Current Biology

A vast icefish breeding colony discovered in the Antarctic

Graphical abstract

Antarctic icefish found brooding ~1,700 eggs per nest

50 cm

79% of 16,160 imaged nests occupied, the most extensive fish brooding colony discovered to date.

50 cm
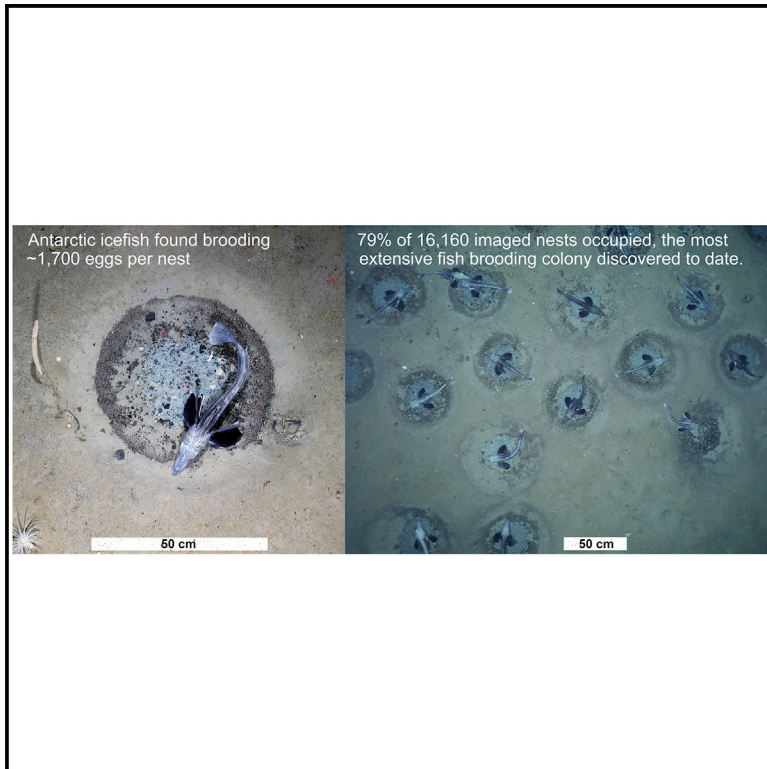
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In brief

In this report, Purser et al. describe the largest yet discovered fish breeding colony ecosystem. Found in the Weddell Sea, Antarctica and covering at least 240 km^2 of seafloor, *Neopagetopsis ionah* icefish brood eggs in ~60-cm-diameter nests at a density of 0.26 nests m^{-2}.

Highlights

- A vast icefish breeding colony has been discovered in the southern Weddell Sea

- Extremely high benthic biomass provides food for predators and scavengers

- Oceanographic conditions influence brooding habitat suitability for icefish

- Unique ecosystem supports establishment of a marine protected area (MPA)

CellPress

Report

A vast icefish breeding colony discovered in the Antarctic

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SUMMARY

A breeding colony of notothenioid icefish (*Neopagetopsis ionah*, Nybelin 1947) of globally unprecedented extent has been discovered in the southern Weddell Sea, Antarctica. The colony was estimated to cover at least ~240 km^2 of the eastern flank of the Filchner Trough, comprised of fish nests at a density of 0.26 nests per square meter, representing an estimated total of ~60 million active nests and associated fish biomass of >60,000 tonnes. The majority of nests were each occupied by 1 adult fish guarding 1,735 eggs (±433 SD). Bottom water temperatures measured across the nesting colony were up to 2°C warmer than the surrounding bottom waters, indicating a spatial correlation between the modified Warm Deep Water (mWDW) upflow onto the Weddell Shelf and the active nesting area. Historical and concurrently collected seal movement data indicate that this concentrated fish biomass may be utilized by predators such as Weddell seals (*Leptonychotes weddellii*, Lesson 1826). Numerous degraded fish carcasses within and near the nesting colony suggest that, in death as well as life, these fish provide input for local food webs and influence local biogeochemical processing. To our knowledge, the area surveyed harbors the most spatially expansive continuous fish breeding colony discovered to date globally at any depth, as well as an exceptionally high Antarctic seafloor biomass. This discovery provides support for the establishment of a regional marine protected area in the Southern Ocean under the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) umbrella.

RESULTS AND DISCUSSION

Neopagetopsis ionah breeding colony discovery

Nest building and egg guarding is a common parental care behavior of channichtyids, previously observed in isolation or in clusters of a few tens of nests, in the Weddell Sea and elsewhere.[1–5] Here, we report the first observations of a *Neopagetopsis ionah* (Nybelin 1947)[6] breeding colony (Figures 1A and 1B) where brooding was observed occurring simultaneously across tens of thousands of nests, arrayed over many square kilometers of seafloor (Figures 2A and 2B). *N. ionah* exhibits a broad, potentially circumpolar Antarctic and sub-Antarctic distribution. Benthopelagic adults have been recorded in the Weddell Sea,[2] Kapp Norvegica, Halley Bay, Vahsel Bay,[7] the Arctic Peninsula,[8] and the Ross Sea,[9] with pelagic juveniles sampled

from the Weddell Sea, South Shetland Islands,[10] and McMurdo Sound.[11] We identified 16,160 fish nests within an area of 45,600 m^2 of seafloor directly imaged by the Ocean Floor Observation and Bathymetry System (OFOBS)[10] camera sled, towed behind the research vessel *RV Polarstern*[12] during four survey station deployments made across the eastern flank of the Filchner Trough (Figures 1A and 1B; Video S1).

Breeding colony extent, fish nest form, and distribution

Four towed camera surveys were conducted from the eastern region of the Filchner Sill, up the eastern Filcher Trough flank, and onto the flat summit of the eastern Filchner Shelf (67-1, Figure 2B). The deepest and shallowest extents of the breeding colony were identified at 535-m and 420-m depth, respectively (Figure 2B; Table S1). All images collected between these two
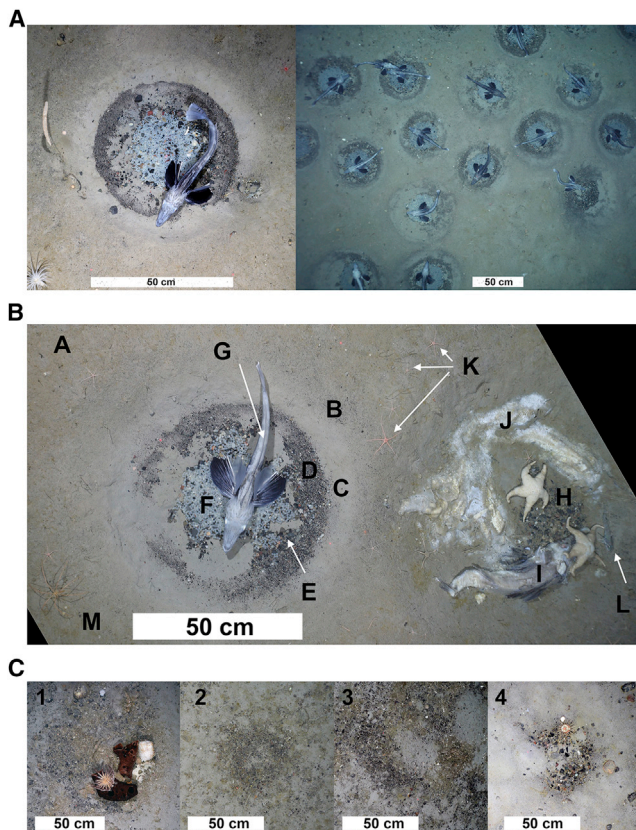
Figure 1. Seafloor images of the most expansive icefish breeding colony discovered to date

(A) Left: *Neopagetopsis ionah* in an active fish nest on the eastern flank of the Filchner Trough, 497-m depth. Each ~15-cm-deep nest has been shaped by removing the fine sediment and exposing numerous small stones, upon which the light blue eggs are laid. Right: dense array of active fish nests.

(B) Two fish nests, spaced ~15 cm from each other, imaged from the active nesting area of the Filchner Trough eastern flank. The left nest is in active use, whereas the right nest contains the remains of dead fish only. A: Surrounding seafloor with thin layer of phytodetritus visible. B: Faint rim of very fine black rocky material marks the extreme extent of the active fish nest. C: A ring of uniform gray upper sediments cut through by the nest structure forms the upper sides of each active nest. D: A ring of slightly coarser black rock fragments makes up the lower flanks of the active fish nest. E: The base of the active fish nest is made up of numerous rock fragments from a range of lithologies, presumably carried to the area by ice rafting from a range of Antarctic source lithologies. F: *N. ionah* eggs cover much of the rocky nest base layer. G: Adult fish commonly observed centrally placed within the nest. H: Nest containing dead fish in various states of decay. I: Recently deceased fish being fed on by a starfish. J: At least three additional adult fish carcasses covered with bacterial mat(s). K: Numerous ophiuroids in highest abundance within and surrounding nests containing dead fish. L: Small fish, potentially a scavenger. M: Pycnogonid of ~20-cm diameter, commonly observed in the vicinity of active nests. In this image, several *N. ionah* eggs seem to be visible below the pycnogonid.

(C) Unused nest arrays on the Filchner Sill and elsewhere in the Filchner Trough. 1: Station 26_7; various sessile suspension feeders occupy the center of nests. 2: Station 30_7; small sessile fauna use small rocks within the unoccupied nest as a substrate on which to settle. 3: Station 54_1; some infilling of the center of the unused nest with sediment and hydrodynamically trapped detritus. 4: Station 72_8; softer sediments render the edges of the unused nests less distinct, though the central nest floor is abundant with larger stone fragments. See Figure 1 for locations of stations referred to here.
See also Video S1, Table S1, and Figure S4.

depths (n = 2,145) indicated that active fish nesting was occurring at a remarkably consistent density throughout the breeding colony. Nests were circular and bowl-shaped, with a uniform diameter of ~75 cm, and a depth of ~15 cm. In distribution and form, this *N. ionah* breeding colony was reminiscent of the relative spacing and arrangement of freshwater bluegill (*Lepomis macrochirus*) colonies, though comprising of larger nests and fish.[13] Of the total 16,160 nests directly imaged by camera, 12,020 (79%) were under active use, containing either a fish and eggs or eggs alone, with the nesting fish absent. In nests containing eggs, an average of 1,735 eggs (standard deviation = 433) were present (Figures 1A and 1B). These egg abundances were ~25% higher than reported for this species in nests observed at the southern extreme of the Filchner Trough,[4] indicating potentially more favorable conditions for *N. ionah* toward the Filchner Sill than close to the Antarctic mainland, at the southern extreme of the trough.[4] A mean density of 0.26 active nests m^{-2} (standard deviation = 0.083) was observed, with a peak density of 1.49 active nests m^{-2} at 497-m depth (Figure S4). In addition to nests under active use, unoccupied nests, those containing fish but no eggs, and nests containing dead fish, were also quantified. 15% of nests were empty (0.06 empty nests m^{-2} [standard deviation = 0.015]), 0.25% contained fish but no eggs (0.001 fish occupied eggless nests m^{-2} [standard deviation = 0.002]), and 9% of nests contained at least one dead fish (0.04 dead fish nests m^{-2} [standard deviation = 0.013]) (Table S1).

A spacing of ~25 cm was common between nests in even the most densely populated areas, with no occurrences of direct physical contact between neighboring nests observed in any of the 2,145 collected images (Figures 1B and 3A). Individual nests were clearly differentiated from the surrounding seafloor by the absence of any detritus within the nests themselves, and by the smooth, uniform, exposed sediment of the upper section of the nest slopes. In the acoustic data collected, nest delineation was evident in the backscatter signals received up to 100 m ahead and from either side of the OFOBS device, indicating the sloped walls of each nest to present a strongly reflective acoustic surface (Figures 3A and 3B). Below the upper exposed slope, a circular ring of coarse-grained sediments was usually visible, partially covered by slipped sediments in some cases (Figure 1B). Underlying these coarse-grained sediments, the base of the nests generally comprised gravel and/or small pebble-sized rock fragments of various lithologies and coloration. The *N. ionah* eggs, where present, were clearly visible on top of this array of stony material. An adult fish was positioned directly above the center of 76% of the imaged nests (Figures 1A and 1B). Deposition of eggs on gravel is a known strategy employed by other Channichtyids to aid in maintaining aeration and cleanliness,[14] with the bowl-shaped depression form of the nests hypothesized to assist in keeping the eggs from being laterally transported out of the nests by benthic currents. Possibly, the tending fish could further assist in maintaining aeration by fanning the eggs, as has been observed in other nesting fish species.[15]

At depths deeper than 535 m and shallower than 420 m, the OFOBS imaged only occasional empty nests, and only for horizontal distances of ~100 m from the edge of the active breeding colony. At greater distances, no further nests were observed on
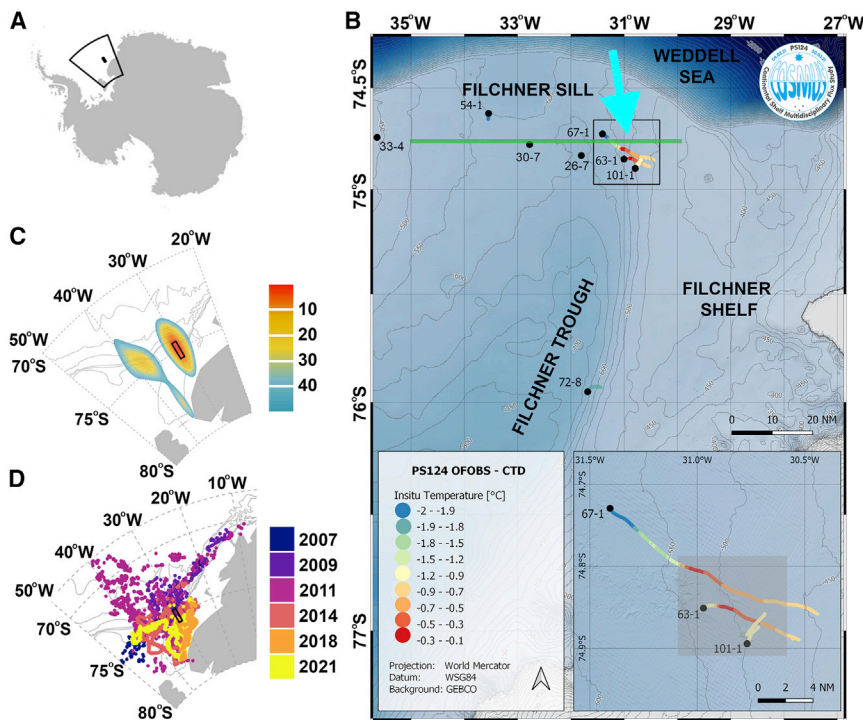
Figure 2. Location of *Neopagetopsis ionah* breeding colony, local seafloor temperature conditions, and Weddell seal behavior

(A) Box indicates area of study.

(B) Map showing Filchner Trough/Weddell Sea interface. Black box (and enlarged inset) defines the area within which the *Neopagetopsis ionah* breeding colony was observed at average density of 0.26 active fish nests m^{-2}. The colored trails indicate the bottom temperatures measured during the deployments. The direction of mWDW inflow is indicated with a blue arrow. The green line represents the cross-section of CTD measurements given in Figure 4.

(C) Weddell seal habitat utilization distributions (%). Values below 50% indicate the core areas of habitat use. The black box represents the area of the eastern Filcher Trough where active *N. ionah* nesting was observed.

(D) State-space modeled tracking data from 46 adult Weddell seals tagged between 2007 and 2021, with the black box again representing the area of observed active *N. ionah* nesting.

See also Tables S1, S2 and S3, and Figures S1, S2, and S3.

the Filchner Trough flank. Active nest use dropped from the consistent density of 0.26 active nests m^{-2} to 0.0 active nests m^{-2} very suddenly, with no gradual spatial decline in nest occupation evident when approaching the extremes of the breeding colony, therefore no edge predation effect was indicated, nor any gradient change in environmental suitability for active nesting.

Five additional OFOBS surveys were made at depths comparable to the active nesting area (gray box, Figure 2B inset), but at distances of up to 80 km. These surveys were made across the Filchner Trough sill to the west, the flat Filchner Shelf plateau to the east, and southward along the trough's eastern slope (Figure 2B). Similarly high densities of fish nest forms, though all empty of icefish and eggs, were observed during three of these survey transects (stations 26-7, 30-7, and 72-8), with occasional nests also imaged at Station 54-1 (Figure 1C). No *N. ionah* nests were imaged from any other OFOBS deployments made during the expedition elsewhere in the Southern Weddell Sea.[12]

Environmental conditions and productivity

Bottom water temperatures at the seafloor interface within the breeding colony area were measured to be −1.0°C to 0°C throughout all survey dives wherever active nesting was observed (Figures 2B, 4A, and S4). These temperatures were characteristic of the modified Warm Deep Water (mWDW). The steep continental slope of the southern Weddell Sea continental shelf is intercepted by numerous troughs, known to act as conduits through which the mWDW can flow upward onto the Weddell Shelf.[10] This topographically guided inflow varies seasonally and interannually in strength, duration, and exact course. Previous expeditions have observed a similar temperature distribution across the area,[16] dominated by an inflow of mWDW across the nesting location active during the COSMUS expedition. mWDW

water has a lower oxygen concentration than the surrounding Antarctic waters, at roughly 65%–75% air saturation (Figure 4B). Outside of the active nesting colony area (gray box, Figure 2B inset), bottom water temperatures were lower at −1.5°C to −2.0°C, with a greater oxygen saturation (>80% air saturation) (Figure 4B). Water column measurements clearly indicate that during the expedition, the mWDW intercepted the Weddell Trough shelf and passed directly over the active breeding colony.

Within the water column above the central Filchner Trough, flanks, and shelves, chlorophyll a (Chl a) and primary production (PP) differed in concentration within the water column above the central Filchner Trough, flanks, and shelves. The highest Chl a measured during the expedition was 1.36 ± 0.09 ug L^{-1} at station 30-7 (Figure 2B), with the regionally highest PP also measured at this station, at a depth concurrent with the Chl a maximum (18.31 ± 1.47 mgC m^{-3} d^{-1}). This station was situated in the bathymetric axis of the Filchner Trough. Chl a and PP decreased from this high toward the western (station 33-1, 0.53 ± 0.03 ug L^{-1}, 6.61 ± 1.03 mgC m^{-3} d^{-1}) and eastern Filchner Trough shelf summits (station 16-1, 1.11 ± 0.05 ug L^{-1}, 4.02 ± 0.55 mgC m^{-3} d^{-1}) (Table S2), indicating higher Chl a and PP levels in the waters above the active and inactive fish nesting areas than elsewhere in the area. Particle volumes across the Filchner Trough showed local mid-water maxima, resulting from particle retention at the density interface between High-Salinity Shelf Water (HSSW) and mWDW. Local maxima above the seafloor (including waters above the active nesting area) were co-located with saline bottom water and indicative of either lateral advection or local resuspension (Figure 4C). From four deployments of an "*in situ* camera" (ISC) system at ∼170-m water depth (Figure S1; Table S3), particle volumes of between 20–40 mm^3 L^{-1} h^{-1} were recorded across the Filchner Sill above the currently unused fish
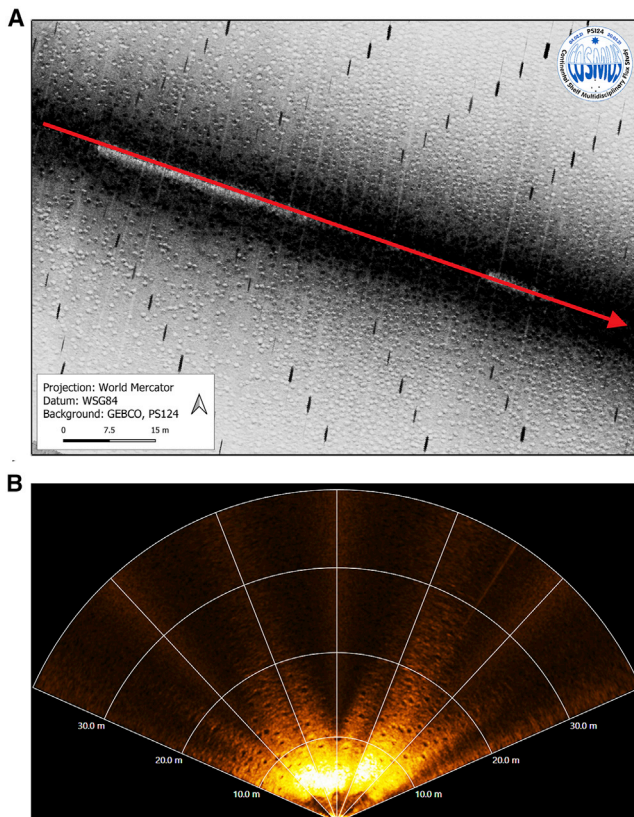
Figure 3. Acoustic data illustrating nest abundance
(A) 540-MHz georeferenced side scan sonar image. Continual and regular distribution of fish nests in the surveyed region of the east Filchner Trough, collected from 3.5-m altitude. The red arrow indicates the course of the OFOBS, which flew at 3.5-m altitude with a speed of 1.5 kts. The array of regularly spaced black lines on either side of the OFOBS course are acoustic interference in the side scan signal caused by the OFOBS DVL positioning system.
(B) Forward-looking sonar image. Fish nests from 2-m altitude ahead of the OFOBS device appear as dark dots.
See also Table S1.

nest areas (station 26-7 and 54-1, Figure 2B; and DF2 and DF3, Figure S1). Particle volume was comparable in waters above the southern fish nest site, not in active nesting use at the time of the expedition (station 72-8, Figure 2B; and DF4, Figure S1), but consistently lower, at around 15 mm³ L⁻¹ h⁻¹ above the southerly Filchner shelf seafloor where no nest forms were observed (station 68-5, Figure 2B;, and DF5, Figure S1). The majority of particles measured were less than 300 μm in equivalent spherical diameter. The strong increase in particle number during nighttime deployments combined with a decrease in mean size seen for DF4, and to a lesser extent for DF3, point toward aggregate fragmentation through zooplankton grazing. Spatial particle distribution based on Underwater Vision Profiler (UVP) profiles through the full water column revealed an increased particle load within the bottom layer of Filchner Trough waters, reaching maximum values of 0.6 ppm in the benthic waters of the eastern flank and 2.2 ppm in those of the central Trough (Figure 4C).

In summary, these observations indicate an increased particulate food source availability in Filchner Trough bottom waters,

potentially supporting a benthic food web utilized by the nesting fish, with upper water concentrations of particulates highest above the active and historically active fish nesting areas of the Filchner Trough and Sill. These upper water particulates could support juvenile *N. ionah,* known to migrate into overlying waters following hatching[17] by supporting the pelagic food chain, including small prey fauna utilized by *N. ionah,* such as the Antarctic silverfish (*Pleuragramma Antarctica*).[18–21]

Benthic and pelagic fauna associated with the active breeding colony

The epifauna community associated with the active breeding colony was characterized by low abundances and diversities, with the community being numerically dominated by brittle stars and star fish. Also conspicuous were large pycnogonids (>15-cm diameter), which were occasionally observed close to *N. ionah* eggs or egg husks observed outside of fish nests (Figure 1B), eggs potentially washed out by currents or fish movements, if not directly displaced by scavenging or predatory organisms. These community characteristics match the description of an undefined community for the Filchner region (group "C" sensu Pineda-Metz et al.[22]). Our observations, in combination with pending analysis of infauna, support the identification of the breeding colony area as a newly described benthic invertebrate community for the Weddell Sea, shaped by the presence of fish nests and the active guarding behavior of *N. ionah* adult inhabitants. In the vicinity of recently dead *N. ionah* individuals, ophiuroids, starfish, octopi, and various fish species opportunistically feeding were also observed (Figure 1B).

Though associated epifauna abundances were low, the locally elevated biomass, primarily made up of *N. ionah*, as well as the heavy reworking of the upper sedimentary structures by the nesting fish (excavation of ~20 liters of sediment from each nest during nest construction, or ~1.2 million cubic meters of excavated material across the surveyed area) may fuel the local benthic microbial loop[23,24] with the elevated carcass concentrations observed within the 0.04 dead fish containing nests m⁻² (standard deviation = 0.013)[25] regularly observed to be covered by microbial mat (Figure 1B), and provide new habitat for sessile invertebrates, elevating local blue carbon concentrations[26,27] following nest abandonment (see "Abandoned fish nests" section below). Although there is no published evidence that *N. ionah* is strictly semelparous, post-spawning individuals are known to have poor and dissipated body conditions,[3] which after several months of egg tending could result in high mortality rates.[28] The shallow slope angle of the eastern slope of the Filchner Trough and low abundance of drop stones or other naturally occurring hydrodynamic structural traps renders the biogenic depressions produced by nesting fish the most efficient local hydrodynamic traps. Across the collected image data, nests represent the most pronounced and abundant sites for accumulation of detritus on the seafloor, detritus originating from the elevated water column particulate concentrations (Figure 4C) and material from the breeding colony area, such as the occasionally numerous *N.ionah* fish carcasses observed within individual unoccupied nests (at least four carcasses appear to be present in the right-hand nest in Figure 1B). No occurrences of more than two live fish within a single nest were observed during the study, indicating that these higher carcass concentrations are likely the
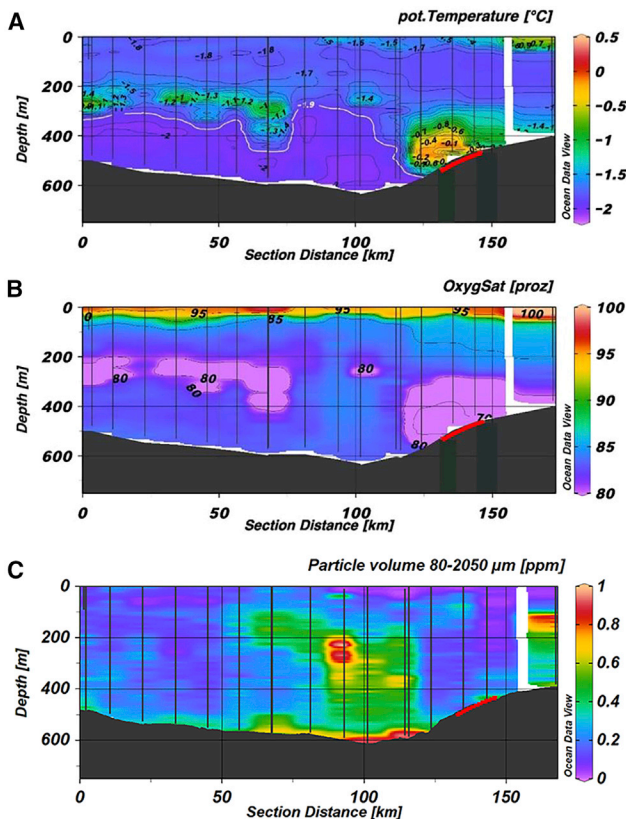
Figure 4. Temperature and oxygen saturation across the Filchner Trough during the COSMUS expedition

Data collected from transect line shown in green in Figure 1.

(A) Temperatures measured with the ship's CTD system and microCAT temperature sensor on the OFOBS.

(B) Calculated oxygen saturation levels. The RED bars on each plot mark the slope area covered by the active breeding colony.

(C) Abundance of particles 80–2050 μm ESD (equivalent spherical diameter). Increased numbers above the seafloor point toward either increased food source availability or local resuspension. Graph coordinates: (35.225°W 74.747°S; 29.421°W 74.921°S)

See also Tables S2 and S3, and Figures S1, S2, S3, and S4.

result of accumulation of carcasses after death, especially given the near neutral buoyancy of many notothenioid fish,[29,30] facilitating transport by even moderate currents. These carcasses act as foci for scavengers feeding on the fleshier fish tissues, with bacterial mats utilizing older remains (Figure 1B). Thus, these carcasses act as local food resource hotspots for other pelagic and benthic organisms. Dead female carcasses were previously observed close to individual fish nests at the extreme south of the Filchner Trough and hypothesized to be associated with the annual breeding cycle of the fish, providing food for vertically migrating scavenging amphipods.[2,4,31] Presumably, the higher nest density at this northerly Filchner Trough breeding site results in a greater periodic flux of carcasses for the local scavenging community (Table S3). During the current survey, only occasional amphipods were observed in association with carcasses. These typical Antarctic scavengers[32] were also observed at 170-m depth within the water column above the Filchner Trough, in images collected by the drifting sediment

traps. A temporally patchy distribution was recorded in the trap data, perhaps indicative of diurnal depth migration and benthic foraging. No amphipods were observed in the water column in the lower Chl *a*, lower productivity waters overlying the adjacent fish-nest-free areas of the Filchner Shelf (Tables S2 and S3).

Additional benthopelagic fish species observed in association with the breeding colony included individuals of other species of the Channichthyidae family,[33] and small individuals (<10 cm length) of unidentified species were observed feeding directly on icefish carcasses. Skates were also observed, occasionally directly observed to swim directly into occupied nests and underneath living, nest-guarding *N. ionah* fish, presumably with the intent of feeding on eggs.

In the pelagic and ice interface domains above the Filchner Trough, satellite tracking data of 46 Weddell seals (*Leptonychotes weddellii*, Lesson 1826[34]) instrumented with GPS and CTD systems across the Weddell Sea during the current and previous expeditions (2007–2021) was conducted.[2,12,35] Tracking results from the COSMUS expedition and throughout the previously instrumented years indicate that the highest seal densities and their greatest habitat use was recorded across the area above the *N. ionah* breeding colony area[2] (Figure 2B). At the time of the COSMUS expedition, the Weddell seals were in the post-breeding and molting phase of their annual cycle, and fattening up for the forthcoming winter. Weddell seals in the Ross Sea are known to forage periodically on *N. ionah*.[36] In the Filchner Trough area, they regularly dive to the benthos, and from the CTD data logged directly by the diving seals, these dives were primarily into mWDW waters, to depths associated with this newly discovered *N. ionah* breeding colony, offering an unprecedentedly high concentration of fish for possible predation. Logged dives to the surrounding fish-nest-free seafloor, into the cooler ice shelf water (ISW) were less numerous[37,38] (Figure 2C). The high philopatry exhibited by Weddell seals and tendency for pack-ice foraging seals to stay within the pack-ice, coupled with the potentially annually abundant *N. ionah* concentrations on the Filchner Trough flank, or historically, on the adjacent Filchner Sill, may well account for the integrated high abundances of seals logged across the area during 2007–2021. *N. ionah* has not been reported in the stomach or scat contents of sampled Weddell Sea seals in the past,[39,40] but these analyses are limited to the identification of the last meal consumed by an individual and the presence of well-preserved otoliths in the samples. Further, there is currently no dietary isotopic data published for this region. Other diving seal species, such as adult male elephant seals (*Mirounga leonina*) have also been reported from the Filchner Trough area, though in far less abundant numbers (Figures 2B and 1C).

Abandoned fish nest arrays across the Filchner Trough and Sill

Four OFOBS deployments made at distances of up to 80 km from the breeding colony, across the similarly deep Filchner Sill (station 26-7, 30-7), western Filchner Trough slope (station 54-1), and southerly Filchner Trough eastern flank (station 72-8) also imaged fish nest depressions on the seafloor (Figure 2B). Throughout these OFOBS deployments, nest abundances were roughly comparable to those observed across the active

breeding colony, but not a single nest was occupied by *N. ionah* or eggs, and all showed signs of age and a degree of degradation or colonization by other fauna. The gravel exposed during nest construction appears to have provided a substrate suitable for sessile organisms, such as tube dwelling polychaetes, bryozoan colonies, and sponges, to colonize following nest abandonment, thus enhancing local biomass and diversity (Figure 1C). The number of polychaete tubes and the size of bryozoan colonies increased from east to west, suggesting the empty nests found closer to the western flank of the Filchner Trough were likely to be the oldest surveyed during the COSMUS expedition. The deployment to the south showed a greater infilling of the nest forms with sediments than was observed at the abandoned northerly sill nests, indicating either a lower current velocity or increased particle flux. Similar observations of empty nests were made in the austral summers of 2013/14[2] and 2015/16 across these regions, though with cameras only covering small areas of seafloor (unpublished data).

Elevated concentrations of phytodetritus were observed within many of the abandoned nests, further indicating the effectiveness of the fish nest structures for the hydrodynamic trapping of material. This localized focusing of food is likely beneficial to colonizing filter and suspension feeders, such as anemones and sponges, observed within these abandoned nests (Figure 1C). The habitat engineering carried out by the nesting fish during nest formation therefore has an influence on local biogeochemical cycling for years following nest abandonment.

Temporal considerations

Data presented here from the COSMUS expedition indicates that a considerable area of the Filchner Trough seafloor was being wholly dominated at time of study by an active *N. ionah* breeding colony. Presumably, on hatching, large numbers of juveniles will enter the ecosystem, which raises important questions on the timing of processes which may operate in the breeding colony area and in surrounding and overlying waters. These questions include the following: (1) how and how often do icefish build individual nests? (2) Are nests reused in successive seasons? (3) How do adult fish behave prior to and post-hatching; do they remain with the eggs throughout the nesting cycle or forage? (4) What role and techniques are employed by predators and egg-eating fauna? (5) What immediate behavioral traits are exhibited posthatching by the juvenile fish? (6) How is mating and spawning conducted? (7) Do Weddell seals actively hunt for fish across the active nest site, and if so, how? In an attempt to address some of these questions, a camera and CTD mooring was assembled during the expedition and deployed at 500-m depth in an area of particularly high active nest abundance (1.47 active nests m^{-2}). Two LED light-and-camera systems were positioned 3 m above the seafloor, to twice daily image the benthos and lower water column for approximately 2 years. Recovery of the mooring and data will be made opportunistically by vessels servicing the Weddell Sea long-term oceanographic mooring array, ideally in 2023 or 2024.

Conclusions

Here, we report the first observations of what may well be a key breeding colony of regional significance in the life cycle of the icefish *Neopagetopsis ionah*, with millions of fish actively guarding egg-filled nests across many square kilometers of seafloor. These fish represent an abundant food resource for higher-order predators such as the Weddell seal, a species which appears to have been actively foraging in the colony area since at least the mid-2000s. In death, fish carcasses provide a food source for scavenging benthic communities, and likely also for pelagic scavengers. Sediment engineering during nest formation has likely influenced benthic biogeochemical processes by re-distributing sediments and providing hydrodynamic traps for the localized increased accumulation of settling organic matter and dead fish. On egg hatching, it is likely that juvenile fish released from this colony play an important role in the food web of the upper pelagic ecosystem, given that young *N. ionah* spend their early years closer to the sea surface and the ice water interface.[41] The locally high Chl *a* and PP measured in the upper waters above the Filchner Trough are indicative of an environment which would likely suit these young fish and their prey. Though the spatial correlation between the active breeding colony area and the mWDW inflow was tightly aligned at the time of the COSMUS expedition, there is uncertainty as to the variability in mWDW course seasonally.[42] The apparent age of the abandoned nests observed across the Filchner Sill and further south on the Filchner Trough eastern flank seems to indicate that the location of the ideal nesting habitat may change over time, or from year to year. Whether the course of the mWDW or another factor such as food availability is crucial in determining nest location suitability is unclear from this current study.

Subsequent research expeditions to the southern Weddell Sea are required to delineate the complete spatial extent of the *N. ionah* breeding colony, to assess whether the mWDW or high surface productivity play the more significant role in determining the most appropriate site for *N. ionah* nesting, and to better understand the local and potentially regional significance of this icefish nesting "metropole" for the species, for surrounding ecosystems and other fauna. We believe our discovery provides support for endeavors to protect the Weddell Sea from anthropogenic impacts by establishing a regional marine protected area under the Southern Ocean under the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR)[43] umbrella.

STAR★METHODS

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ACKNOWLEDGMENTS

AUTHOR CONTRIBUTIONS

A.P., L.H., L.B., E.W., and F.W. ran the OFOBS, collecting all acoustic, image, and positioning data. A.P. and L.B. characterized and quantified all nests imaged during the study. L.B. quantified egg abundances. L.H., L.B., and E.W. analyzed the OFOBS acoustic data. S.T., M.J., and H.H.H. provided the MicroCAT temperature sensor and collated the oceanographic data. H.B. and M.W. tagged the Weddell seals during COSMUS. M.W. integrated the new data with published data on seal activity in the area and analyzed it. C.M.F. and B.G. deployed the drift traps and analyzed the particle size and amphipod data. A.R. collected and analyzed the UVP5 particle data. F.K. and J.B. collected and analyzed the Chlorophyll *a* and primary production data. S.E.A.P.M., P.B.H., and A.P. analyzed the image and video data for fauna analysis. M.H. coordinated the benthic research program of the COSMUS expedition, in association with H.H.H, expedition leader. F.W. was group leader of the benthic imaging team and coordinated this study. A.P. prepared the manuscript with input and approval of all co-authors.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

One or more of the authors of this paper self-identifies as a member of the LGBTQ+ community.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Active *Neopagetopsis ionah* breeding colony images	This paper	https://doi.pangaea.de/10.1594/PANGAEA.932827
Abandoned *Neopagetopsis ionah* nest images	This paper	https://doi.pangaea.de/10.1594/PANGAEA.936205
Neopagetopsis ionah egg count data	This paper	Mendeley Data: https://doi.org/10.17632/xgg9mp77kv.1
UVP data	This paper	https://ecotaxa.obs-vlfr.fr/
Leptonychotes weddellii distribution data 2007-2011	Boehme et al.[35]	N/A
Leptonychotes weddellii distribution data 2014 onward	Nachtsheim et al.[38]	N/A
Software and algorithms		
CARIS HIPS and SIPS 11.3	TeledyneCARIS; v11.3	https://www.teledynecaris.com
R library - "argosfilter"	Freitas[44]	https://CRAN.R-project.org/package=argosfilter
R library – "foiegras"	Jonsen[45]	https://github.com/ianjonsen/foieGras
R library – "adehabitatHR"	Calenge[46]	https://cran.r-project.org/web/packages/adehabitatHR
Zooprocess	Gorsky et al.[47]	https://sites.google.com/view/piqv//
Ecotaxa / Ecopart	Picheral et al.[48]	https://ecotaxa.obs-vlfr.fr/
PAPARA(ZZ)I v2.8	Marcon and Purser[49]	https://github.com/PAPARA-ZZ-I/PAPARA-ZZ-I

RESOURCE AVAILABILITY

Lead contact
Further information and requests for video, image or sensor data relating to this paper should be directed to and will be fulfilled by the lead contact, Autun Purser (autun.purser@awi.com).

Materials availability
This study did not generate any new reagents.

Data and code availability
All data used in the current study is freely available. All still image data from the fish nest OFOBS dives and from adjacent areas of the Weddell Sea are available from the PANGAEA data repository (PANGAEA: https://doi.pangaea.de/10.1594/PANGAEA.932827 and PANGAEA: https://doi.pangaea.de/10.1594/PANGAEA.936205 respectively. Egg count data are available from Mendeley Data: https://doi.org/10.17632/xgg9mp77kv.1. UVP5 data are available at ECOTAXA: https://ecotaxa.obs-vlfr.fr/ on request. All acoustic, CTD and video data are available from the lead contact on request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Animals
The icefish *Neopagetopsis ionah* (Nybelin 1947)[6] was the primary focus of the study. Extensive images of the fish were collected with the OFOB[50] towed platform from a seafloor breeding colony on the eastern flank of the Filchner Trough, Weddell Sea, Antarctica (31°W, 74.8°S). No physical samples were collected, nor were any direct interactions with fish individuals conducted.

METHOD DETAILS

Research expedition overview
The COntinental Shelf MUltidisciplinary flux Study COSMUS expedition on *RV Polarstern*, Feb – Apr 2021, was an interdisciplinary expedition to the southern Weddell Sea, Antarctica, designated expedition PS124[51] (Figure 2a). As part of the benthic research

program, the Ocean Floor Observation and Bathymetry System (OFOBS)[50] was used to collect high resolution still images, HD video, forward and side scan sonar data from several meters above seafloor. The device was deployed 21 times during the expedition (Figure 2b), with four of these deployments revealing the partial extent of a vast notothenioid icefish (*Neopagetopsis ionah*) breeding colony, the most extensive such site discovered to date (Figure 1; Video S1).

The COSMUS expedition also investigated the relationships between ocean heat, mass transport, primary production, benthic community structure and marine mammal behavior in Antarctic shelf waters. From these additional research foci a number of environmental factors, flora and fauna within the surrounding and overlying waters were also investigated during the expedition. Here we present our observations on the distribution of fish nests and fish across this breeding colony, the potential role environmental and nutrient variables may have on determining colony location and on how these elevated fish stocks may play an important role for marine mammals within the Weddell Sea.

Seafloor imagery and bathymetry data acquisition

The Ocean Floor Observation and Bathymetry System (OFOBS) was used to survey the seafloor for this study, the full specifications of which can be found in Purser et al.[50] In summary, this towed platform was equipped with a 26 megapixel stills camera, high resolution video camera and three bathymetric sensors mounted on the OFOBS; 1) A BlueView M900 forward-looking sonar, 2) An Edgetech 2205 bathymetric side scan sonar and 3) an iXblue PHINS 6000 INS navigation system with integrated AML Micro-X sound velocity sensor, AML Micro-X pressure sensor and a Doppler Velocity Log (DVL) system, were installed to further aid with acoustics accuracy and navigation precision. The OFOBS can be towed by ice breaking vessels even in ice covered seas,[52] with the combination of video imagery and side-scan sonar enabling detailed small-scale topography mapping regardless of water depth.[53]

Throughout the PS124 COSMUS expedition all OFOBS deployments were conducted with a still image collection frequency of 1 image every 20 s. Additional manual images could be collected at the discretion of the observer. Each image collected was time-stamped, and position information assigned from the onboard navigation system.

OFOBS is traditionally towed behind a research vessel at a height above seafloor of 1.5 m, and a towing speed of 0.5 kts. This strategy was employed during the deployment that initially discovered the fish nests (Station 21-7). During subsequent deployments a higher flight altitude of 3 – 4 m was maintained, and a faster tow speed of 1.5 kts used. By increasing flight height and tow speed a greater area of seafloor could be inspected during a particular time frame, both optically and acoustically, though with a loss of seafloor image detail resolution. At these higher flight heights and speeds, the presence / absence of eggs within fish nests, and the presence / absence of living or dead fish could still be clearly determined from the image data.

The forward facing acoustic camera could pick up fish nests up to 30 m in front of the OFOBS clearly, with the side scan system allowed mapping of individual nests to distances of 50 m on either side of the OFOBS.

Bathymetric processing

The OFOBS sidescan high and low frequency data were processed using CARIS HIPS and SIPS 11.3 software in a UPS South WGS84 N,E (EPSG: 32761) projection. The data was processed to reduce movement created from the offset between the PHINS 6000 INS navigation system and the Edgetech DVL instrument mounted on the OFOBS, and to convert the raw data into usable products. The sidescan data on collection showed a distinct water column band directly under the OFOBS, which was removed and the imagery enhanced. Additionally, the bathymetry was cleaned for outliers or erroneous soundings.

Seafloor fauna qualitative analysis

The images collected with OFOBS during the COSMUS cruise were qualitatively assessed for fauna presence / absence across all deployments made within the Filchner Trough, and across the Filchner Sill and Filchner Shelf. Fauna observed were used to place the areas surveyed into the Weddell Sea seafloor ecosystem categories established during previous cruises to the region.[2,22,54] For the active fish nest area, an undescribed ecosystem, broad fauna categories were identified.

Seal distribution in the Weddell Sea

Previously collected adult Weddell seal (*Leptonychotes weddellii*) satellite tracking data from the Weddell Sea was collated from PANGAEA and freely available published online data. This data consists of individuals tracked in 2007 (n = 4), 2009 (n = 8), 2011 (n = 19), 2014 (n = 6), 2018 (n = 4) and 2021 (n = 5). The 2007-2011 data are published in Boehme et al.[35] (hereafter BAS data), the 2014 data are published in Nachtsheim et al.[38] (hereafter PS82), and deployment and immobilisation methods can be found in these articles. Data from 2018 (hereafter PS111) and 2021 (hereafter COSMUS) are unpublished; field methods are available in expedition reports from both 2018[55] and 2021.[51] All satellite trackers were deployed post-moult in February – March each year. Data analyses were done using R programming language.[56] We used satellite telemetry data from individuals whose tracks lasted longer than 10 days. The BAS data were not strictly movement data, but were data collected on the haul out behavior of individual Weddell seals[35] with locations labeled either that seals were hauled out on the ice, in the water at the surface, or diving. We only used points where the animals were in the water, although Weddell seals are known to haul out close to foraging areas.[57]

The inherent error that exists in satellite tracking data from 31 adult Weddell seals were filtered using a swimming speed cut-off of 3 m s^{-1} with the speed-distance-angle filter[58] in the R libraries "argosfilter"[44] and "foiegras"[45,59,60]. Data were then interpolated to a 24 h timestep using a random-walk model in R library "foiegras"[59–61]. Core habitat use (i.e., 50% kernel utilization distributions) was

then calculated for all individuals combined using the R library "adehabitatHR"[46]. H-values were selected using the *ad hoc* method.[62] Kernel densities were plotted for illustrative purposes over the fish-nests area.

Environmental parameter assessment

Hydrographic properties were measured with a shipboard Conductivity-Temperature-Depth (CTD) profiler and a Seabird SBE37 (microcat) CTD-recorder, mounted directly on the OFOBS frame. The CTD/Rosette was operated using the standard SeaBird SBE911plus setup, equipped with double sensors for temperature, salinity, and oxygen. The CTD data was checked for spikes manually, using the standard, SBE Data Processing-based, routines at the Alfred Wegener Institute. The accuracy of the lowered-CTD temperature data was better than $\pm 0.01°C$. The accuracy of the OFOBS-CTD temperature data was better than $\pm 0.1°C$. We used potential temperature and saturated oxygen from CTD stations along 75°S to relate the high density of fish nests to the presence of the oxygen-depleted modified Warm Deep Water (mWDW).

Additionally, for chlorophyll a and primary productivity analysis, water was collected with the AWI's new, state of the art, trace metal clean sampling infrastructure, including a Teflon CTD equipped with GoFlo bottles (12 L/bottle capacity). After collection, water was filtered onto glass fiber filters (GF/F, Whatman) and analyzed for chlorophyll a concentration on a Trilogy fluorometer (Turner Design) using the non acidification method.[63] To measure primary production rates, 0.05 MBq of ^{14}C-bicarbonate (Perkin Elmer) was added to 125 mL polycarbonate (PC) bottles and incubated in on-deck incubators at ambient temperatures and depth-appropriate light conditions. After 24 h, samples were filtered onto 0.2 mm PC filters (Whatman/GE), acidified with 250 mL of 1N HCl in order to convert any remaining inorganic bicarbonate to CO_2 and allowed to degas for 24 h prior to adding 5 mL of Ultima Gold (Perkin Elmer) scintillation cocktail and running them on a liquid Scintillation counter (Perkin Elmer).[64] Primary production rates were then calculated.[65]

QUANTIFICATION AND STATISTICAL ANALYSIS

Fish nest characterization and quantification

Still images were taken with the OFOBS timer every 20 s through each of the four OFOBS deployments. Of the four OFOBS dives carried out across the active brooding ground, fish nests were characterized and quantified for images collected during Station 63-1, 67-1 and 101-1. During these three deployments a flight height of 3 - 4 m was maintained, as well as a continuous towed speed of 1-5 kt, making the datasets collected during each deployment directly comparable. Images collected during the colony discovery dive (Station 21-7) were taken from a lower flight altitude, covered less seafloor with each image, and were made at a slower towing speed. These images were therefore excluded from the spatial analysis as they were not directly comparable with the other station datasets. Images from the 3 latter deployments were inspected using the PAPARA(ZZ)I v2.8 software application.[49] Using this software, the seafloor area covered by each image was determined from the 50 cm spaced laser points visible in all images. All nests observed in each image were logged as belonging to one of the following categories: 'nest, no fish', 'nest, at least one dead fish', 'nest, with eggs and no fish', 'nest, with eggs and one fish' and 'nest, with eggs and more than one fish'. The densities of each of these categories of nests was then computed for each deployment.

The three dives analyzed for nest quantification cut across an area of ~240 km² of the eastern flank of the Filchner Trough. This area of trough flank was exposed to mWDW, and of uniform slope angle, depth and aspect. Because of these uniformities, we hypothesized it as likely that this 240 km² of Weddell Sea seafloor to be populated by actively nesting fish, at comparable densities as observed directly by the OFOBS during the cross-cutting transects.

Egg abundance estimation

Average egg abundance was determined by counting individual eggs in images from 18 different nests randomly selected from close up images recorded during the initial breeding colony discovery dive (Station 21-7). The PAPARA(ZZ)I v2.8 software application was used to manually mark eggs on each image to compute a nest total.[49] The range of egg abundances was determined from the average of these measurements.

Particle size and volume distribution from sediment traps

Particle abundances below the euphotic zone at 170 m water depth over time were imaged with the *In Situ* Camera (ISC)[66,67] attached to a surface-tethered, free-drifting sediment trap array at 170 m water depth during four deployments (Figure S1; Table S3) . The ISC consisted of an industrial camera illuminated by an infrared backlight which imaged a water volume of 62.3 mL at a frequency of 0.2 Hz. Images were analyzed using Python and Fiji.[68] Particle contours were determined using a threshold value. Based on these contours, particles were cropped and saved in a separate folder. For analysis of organic matter particles, images featuring large swimmers (e.g., amphipods) were removed prior to analysis. The area of each particle was determined from particle contours and converted to equivalent spherical diameter (ESD) using the correct pixel to mm ratio. Particle volume was calculated from the ESD. Because of the resolution limit of the ISC, only particles > 107 μm ESD were included in further analyses.

The particle distribution in the water column along the Filchner Sill was assessed with the Underwater Vision Profiler 5 hd (UVP 5,[48] HYDROPTIC, France). The UVP 5 was mounted inside the CTD frame and operated in autonomous pressure mode. Images were acquired with a maximum frequency of 20 Hz during every downcast. The sampling volume was approximately 1 L, with a particle

quantification threshold of 2 pixels ($\sim$80 μm ESD). Post-processing was accomplished using the ImageJ based software Zooprocess[47] as well as the Ecotaxa platform and the Ecopart export tool.[69]

Water column amphipod abundance

Amphipods, where present, were recorded in the images captured by the ISC (Figure S1; Table S3). The times at which each amphipod was imaged was logged. The total number of images of amphipods captured by the ISC was 23 for DF2, 41 for DF3, 28 for DF4, and 0 for DF5. To avoid multiple-counting, amphipods were only counted as separate individuals if they appeared at least 10 min apart (upper estimate), or, for an even more conservative estimate, at least one h apart (lower estimate) in the image dataset (Table S3). In one instance, two individuals appeared in the same image. From the images alone it was not possible to tell individuals apart, and because amphipods exhibit swarm-forming behavior,[70] the true number of amphipods captured by the ISC during deployments DF2-DF4 were likely higher than the conservative estimates given here.