to already-consumed squid, assuming that for each sheet a spent female squid reached the seafloor.

The 64 occurrences of squid and egg sheets are to our knowledge the largest number of natural deep-sea food falls of medium-sized nekton reported to date (electronic supplementary material, table S1). Smith [10] reported 12 food falls in the Catalina Basin, of which eight may have had a pelagic origin. Roper & Vecchione [23] reported two presumably spent brachioteuthid squid on the seafloor, which were consumed by brittle stars and a crab. These authors state that ‘spent, dying squids that sink to the bottom could provide a significant source of energy to the deep benthic fauna’ (p. 59).

We estimate that the average observed carcass, excluding egg sheets, of 351 mm mantle length ($n = 7$; see also electronic supplementary material, SM1) weighs 1.9 kg [30]. Assuming a scavenging rate of 5 kg d⁻¹ [5,31], such a carcass would take an average of 9 h to be consumed. However, Collins *et al.* [31] also report that in three of nine experimental squid falls, the bait remained untouched and in two experiments little of the bait was consumed within the experimental period. Therefore, 9 h may be an underestimate, and squid may lie longer on the seafloor. In any case, provided the rarity of observations in the literature, our encounters with these food falls were likely fortunate, and there is potential for high squid carcass turnover on the seafloor in certain areas of the Gulf of California. The high concentration of squid remains in some areas (up to 0.023 m⁻²) also suggests a regional abundance of these food falls, but the absence of carcass observations during the majority of the dives indicates heterogeneity in their deposition. Additionally, we encountered remains more than 450 km apart, supporting the notion that this carbon input is not limited to just one basin within the Gulf of California. The finding of squid remains in two separate years between February and April suggests an annual event that is spread over at least three months, but

whether or not the deposition of squid carcasses is a continuous, episodic or seasonal process remains a matter of speculation.

Our data allowed careful estimations of the role of squid carcass deposition in local carbon budgets. If we assume that for each egg sheet, a squid carcass was also deposited, then the density of carcasses would be 0–0.023 m⁻² for a single dive location (electronic supplementary material, table S2). Assuming that the pulse of carcasses is an annual event, the carcasses could locally contribute from 0.05 to 12.07 mg C m⁻² d⁻¹ to the deep seafloor in the areas where they were observed (electronic supplementary material, SM1 and table S2). Estimates of POC flux to the deep seafloor greater than 1000 m in the Gulf of California are absent, to our knowledge. Published records of POC flux measured by sediment traps in the Guaymas Basin, Gulf of California at 475 m ranged from 2 to 58 mg POC m⁻² d⁻¹ (mean = 21 mg POC m⁻² d⁻¹) [32]. A direct comparison would suggest that squid food falls may locally contribute the equivalent of 0.2–57.4% of the mean annual sediment trap flux. However, we should emphasize that (i) the measured POC flux from sediment traps is from shallower depths than the observed squid remains, and (ii) the squid food fall calculations are based on individual dives and squid carcasses were observed on only some of the benthic dives (11 of 80 dives). Our estimated values of carbon associated with the carcasses of what is probably a single squid species are locally relatively high. They exceed estimates for other nekton food falls [5,10], but they are less than estimates for certain gelatinous zooplankton species [4,6,8]. Our estimations may be conservative because our calculations are based on female squid only while male squid are also semelparous. Also, we have assumed that the observed carcasses were the only carcasses deposited in that area that year (i.e. not taking into account scavenging rates), while deposition must occur more often. Our estimate of the area observed by the ROV may be conservatively large, meaning that the density may be higher than our current measurements. Finally, our calculations only included the carbon associated with the squid bodies and the squid bodies presumed to have been deposited with the egg sheets, but not the hatched-out egg sheets themselves. An overestimation of our calculated flux could result if the squid have a lower body mass than estimated here, because female squid mobilize nutrients from their mantle and digestive gland to fuel the long brooding time [26,28]. Also, it is possible that in some cases the squid associated with the egg sheet observed on the sediment was consumed by benthopelagic predators before it reached the seafloor. Finally, it is possible that some of the egg sheet fragments observed in the Cerralvo Trough originated from the same squid, while we counted them as separate food falls. The Gulf of California is a suitable area to investigate the role of nektonic carrion in benthic carbon budgets and future research efforts should focus on performing standardized survey studies using *in situ* observations.

These first quantitative estimates of squid carrion in the deep sea and the associated scavenging fauna suggest that sinking squid could be an important local source of carbon, but this source is currently not taken into account in carbon budgets. By feeding intensively on mesopelagic prey [33], and through high growth and metabolic rates [34], gonatid squid very efficiently capture carbon that is stored in mesopelagic communities, including myctophids, which comprise some of the largest fish biomasses on the planet [35]. As they descend to meso- and bathypelagic depths for reproduction

and subsequent death, gonatids, and probably other squids, transport carbon from the epi- and mesopelagic layers to the deep seafloor. This pathway circumvents the conventional carbon pump concept of passively sinking particles, and results in rapid transportation of carbon to the deep sea [22]. Our results shed light on a process that is probably of global importance, and one that further links the largest habitats on the planet, the deep seafloor and the pelagic realm. Squid populations worldwide are massive, supporting large industrial fisheries [36]. Annually, sperm whales alone are estimated to consume as much squid as all human fisheries combined [37]. Because of the single reproductive cycle, and the typically short lifespan of squids, populations may provide the deep sea with annual pulses of carbon worldwide, as suggested from the diets of abundant deep-sea scavengers [20–22]. The squid-associated carbon flux is probably also dynamic. Squid populations respond flexibly and in some cases positively to regional environmental change [15–16]. Together with overexploitation of fishes, this has resulted in a trend observed in different marine systems where cephalopods are proliferating [17]. Such potential ecosystem shifts probably change the squid-associated carbon flux to the seafloor and may locally result in an alteration of the ocean carbon pump.

Ethics. Our study is mostly based on deep-sea video observations. The three ROV-captured squid specimens were flash-frozen at -80 C , and subsequently defrosted and preserved in formalin for preservation and examination. The expedition ‘MBARI’s 2012 Gulf of California Expedition, R/V *Western Flyer*.’ (Cruise no. F2011-068) was approved by the Mexican government via permits CTC/001340 (from La Secretaria de Relaciones Exteriores) and H00/

INAPESCA/DGIPPN/831 (Secretaria de Agricultura, Ganadería, Desarrollo Rural, Pesca Y Alimentación). The expedition ‘2015 R/V *Western Flyer* Gulf of California Expedition.’ (Cruise no. F2014-075) was approved by the Mexican government via permits CTC/01700/15 (La Secretaria de Relaciones Exteriores) and DGOPA-02919/14 (Secretaria de Agricultura, Ganadería, Desarrollo Rural, Pesca Y Alimentación).

Data accessibility. The data are made available in electronic supplementary material, tables S1 and S2. ROV track coordinates on which the distances (d) calculated in electronic supplementary material, SM1 are based and the images of food falls can be found at <http://mbari.org/squid-carrion-images>.

Authors’ contributions. H.J.T.H. conceived of the study, designed the study, helped collect the field data, analysed the data and drafted the manuscript. S.L.B. helped collect the field data, analysed the data and helped to draft the manuscript. S.H.D.H. and B.H.R. collected field data and helped to draft the manuscript. All authors gave final approval for publication.

Competing interests. We have no competing interests.

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