ECOLOGY

Abyssal hydrothermal springs—Cryptic incubators for brooding octopus

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Does warmth from hydrothermal springs play a vital role in the biology and ecology of abyssal animals? Deep off central California, thousands of octopus (*Muusoctopus robustus*) migrate through cold dark waters to hydrothermal springs near an extinct volcano to mate, nest, and die, forming the largest known aggregation of octopus on Earth. Warmth from the springs plays a key role by raising metabolic rates, speeding embryonic development, and presumably increasing reproductive success; we show that brood times for females are ~1.8 years, far faster than expected for abyssal octopods. Using a high-resolution subsea mapping system, we created landscape-scale maps and image mosaics that reveal 6000 octopus in a 2.5-ha area. Because octopuses die after reproducing, hydrothermal springs indirectly provide a food supplement to the local energy budget. Although localized deep-sea heat sources may be essential to octopuses and other warm-tolerant species, most of these unique and often cryptic habitats remain undiscovered and unexplored.

INTRODUCTION

Of all the hurdles faced by animals in the deep sea, cold may be the most challenging. Metabolism slows as temperature drops, and metabolic cold adaptation or thermal compensation (*1–3*) rarely allows cold-water ectotherms to approach the higher physiological rates of related warm-water taxa [e.g., (*4*)]. Consequently, growth, locomotion, reproduction, and similar integrative physiological processes are typically slow in deep- or cold-water species, often leading to delayed development, low birth rates, and long lives. Embryonic development, in particular, is sluggish in polar and deep-sea marine ectotherms; rates for species inhabiting waters near 0°C can be 4 to 33 times slower than related taxa from waters 10°C warmer [i.e., Q_{10} ~ 4 to 33; (*2*, *5*)]. In comparison, a similar 10°C warming for temperate or tropical taxa typically speeds development by only a factor of ~2 to 3.

How then do deep-sea animals ensure reproductive success? On a macroevolutionary level, egg-laying ectotherms in cold habitats, including octopods, generally have fewer, larger eggs than those in warm environments (*6*, *7*). Although factors responsible for this pattern of maternal investment are not fully understood, large eggs, along with their longer developmental times, are needed to produce large, well-developed hatchlings and juveniles capable of feeding and surviving in food-poor deep-sea habitats (*8–12*). Within species, microevolutionary processes and phenotypic plasticity can fine-tune these reproductive traits to maximize fitness (*7*). Ultimately, the growth and resilience of deep-sea populations are influenced by environmental and biological factors that affect rates of reproduction, recruitment, and adult survival.

Brood success, the proportion of eggs completing development and reaching a hatchling stage, depends on endogenous factors affecting embryogenesis and hatchling competence, as well as exogenous mortality sources (e.g., predation) that act independently to reduce the number of embryos surviving to hatching. First, embryos must be developmentally competent, that is, metabolically capable of completing normal embryogenesis from fertilization to a feeding hatchling stage. Octopod mothers must equip each egg with sufficient energy (i.e., yolk) to support the costs of embryonic development and early juvenile success, trading fecundity for egg size (*10*, *13*, *14*), but must also retain enough energy to sustain maternal care throughout incubation (*15*).

Temperature plays a pivotal role in brood success. Warming generally hastens the pace of embryogenesis and shortens the duration of incubation but also affects the health and survival of developing embryos or hatchlings, as well as the energetic cost of development (*16–22*). Second, developing embryos are exposed to risk of infection, injury, predation, or other mortality sources unrelated to their developmental competence. Brood survival, the proportion of eggs in a clutch avoiding external mortality factors, is a function of both the intensity of external mortality (i.e., % loss year^{-1}) and the duration of brooding. Thus, brood survival may decrease with lengthier incubation periods (*23*).

If brood success and subsequent population growth or resilience decline as brood duration lengthens, then selection should favor physiological or behavioral traits that shorten development (*24*). Considering the effects of warming on developmental rates, adaptations that enable breeding in localized warm spots may be a key to higher reproductive success for thermally tolerant deep-sea species.

Warmth appears to play an important role in reproduction for thousands of octopus (*Muusoctopus robustus*) found brooding among deep-sea hydrothermal springs on a hillock bordering Davidson Seamount off Central California (3175- to 3300-m depth, 35.518911°N, 122.64085°W). Male and female *M. robustus* migrate to these thermal springs known as the Octopus Garden

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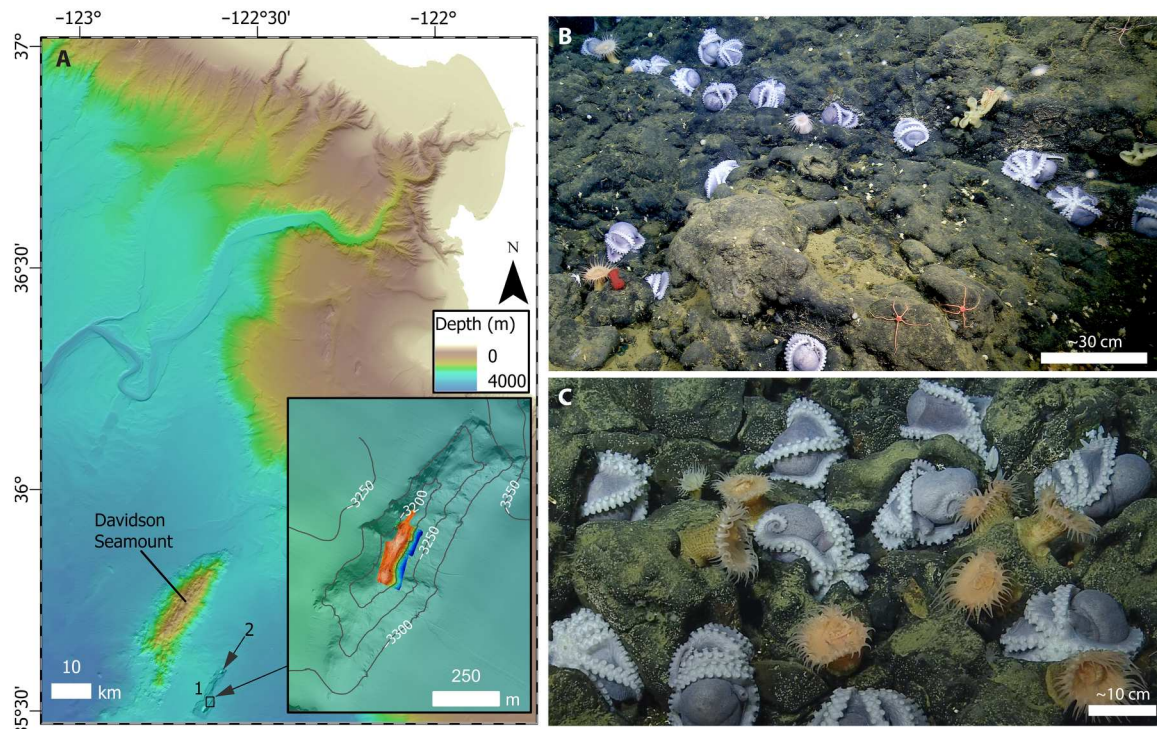*Corresponding author. Email: barry@mbari.org

Fig. 1. Location and appearance of the Octopus Garden. (**A**) Map of Davidson Seamount and hydrothermal springs/octopus nursery sites. (1) Octopus Garden. (2) Octocone. Inset: Detail of the Octopus Garden hillock. Contour lines in meters. Central area mapped in high resolution (2.5 ha) indicated by central depth-color section. (**B**) *Muusoctopus robustus* females nesting in cracks influenced by hydrothermal springs. (**C**) Octopus with anthozoan anemones that benefit from the *M. robustus* carbon subsidy.

[Fig. 1 and movie S1; (*25*)], where in addition to the effects of warming on development, breeding in aggregations may improve mate finding, reducing Allee effects observed in sparse populations (*26*).

Beyond their role in the thermal ecology of *M. robustus*, hydrothermal springs may indirectly boost the carbon budget for the local biological community. Most cephalopods, including male and female *M. robustus*, are semelparous—dying shortly after reproducing. Thus, immigration to the Octopus Garden is one-way; each *M. robustus* eventually adds to the organic carbon pool available to support the local bentho-pelagic community.

Here, we examine the influence of hydrothermal springs on *M. robustus* reproduction as well as ecological interactions and energy flow in the resident biological community; we propose the Octopus Garden as a case study for the eco-physiological influence of thermal springs on deep-sea biological communities. We use advanced undersea robotics, including remotely operated vehicles (ROVs), high-resolution subsea mapping technologies, and time-lapse imaging, to generate landscape-scale maps of bathymetry and seafloor imagery and to observe faunal behavior.

RESULTS

The physical setting: Temperature and oxygen variation at the Octopus Garden

Water temperature at the Octopus Garden varied over space and time. Temperature ranged from ambient (~1.6°C) to near 10.8°C in crevices and cracks bathed by shimmering waters (movie S2)

from hydrothermal flows. Waters surrounding developing embryos were warm ($\bar{x}$ = 5.1°C, σ = 1.3, N = 26) but dropped to near ambient within a short distance (<1 m). Evidence of hydrothermal venting at the Octopus Garden was minor above the seafloor (table S1). Temperature anomalies 5 to 10 m above the bottom (mab) were 0.02 (0.02) °C [$\bar{x}$ (σ)] and 0.07°C (maximum). Oxygen anomalies reaching −3 μmol O_2 kg^{-1} were observed up to ~5 to 10 mab but were within the range of oxygen variation measured during ROV dives in comparable areas lacking hydrothermal springs.

Temperature varied moderately and predictably over time; measurements logged every 5 or 60 min over deployment periods of 3 to 12 months ranged from ~3° to 10.8°C. Variation in temperature was aligned primarily with semidiurnal tides (Fig. 2), presumably due to the influence of tidal currents on hydrothermal flow or mixing with ambient waters. Similar periodicity was observed ~1 m from nests, though with only minor (~0.3° to 0.5°C) temperature fluctuations. No anomalous high temperature (>11°C) events were detected.

Oxygen was moderately low in spring waters (Fig. 2C), and conditions across the Octopus Garden reflected the admixture of ambient (~105 to 125 μM O_2) and diffuse vent (~50 μM O_2) fluid sources. Oxygen levels measured among eggs averaged 95.6 μM O_2 (σ = 13.5, N = 46).

M. robustus distribution and abundance at the Octopus Garden

M. robustus abounds at the Octopus Garden, particularly on slopes near the crest of the hillock (Fig. 3A). The 2.5-ha image mosaic from
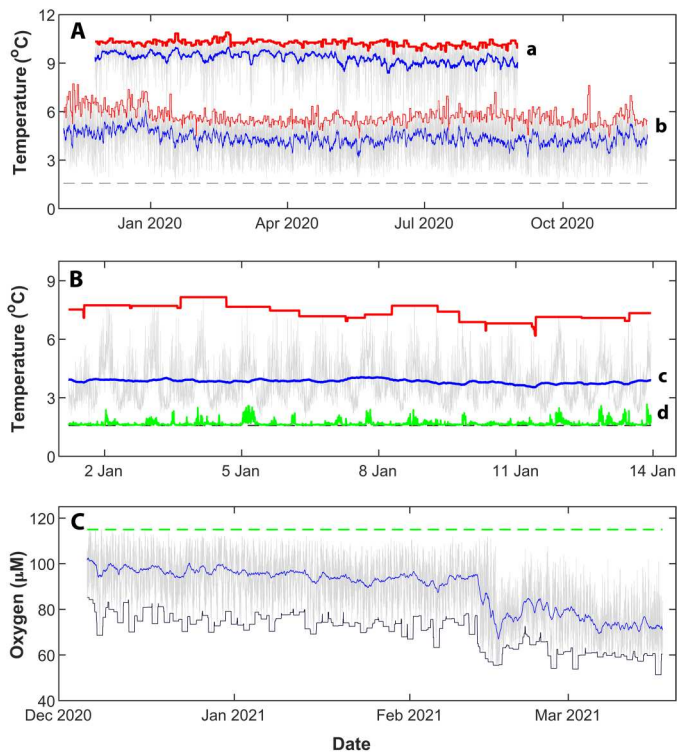
Fig. 2. Time series of temperature and oxygen in the Octopus Garden. (**A**) Hourly observations at two locations over ~1 year. (a) Sensor 1 in crevice with high observed temperature. (b) Sensor 2 near base of octopus nest. Red lines, running maximum temperature. Blue lines, running mean temperature. Dashed black line, ambient temperature. (**B**) Short-term (2-week) temperature measurements using a 5-min measurement interval. (c) Sensor in base of octopus nest. (d) Sensor (green line) positioned 1 m from *M. robustus* nest. Line colors as in (A). (**C**) Oxygen measurements in base of octopus nest. Dashed green line, ambient oxygen level. Blue line, running mean. Black line, running minimum O_2. Downward shift in oxygen near end of February thought to be caused by octopus repositioning the O_2 sensor.

the center of the Octopus Garden (Fig. 3B) revealed 5718 octopus (0.23 octopus·m^{-2}); the total population on the ~333-ha hillock (Fig. 1A) could easily exceed 20,000 individuals. Octopus have a patchy distribution (0 to 20 individual m^{-2}) with aggregations of brooding females nestled in warm spring waters (~5° to 11°C) flowing from depressions, crevices, and fractures (Fig. 3, B to D). Nests were generally found along the steeper slopes (Fig. 3A), and using the coregistered imagery and bathymetry, the mean slope of nest locations ($\bar{x} = 38.9°$, $\sigma = 17.9$, $N = 4707$) was somewhat steeper ($t = 17.7$, $P < 0.0001$) than the general Octopus Garden area ($\bar{x} = 34.8°$, $\sigma = 15.8$, $N = 1,048,575$).

The presence of male and female adults, developing eggs, and hatchlings of *M. robustus* (Fig. 4) indicates that the site is used exclusively for reproduction; we observed no intermediate-sized individuals or evidence of feeding. Most octopus (82%) were brooding females (e.g., Figs. 3, B to E, and 4D), with clutch sizes near 58 ($N = 2$). "Migrators" (3% of total) were individuals crawling across the seabed, presumably females searching for nesting sites or males seeking mates. Embryos in all stages of development (fig. S1) were seen during all seasons, indicating asynchronous spawning. Early stage eggs were large ($\bar{x}$ length = 30 mm, $\sigma = 3$ mm, $N = 43$) and

increased in length to 42 mm ($\sigma = 4$ mm, $N = 6$) in late stages (fig. S2). We occasionally saw hatchlings, which swam off into the dark; shrimp and anemones would attack hatchlings if they were nearby. *M. robustus* is semelparous and many senescent (14%) or dead (0.4%) adults, presumably postbreeding females and males, were observed in all seasons.

Resident faunal abundance at the Octopus Garden
A rich megafaunal assemblage is associated with *M. robustus*; cnidarians (anemones and corals), echinoderms (sea stars, brittle stars, and feather stars), crustaceans (shrimp and amphipods), gastropod snails, sponges, annelid worms, and fishes are common at the Octopus Garden (table S2). The abundance of *M. robustus* is significantly correlated with the abundance of nonoctopod megafauna ($R^2 = 0.54$, $N = 130$, $P < 0.0001$), and especially anthozoan anemones ($R^2 = 0.75$, $N = 130$, $P < 0.0001$; fig. S3).

M. robustus brood duration
Embryonic development by *M. robustus* at the Octopus Garden was complete in under 2 years, estimated from either the chronology of embryo developmental stages ($\bar{x} = 1.8$ years, $\sigma = 0.5$ years, $N = 30$; table S3) or female residence time ($\bar{x} = 1.6$ years, $\sigma = 1.1$ years, $n = 36$; table S4). This relatively short brood duration is very near the period (1.6 years; 95% confidence interval = 1.4 to 1.9 years) predicted for a temperature of 5.1°C, based on the global compilation of octopod brood periods versus temperature (Fig. 5). Although the incubation period for *M. robustus* in ambient waters is expected to be long, estimates are complicated by the uncertainty of extrapolating temperature versus brood period relationships beyond the range currently known for octopods. Using several approaches, we estimated its brood duration at 1.6°C to be at least 5 to 8 years (see Supplementary Text).

Potential effects of external mortality risk on hatch success
A survivorship model comparing brood survival versus the duration of exposure to external mortality (brood period) indicates that survival is expected to be reduced for species with long brood periods, particularly for higher rates of annual external mortality (fig. S4). Brood survival is high for species with short brood periods (e.g., <0.5 years), even under an external mortality of 25% $year^{-1}$. As brood period increases beyond a few years, brood survival declines markedly. Thus, assuming embryos are developmentally competent and can hatch normally, brood success may be influenced primarily by brood duration and the severity of external mortality.

Time-lapse observations of the Octopus Garden
We recorded 12,256 images of an aggregation of *M. robustus* and other megafauna at the Octopus Garden, at 20-min intervals over 6 months (3 March 2022 to 26 August 2022). Photographs captured various activities and behaviors of these octopus and their potential predators and scavengers. The dominant activity of most octopus visible in images (~12 individual) was brooding by females (Figs. 1 and 3 and movie S3). At least two females died before hatching of their clutch, after which predator-scavenger taxa (gastropods, shrimp, amphipods, and fishes) attacked developing eggs or their egg sheaths. Carcasses of postbreeding females were pushed aside by live nesting females, and eventually disappeared (perhaps removed by macrourid or ophidiid fishes), or were scavenged by various residents such as buccinid snails and large anthozoan
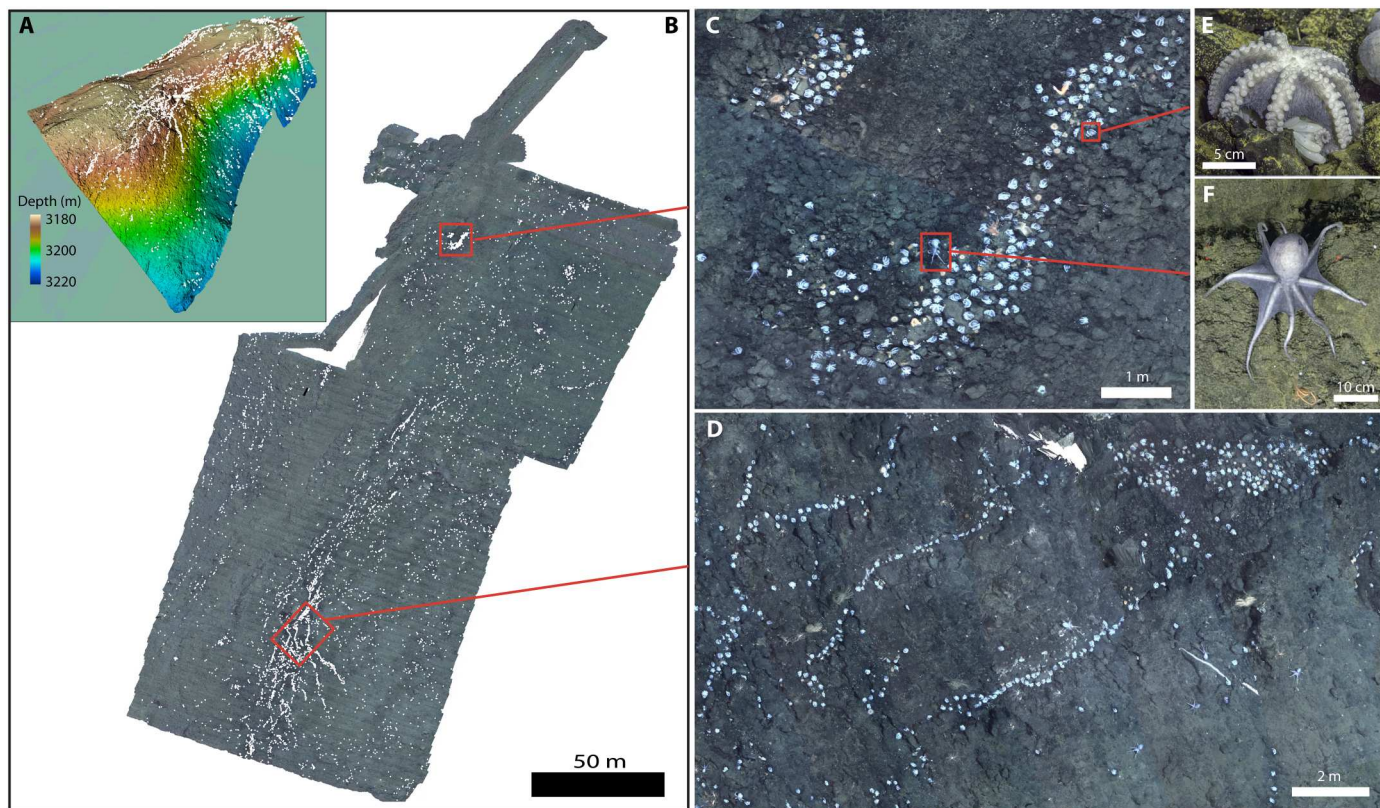
Fig. 3. Bathymetry and photomosaic of the Octopus Garden. (**A**) Color-gradient perspective view of bathymetry in the central 2.5 ha of Octopus Garden. White dots indicate *M. robustus* locations. (**B**) Map view of image mosaic of central Octopus Garden. *M. robustus* as in (A). (**C** and **D**) Close-up of portions of image mosaic showing aggregations of *M. robustus* and benthic megafauna in pools (C) and cracks (D). (**E**) Photograph of brooding *M. robustus* in typical inverted position similar to most octopus visible in (B) to (D). (**F**) Photograph of migrating *M. robustus* similar to several adults visible in (C) and (D). See methods for repositories of bathymetry and photomosaic datasets.

anemones. It is unclear whether unprotected late-stage embryos were consumed by predators or if scavengers (e.g., snails and shrimp) facilitated their hatching by opening their egg sheaths. Once a brooding site was vacant, it was reoccupied within 14 days. The photo series also captured instances of mating with males wandering through the setting and visitation by fishes when carcasses of *M. robustus* were present.

Benthic carbon subsidy from *M. robustus*

Biomass from the immigration and death of *M. robustus* at the Octopus Garden represents a substantial carbon subsidy to the local benthic community. For the 4871 live *M. robustus* identified in the 2.5-ha image mosaic and a population turnover of 57% per year (based on a brood period of 1.75 years), an estimated ~2784 die each year. Using a mean body mass of 406 g wet wt. (SE = 52.4, $N = 6$), the total energy content (E) of *M. robustus* individuals was estimated to be 1.08 MJ. The ambient flux of particulate organic carbon (POC) from surface waters to the Octopus Garden was assumed to equal the flux measured at a nearby long-term abyssal study site [(27); 8.1 mgC m^{-2} day^{-1}]. Converted to energy (28), the POC flux to the Octopus Garden equals 458 J m^{-2} day^{-1} (table S6). We observed no evidence of chemosynthesis (e.g., microbial films, suspended particulates, or known chemosynthetic invertebrates) and assumed that dying *M. robustus* individuals represent

the major C subsidy. Thus, the input of octopus biomass represents a carbon subsidy (Eq. 8) of 330.2 J m^{-2} day^{-1}, supplementing the ambient flux of organic carbon from surface productivity by 72%.

DISCUSSION
Reproductive benefits from warm-spring brooding

The remarkable aggregation of ~6000 *M. robustus* nesting at 3200-m depth among hydrothermal springs at the Octopus Garden suggests strongly that this breeding behavior provides a reproductive advantage. Selection should act most strongly on maternal factors that influence the survival of offspring to the point of nutritional independence (16). Like those of other cold-water octopods, the large eggs of *M. robustus* require a longer development time (29) that presumably increases the survival of hatchlings. Among many factors influencing reproductive success, mate finding, the effects of warming on development, and the exposure of eggs to external mortality risk during embryogenesis may be influenced by group nesting in thermal springs.

The potential rarity of mating encounters for sparsely distributed deep-sea populations is thought to favor aggregated breeding to increase mating opportunities (30), but its importance for *M. robustus* is unclear. We observed mating by *M. robustus* at the Octopus Garden during ROV observations and in time-lapse images (movie
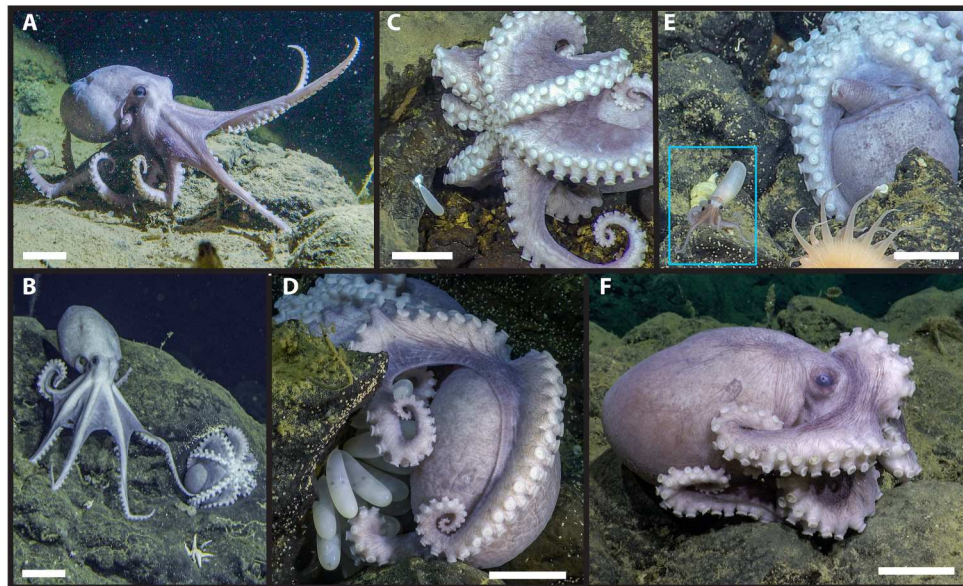
Fig. 4. *M. robustus* at the Octopus Garden. (**A**) Migrating female. (**B**) Adult male approaching/probing female during courtship. (**C**) Female with first, newly spawned egg of brood. (**D**) Brooding female with partially developed eggs. (**E**) Hatchling (light blue box). (**F**) Senescing postbreeding female. Scale bars, ~5 cm.
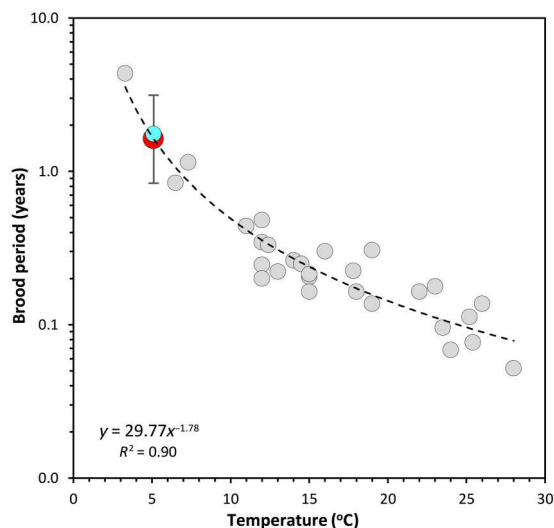

Fig. 5. Brood period versus environmental temperature. Gray dots represent octopus species worldwide (table S5), fit to a power function [$BP = 29.77*(Temp.)^{-1.78}$, $R^2 = 0.90$], where BP represents brood period. Red and blue dots (overlapping) indicate the predicted (1.7 years) and observed (1.8 years) BP, respectively, for *M. robustus* at the mean nest temperature (5.1°C) in the Octopus Garden. Error bars shown are 95% confidence limits for the predicted brood period.

S3), but mating encounters are not likely to be restricted to nesting areas. *M. robustus* is generally rare in the region outside the Octopus Garden), but multiple individuals have been seen near deep-sea food falls (*25*) where mating would presumably be common.

Brood temperature plays a crucial role in octopod embryogenesis and hatchling competence. Across a species' natural temperature range, octopod embryogenesis is generally faster in warmer waters

(*18*, *19*, *21*, *22*, *31*, *32*), though faster development is not necessarily an indicator of normal development or high hatching success. Warming, if stressful, can result in a collection of developmental setbacks including a reduced percentage of embryos completing embryogenesis (reduced hatch survival) (*19*), premature hatching (*21*), smaller hatchling size (*21*, *31*), reduced hatchling yolk reserves (*22*, *31*) and lower hatchling survival (*19*, *20*). On the other hand, warming may be beneficial if brooding occurs near a species' temperature optimum. For example, warming from 13° to 16°C for *Octopus tehuelchus* produced larger hatchlings, despite a shorter brood period. Hatchlings from the cooler incubation temperature were smaller but had larger internal yolk reserves (*18*). Larger size and greater yolk reserves can each be beneficial; larger hatchlings are more capable foragers as early juveniles, but larger yolk reserves provide a buffer against starvation while learning to feed or surviving periods of low food availability (*18*).

Beyond its shorter brood period, we have few clues concerning the effect of warming on *M. robustus* embryogenesis, however, scant observations from ROV observations and time-lapse images suggest that broods at the Octopus Garden produce healthy, capable hatchlings. In two nests visible after the death of the brooding female, we found ~40 large, late-stage embryos appearing very close to hatching; if so, this indicates a potential hatch success of >70% (original broods ~55 eggs), comparable to the highest hatch percentage observed for *Octopus maya* eggs incubated under a range of temperatures (*19*). If thermal stress leads to several concurrent developmental symptoms, then the high hatch percentages in these nests suggests that other developmental traits were normal (e.g., large size, high hatchling competence).

The effects of warming on the energetic cost of embryogenesis and its influence on energy allocation by females among eggs, fecundity, and somatic tissues to support brooding are not known for *M. robustus* but may be important if they affect reproductive success. The cost of embryogenesis is the product of embryo metabolic rate and the duration of embryogenesis. Warming raises

metabolic rates and shortens brood periods and can also alter total energy costs, depending on the temperature sensitivities of metabolism and embryogenesis (17). If embryogenesis is more sensitive to warming than metabolic rate (i.e., developmental efficiency increases), then the total energy required for development may decrease in warmer waters. Conversely, energy needs may rise if efficiency decreases.

Eggs, when spawned, have a finite energy supply (yolk), and temperature variation can affect embryogenesis or the condition of the brooding female. Under optimal conditions, normal, presumably large hatchlings use the remaining internal yolk reserve to support their survival and bridge the transition to nutritional independence. On the other hand, eggs developing under suboptimal temperatures or with insufficient yolk stores may fail during embryogenesis or emerge as smaller, less competent hatchlings. For brooding females, the energy to support maternal care may be shaped by poorly known factors such as feeding success before nesting, reproductive energy allocation, or the energy required to support their higher metabolic rates in warm springs. Our observations of the senescence and death of some brooding females before brood hatching (movie S3) suggest that they were weakened by starvation and had too little energy to complete brooding. Predator/scavenger species (e.g., snails and shrimp) attacked developing embryos soon after maternal care ended, though many may have hatched unscathed. Although the fate of these unprotected broods is unclear, failure of maternal care may have affected their survival.

Apart from energy concerns, the shorter brood period for *M. robustus* in thermal springs at the Octopus Garden can have profound effects on brood success and population growth for *M. robustus*. If embryos are developmentally competent in warmer waters (i.e., energy concerns are minor and embryogenesis and hatching are expected to be normal), then mortality due to external risk, rather than endogenous metabolic processes, may be the major source of variation in brood success. Brooding females provide maternal care, shielding embryos from predation, injury, infection, or other risks (33). If embryo mortality due to external factors is nonzero and persists throughout development, then brood survival should decrease with longer brood periods or with higher mortality risk. Consequently, exposure to exogenous risk is brief for species with brood periods of days to weeks, resulting in presumably low embryo mortality. In contrast, the impact of external mortality risk on brood survival may be paramount for octopods in cold waters with years-long incubations, even under low annual rates of mortality.

Globally, brood periods for octopuses vary logarithmically with temperature (Fig. 5), but brood duration for most deep-sea or polar species are unknown and expected to be quite long (34). *Graneledone pacifica*, a northeast Pacific octopod inhabiting waters near 3°C, has the longest known brood period for any animal, exceeding 4 years (35). Whether *M. robustus* nests in ambient (1.6°C) waters anywhere in its range is unknown, but its expected brood period would exceed that of *G. pacifica* by at least several years, increasing the potential impact of external mortality sources on brood survival. The actual mortality risk for *M. robustus* from predation or other external factors during development is unknown but is nonzero; brood predation has been observed in other octopuses [e.g., (36)] and our observations of *M. robustus* during ROV dives and in time-lapse images at the Octopus Garden show that several taxa (anemones, shrimp, and snails) will attack developing eggs and hatchlings. Assuming that embryogenesis and hatchling conditions are normal regardless of brood duration, then a shorter brood period should increase reproductive success, particularly as external mortality risk increases.

Despite the apparent reproductive success of *M. robustus* at the Octopus Garden, nesting in warm springs is risky. Once laid, eggs are immovable and exposed to potentially lethal variation in environmental conditions. Brood failure is likely unless environmental conditions are suitable to embryos throughout nearly 2 years of incubation. Observations of a congener (*Muusoctopus* sp.) brooding in hydrothermal springs off Costa Rica (37) found only undeveloped eggs, perhaps from thermal or hypoxic stress, even though environmental conditions were similar to the Octopus Garden. The mild warming and apparent long-term temperature stability at the Octopus Garden (Fig. 2) may be critical to hatch success.

Adaptation to warm spring brooding

Deep-sea octopuses that nest on the seafloor require exposed rock surfaces for egg laying (38). *M. robustus*, after spending much of its life foraging over the muddy abyssal landscape, finds its way to relatively rare rocky habitat on seamounts to reproduce, resulting in localized breeding groups [e.g., (39)]. Aggregation in rocky areas, with or without thermal springs, may have influenced reproductive success by enhancing mate finding (40, 41). However, not all rock surfaces are suitable; even rocky outcrops on seamounts are often covered with a veneer of sediment unsuitable for egg attachment. Currents sweeping over the knoll housing the Octopus Garden, weak flow from hydrothermal springs, and perhaps also the nesting behavior of *M. robustus*, act to resuspend and sweep away fine sediments to maintain open space. Whether the use of thermal springs by *M. robustus* arose in part from the availability of suitable nesting space or the ancestral affinity of enteroctopodids for warm brooding sites (42) is unknown.

Octopods have several traits that may have facilitated the exploitation of thermal springs by *M. robustus*. On the basis of temperature measurements and ROV observations, *M. robustus* clearly chooses warm nest sites, positioning eggs in warm locations using behavioral thermoregulation, similar to ectotherms worldwide (43). Physiological plasticity allows at least some octopuses to adjust their metabolism across a broad temperature range. For example, *Octopus vulgaris* exhibits up to a 5× range in brood period across ~10°C (44), though warmer temperatures may compromise hatchling competence. Rapid development of *M. robustus* embryos in warm waters (~3° to 10°C) indicates similar developmental plasticity. Chemoreception is also well developed in cephalopods (45), and waterborne cues from hydrothermal springs and conspecifics may act as beacons for migrating *M. robustus*.

Nesting in localized deep-sea warm spots may be common for local *M. robustus* populations, but it is unclear whether this pattern is consistent across the metapopulation. Is *M. robustus* an obligate hydrothermal spring nester? In addition to the Octopus Garden, thousands of *M. robustus* brooding under very similar conditions were found at hydrothermal springs ("Octocone") only 8 km northeast of the Octopus Garden [Fig. 1 (25)]. Nesting females have also been observed along the flanks of hydrothermal vents, though no temperature measurements were performed (46). We found no reports of *M. robustus* brooding in areas distant from deep-sea heat sources and could not find individuals nesting in ambient waters at the Octopus Garden. Whether *M. robustus* requires warming for

brooding is unclear; too little is known concerning both the distribution of *M. robustus* and the abundance of hydrothermal springs.

Benthic production fueled by octopus carbon subsidy

As a nexus for *M. robustus* reproduction, hydrothermal springs catalyze a carbon subsidy for the resident benthic community, adding octopus biomass totaling ~72% of the ambient carbon flux from surface waters. This higher food input to the community supports an assemblage of benthopelagic invertebrates and fishes richer than the relatively depauperate benthic community distant from breeding grounds. Carcasses of *M. robustus* are consumed by species ranging from benthopelagic fishes (e.g., Macrouridae and Ophidiidae) to small crustaceans [Decapoda (e.g., shrimps) and Peracarida (e.g., amphipods)] and undoubtedly by a resident microbial assemblage. The feeding activities of these direct octopus scavengers, in turn, redistribute (as smaller particles) and repackage (as fecal and dissolved materials) octopus carbon for a broader trophic assemblage. Not unexpectedly, the abundance of *M. robustus* across the Octopus Garden was correlated with the densities of other invertebrates (fig. S3). Anthozoan anemones, direct predators and scavengers of *M. robustus*, are commonly positioned within centimeters of nesting octopus (movies S1, S2, and S3, and Fig. 1C) and hydrothermal fluids; they too may benefit from warmer temperatures enabling more rapid movement and higher growth rates in conjunction with the subsidy provided by *M. robustus*.

Given the generally low food availability in deep-sea ecosystems, carbon subsidies associated with abyssal aggregations like *M. robustus* (particularly semelparous species) should have larger impacts on local energy budgets than in energy-rich shallow or terrestrial ecosystems. Breeding aggregations worldwide generate food subsidies for local biological communities (47), but few such carbon subsidies are known from deep-sea environments [e.g., (48)]. The C subsidy at the Octopus Garden is proportionately large because abyssal habitats are food poor. A subsidy of the same biomass would represent only ~17% of surface productivity exported to 200 m on the continental shelf and well less that 1% of kelp production [~1 kgCm^{-2} year^{-1}; (49)] in nearshore macroalgal ecosystems.

Population growth and thermal spring brooding

Why do not more deep-sea species brood in hydrothermal springs? Adaptations that favor brooding in deep-sea hydrothermal springs depend on a range of physiological and environmental factors. Assuming that thermal springs are common, species' phenotypic plasticity, their scope for adaptation, and physiological trade-offs may favor brooding in hydrothermal springs. If brood survival represents a key life-history bottleneck for population growth, shorter incubation times in warm waters may increase brood success and elevate population fitness. Nevertheless, the transition from brooding in ambient waters to aggregating in warm sites may be complex.

Conversely, brooding in thermal springs may result in marginal or negative fitness benefits for many taxa. Shifting a species' thermal window of performance (50) to improve embryogenesis in warmer waters may drive physiological trade-offs (51) that impair function at ambient temperatures, compromising aerobic activities that contribute to growth, survival, and reproduction for juveniles and adults. If the potential fitness gain from a shorter brood period is small (i.e., brood survival is not a strong driver of population growth), then warm brooding may have little or no value. For example, *G. pacifica* could seemingly benefit from shortening of

its record-holding brood period, yet its reproductive mode is successful as is. Adaptations favoring brooding by *M. robustus* in thermal springs or similar localized warm sites might have eliminated their ability to nest in ambient waters, vastly limiting where they can reproduce.

Hydrothermal springs: Common, but cryptic?

Early studies of heat flow through oceanic crust focused on ridge crests where venting of hot fluids was expected. Anomalously warm temperatures and elevated optical backscatter in hydrothermal plumes reaching hundreds of meters from venting sites helped focus the search, culminating in the discovery of hydrothermal vents in the 1970s (52); the near-simultaneous discovery of marked vent-associated biological communities was a surprise (53, 54). More recent research on heat flux through old oceanic crust (>1 Ma) on ridge flanks indicates that most heat must move through channelized low-temperature (i.e. above ambient) flows along faults and vertical conduits (55), particularly near seamounts and other rough seabed topography (56). Exploration over seamounts and ridge flanks, though limited, supports this hypothesis (57–59). Unlike ridge-crest vents where vigorous flows of hot, chemically rich fluids fuel chemosynthetic biological communities, ridge-flank systems are characterized by weaker, cooler flows with little suspended material and lack mineral chimneys or massive chemosynthetic communities (59), making them difficult to locate with water column surveying techniques that proved useful in ridge-crest systems.

How then, to search for deep-sea hydrothermal springs and octopus gardens? The deep-sea floor is immense and decisions concerning where to apply pin-point exploration systems (e.g., ROVs and human-occupied submersibles) depend on geophysical surveys providing detailed seabed bathymetry, bottom characteristics (e.g., hard rock and sediment), and sub-seabed fluid pathways that may be linked to seafloor fluid discharge. On a large scale, marine sediments sufficiently thick to redistribute crustal heat loss through advective heat transport may result in fluid venting on ridge-flanks where draped sediments are interrupted along faults, fracture zones, hot spots, or other structures creating conduits for fluid expression. Each of the three known deep-sea octopus nurseries at hydrothermal springs are on small basaltic outcrops with similar outcrop-sediment abutments along the eastern Pacific margin (57–60). The distribution of such conditions across the world ocean depends in part on basin-scale processes. For example, the geologic settings produced by slow-spreading centers of the Atlantic differ from those in the medium to fast-spreading centers in the Pacific. Outcrops akin to the Octopus Garden site exist in the Atlantic but are less common than observed in the Pacific. Nevertheless, deep-sea hydrothermal springs with low-temperature fluid discharge are far more common than currently known, discharging a volumetric flux of warmed, altered seawater to the oceans that is comparable to the global riverine fluid discharge (61). Considering the existing regional-scale geophysical and chemical surveys and the distribution of seamounts where exposed basaltic crust is possible (56, 62, 63) there must be many thousands of ridge-flank hydrothermal systems that remain to be found.

Once narrowed to a likely geologic setting, high-resolution bathymetry and sub-bottom profiling may indicate sites for focused exploration using autonomous, remotely operated, or

human-occupied vehicles. Near-bottom surveys of temperature and oxygen may detect the hydrothermal plumes from thermal springs, though sensors may need to be within ~5 mab considering the limited range of temperature anomalies detected at the Octopus Garden. High-resolution imaging is likely to be equally or more important; without their high densities of light-colored octopus, cryptic venting of cool to warm fluids at the Octopus Garden, Octocone, and Dorado hydrothermal springs (14, 26, 45, 46) would have gone unnoticed. Only upon approaching brooding octopus for a close-up view did observers see the startling shimmering boundary of ambient and warm venting fluids (movie S2). Once found, detailed observations of faunal assemblages in relation to local environmental conditions can commence. For example, the co-registered bathymetry (5-cm resolution) and stereo imagery generated by the Low Altitude Survey System (LASS) (fig. S5) at the Octopus Garden highlighted the tight alignment of octopus nests with crevices and fractures throughout the 2.5-ha survey area (Fig. 3).

Brooding aggregations of octopuses or other species may occur in only a subset of hydrothermal spring locations. Key habitat features for *M. robustus* include exposed rock surfaces (manganese crusts are often used as nest sites) and warm (ca. 3° to 10°C) seawater. We assume that surrounding fluids must not be toxic (e.g., low HS⁻) or have physiologically stressful oxygen or pH levels. Temperature stability is likely to be critical; mean temperature in nests must be above ambient to accelerate development but cannot exceed a threshold (currently unknown) for hyperthermic stress, even for short periods. The long-term stability of ridge flank heat flow (64) may result in the near-permanence of suitable warm brooding sites, their dependability perhaps enhancing the fidelity of multiple generations of octopods. Other characteristics may be secondary; abundant crevice space may buffer temperature variability by retaining hydrothermal fluids or provide protection from potential predators. Large abyssal fishes [cusk-eels (Ophidiidae) and grenadiers (Macrouridae)] were seen foraging among nesting *M. robustus* in time-lapse images, though it is unclear if they were attacking live females and embryos or scavenging decaying animals. We also observed pits thought to be created by foraging beaked whales (*Berardius bairdii*) on the muddy seafloor, though no evidence of whale predation was detected near thermal springs.

The Octopus Garden, Octocone, and similar octopus nurseries merit consideration for protection as vulnerable marine ecosystems [VMEs; (65)] as these densely populated brooding sites are reproductive hot spots for local octopus populations (66). Both sites lie within the Monterey Bay National Marine Sanctuary, which affords some protection from disturbance. Fishing, deep-sea mining, and other human activities are currently a minor threat; deep-sea mining to harvest the modest ferromanganese crust on basalt outcrops at the Octopus Garden seems unlikely. Commercial fishing is permitted in much of the Sanctuary (including the Octopus Garden) but rarely exceeds 1500-m depth, shallower than the known depth range of *M. robustus* at the Octopus Garden or its abyssal foraging areas (~2300 to 3600 m). However, their protection from these threats in the future is uncertain. To date, no octopuses have been designated as VME indicators by any North Pacific Regional Fishery Management Organizations, though until recently, these dense octopus nurseries were unknown.

Ridge-flank thermal springs and other localized sites of low-temperature warming in deep-sea environments seem likely to play an important and largely undiscovered role in the ecology and evolution of deep-sea populations, as well as the dynamics and energy flow of deep-sea benthic communities. As exploration and sampling of deep-sea habitats expand, reports of animals exploiting localized warm sites are becoming common. In addition to our observations, nesting octopuses have been reported near localized, warm deep-sea habitats in several areas along the Eastern Pacific Margin, and rapid development has been suggested for cephalopods in warm anomalies near methane seeps or hydrothermal vents. Similarly, deposition of skate egg cases in diffuse hydrothermal flows (67) and active methane seeps (68), or group-nesting in warm anomalies by abyssal Antarctic icefish (69), are behaviors that accelerate development and presumably benefit the population dynamics of species drawn to deep-sea warmings.

The sea floor over 2 km deep covers roughly 60% of Earth's surface and outside the ocean science community is generally thought of as a vast, largely homogeneous frontier. Vast indeed, efforts continue to map large areas where we have only grainy views of the seafloor and scant information concerning potentially vital heterogeneities and anomalies—warm spots, seamounts, vents, and others. Most of these "island" habitats remain unseen and unknown, including their potentially large influence for deep-sea populations and broad indirect influence of the structure and function of deep-sea ecosystems. Precautionary stewardship of poorly known abyssal resources and continued exploration of unknown deep-sea environments are essential to discover and protect habitats that may play disproportionately large roles in the dynamics of populations and the biodiversity of deep-sea ecosystems.

MATERIALS AND METHODS
Study site
The Octopus Garden is located on a small abyssal hillock (~3200-m depth) flanking Davidson Seamount (Fig. 1) where large aggregations of octopus (*M. robustus*) were found nesting in cool to warm hydrothermal waters that circulate through fractured basalt basement rock and emerge along localized fractures and depressions (70). Studies of *M. robustus* at the Octopus Garden were performed during 14 dives of the ROV *Doc Ricketts*, operated from the R/V *Western Flyer* by the Monterey Bay Aquarium Research Institute (MBARI) (table S7). The *Doc Ricketts* has high definition video cameras for close-up imagery of benthic communities and *M. robustus* behavior, onboard conductivity, temperature, depth, and oxygen sensors, manipulator arms, and sample drawers. Sparse collections of *M. robustus* provided specimens for morphometrics and related analyses. Results from this study are drawn from 12 research cruises from 2019 to 2021.

High-resolution seafloor mapping and imaging
We characterized the distribution and abundance of octopus and other animals at the Octopus Garden and assessed linkages between faunal patterns and hydrothermal springs, using a unique ROV-mounted high-resolution mapping system (fig. S5) to create a landscape-scale (2.5 ha) map of the Octopus Garden encompassing ~8% of the hillock. The MBARI LASS is operated from ROVs (71). The LASS combines three seafloor mapping sensors with an inertial navigation system (INS), all mounted on a frame that rotates to face the seafloor, regardless of slope. A 400-kHz

multibeam sonar provides 5-cm lateral resolution bathymetry, a 90° field of view Wide Swath Subsea Lidar collects 1-cm resolution bathymetry, and color stereo still cameras illuminated by strobe lights image the seafloor at 2.5-mm resolution. LASS data are processed using the MB-System software package (www.mbari.org/technology/mb-system/). The multibeam and lidar bathymetry are cleaned using a combination of automated filtering (MBclean and MBvoxelclean) and interactive editing (MBeditviz). Because the INS navigation drifts over time, adjustment of the navigation model so that features mapped in overlapping swathes match is a vital component of the processing. The navigation adjustment is accomplished using the MB-System tool MBnavadjust with the LASS multibeam. Photomosaicing is accomplished using MBphotomosaic, which projects the pixels from each of the source images onto a topography model from the multibeam data to determine their location in the destination image. Multibeam sonar data collected using the LASS during 2021 (table S7) were used to create a gridded 5-cm scale bathymetric map of a portion of the Octopus Garden, and a 3-mm-resolution image mosaic of the survey area was created using >10,000 images from the left stereo camera.

High-resolution bathymetry and photomosaic datasets are archived at the Marine Geoscience Data System (MGDS; www.marine-geo.org/index.php) and are accessible as an expedition compilation (OctopusGarden_MBARI). The photomosaic is archived as 10 subsections (fig. S6) owing to their large storage size.

Environmental conditions and variability

To characterize environmental conditions at the Octopus Garden, we measured temperature, oxygen, and salinity in and out of nests and crevices influenced by hydrothermal flows. Single point "spot measurements" of temperature and oxygen were made during surveys of nests and embryo conditions using thermistor and oxygen sensors (Pyroscience Firesting FS02, OXROB10) connected directly to the ROV. These sensors were attached to a short rod (ca. 2-cm diameter by 30-cm length) and positioned precisely by the ROV manipulator arm (fig. S1 and movie S4).

Time-series measurements of temperature and oxygen were collected in various nests and crevices where hydrothermal waters were emanating or in nearby nonvent locations at the Octopus Garden over periods of 3 to 14 months. Temperature (Seabird Electronics SBE model 39 Plus) and oxygen (Aanderaa optode models 3830 and 3966) sensors connected to SBE SeaCat 19 Plus data loggers recorded conditions every 5 min from December 2020 to March 2021. Four additional temperature sensors (ibutton) logged water temperature in venting/nesting areas every 1 or 2 hours over 11 to 13 months (September 2019 to December 2020).

Water temperature, depth, and the altitude of the ROV *Doc Ricketts* above the seafloor were measured continuously during all dives used for biological studies at the Octopus Garden. Temperature was measured using a Seabird Electronics CTD mounted 2 m above the base of the ROV. Altitude (meters above the bottom) was measured using an ROV-mounted downward-looking depth sensor. Anomalies from the mean temperature ~20 mab were compared for all ROV dives to assess mixing of the thermal plume emanating from hydrothermal springs (table S1).

Comparison of the slope of the seafloor in octopus nests to the slope of the bottom in the 2.5-ha mapped area was performed by extracting the 5-cm bathymetry slope for the location of all nesting females ($N = 4707$), then comparing those to the slopes of the entire 2.5-ha focus area ($N = 1,048,475$) using a two-tailed Fisher's F = test.

Time-lapse imagery of Octopus Garden community dynamics

We used a time-lapse camera system (fig. S7) to capture dynamic changes in the behavior of *M. robustus* and the associated biological community at the Octopus Garden. The system, a Canon EOS-R5 camera with an RF 85 mm, f/2 macro lens, and twin electronic strobes, was mounted in pressure housings with control electronics and batteries. Photographs of a ca. 0.7- to 1.0-m-wide view of the Octopus Garden (e.g., Fig. 1C) were taken at 20-min intervals from early March to late August 2022.

Octopus and megafaunal abundance

The abundance of *M. robustus* at the Octopus Garden was determined from direct counts using the high-resolution LASS image mosaic covering 2.5 ha of the hillock (Fig. 3B and fig. S6). Octopus were marked in the mosaic as colored codes for different categories of individuals; migrating, nesting, senescing, and dead octopus, based on behavior and postures drawn from ROV observations. Migrating individuals typically have arms extended in an upright position as they crawl over the seafloor. Nesting females are often positioned "mouth-up" with tentacles wrapped around their body and encircling their clutch of developing embryos. Senescent *M. robustus* are often positioned mantle up with arms curled and held somewhat near the body. Ventilation (indicated by mantle contractions) in senescent individuals is slow (<3 min^{-1} compared to 7+ min^{-1} for active individuals), and color is often lighter. Carcasses are difficult to distinguish from senescent individuals in still images but are often on their side with relaxed arms.

Matlab scripts were developed (J.P.B.) to locate the coordinates of each colored octopus code through a series of filtering steps based on color, shape, and size. The coregistration of the photomosaic and bathymetric maps created by the LASS mapping system allowed the precise locations of octopus in relation to bathymetry to be determined.

The abundance of nonoctopod megafauna was assessed from counts in a subsample of the 3-mm-scale Octopus Garden image mosaic. We (J.P.B.) superimposed a 1-m by 1-m grid over each of 10 subsections of the 3-mm-resolution image mosaic (fig. S6) using Photoshop software; subsections were used because of the slow display time of the very large file size for the entire mosaic. All visible animals (ca. >3 to 5 cm) were identified (MBARI Deep-sea Guide) to the lowest taxon possible and counted in 5 to 15 plots (1 m by 1 m) positioned randomly in each mosaic subsection (fewer plots were counted in smaller subsections). A total of 85 randomly positioned plots were counted. Owing to the patchiness of *M. robustus*, another 45 plots were positioned haphazardly in regions of photomosaic subsections containing >2 octopus m^{-2} (i.e., octopus-rich locations). Comparisons of *M. robustus* versus megafaunal abundance in all plots were performed for counts of total megafauna (all identifiable animals) and anemones (Anthozoa) using Microsoft Excel XLStat 2021.4.1.1215.

Rates of *M. robustus* embryonic development

The rate of embryogenesis for *M. robustus* at the Octopus Garden was determined by observing the change in embryo's developmental stages between expeditions. Octopus development progresses from

eggs to hatchlings through 20 well-described stages [Naef Stages; (72)]. We documented the developmental stages of embryos in 31 haphazardly selected nests that were resurveyed at least once over five expeditions from April 2019 to March 2021. During each visit, females were gently nudged aside (ca. 5 to 20 cm) with a probe to view their clutch of ~55 eggs (fig. S1E and movie S4). We assessed the Naef Stage of most embryos visible on the basis of published images of Naef Stages for *O. vulgaris* (72) and *Enteroctopus megalocyathus* (73). For *M. robustus*, close-up video observations were sufficient to assign an approximate Naef stage for developing eggs (fig. S1). During a single visit, all embryos within a nest appeared to be very near the same stage of development. Nest conditions (temperature measured within 1 to 3 cm of eggs, oxygen for some nests) and imagery of females and embryos were recorded during each visit. On successive expeditions, maps of nesting areas were used to relocate previously surveyed nests and reassess embryo development and female identity.

Duration of *M. robustus* brood period

To estimate the brood period of *M. robustus* from successive changes in embryonic stages, we assumed that development in *M. robustus* was similar to most octopuses, with an asymptotic progression of Naef stages (I–XX) versus time [e.g., (73)]. We developed a generalized relationship between Naef stage and fractional embryonic development (*F*) using an aggregate of development patterns for six octopuses by

digitizing figures of Naef stage versus age (days of development) for six octopus species [*E. megalocyathus* (73), *Octopus bimaculoides* (74), *O. maya* (19, 75, 76), *Octopus mimus* (32), *O. tehuelchus* (18), and *Octopus tetricus* (77, 78)] over a range of incubation temperatures.

For each developmental series, we converted the days of development to fractional development as

$$F_i = \left(\frac{D_i}{D_{max}}\right)\left(\frac{S_{max}}{20}\right) \quad (1)$$

where F_i = fractional development for observation i, D_i = days of development for observation i, D_{max} = the reported brood period for the species, and S_{max} = maximum reported Naef stage.

Fractional development (*F*) was plotted versus Naef Stage for all species pooled and then modeled using asymptotic nonlinear regression (fig. S8) as

$$F = 0.3772e^{(Stage \cdot 0.0602)} - 0.3153 (R^2 = 0.88) \quad (2)$$

F was calculated using Eq. 1 and the Naef stage of development for larvae observed in each nest during each observation period (i.e., Date$_1$ and Date$_2$).

Brood period (*P*) was calculated for each nest on the basis of *F* and the time between successive observations.

For nests with the same female present for both visits

$$P(days) = \frac{(Date_2 - Date_1)}{(F_2 - F_1)} \quad (3)$$

For nests with a different female on the second observation date

$$P(days) = \frac{(Date_2 - Date_1)}{[(F_{Stage20} - F_1) + (F_2 - F_0)]} \text{ or simplified}$$

$$P(days) = \frac{(Date_2 - Date_1 - I)}{(1 - F_1 + F_2)} \quad (4)$$

where *I* = the estimated period (14 days) between clutch hatching for female 1 and egg laying by female 2.

Equation 2 or 3 was then used to estimate *F* for *M. robustus*, on the basis of observed Naef stages of *M. robustus* embryos.

Female nest residence time

An independent estimate of *M. robustus* brood period was calculated from the residence time of brooding females on nests, assuming that females were present on nests only so long as to lay and incubate eggs to hatching. For each repeat visit to a marked nest, we identified females on the basis of scarring on their mantle or arms (fig. S9).

Brood period was estimated as the reciprocal of the mean rate of nest turnover, calculated as the proportion of nests having different females for pairs of expeditions spanning periods of 79 to 594 days. The number of nests surveyed ranged from 2 to 15 among expedition pairs (table S4).

Expected *M. robustus* brood period in relation to habitat temperature

The expected brood period (years) for *M. robustus* at the Octopus Garden was calculated from a log-linear function of brood period (*BP*) versus habitat temperature (*T*) developed from reports of octopus reproductive biology worldwide. For all species known (table S5), we fit a power function for brood period versus temperature as

$$BP = 29.77 \ T^{-1.78} (R^2 = 90) \quad (5)$$

Effect of external mortality risk on hatch success

We used a simple model to estimate the percentage of the initial brood surviving to hatching, assuming that the annual mortality rate (*M*, in % year^{-1}) due to predation or other external risks acts throughout the brooding period. Using finite (i.e,. annual) mortality rates of *M* equaling 1, 5, 10, and 25% year^{-1}, we calculated the instantaneous mortality (z) of

$$z = \ln(1 - 0.01 \cdot M) \quad (6)$$

Hatch success (percentage of embryos hatched) was then modeled as a survivorship curve as

$$HS = 100 - 100(1 - e^{(M \cdot y)}) \quad (7)$$

where *y* is the *n*th year of incubation (fig. S4).

Benthic community carbon Subsidy from *M. robustus*

The carbon subsidy for the benthic community at the Octopus Garden resulting from the immigration and subsequent death of *M. robustus* was estimated from the population size, turnover, and mass of *M. robustus* (table S6). The water content (83.3%) and energy content (15.97 MJkg^{-1}) of *M. robustus* were assumed to be equal to *E. megalocyathus* (73). The annual *M. robustus* energy

input (S) at the Octopus Garden was calculated from population size (P), turnover proportion (t), energy content (E), and area (A), as

$$S = \frac{(PtE)}{A} \qquad (8)$$

assuming that all octopuses died following breeding and remained in the area (consistent with our observations of senescing individuals and carcasses; movie S3).

The sinking flux of organic carbon from surface waters was assumed to equal the mean flux reported (27) for 3400-m depth at Station M located ca. 75 km southwest (8.1 mg Cm^{-2} day^{-1}). Carbon flux was converted to energy flux assuming the mean energy content of sinking POC is 56.6 J mg^{-1}C (28).

Faunal collections

All faunal collections were permitted under scientific collecting licenses registered under J.P.B. with the California Department of Fish and Wildlife (D−0023646428−5) and through MBARI's permit for scientific collections through the Monterey Bay National Marine Sanctuary. Use of animal (octopus) subjects for collections and field observations supporting this study were in close alignment with the requirements of the United States Animal Welfare Act, and the methods required for field studies involving animals (including cephalopods) outlined in Directive 2010/63/EU (www.legislation.gov.uk/eudr/2010/63) concerning the protection of animals used for scientific purposes. Octopus collections were minimal and included carcasses or live adults (<10) and clutches of eggs attached to sensors deployed in the field.

Statistical analysis

Spectral analyses were performed to identify the dominant periods of variability in temperature and oxygen data series. We calculated power spectra using the MatLab FFT function after processing the raw data series by truncation to a power of 2, subtracting the mean, and detrending.

Supplementary Materials
This PDF file includes:
Figs. S1 to S11
Tables S1 to S10
Supplementary Text
Legends for movies S1 to S4
Legends for data S1 and S2
References

Other Supplementary Material for this manuscript includes the following:
Movies S1 to S4
Data S1 and S2

REFERENCES AND NOTES

1. A. Clarke, A reappraisal of the concept of metabolic cold adaptation in polar marine invertebrates. *Biol. J. Linn. Soc.* **14**, 77–92 (1980).
2. L. S. Peck, A cold limit to adaptation in the sea. *Trends Ecol. Evol.* **31**, 13–26 (2016).
3. L. S. Peck, Antarctic marine biodiversity: Adaptations, environments and responses to change. *Oceanogr. Mar. Biol.* **56**, 2–133 (2018).
4. O. Heilmayer, T. Brey, H. O. Pörtner, Growth efficiency and temperature in scallops: A comparative analysis of species adapted to different temperatures. *Funct. Ecol.* **18**, 641–647 (2004).
5. H. O. Pörtner, L. Peck, G. Somero, Thermal limits and adaptation in marine Antarctic ectotherms: An integrative view. *Philos. Trans. R. Soc. B Biol. Sci.* **362**, 2233–2258 (2007).
6. C. M. Ibáñez, E. L. Rezende, R. D. Sepúlveda, J. Avaria-Llautureo, C. E. Hernández, J. Sellanes, E. Poulin, M. C. Pardo-Gandarillas, Thorson's rule, life-history evolution, and diversification of benthic octopuses (Cephalopoda: Octopodoidea). *Evolution* **72**, 1829–1839 (2018).
7. S. C. Stearns, *The Evolution of Life Histories* (Oxford Univ. Press, 1992).
8. M. J. Angilletta Jr., C. E. Oufiero, A. D. Leaché, Direct and indirect effects of environmental temperature on the evolution of reproductive strategies: an information-theoretic approach. *Am. Nat.* **168**, E123–E135 (2006).
9. N. Marshall, Egg size in Arctic, Antarctic and deep-sea fishes. *Evolution* **7**, 328–341 (1953).
10. E. Ramirez-Llodra, Fecundity and life-history strategies in marine invertebrates. *Adv. Mar. Biol.* **43**, 87–170 (2002).
11. V. Laptikhovsky, Latitudinal and bathymetric trends in egg size variation: a new look at Thorson's and Rass's rules. *Mar. Ecol.* **27**, 7–14 (2006).
12. G. Thorson, Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.* **25**, 1–45 (1950).
13. C. C. Smith, S. D. Fretwell, The optimal balance between size and number of offspring. *Am. Nat.* **108**, 499–506 (1974).
14. M. J. Angilletta, C. E. Oufiero, M. W. Sears, Thermal adaptation of maternal and embryonic phenotypes in a geographically widespread ectotherm. *Int. Congr. Series* **1275**, 258–266 (2004).
15. T. Cortez, B. G. Castro, A. Guerra, Reproduction and condition of female Octopus mimus (Mollusca: Cephalopoda). *Mar. Biol.* **123**, 505–510 (1995).
16. A. K. Pettersen, C. R. White, R. J. Bryson-Richardson, D. J. Marshall, Linking life-history theory and metabolic theory explains the offspring size-temperature relationship. *Ecol. Lett.* **22**, 518–526 (2019).
17. D. J. Marshall, A. K. Pettersen, M. Bode, C. R. White, Developmental cost theory predicts thermal environment and vulnerability to global warming. *Nat. Ecol. Evol.* **4**, 406–411 (2020).
18. R. Braga, S. Van der Molen, J. Pontones, N. Ortiz, Embryonic development, hatching time and newborn juveniles of Octopus tehuelchus under two culture temperatures. *Aquaculture* **530**, 735778 (2021).
19. C. Caamal-Monsreal, I. Uriarte, A. Farias, F. Díaz, A. Sánchez, D. Re, C. Rosas, Effects of temperature on embryo development and metabolism of O. maya. *Aquaculture* **451**, 156–162 (2016).
20. K. Hamasaki, T. Morioka, Effects of temperature on egg incubation period, and paralarval survival and growth of common octopus, octopus vulgaris reared in the laboratory. *Aquac. Sci.* **50**, 407–413 (2002).
21. T. Repolho, M. Baptista, M. S. Pimentel, G. Dionísio, K. Trübenbach, V. M. Lopes, A. R. Lopes, R. Calado, M. Diniz, R. Rosa, Developmental and physiological challenges of octopus (Octopus vulgaris) early life stages under ocean warming. *J. Comp. Physiol. B* **184**, 55–64 (2014).
22. I. Uriarte, E. Martínez-Montaño, V. Espinoza, C. Rosas, J. Hernández, A. Farías, Effect of temperature increase on the embryonic development of Patagonian red octopus Enteroctopus megalocyathus in controlled culture. *Aquacult. Res.* **47**, 2582–2593 (2016).
23. A. Hirst, A. López-Urrutia, Effects of evolution on egg development time. *Mar. Ecol. Prog. Ser.* **326**, 29–35 (2006).
24. J. Bernardo, Maternal effects in animal ecology. *Am. Zool.* **36**, 83–105 (1996).
25. C. King, J. Brown, E. Burton, A. Kahn, A. Hartwell, A. Wood, D. Hardin, Octopus gardens and a whale fall in monterey bay national marine sanctuary. *Oceanography* **33**, 50–51 (2020).
26. P. A. Stephens, W. J. Sutherland, Consequences of the Allee effect for behaviour, ecology and conservation. *Trends Ecol. Evol.* **14**, 401–405 (1999).
27. K. L. Smith, H. A. Ruhl, C. L. Huffard, M. Messié, M. Kahru, Episodic organic carbon fluxes from surface ocean to abyssal depths during long-term monitoring in NE Pacific. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 12235–12240 (2018).
28. E. Grabowski, R. M. Letelier, E. A. Laws, D. M. Karl, Coupling carbon and energy fluxes in the North Pacific Subtropical Gyre. *Nat. Commun.* **10**, 1–9 (2019).
29. D. J. Marshall, T. F. Bolton, Effects of egg size on the development time of non-feeding larvae. *Biol. Bull.* **212**, 6–11 (2007).
30. J. D. Gage, P. A. Tyler, *Deep-Sea Biology: A Natural History of Organisms at the Deep-Sea Floor* (Cambridge Univ. Press, 2012).
31. M. Nande, P. Domingues, C. Rosas, Effects of temperature on the embryonic development of octopus vulgaris. *J. Shellf. Res.* **37**, 1013–1019 (2018).
32. I. Uriarte, V. Espinoza, M. Herrera, O. Zúñiga, A. Olivares, P. Carbonell, S. Pino, A. Farías, C. Rosas, Effect of temperature on embryonic development of Octopus mimus under controlled conditions. *J. Exp. Mar. Biol. Ecol.* **416-417**, 168–175 (2012).

33. M. Narvarte, R. A. González, L. Storero, M. Fernández, Effects of competition and egg predation on shelter use by Octopus tehuelchus females. *Mar. Ecol. Prog. Ser.* **482**, 141–151 (2013).

34. I. M. Barratt, M. P. Johnson, A. L. Allcock, Fecundity and reproductive strategies in deep-sea incirrate octopuses (Cephalopoda: Octopoda). *Mar. Biol.* **150**, 387–398 (2007).

35. B. Robison, B. Seibel, J. Drazen, Deep-sea octopus (Graneledone boreopacifica) conducts the longest-known egg-brooding period of any animal. *PLOS ONE* **9**, 7–10 (2014).

36. T. J. Anderson, Habitat selection and shelter use by Octopus tetricus. *Mar. Ecol. Prog. Ser.* **150**, 137–148 (1997).

37. A. M. Hartwell, J. R. Voight, C. G. Wheat, Clusters of deep-sea egg-brooding octopods associated with warm fluid discharge: An ill-fated fragment of a larger, discrete population? *Deep-Sea Res. Pt I* **135**, 1–8 (2018).

38. J. R. Voight, The distribution of octopuses of Graneledone (Cephalopoda : Octopodidae) in reference to deep-sea features. *Malacologia* **42**, 63–74 (2000).

39. J. C. Drazen, S. K. Goffredi, B. Schlining, D. S. Stakes, Aggregations of egg-brooding deep-sea fish and cephalopods on the Gorda Escarpment: A reproductive hot spot. *Biol. Bull.* **205**, 1–7 (2003).

40. J. Gascoigne, L. Berec, S. Gregory, F. Courchamp, Dangerously few liaisons: A review of mate-finding Allee effects. *Popul. Ecol.* **51**, 355–372 (2009).

41. A. M. Kramer, L. Berec, J. M. Drake, Editorial: Allee effects in ecology and evolution. *J. Anim. Ecol.* **87**, 7–10 (2018).

42. C. M. Ibáñez, M. C. Pardo-Gandarillas, F. Peña, I. G. Gleadall, E. Poulin, J. Sellanes, Phylogeny and biogeography of Muusoctopus(Cephalopoda: Enteroctopodidae). *Zool. Scr.* **45**, 494–503 (2016).

43. M. J. Angilletta Jr., P. H. Niewiarowski, C. A. Navas, The evolution of thermal physiology in ectotherms. *J. Therm. Biol.* **27**, 249–268 (2002).

44. A. Caverivière, F. Domain, A. Diallo, Observations on the influence of temperature on the length of embryonic development in (Senegal). *Aquat. Living Resour.* **12**, 151–154 (1999).

45. G. Polese, C. Bertapelle, A. Di Cosmo, Role of olfaction in Octopus vulgaris reproduction. *Gen. Comp. Endocr.* **210**, 55–62 (2015).

46. D. A. Clague, J. B. Paduan, D. W. Caress, J. McClain, R. A. Zierenberg, Lava Flows Erupted in 1996 on North Gorda ridge segment and the geology of the Nearby Sea Cliff hydrothermal vent field from 1-M Resolution AUV mapping. *Front. Mar. Sci.* 7, 10.3389/fmars.2020.00027, (2020).

47. S. Bauer, B. J. Hoye, Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science* **344**, 1242552 (2014).

48. H. J. T. Hoving, S. L. Bush, S. H. D. Haddock, B. H. Robison, Bathyal feasting: post-spawning squid as a source of carbon for deep-sea benthic communities. *Proc. Biol. Sci.* **284**, 20172096 (2017).

49. R. J. Miller, D. C. Reed, M. A. Brzezinski, Partitioning of primary production among giant kelp (Macrocystis pyrifera), understory macroalgae, and phytoplankton on a temperate reef. *Limnol. Oceanogr.* **56**, 119–132 (2011).

50. H. O. Pörtner, Oxygen- And capacity-limitation of thermal tolerance: A matrix for integrating climate-related stressor effects in marine ecosystems. *J. Exp. Biol.* **213**, 881–893 (2010).

51. H. O. Pörtner, A. P. Farrell, Physiology and climate change. *Science* **322**, 690–692 (2008).

52. R. M. Haymon, E. T. Baker, J. A. Resing, S. M. White, K. C. Macdonald, Hunting for Hydrothermal Vents Along the Galápagos Spreading Center. *Oceanography* **20**, 100–107 (2007).

53. C. R. Fisher, K. Takai, N. Le Bris, Hydrothermal vent ecosystems. *Oceanography* **20**, 14–23 (2007).

54. C. Van Dover, *The Ecology of Deep-Sea Hydrothermal Vents* (Princeton Univ. Press, 2000).

55. A. Fisher, K. Becker, Channelized fluid flow in oceanic crust reconciles heat-flow and permeability data. *Nature* **403**, 71–74 (2000).

56. C. G. Wheat, M. J. Mottl, A. T. Fisher, S. Hulme, Formation waters delineate diverse hydrogeologic conditions at a plate scale: Eastern flank of the Juan de fuca ridge. *Geochem. Geophys. Geosyst.* **23**, e2022GC010665 (2022).

57. C. G. Wheat, M. J. Mottl, Composition of pore and spring waters from Baby Bare: Global implications of geochemical fluxes from a ridge flank hydrothermal system. *Geochim. Cosmochim. Acta* **64**, 629–642 (2000).

58. A. T. Fisher, C. G. Wheat, C. Geoffrey, C. G. Wheat, Seamounts as conduits for massive fluid, heat, and solute fluxes on ridge flanks. *Oceanography* **23**, 74–87 (2010).

59. C. G. Wheat, A. M. Hartwell, J. McManus, A. T. Fisher, B. N. Orcutt, L. E. M. Schlicht, S. Niedenzu, W. Bach, Geology and fluid discharge at dorado outcrop, a low temperature ridge-flank hydrothermal system. *Geochem. Geophys. Geosyst.* **20**, 487–504 (2019).

60. M. J. Mottl, G. Wheat, E. Baker, N. Becker, E. Davis, R. Feely, A. Grehan, D. Kadko, M. Lilley, G. Massoth, C. Moyer, F. Sansone, Warm springs discovered on 3.5 Ma oceanic crust, eastern flank of the Juan de Fuca Ridge. *Geology* **26**, 51–54 (1998).

61. C. G. Wheat, J. McManus, M. J. Mottl, E. Giambalvo, Oceanic phosphorus imbalance: Magnitude of the mid-ocean ridge flank hydrothermal sink. *Geophys. Res. Lett.* **30**, 1895 (2003).

62. M. Hutnak, A. T. Fisher, R. Harris, C. Stein, K. Wang, G. Spinelli, M. Schindler, H. Villinger, E. Silver, Large heat and fluid fluxes driven through mid-plate outcrops on ocean crust. *Nat. Geosci.* **1**, 611–614 (2008).

63. P. Wessel, D. T. Sandwell, S. S. Kim, The global seamount census. *Oceanography* **23**, 24–33 (2010).

64. C. G. Wheat, A. T. Fisher, J. McManus, S. M. Hulme, B. N. Orcutt, Cool seafloor hydrothermal springs reveal global geochemical fluxes. *Earth Planet. Sci. Lett.* **476**, 179–188 (2017).

65. J. A. Ardron, M. R. Clark, A. J. Penney, T. F. Hourigan, A. A. Rowden, P. K. Dunstan, L. Watling, T. M. Shank, D. M. Tracey, M. R. Dunn, S. J. Parker, A systematic approach towards the identification and protection of vulnerable marine ecosystems. *Mar. Policy* **49**, 146–154 (2014).

66. C. Gros, J. Jansen, C. Untiedt, T. R. R. Pearman, R. Downey, D. K. A. Barnes, D. A. Bowden, D. C. Welsford, N. A. Hill, Identifying vulnerable marine ecosystems: An image-based vulnerability index for the Southern Ocean seafloor. *ICES J. Mar. Sci.* **80**, 972–986 (2023).

67. P. Salinas-de-León, B. Phillips, D. Ebert, M. Shivji, F. Cerutti-Pereyra, C. Ruck, C. R. Fisher, L. Marsh, Deep-sea hydrothermal vents as natural egg-case incubators at the Galapagos Rift. *Sci. Rep.* **8**, 1–7 (2018).

68. A. Sen, T. Himmler, W. L. Hong, C. Chitkara, R. W. Lee, B. Ferré, A. Lepland, J. Knies, Atypical biological features of a new cold seep site on the Lofoten-Vesterålen continental margin (northern Norway). *Sci. Rep.* **9**, 1762 (2019).

69. A. Purser, L. Hehemann, L. Boehringer, S. Tippenhauer, M. Wege, H. Bornemann, S. E. A. Pineda-Metz, C. M. Flintrop, F. Koch, H. H. Hellmer, P. Burkhardt-Holm, M. Janout, E. Werner, B. Glemser, J. Balaguer, A. Rogge, M. Holtappels, F. Wenzhoefer, A vast icefish breeding colony discovered in the Antarctic. *Curr. Biol.* **32**, 842–850.e4 (2022).

70. C. King, J. Brown, Corals, sponges, and an octopus garden in Monterey Bay National Marine Sanctuary. *Oceanography* **32**, 52–53 (2019).

71. D. W. Caress, H. J. Thomas, E. J. Martin, J. A. Hamilton, M. Risi, L. Bird, R. Henthorn, G. Troni, B. Hobson, C. K. Paull, J. Barry, K. L. Maier, M. W. Schwehr, S. Rock, E. Trauschke, E. Slattery, C. Dawe, M. Burczynski, D. J. Osborne, 1-cm Resolution Seafloor Surveys Combining Wide Swath Lidar, Multibeam Sonar, Stereo Cameras, and INS on an Articulating ROV Toolsled. AGU Fall Meeting 2018, OS33day-1920 (2018).

72. A. Deryckere, R. Styfhals, E. A. G. Vidal, E. Almansa, E. Seuntjens, A practical staging atlas to study embryonic development of Octopus vulgaris under controlled laboratory conditions. *BMC Dev. Biol.* **20**, 1–18 (2020).

73. I. Uriarte, V. Espinoza, R. Gutiérrez, O. Zúñiga, A. Olivares, C. Rosas, S. Pino, A. Farías, Key aspects of egg incubation in Patagonian red octopus (Enteroctopus megalocyathus) for cultivation purposes. *Aquaculture* **424-425**, 158–166 (2014).

74. L. E. Ibarra-García, J. M. Mazón-Suástegui, C. Rosas, D. Tovar-Ramírez, G. Bárcenas-Pazos, R. Civera-Cerecedo, A. I. Campa-Córdova, Morphological and physiological changes of Octopus bimaculoides: From embryo to juvenile. *Aquaculture* **497**, 364–372 (2018).

75. A. Sanchez-García, G. Rodríguez-Fuentes, F. Díaz, C. E. Galindo-Sánchez, K. Ortega, M. Mascaró, E. López, C. Caamal-Monsreal, O. Juárez, E. Noreña-Barroso, D. Re, C. Rosas, Thermal sensitivity of O. maya embryos as a tool for monitoring the effects of environmental warming in the Southern of Gulf of Mexico. *Ecol. Indic.* **72**, 574–585 (2017).

76. O. E. Juárez, C. E. Galindo-Sánchez, F. Díaz, D. Re, A. M. Sánchez-García, C. Camaal-Monsreal, C. Rosas, Is temperature conditioning Octopus maya fitness? *J. Exp. Mar. Biol. Ecol.* **467**, 71–76 (2015).

77. S. Spreitzenbarth, A. Jeffs, Temperature induced changes in the development of embryos and paralarvae of the merobenthic octopus, octopus tetricus. *Aquaculture* **538**, 736547 (2021).

78. S. Spreitzenbarth, A. Jeffs, Egg survival and morphometric development of a mero-benthic octopus, Octopus tetricus, embryos in an artificial octopus egg rearing system. *Aquaculture* **526**, 735389–735389 (2020).

79. J. B. Wood, E. Kenchington, R. K. O'Dor, Reproduction and embryonic development time of Bathypolypus arcticus, a deep-sea octopod (Cephalopoda : Octopoda). *Malacologia* **39**, 11–19 (1998).

80. K. Mangold, S. von Boletzky, D. Frösch, Reproductive biology and embryonic development of Eledone cirrosa (Cephalopoda: Octopoda). *Mar. Biol.* **8**, 109–117 (1971).

81. J. A. A. Perez, M. Haimovici, Sexual maturation and reproductive cycle of Eledone massyae, Voss 1964 (Cephalopoda: Octopodidae) in southern Brazil. *Bull. Mar. Sci.* **49**, 270–279 (1991).

82. S. H. Gabe, Reproduction in the Giant Octopus of the North Pacific, Octopus dofleini martini. *Veliger* **18**, 146–150 (1975).

83. N. Ortiz, M. E. Ré, F. Márquez, N. G. Glembocki, The reproductive cycle of the red octopus Enteroctopus megalocyathus in fishing areas of Northern Patagonian coast. *Fish. Res.* **110**, 217–223 (2011).

84. H. Overath, S. von Boletzky, Laboratory observations on spawning and embryonic development of a blue-ringed octopus. *Mar. Biol.* **27**, 333–337 (1974).

85. T. J. Anderson, Morphology and biology of Octopus maorum Hutton 1880 in northern New Zealand. *Bull. Mar. Sci.* **65**, 657–676 (1999).

86. M. A. Collins, P. G. K. Rodhouse, Southern ocean cephalopods. *Adv. Mar. Biol.* **50**, 191–265 (2006).

87. B. Ignatius, M. Srinivasan, Embryonic development in Octopus aegina Gray, 1849. *Curr. Sci.* **91**, 1089–1092 (2006).

88. J. W. Forsythe, R. T. Hanlon, Effect of temperature on laboratory growth, reproduction and life span of Octopus bimaculoides. *Mar. Biol.* **98**, 369–379 (1988).

89. R. T. Hanlon, Laboratory rearing of the Atlantic reef octopus, Octopus briareus Robson, and its potential for mariculture. *Proc. World Maric. Soc.* **8**, 471–482 (1977).

90. H. Ito, Some Observation on the Embryonic Development of Paroctopus conispadiceus (Mollusca: Cephalopoda). *Bull. Hokkaido Regional Fish. Res. Lab.* **8**, 93–105 (1983).

91. W. F. Van Heukelem, Growth and life-span of Octopus cyanea (Mollusca: Cephalopoda). *J. Zool.* **169**, 299–315 (1973).

92. L. Opresko, R. Thomas, Observations on Octopus joubini: Some aspects of reproductive biology and growth. *Mar. Biol.* **31**, 51–61 (1975).

93. N. Kaneko, Y. Oshima, Y. Ikeda, Egg brooding behavior and embryonic development of Octopus laqueus (Cephalopoda: Octopodidae). *Molluscan Res.* **26**, 113–117 (2006).

94. G. L. Voss, R. B. Toll, The systematics and nomenclatural status of the Octopodinae described from the Western Atlantic Ocean, in *Systematics and Biogeography of Cephalopods*, N. A. Voss, M. Vecchione, M. J. Sweeney, Eds. (Smithsonian Institution Press, 1998), pp 277–599.

95. J. Semmens, Z. Doubleday, K. Hoyle, G. Pecl, A multilevel approach to examining cephalopod growth using Octopus pallidus as a model. *J. Exp. Biol.* **214**, 2799–2807 (2011).

96. S. A. Osborn, Fecundity and embryonic development of *Octopus rubescens* Berry from Monterey Bay, California (San Jose State University, 1995).

97. O. O. Iribarne, Life history and distribution of the small south-western Atlantic octopus, *Octopus tehuelchus. J. Zool.* **223**, 549–565 (1991).

98. L. M. Joll, Mating, egg-laying and hatching of Octopus tetricus (Mollusca: Cephalopoda) in the laboratory. *Mar. Biol.* **36**, 327–333 (1976).

99. T. N. Stranks, The systematic and nomenclatural status of the Octopodinae described from Australia (Mollusca: Cephalopoda), in *Systematics and Biogeography of Cephalopods*, N. A. Voss, M. Vecchione, R. B. Toll, M. J. Sweeney, Eds. (Smithsonian Institution Press, 1998), pp. 529–547.

100. C. Lu, T. Stranks, Synopsis of Pareledone and Megaleledone species, with description of two new species from East Antarctica (Cephalopoda: Octopodidae). *Memoirs of the National Museum of Victoria* **54**, 221–242 (1994).

101. V. Laptikhovsky, A. Salman, B. Önsoy, M. Akalin, B. Ceylan, Reproduction in rare bathyal octopods Pteroctopus tetracirrhus and Scaeurgus unicirrhus (Cephalopoda: Octopoda) in the east Mediterranean as an apparent response to extremely oligotrophic deep seas. *Deep Sea Res. Part I: Oceanogr. Res. Pap.* **92**, 85–92 (2014).

102. I. Uriarte, O. Zúñiga, A. Olivares, A. Vespinoza, V. Černá, A. Farías, C. Rosas, Morphometric changes and growth rate during embryonic development of Robsonella fontaniana. *Vie et Milieu/Life Environ.* **59**, 315–323 (2009).

103. R. Gutiérrez, I. Uriarte, G. Yany, A. Farías, Productive performance of juvenile Patagonian red octopus (Enteroctopus megalocyathus) fed with fresh preys: Are relevant the quantity of protein and energy on diets? *Aquacult. Res.* **46**, 64–75 (2015).