Deep–Sea Research I 183 (2022) 103719

Contents lists available at ScienceDirect

Deep-Sea Research Part I

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

The abyssal voyage of the argonauts: Deep-sea in situ observations reveal the contribution of cephalopod egg cases to the carbon pump

H.J.T. Hoving [a,*], D. Amon [b], Y. Bodur [c,d], M. Haeckel [a], D.O.B. Jones [e], P. Neitzel [a], E. Simon-Lledó [e], C.R. Smith [f], J.B. Stauffer [a], A.K. Sweetman [g], A. Purser [a]

[a] GEOMAR Helmholtz Centre for Ocean Research Kiel, 24105, Kiel, Germany
[b] SpeSeas, D'Abadie, Trinidad and Tobago
[c] UiT - The Arctic University of Norway, 9037, Tromsø, Norway
[d] Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, 27570, Bremerhaven, Germany
[e] National Oceanography Centre, Southampton, SO14 3ZH, United Kingdom
[f] Department of Oceanography, University of Hawaii at Manoa, 96822, Honolulu, Hawaii, USA
[g] Heriot-Watt University, Edinburgh, EH14 4AS, Scotland, United Kingdom

ARTICLE INFO

Keywords:
Argonauta
Calcium carbonate
Calcite
Biological carbon pump
Food falls
Nekton

ABSTRACT

Calcifying plankton in the upper ocean produce calcium carbonate ($CaCO_3$) shells that sink to the seafloor after death resulting in the vertical transport of inorganic carbon in shells and organic carbon in carcasses. In situ observations of pelagic detritus on the abyssal plain are very scarce. Carcasses are rapidly scavenged and shells may dissolve owing to undersaturation of deep waters with respect to $CaCO_3$. We observed more than 300 egg cases of the epipelagic cephalopod *Argonauta* sp. in 9 large seafloor image surveys investigated across the Clarion Clipperton Zone in the Pacific between 2010 and 2020. Females of this octopus produce calcite egg cases that are used for buoyancy and as substrate on which to attach their eggs in the water column. These cases sink to the seafloor, presumably upon death of the octopus. In one area, between 3970 and 4551 m water depth surveyed in 2019, we documented more than 200 complete and fragments of egg cases (5.84 $\pm$ 1.8 cm in size) on the seafloor, complete and broken and in various states of dissolution. Here, we present observations of egg case dissolution in situ and of 99 white deposits that were likely largely dissolved egg cases. Our observations reveal a previously undocumented pathway of epipelagic inorganic carbon to the abyssal plain. Preliminary estimations indicate that the local contribution of *Argonauta* egg cases to the vertical transport of carbonates is likely small compared to other planktonic calcifiers, but the geographic extent of the deposition in the eastern Pacific is apparently large. This study highlights the need for in situ observations to discover and document carbon fluxes in the deep sea, and for consideration of life history traits in unraveling elusive pathways within the biological pump.

1. Introduction

The deep ocean is a sink for carbon. Unraveling pathways in the vertical transport of carbon ("carbon pump") is crucial for our understanding of carbon dioxide sequestration, a major ecosystem service of the deep ocean (Thurber et al., 2014). One biological pathway in the carbon pump is the uptake of carbon dioxide from the atmosphere via primary producers (algae) in the sunlit upper layers of the ocean. Aggregation and sinking of dead algal and other detrital material, and the subsequent repackaging of particulate organic matter by consumers within the ocean water column results in the flux of carbon to the deep seafloor (Robinson et al., 2010). The pace of the biological carbon pump may be enhanced by vertical migration of plankton and nekton (Hernández-León et al. 2019). The sinking of dead, larger pelagic organisms (gelatinous zooplankton, cephalopods, fishes, megafauna) to the seafloor is another pathway in the vertical carbon flux with these parcels of organic matter providing local enrichments known as food falls (Stockton and E DeLaca, 1982) nourishing scavengers (Soltwedel et al., 2003), and contributing to local carbon budgets (Smith et al., 2014; Hoving et al., 2017; Lebrato et al., 2012; Sweetman and Chapman 2015; Smith 1985). Observations of pelagic food falls in the deep sea are extremely rare (Soltwedel et al., 2003; Higgs et al. 2014; Amon et al.,

* Corresponding author.
E-mail address: hhoving@geomar.de (H.J.T. Hoving).

https://doi.org/10.1016/j.dsr.2022.103719
Received 13 June 2021; Received in revised form 24 January 2022; Accepted 1 February 2022
Available online 22 February 2022
0967-0637/

2016) but their role in subsidizing food-deprived abyssal plain ecosystems may be significant (Drazen et al., 2012) although temporally and spatially heterogeneous (Hoving et al. submitted).

Another pathway in the biological pump is maintained by calcifying organisms. Calcifying plankton such as foraminifera, ostracods and pteropods take up inorganic CO_3^{2-} ions from water to produce relatively heavy carbonate shells that sink fast to the deep ocean floor after the death of the individual (Volk and Hoffert 1985). The transport of $CaCO_3$ to the deep sea via detrital calcareous shells is a major pathway in the (inorganic) carbon pump and at the seafloor the dissolution and burial of $CaCO_3$ provide final sinks for anthropogenic CO_2 (Archer et al., 2009). One of the challenges in quantifying fluxes of carbonate from calcifiers to abyssal depths (3000–6000 m) is that $CaCO_3$ shells of epi- and mesopelagic fauna dissolve at depths below the dissolution horizon of aragonite and calcite owing to undersaturation with respect to $CaCO_3$ (Zeebe and Wolf-Gladrow 2001). Calcium carbonate shells of pelagic calcifiers therefore do not accumulate on the abyssal seafloor, and depending on the water depth and the form of $CaCO_3$ they may be absent or reduced in abyssal sediment traps (Betzer et al., 1984).

The Argonautidae or paper nautilus, are a family of epipelagic octopods that occur in shallow open ocean waters in tropical and subtropical regions around the world (Finn 2013). Female argonauts produce an external calcium carbonate (calcite) egg case (Mitchell et al., 1994; Oudot et al., 2020) that is held by webs on two arms. The egg case is used for buoyancy control (Finn and Norman 2010) and as brood chamber to attach the eggs (Conrad 1854; NaefCephalopoda,). The argonaut egg case is evolutionarily unrelated to the molluscan shell, and is produced by glands on the arms rather than by an internal shell sac as in other cephalopods (Finn and Norman 2010). The males are dwarfed and have about 8% of the female length and 0.17% of the female weight, and they do not produce an egg case. Mass stranding of hundreds to thousands of argonaut egg cases, sometimes with female and eggs, have been documented on beaches worldwide (Norman 2003; Okutani and Kawaguchi 1983; Rosa and Seibel 2010), with these attributed to reproductive, meteorological or oceanographic events. The episodic occurrence of argonaut egg cases in the neritic zone suggests that similar deposition of carcasses and egg cases must occur in the open ocean as the species has a holopelagic oceanic lifestyle. Observations from the deep seafloor are to the best of our knowledge currently not present in the literature. Benefitting from extensive seafloor observations in waters >3400 m, obtained during deep-sea expeditions in the Clarion Clipperton Zone (CCZ), in the Pacific between 2010 and 2021, we present regional datasets of submersible and camera observations of *Argonauta* sp.egg case deposition which includes the deepest reported cephalopod related food fall to date. We provide in situ dissolution observations and using the best studied example, from 2019, we provide detailed observations of the deposition and quantified how much calcium carbonate is associated with this event, and discuss how this phenomenon may contribute to the transport of carbon to the abyssal plain.

2. Material and methods

Regional seabed image datasets (Supplementary Table 1) from 12 abyssal sites, which cover nine areas across the CCZ in the Central Pacific (UK-1: Amon et al., 2016; TOML-B, TOML-C, and TOML-D: Simon-Lledó et al., 2020; APEI-6: Simon-Lledó et al., 2019a; APEI-6 Seamount: Jones et al., 2021; BGR-east and NORI-D: this study) and three areas within Kiribati (Kiribati A-C; Simon-Lledó et al., 2019b) (Fig. 1), were re-annotated manually for argonaut egg cases (Fig. 2). These datasets were collected with a variety of imaging platforms (ROV, AUV, or towed camera system) but all had the ability to discriminate organisms greater than 10 mm in maximum dimension (see e.g. Multimedia Component 1). As such, identifying argonaut egg cases several times larger than the minimum size cut off is assumed to be robust and include all records of intact or broken egg cases present. These datasets included a total of 91,152 images covering a seafloor area of 597,360 m^2. The datasets spanned latitudes from 0 to 17°N, longitudes from 172 to 115°W, and depths from 3480 to 5575 m (Fig. 1).

One area of the CCZ was investigated in more detail for this paper, referred to as the SO268 area. Between March 7 and May 10, 2019, during the cruise SO268 on RV SONNE, 14 seafloor transects (of which 13 were successful) were collected with the towed camera Ocean Floor Observation System (OFOS) at depths from 3970 to 4551 m in the CCZ (Multimedia Component 2). The OFOS consisted of a steel frame with a downward looking 23 megapixel still camera (iSiTEC, CANON EOS 5D Mark III) that was set to take an image every 15 s, and a telemetry, which transmitted a high definition preview via the ship's fiber optic cable. An altimeter enabled constant distance from the ground (1.7 m), and a pair of tri-lasers (iSiTEC, custom built; 50 cm apart) were used to provide information on the size of the observed fauna and objects. OFOS was towed at a ship speed of 0.2–0.5 knots. A total of 41,134 images were

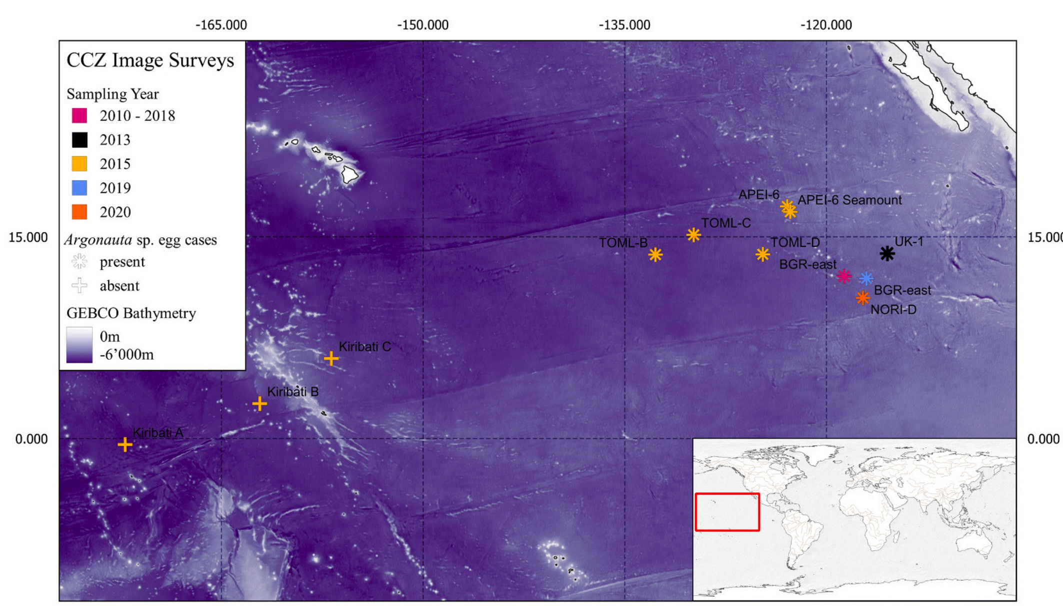

Fig. 1. Locations in the Central Pacific where seafloor observations were collected and that were annotated for the presence of *Argonauta* sp. shells.

Fig. 2. *Argonauta* egg cases observed by ROV KIEL6000 in the area BGR-east during SO268 in 2019: a) an intact egg case and b) a partially degraded egg case. The distance between the laser dots is 6.3 cm.

collected. The seafloor area captured within each image was determined by measuring the spacing of the laser points in a subset of 3663 images using the PAPARA(ZZ)I software application (Marcon and Purser 2017). This resulted in an average image area of 10.85 m^2. The 13 seafloor transects covered a total area of 446,293 m^2. ROV surveys by ROV KIEL6000 in the study region also documented the egg cases opportunistically. These images were used as reference material and for illustration.

All images were manually analyzed for the presence of food falls, egg cases and the white substance that presumably remains after dissolution of the egg case. When possible the "shell length" (hereafter called "egg case length") was measured according to the definition of Finn (2013) with ImageJ using the lasers as scale.

The in situ consumption and dissolution of one egg case was documented by a time-lapse camera on a lander system (KC Denmark) deployed to the seabed in the NORI-D area during cruise NORI-D Campaign 5D in the eastern CCZ (10° 20.103' N 117° 10.445' W) on May 31st' 2021 at a depth of 4288 m. The time-lapse camera system includes an Ocean Imaging Systems DSC24000 deep-sea camera (The DSC24000 contains a Nikon 7100 digital single lens reflex camera). The acceptance angles of the camera lens were 40° (vertical) and 57° (horizontal). The camera was powered by a Deep-Sea Power and Light 24 V external battery and light was provided by a 300 J strobe mounted facing down at an angle of 45°, at a distance of 1.17 m from the camera. The camera system took a picture every 8 h during 3 months and was set to ISO 200, f/16 and 1/25 s exposure. The last photograph was taken on August 30, 2021 when the battery ran out. The camera was recovered on Nov 19, 2021 during cruise NORI-D Campaign 5 E. Both cruises used the multi-purpose vessel *Maersk Launcher*.

3. Results

A total of 316 complete and broken argonaut egg cases, as well as 123 potential argonaut egg case remnants, were observed in the regional datasets (density of 0–61.7 egg cases per hectare), with egg cases seen at 9 of the 12 sites. Egg cases were not observed within the Kiribati EEZ, the westernmost samples in the region assessed. The Kiribati samples were the smallest in the regional dataset (combined total in 3 sites: 4074 images covering 14,666 m^2). In contrast, egg cases were present in all the abyssal areas assessed in the eastern CCZ (Multimedia Component 1).

In the detailed observations in BGR-east (2019) made during cruise SO268, 211 individual argonaut egg cases (Fig. 2) were observed on the seafloor between 3970 and 4551 m water depth. The egg case length ranged from 2.25 to 12.75 cm, with an average egg case length of 5.84 ± 1.8 cm (n = 139). Such an egg case length corresponds with an egg case mass of 2.39 g based on published length mass relationships (Finn 2013). Egg cases were observed intact, broken and partially degraded (Figs. 2 and 3). In some instances, more than one egg case was observed in one image. The only potential scavengers we observed associated with an argonaut egg case were a galatheid crab and sea urchins. Additionally, we observed 99 instances of white deposits of similar dimensions as the egg cases (Fig. 3). When we assume that the white masses were partly dissolved argonaut egg cases, the average density of egg cases was 0.00069 egg case/m^2, which correlates with a density of one egg case per 1449 m^2 of seafloor.

The average egg case was 5.84 ± 1.8 cm in length, which corresponded to a mass of 2.38 g/egg case based on published length mass relationships (Finn 2013). From this, the contribution of argonaut egg cases during the period of observation was 1.64 mg egg case mass/m^2.

The top 1 cm of sediment samples obtained during SO268 has a POC content of 0.7–1.0 wt% and a $CaCO_3$ content of 0.5–2 wt%, resulting in a POC/$CaCO_3$ mass ratio of 0.5–1.4.

In situ observations of a single *Argonauta* egg case from a time-lapse deployment show the majority of the decomposition process from shortly after deposition to almost complete decomposition (Fig. 3). Although the arrival of the egg case at the seafloor is not observed, the initial images show a complete specimen, with no indication of dissolution, that we assume is relatively newly deposited. At the end of the 90-day period there is little remaining material. This observation suggests that decomposition at this site takes at least 90 days. In addition to the decomposition process, the time-lapse images captured a small gastropod that is attracted to the egg case and interacts with it (Multimedia Component 4). The image resolution is not sufficient for confident identification (although see more detailed observations in Multimedia Component 3).

4. Discussion

Remains of pelagic organisms that fall onto the deep seafloor may regionally be important vectors of organic matter that nourish deep-sea fauna, but observations are very few (Soltwedel et al., 2003; Hoving et al., 2017; Sweetman and Chapman 2015). The reason for this paucity in data is that observations made during oceanographic campaigns provide snapshots of a surveyed ecosystem, potentially missing stochastic, short-term deposition events. Therefore, there may be a temporal and spatial mismatch between campaigns and the deposition of pelagic carcasses. Also, medium-size carcasses of cephalopods are rapidly scavenged, usually within 24 h, without leaving visual traces of the carcass (Collins et al., 1999). Our observations of several hundreds of argonaut egg cases on the seafloor at water depths exceeding 3400 m is the highest number of cephalopod remains reported to date in waters of greater than 200 m depth. The only other published reports of cephalopod remains in the deep sea include post-spawning female gonatids at 1000–1500 m in the Gulf of California (Hoving et al., 2017), carcasses of *Brachioteuthis,* observed off Cape Hatteras North Carolina (Roper and Vecchione 1996), and remains of *Illex* observed at 815 m by ROV (https://oceanexplorer.noaa.gov/okeanos/explorations/ex1711/logs/dec2/welcome.html).

Female argonauts with egg cases have been observed in large

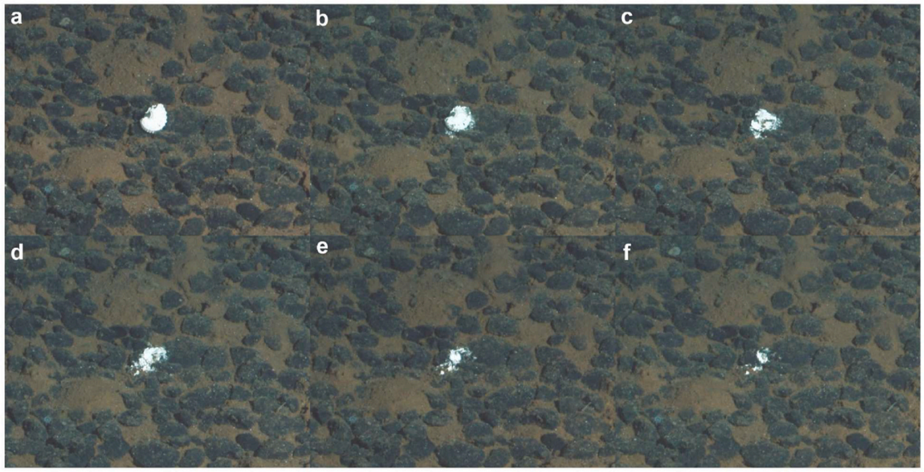

Fig. 3. In situ observations of the decomposition of one *Argonauta* sp. egg case as observed with a stationary time-lapse camera mounted on a deep-sea lander in NORI-D area (4288 m). A) 31. May 2021; B) after 18 days; C) after 36 days; D) after 54 days; E) after 72 days; F) after 90 days.

numbers at the sea surface in the equatorial Pacific Ocean (Conrad 1854). Their frequent strandings on beaches worldwide (Norman 2003), sometimes in 100s or even 1000s of individuals (Okutani and Kawaguchi 1983), and their occurrences in the stomachs of pelagic predators (Hernández-García, 2002) strongly supports the hypothesis that their abundance and importance in the upper ocean ecosystem worldwide is significant. *Argonauta* spp. feed on pteropods and other plankton, and have been observed associated with jellyfish (Heeger et al.1988). The egg cases we observed in the Clarion Clipperton Zone likely belong to *A. nouryi* (Finn 2013). In the open ocean females of this species may cling to each other forming chains of up to 18 animals (Rosa and Seibel 2010). Egg cases of *A. nouryi*, sometimes including a female argonaut with eggs, strand on beaches in the southern part of the Gulf of California during late winter and early spring (January to March) (Gonzales-Peralta 2006). Yet, despite numerous encounters of animals and egg cases in shallow water, argonauts or their egg cases have not been reported previously from the abyssal seafloor. The seasonal findings of argonauts on the beaches in the Gulf of California between January and March corresponds with our regional observations in March and April. Whether the deposition of argonaut egg cases on the abyssal seafloor is incidental, seasonal or continuous is unknown. The virtual absence of scavengers associated with the egg cases we observed may indicate that the bodies were already consumed at the surface or in the water column before the egg cases reached the seafloor, or that the egg cases were on the seafloor for some time before the surveys were conducted, and that a period of seafloor scavenging was missed. The time lapse images of in situ decomposition of the egg case showed that organisms, potentially scavengers such as amphipods and snails, are attracted to the egg case itself. They were small taxa, and in the current study only observable in the time lapse sequence of the images. They were not visible on the individual images taken by OFOS.

The observations of calcite argonaut egg cases (McClintock et al., 2011) on the abyssal seafloor was fortunate, given that carbonate structures are prone to dissolve at the water depths in that region as a result of undersaturation with respect to the respective carbonate mineral (i.e., calcite, aragonite). In addition, carbonate dissolution has also been shown to occur in the upper 1000 m of the water column (Sulpis et al., 2021). Argonaut egg cases probably sink relatively fast compared to other smaller carbonate detritus, and dissolution may not impact the egg cases in the upper 1000 m. $CaCO_3$ concentrations in Holocene surface sediments of the CCZ study area are typically below 1 wt%, since carbonate dissolution rates in the Equatorial Pacific peak in the surface sediments at 4–5 km water depth (Sulpis et al., 2021). The in situ decomposition of the egg case shows that it takes approximately 90 days until the egg case is in the state that we here described as the "white deposits". Decomposition of the shell is probably from dissolution potentially enhanced by faunal scavenging. The exact dissolution rate is highly dependent on depth, water chemistry but also the morphology and chemical composition of the carbonate structure. Argonaut egg cases consist of a central organic (protein; 1.8% of total composition) layer sandwiched between two layers of calcite (98.2%) (Oudot et al., 2020). It is not clear if scavenging activity is an important mechanism for decomposition or whether scavenging activities target the organic or inorganic parts of the egg case. Seasonal strandings suggest an annual life cycle, and potentially annual abyssal deposition. It should also be noted that some of the egg cases in our study were broken, which may bias the calculations. Egg case production is likely fast and an egg case with a maximum length of 17.4 cm was estimated to be built over a period of 4–5 months (Stevens et al., 2015). When we focus on the 2019 BGR east region and assume that the white masses are partly dissolved argonaut egg cases, egg case density was 0.00069 egg case/m^2. This could represent an annual flux of 1.64 mg m^{-2} yr^{-1} $CaCO_3$. Given that all open-ocean calcifiers including coccolithophorids, Foraminifera, and all pteropods contribute an estimated 2.5 g m^{-2} yr^{-1} to the $CaCO_3$ flux (Milliman and Droxler 1996; Tsurumi et al., 2005), the *Argonauta* sp. egg cases would therefore regionally contribute annually 0.06% to the total $CaCO_3$ flux of global open ocean calcifiers. How much of this $CaCO_3$ is incorporated in deep-sea sediment is hard to calculate, because it will undergo dissolution in sediments below the CCD. Since our study documents a potentially fast dissolution of the egg cases, once they have reached the seafloor (Fig. 3), it is difficult to compare this deposition flux to the total $CaCO_3$ flux of 3.75–12 mg m^{-2} yr^{-1}, derived by integration over the top 1 cm of the sediment (having a $CaCO_3$ content of 0.5–2 wt%, a porosity of 0.9–0.92 and a sedimentation velocity of 0.3 cm/kyr, thus representing a time interval of ~3000 yr with ongoing dissolution). The calcium carbonate flux from egg cases is clearly not representing a steady state.-

While the overall contribution of *Argonauta* sp. egg cases is small in the context of our current knowledge of the carbon cycle on the CCZ abyssal plain, our in situ observations reveal a taxon-specific pathway of epipelagic nektonic carbon that has thus far not been recognized in abyssal ocean carbon budgets. The documentation of multiple smaller pathways will eventually contribute to an integrative and detailed understanding of the biological pump. Also, the area over which *Argonauta* sp. egg cases were observed suggests that it is not a local phenomenon. The observation of sunken *Argonauta* sp. egg cases on the abyssal plain was only possible via in situ optical observations, emphasizing the need to explore the oceans using towed cameras, ROVs and AUVs equipped with cameras. Imagery analysis from future seafloor surveys in other areas of the global oceans should consider quantification of egg cases.

Automated image analysis may be particularly suitable for detection of *Argonauta* sp. egg cases, in images, which renders them in stark contrast with the darker background of abyssal plain seafloor. The finding of egg cases, a sex-specific trait, of epipelagic cephalopods illustrates the need to consider life history information when studying the biological pump, a combination of disciplines that deserves further attention in future research.

Data availability

Image data for SO268 are available on PANGAEA https://doi.org/10.1594/PANGAEA.935856 and the analyzed image data are available as an electronic supplement.

Author contributions

HJH wrote the first draft, all authors contributed to reviewing and editing; AP, MH and YB performed fieldwork; AP carried out data quality assessment and image archiving; PN, ESL, JS and HJH analyzed imagery and data; MH and HJH acquired funding; ESL and DOBJ, DA and CRS provided observations and/or images from additional field campaigns. AKS generated the funding for, and carried out the 90-d time-lapse camera lander deployment in the NORI-D license area.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are indebted to the professional assistance of the captain and crew of RV SONNE during cruise SO268 and the GEOMAR team operating ROV Kiel 6000. This research was funded by the German Ministry of Research (BMBF) in the framework of the MiningImpact project (grant no. 03F0812A-H) as part of the Joint Programming Initiative of Healthy and Productive Seas and Oceans (JPI Oceans). HJH is funded by the DFG (Deutsche Forschungsgemeinschaft) under grant HO 5569/2-1 (Emmy Noether Junior Research Group). DOBJ, ESL and AKS have received funding from UK Natural Environment Research Council through the Seabed Mining And Resilience To EXperimental impact (SMARTEX) project (Grant Reference NE/T003537/1). DOBJ, ESL and AKS have also received support from TMC the metals company Inc. (The Metals Company) through its subsidiary Nauru Ocean Resources Inc. (NORI). NORI holds exploration rights to the NORI-D contract area in the CCZ regulated by the International Seabed Authority and sponsored by the government of Nauru. This is contribution TMC/NORI/D/001. DA and CRS received support through the ABYSSLINE Project funded by UK Seabed Resourced Limited. The funders had no role in the design and conduct of the study; collection, management, analysis, and interpretation of the data; preparation, review, or approval of the manuscript; and decision to submit the manuscript for publication.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr.2022.103719.

References

Amon, Diva, Hilario, A., Arbizu, P.M., Smith, C.R., 2016. Observations of organic falls from the abyssal Clarion-Clipperton zone in the tropical Eastern Pacific Ocean. Mar. Biodivers. 47, 311–321. https://doi.org/10.1007/s12526-016-0572-4.

Amon, D.J., Ziegler, A.F., Dahlgren, T.G., Glover, A.G., Goineau, A., Gooday, A.J., Wiklund, H., 2016. Insights into the abundance and diversity of abyssal megafauna in a polymetallic-nodule region in the eastern Clarion-Clipperton Zone. Sci Rep 6, 30492. https://doi.org/10.1038/srep30492.

Archer, David, Eby, Michael, Brovkin, Victor, Ridgwell, Andy, Cao, Long, Mikolajewicz, Uwe, Caldeira, Ken, et al., 2009. Atmospheric lifetime of fossil fuel carbon dioxide. Annu. Rev. Earth Planet Sci. 37 (1), 117–134. https://doi.org/10.1146/annurev.earth.031208.100206.

Betzer, P., Byrne, Robert, Acker, James, Lewis, C., Jolley, R., Feely, Richard, 1984. The oceanic carbonate system: a reassessment of biogenic controls. Science (New York, N.Y.) 226 (December), 1074–1077. https://doi.org/10.1126/science.226.4678.1074.

Collins, Martin A., Yau, Cynthia, Nolan, Conor P., Bagley, Phil M., Priede, Imants G., 1999. Behavioural observations on the scavenging fauna of the patagonian slope. J. Mar. Biol. Assoc. U. K. 79 (6), 963–970. https://doi.org/10.1017/S0025315499001198.

Conrad, T.A., 1854. Monograph of the genus Argonauta, linne, with descriptions of five new species. J. Acad. Nat. Sci. Phila. 2, 331–334.

Drazen, Jeffrey, Bailey, David, Henry, Ruhl, Smith, Kenneth, 2012. The role of carrion supply in the abundance of deep-water fish off California. PLoS One 7 (November), e49332. https://doi.org/10.1371/journal.pone.0049332.

Finn, Julian K., 2013. Taxonomy and biology of the argonauts (cephalopoda: Argonautidae) with particular reference to Australian material. Molluscan Res. 33 (3), 143–222. https://doi.org/10.1080/13235818.2013.824854.

Finn, Julian, Norman, Mark, 2010. The argonaut shell: gas-mediated buoyancy control in a pelagic Octopus. Proceedings. Biological Sciences/The Royal Society 277 (October), 2967–2971. https://doi.org/10.1098/rspb.2010.0155.

Gonzales-Peraltа, A., 2006. Mass stranding of Argonauta spp. (cephalopoda: Argonautidae) in the Gulf of California, Mexico. In: *Cephalopod Life Cycles, CIAC*. Hobart.

Heeger, T., Piatkowski, Uwe, Möller, H., 1988. Predation on Jellyfish by the cephalopod Argonauta argo. Mar. Ecol. Prog. Ser. 88 (November), 293–296. https://doi.org/10.3354/meps088293.

Hernández-García, Vicente, 2002. Contents of the digestive tract of a false killer whale (pseudorca crassidens) stranded in gran canaria (canary Islands, Central East atlantic). Bull. Mar. Sci. 71 (July), 367–369.

Higgs, Nicholas D., Gates, Andrew R., Jones, Daniel O.B., 2014. Fish food in the deep sea: revisiting the role of large food-falls. PLoS One 9 (5), e96016. https://doi.org/10.1371/journal.pone.0096016.

Hoving, H.J.T., Bush, S.L., Haddock, S.H.D., Robison, B.H., 2017. Bathyal feasting: post-spawning squid as a source of carbon for deep-sea benthic communities. Proc. Biol. Sci. 284 https://doi.org/10.1098/rspb.2017.2096, 1869.

Jones, D.O.B., Simon-Lledó, E., Amon, D.J., Bett, B.J., Huvenne, V.A.I., et al., 2021. Environment, ecology, and potential effectiveness of an area protected from deep-sea mining (Clarion Clipperton Zone, abyssal Pacific). Prog. Oceanogr. 197, 102653. https://doi.org/10.1016/j.pocean.2021.102653.

Lebrato, Mario, Pitt, Kylie, Sweetman, Andrew, Jones, Daniel, Cartes, Joan, Oschlies, Andreas, Condon, Robert, et al., 2012. Jelly-falls historic and recent observations: a review to drive future research direction. Hydrobiologia 690 (January), 227–245.

Hernández-León, Santiago, Olivar, María Pilar, Luz Fernández de Puelles, María, Bode, Antonio, Castellón, Arturo, López-Pérez, Cristina, Tuset, Víctor M., González-Gordillo, José Ignacio, 2019. Zooplankton and micronekton active flux across the tropical and subtropical atlantic ocean. Front. Mar. Sci. 6:535. https://www.frontiersin.org/article/10.3389/fmars.2019.00535.

Marcon, Yann, Purser, Autun, 2017. PAPARA(ZZ)I: an open-source software Interface for annotating photographs of the deep-sea. Software 6 (February), 69–80. https://doi.org/10.1016/j.softx.2017.02.002.

McClintock, James, Amsler, Margaret, Angus, Robert, Challener, Roberta, Julie Schram, Amsler, Charles, Mah, Christopher, Cuce, Jason, Baker, Bill, 2011. The Mg-calcite composition of antarctic echinoderms: important Implications for predicting the impacts of ocean acidification. J. Geol. 119 (September), 457–466. https://doi.org/10.1086/660890.

Milliman, J.D., Droxler, A.W., 1996. Neritic and pelagic carbonate sedimentation in the marine environment: Ignorance is not bliss. Geol. Rundsch. 85 (3), 496–504. https://doi.org/10.1007/BF02369004.

Mitchell, P.R., Phakey, P.P., Rachinger, W.A., Hirsch, K.F., Smillie, A.C., 1994. Ultrastructural Observations of the Argonaut Shell" 8 (March): 35–46.

Naef, A. n.d. Cephalopoda. Fauna e Flora Del Golfo Di Napoli. Monograph. Jerusalem.

Norman, M., 2003. Cephalopods: a world guide. Hackenheim: Conchbooks 1–320.

Okutani, T., Kawaguchi, T., 1983. A mass occurrence of Argonauta argo (cephalopoda: octopoda) along the coast of shimane prefecture, western Japan sea. Japanese Journal of Malacology 41, 281–290.

Oudot, Morgane, Ben Shir, Ira, Schmidt, Asher, Plasseraud, Laurent, Broussard, Cédric, Pascal, Neige, Marin, Frédéric, 2020. A nature's curiosity: the argonaut 'shell' and its organic content. Crystals 10 (September). https://doi.org/10.3390/cryst10090839.

Robinson, Carol, Steinberg, Deborah K., Anderson, Thomas R., Arístegui, Javier, Carlson, Craig A., Frost, Jessica R., Ghiglione, Jean-François, et al., 2010. Mesopelagic zone ecology and biogeochemistry – a synthesis. Deep Sea Res. Part II Top. Stud. Oceanogr. 57 (16), 1504–1518. https://doi.org/10.1016/j.dsr2.2010.02.018.

Roper, Clyde, Vecchione, Michael, 1996. In situ observations on Brachioteuthis beanii Verrill: paired behaviour, probably mating (cephalopoda, oegopsida). Am. Malacol. Bull. 12 (1/2), 55–60.

Rosa, Rui, Seibel, Brad A., 2010. Voyage of the argonauts in the pelagic realm: physiological and behavioural ecology of the rare paper nautilus, Argonauta nouryi. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 67 (7), 1494–1500. https://doi.org/10.1093/icesjms/fsq026.

Simon-Lledó, E., Bett, B.J., Huvenne, V.A.I., Schoening, T., Benoist, N.M.A., Jones, D.O.B., 2019a. Ecology of a polymetallic nodule occurrence gradient: Implications for deep-sea mining. Limnol Oceanogr 64, 1883–1894. https://doi.org/10.1002/lno.11157.

Simon-Lledó, E., Thompson, S., Yool, A., Flynn, A., Pomee, C., Parianos, J., 2019b. Preliminary Observations of the Abyssal Megafauna of Kiribati. Frontiers in Marine Science 6. https://doi.org/10.3389/fmars.2019.00605.

Simon-Lledó, E., Pomee, C., Ahokava, A., Drazen, J.C., Leitner, A.B., Flynn, A., Parianos, J., 2020. Multi-scale variations in invertebrate and fish megafauna in the mid-eastern Clarion Clipperton Zone. Prog. Oceanogr. 187, 102405. https://doi.org/10.1016/j.pocean.2020.102405.

Smith, Craig R., 1985. Food for the deep sea: utilization, dispersal, and flux of nekton falls at the santa catalina basin floor. Deep-Sea Res. Part A. Oceanographic Research Papers 32 (4), 417–442. https://doi.org/10.1016/0198-0149(85)90089-5.

Smith Jr., K.L., Sherman, A.D., Huffard, C.L., McGill, P.R., Henthorn, R., Von Thun, S., Ruhl, H.A., Kahru, M., Ohman, M.D., 2014. Large salp bloom export from the upper ocean and benthic community response in the abyssal northeast pacific: day to week resolution. Limnol. Oceanogr. 59 (3), 745–757. https://doi.org/10.4319/lo.2014.59.3.0745.

Soltwedel, Thomas, von Juterzenka, Karen, Premke, Katrin, Klages, Michael, 2003. What a lucky shot! Photographic evidence for a medium-sized natural food-fall at the deep seafloor. Oceanol. Acta 26 (5), 623–628. https://doi.org/10.1016/S0399-1784(03)00060-4.

Stevens, Kevin, Iba, Yasuhiro, Suzuki, Akihiko, Mutterlose, Jörg, 2015. Biological and environmental signals recorded in shells of Argonauta argo (cephalopoda, octobrachia) from the sea of Japan. Mar. Biol. 162 (October) https://doi.org/10.1007/s00227-015-2750-5.

Stockton, William L., E DeLaca, Ted, 1982. Food falls in the deep sea: occurrence, quality, and significance. Deep-Sea Res. Part A. Oceanographic Research Papers 29 (2), 157–169. https://doi.org/10.1016/0198-0149(82)90106-6.

Sulpis, Olivier, Jeansson, Emil, Dinauer, Ashley, Lauvset, Siv, Middelburg, Jack, 2021. Calcium carbonate dissolution patterns in the ocean. Nat. Geosci. 14 (June) https://doi.org/10.1038/s41561-021-00743-y.

Sweetman, Andrew, Chapman, Annelise, 2015. First assessment of flux rates of Jellyfish carcasses (Jelly-Falls) to the benthos reveals the importance of gelatinous material for biological C-cycling in Jellyfish-dominated ecosystems. Front. Mar. Sci. 2:47. https://www.frontiersin.org/article/10.3389/fmars.2015.00047.

Thurber, A.R., Sweetman, A.K., Narayanaswamy, B.E., Jones, D.O.B., Ingels, J., Hansman, R.L., 2014. Ecosystem function and services provided by the deep sea. Biogeosciences 11 (14), 3941–3963. https://doi.org/10.5194/bg-11-3941-2014.

Tsurumi, M., Mackas, D.L., Whitney, F.A., DiBacco, C., Galbraith, M.D., Wong, C.S., 2005. Pteropods, eddies, carbon flux, and climate Variability in the Alaska gyre. Deep Sea Res. Part II Top. Stud. Oceanogr. 52 (7), 1037–1053. https://doi.org/10.1016/j.dsr2.2005.02.005.

Volk, T., Hoffert, M.I., 1985. ocean carbon pumps: analysis of relative strength and efficiencies of in ocean-driven circulation atmospheric CO2 changes. In: Sundquist, E.T., Broecker, W.S. (Eds.), The Carbon Cycle and Atmospheric CO2: Natural Variation Archean to Present. American Geophysical Union, Washington D. C., pp. 99–110. Washington).

Zeebe, Richard, Wolf-Gladrow, Dieter, 2001. CO2 in Seawater: Equilibrium, Kinetics, Isotopes.