Reference: *Biol. Bull.* **205:** 1–7. (August 2003)

Aggregations of Egg-Brooding Deep-Sea Fish and Cephalopods on the Gorda Escarpment: a Reproductive Hot Spot

JEFFREY C. DRAZEN*, SHANA K. GOFFREDI, BRIAN SCHLINING, AND DEBRA S. STAKES

Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, California 95039-9644

Localized areas of intense biological activity, or hot spots, in the deep sea are infrequent but important features in an otherwise sparsely occupied habitat (1). Hydrothermal vents, methane cold seeps, and the tops of seamounts are well documented areas where dense communities persist for generations (2–5). Reproductive aggregations where conspecifics concentrate for the purposes of spawning or egg brooding could be thought of as transient hot spots. It is likely that they occur in populations with low densities to maximize mate location and increase reproductive success (6). However, only a few deep-sea reproductive aggregations have ever been documented (7–9), demonstrating the paucity of present-day information regarding reproductive behavior of deep-sea animals. In this paper we describe a unique multispecies reproductive aggregation located on the Gorda Escarpment, California. We document some of the highest fish and octopus densities ever reported in the deep sea, with most individuals of both species brooding eggs. We describe the nesting behavior of the blob sculpin, Psychrolutes phrictus*, and the egg-brooding behavior of an octopus,* Graneledone *sp. observed during annual dives of a remotely operated vehicle (ROV) on the Gorda Escarpment. The animals are concentrated at the crest of the local topography and near cold seeps where they may benefit from enhanced current flow and local productivity. These findings provide new information on the reproductive behaviors of deep-sea animals. More importantly, they highlight how physical and bathymetric heterogeneity in the environment can result in reproductive hot spots, which may be a critical resource for reproductive success in some deep-sea species.*

Fifteen ROV dives were conducted on the Gorda Escarpment and Mendocino Ridge during three visits in August 2000, August 2001, and July 2002 (Fig. 1). The Gorda Escarpment is a submarine plateau offshore of northern California. The Mendocino Ridge extends westward from its northern edge at 40.35° N. The Escarpment's northern side is characterized by steep topography, frequent rocky outcrops and talus fields, sediment slumps, and drainage channels (10). The depth of investigation ranged from 1300 to 3000 m.

Reproductive aggregations of both blob sculpin and octopus were present at Site 1 (Fig. 1). The biomass of *P. phrictus* alone at this site was equivalent to the average total biomass of fishes on the continental slope. Likewise, the density of *Graneledone* sp. was considerably greater than previously published estimates (Fig. 2). Eighty-four individuals of *P. phrictus* and 64 nests (Fig. 3A) were observed. They were present at two sites, with the highest density occurring at Site 1 in both August 2000 and August 2001 (Fig. 1). The fish were found over the steepest topography and at a topographic break between the steep northern side of the ridge and the more gently sloping top (Fig. 4). *P. phrictus* and associated nests were absent in July 2002. Two hundred and thirty-two individuals of *Graneledone* sp. (Fig. 3B) were observed across all locations, with the highest densities observed at Site 1 during all three visits (Fig. 1). The octopus co-occurred with the blob sculpin, with 51% of the octopus observed within 5 m of sculpin adults or nests in 2001. Smaller aggregations of brooding blob sculpin and octopus were observed at Site 2.

Site 1 (depth 1547–1603 m; dives T208, T349, T448) was

Received 14 February 2003; accepted 12 May 2003.
* To whom correspondence should be addressed. E-mail: jdrazen@mbari.org

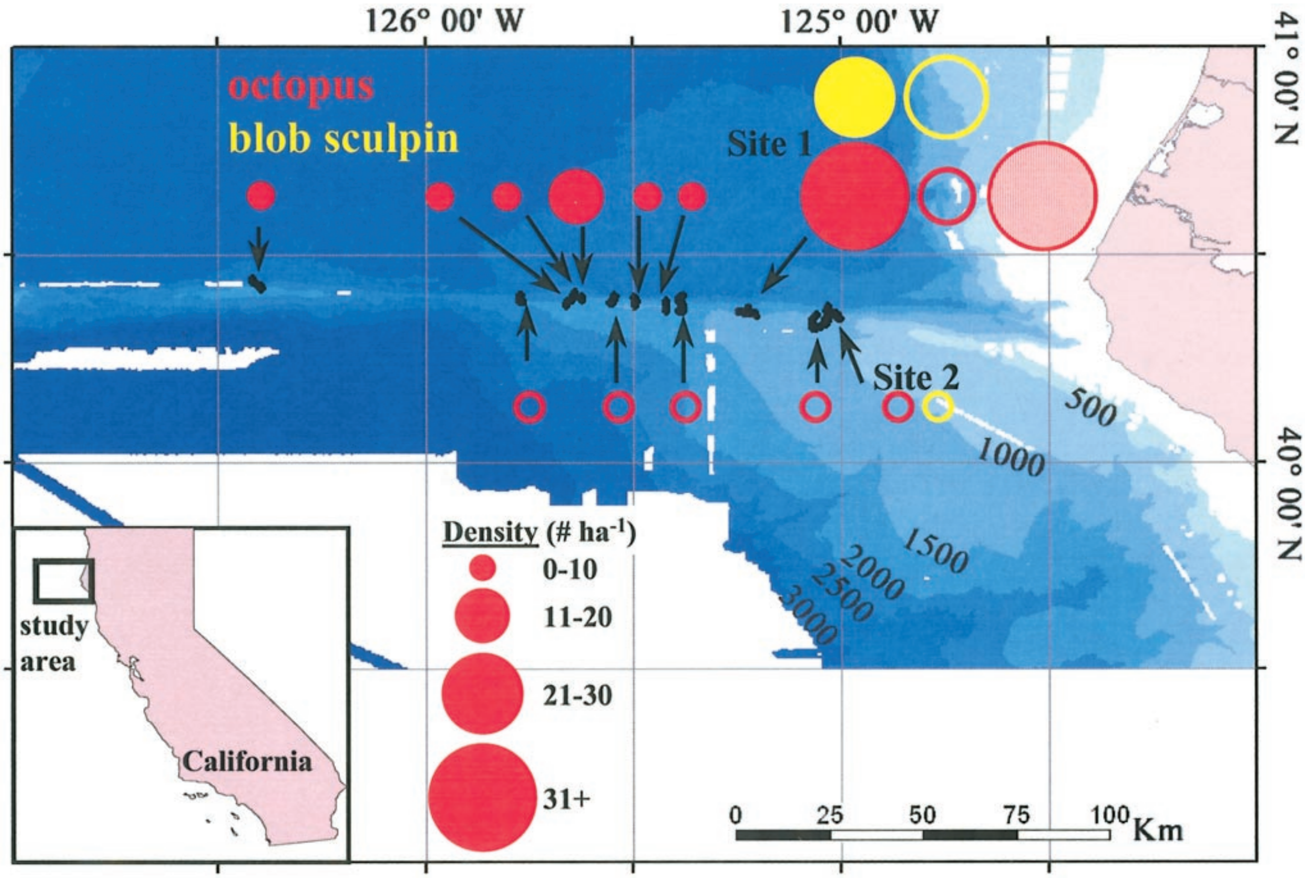

Figure 1. Bathymetric map of the Mendocino Ridge and Gorda Escarpment, showing all dive sites. Depths are in meters. One hundred and fourteen hours of video from ROV bottom time was recorded, annotated, and analyzed. Annotations of all occurrences of discernible animals and geologic features were stored in a searchable database with corresponding environmental (CTDO), observational (time, position), and system (camera zoom) data. Bathymetry is derived from a hull-mounted EM300 sonar system with 20-m pixel resolution. Ultrashort baseline Transponders (Sonardyne, Houston, TX) mounted on the ROV and the ship determine position. Tracklines are derived in a real-time ArcView-based (Environmental Systems Research Institute) navigation system. Closed circles, open circles, and hatched circles are densities (# ha^{-1}) of blob sculpin (yellow) and octopus (red) from dives in 2000, 2001, and 2002 respectively. For each dive the densities reflect the number of animals observed over the surveyed area of seafloor. Areas for density estimates were calculated using the navigation to determine track length and assuming an average observational width of 4 m. Overlap of the dive track was accounted for in the calculations.

characterized by small rocky cliffs and bouldered slopes that shoaled to a sloping talus field in which the gravel and boulders were interspersed with sediment. Site 2 (depth 1534–1583 m; dive T351; Fig. 1) was on a shallowly sloping mud and sand bottom interspersed by boulders, talus, and small rock outcrops. Diffuse cold seeps at the base of several bouldered slopes at both sites were evident by the presence of small patches of vestimentiferan tube worms and vesicomyid clams (10). Sites 1 and 2 were characterized by an average bottom water temperature of 2.4 °C (range = 2.3 – 2.7 °C) and very low oxygen concentration (mean = 1.07 ml l^{-1}; range = 0.73–1.46 ml l^{-1}). The temperature at Site 1 was slightly elevated above ambient (~0.1–0.2 °C) due to local subsurface fluid seepage from the substrate (10).

Blob sculpin attended nests of large (4.0 ± 0.6 mm; n = 50) pinkish eggs (Fig. 3A). The majority of the nests had fish in close attendance (within 3 m), often sitting directly on or touching the eggs. Some nests and fish were observed by themselves primarily in the roughest terrain where it was difficult to see behind nearby rocks and ledges. Eggs were free of sediment, suggesting that the adults cleaned or fanned their nest sites. Brooding fish were almost always found very close to each other, and nests were often on neighboring boulders separated by only 1–2 m. Generally the parent fish did not move when the ROV approached;

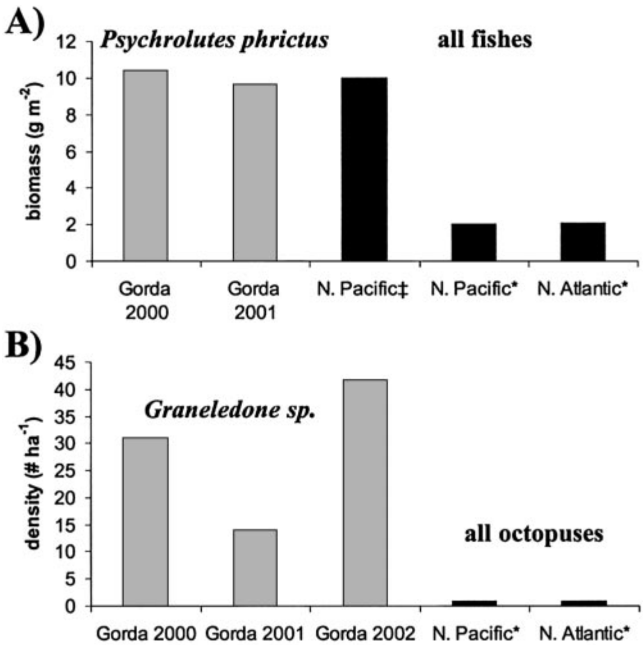

Figure 2. Biomass of blob sculpin (*Psychrolutes phrictus*) and density of octopus (*Graneledone* sp.) at Site 1 (grey bars) compared to "background" averages for total fishes and total octopuses at similar depths elsewhere (black bars). (A) Biomass (g m^{-2}; the metric typically used for fish) of blob sculpin was estimated by assuming an average adult size of 4.5 kg (26). (B) Density of octopuses (# ha^{-1}; typically used for cephalopods). Data from other locations are from trawling* (16, 27, 28; J. R. Voight, pers. comm.) or camera surveys‡ (29).

however, this was also true for fish without eggs, which precluded any conclusions about nest-guarding behavior. The sex of the fish could not be determined from video observations. Fecundity was estimated for four egg masses and ranged from 9375 to 108,125 eggs. The eggs were generally laid on the flat exposed surfaces of large boulders and rock outcrops. Of the 64 egg masses, 57 (89%) had been laid on single rocks; the other seven were each strewn across as many as three neighboring rocks or across large fissures in a flat rock face.

This study presents the first direct evidence of parental care (11) in an oviparous deep-sea fish. It is likely that members of the families Zoarcidae and Liparidae also exhibit parental care, but this has not been confirmed. The zoarcid *Melanostigma atlanticum* was captured in a burrow with its eggs by a box core at 350 m depth (12). The developmental stage of the eggs was not determined; thus, it is unknown whether the parents were in the process of egg laying (one female still retained her eggs) or whether they were staying to guard and ventilate the eggs. Many liparids have large eggs and very low fecundities, suggesting some form of parental care, but no direct evidence has been described (13). Reviews of reproduction in other diverse deep-sea fishes make no note of parental care (1, 14–16).

Individuals of *Graneledone* sp. were observed brooding eggs under their bodies while sitting vertical and motionless with arms curled outwards on boulders, rock outcrops, and ledges (Fig. 3C). An adult specimen of *Graneledone boreopacifica* was collected in July 2002 with 51 eggs. The eggs were 40 mm in length, and many began hatching prematurely when collected; these juveniles still retained egg sacs. Site 1 was revisited in July 2002, and 63 individuals of *Graneledone* sp. were observed in the curled position. Nine of ten individuals in this position were confirmed to be in the process of brooding eggs. In August 2001, 43 eggs of a specimen of *Benthoctopus* sp. were collected from Site 2. This octopus, unlike the others observed, was underneath a small rock with its eggs out of plain view; it was also much smaller than the *Graneledone* sp. (mantle length ~10 cm), and its eggs were only 16 mm long. It was only observed during the course of collecting the rock for geologic examination.

Our observations provide the first evidence of a multispecies reproductive aggregation in the deep sea. To our knowledge, the only other reproductive aggregations described from deep-sea environments are for spawning aggregations of orange roughy (7); another brooding aggregation of octopuses, including a species of *Graneledone*, in the North Pacific (8); and small (2–6 individuals) aggregations of an echinoid (9). In addition, there are reports of aggregations of two echinoderm species in the North Atlantic (17, 18) that may have been for the purpose of reproduction, and pair formation has been documented in a holothuroid (19). Observations over 3 years indicate that the aggregation at Site 1 is either long-lived or recurs at the same location perhaps every year. The aggregations of blob sculpin and octopus exhibit densities and biomass among the highest recorded in the deep sea (Fig. 2). Localized aggregations of this magnitude could have profound influences on local food webs and fauna.

There are several possible explanations for the presence of the dense aggregations of animals on the Gorda Escarpment. For instance, the presence of brooding aggregations of *Benthoctopus* sp. and *Graneledone* sp. in the North Pacific have been explained previously by the availability of both rocky substrate for egg attachment and bivalve prey from nearby cold seeps (8). Rocky substrate for egg attachment is an obvious requisite for spawning by both sculpin and octopus. Rocky substrate, however, occurred at all dive locations yet reproductive aggregations were present at only two locations, suggesting that substrate is not the only criterion involved in site selection for brooding. Furthermore, aggregations of sculpin or octopuses have not been observed on other rocky features, including some within our dive areas on the Gorda Escarpment and Mendocino Ridge and on the Davidson, Guide, and Gumdrop seamounts in the North Pacific. These seamounts have been observed using the Monterey Bay Aquarium Research Institute's ROV at various times of the year, but no aggregations such as we

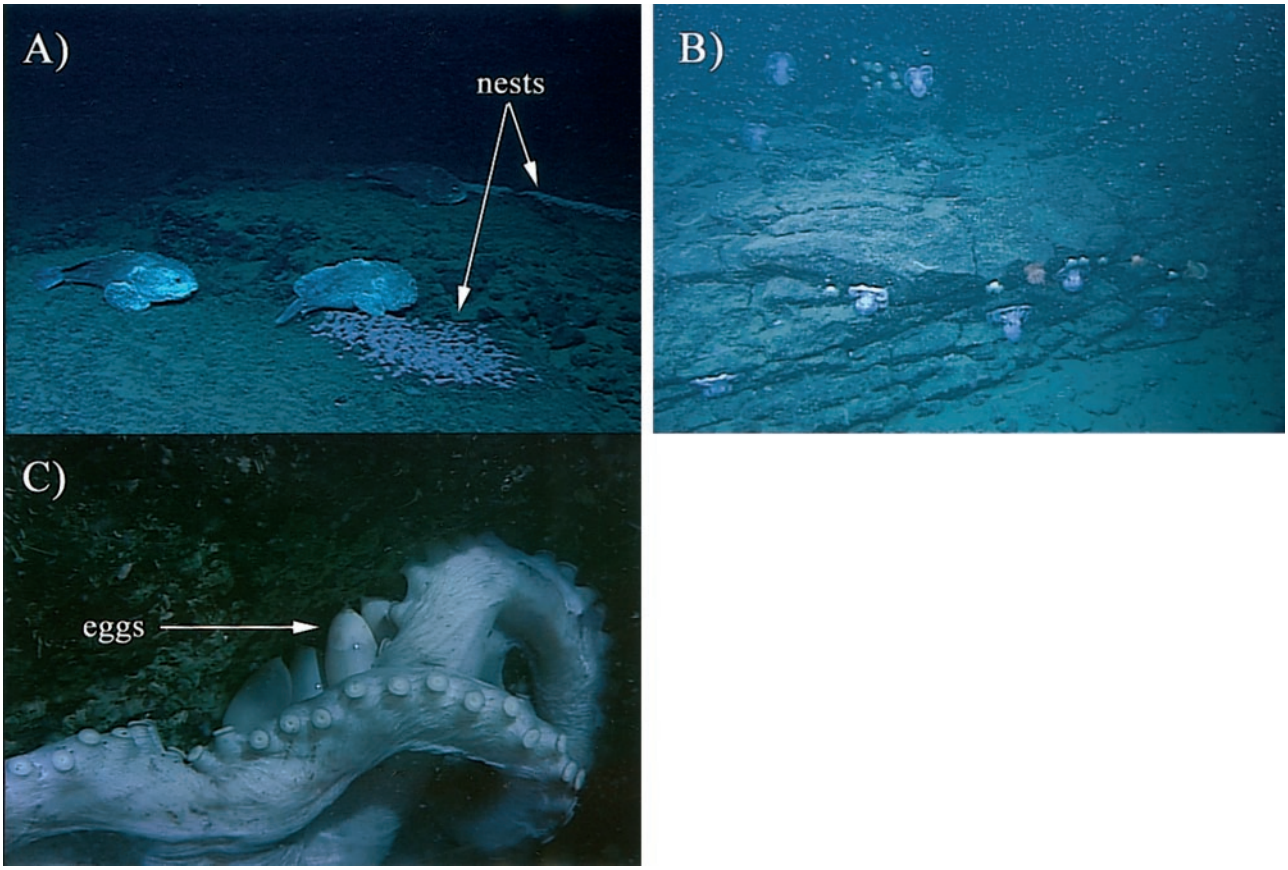

Figure 3. Egg-brooding fish and octopus. (A) Three blob sculpin, *Psychrolutes phrictus*, attending nests. The fish on the left has a nest just outside of the field of view. Size-calibrated images were used to determine fish egg size and fecundity. When the camera had zoomed such that the plane of focus was narrow, then the horizontal dimension of the field of view (field width) could be determined (30). From the resulting calibrated images, Optimas image analysis software (ver. 6) (Optimas Corporation, Bothell, WA) was used to measure fish egg diameters. Occasionally when field width could be used to calibrate the size of objects in the video, the Optimas software was used to calculate the area of fish egg masses. The eggs appeared to be laid in a thin layer across the rocks, and in a few cases they were piled on top of each other near the center of the mass. Consequently, egg numbers were estimated by assuming that a single layer of eggs was placed across the nest area as closely together as possible. (B) Eight egg-brooding individuals of *Graneledone* sp. on a rock outcrop. (C) A specimen of *Graneledone* sp. showing eggs protected under arms and mantle.

describe have been found (J. Drazen, unpubl. data). Likewise, on more than 200 dives in the Monterey Bay area at depths greater than 1000 m and often in areas of rocky substrate (*i.e.*, canyon walls and slopes), no brooding octopuses were observed (although octopuses are common) and only 13 blob sculpin were seen, none with eggs.

The presence of cold seeps can dramatically influence the local productivity of surrounding deep-sea communities by transfer of organic nutrients (2). Diffuse cold seeps were observed at both sites of sculpin and octopus aggregations, suggesting that enhanced local productivity from cold seeps on the Gorda Escarpment may also influence the aggregations. This is unconfirmed, however, because only six octopus were seen in the immediate vicinity of seep organisms and the distribution of nesting blob sculpin was much broader than that of the seeps (Fig. 4).

Cold seeps are related to the upward flow of warm, methane-rich pore fluids from depth; this flow has also generated slight increases in temperature (0.1–0.2 °C above ambient) at Site 1 (10). Increases in temperature could shorten egg development times, which would be an advantage to species that invest parental care. Assuming a Q_{10} of 2, an increase of 1.5 °C would be required for a 10% reduction in incubation time. Similar conclusions were drawn for benthic octopus brooding near cold seeps at the Baby Bare site off of Washington State (8). However, temperature elevations of this magnitude around cold seeps are very unlikely. Furthermore, animal occurrences did not

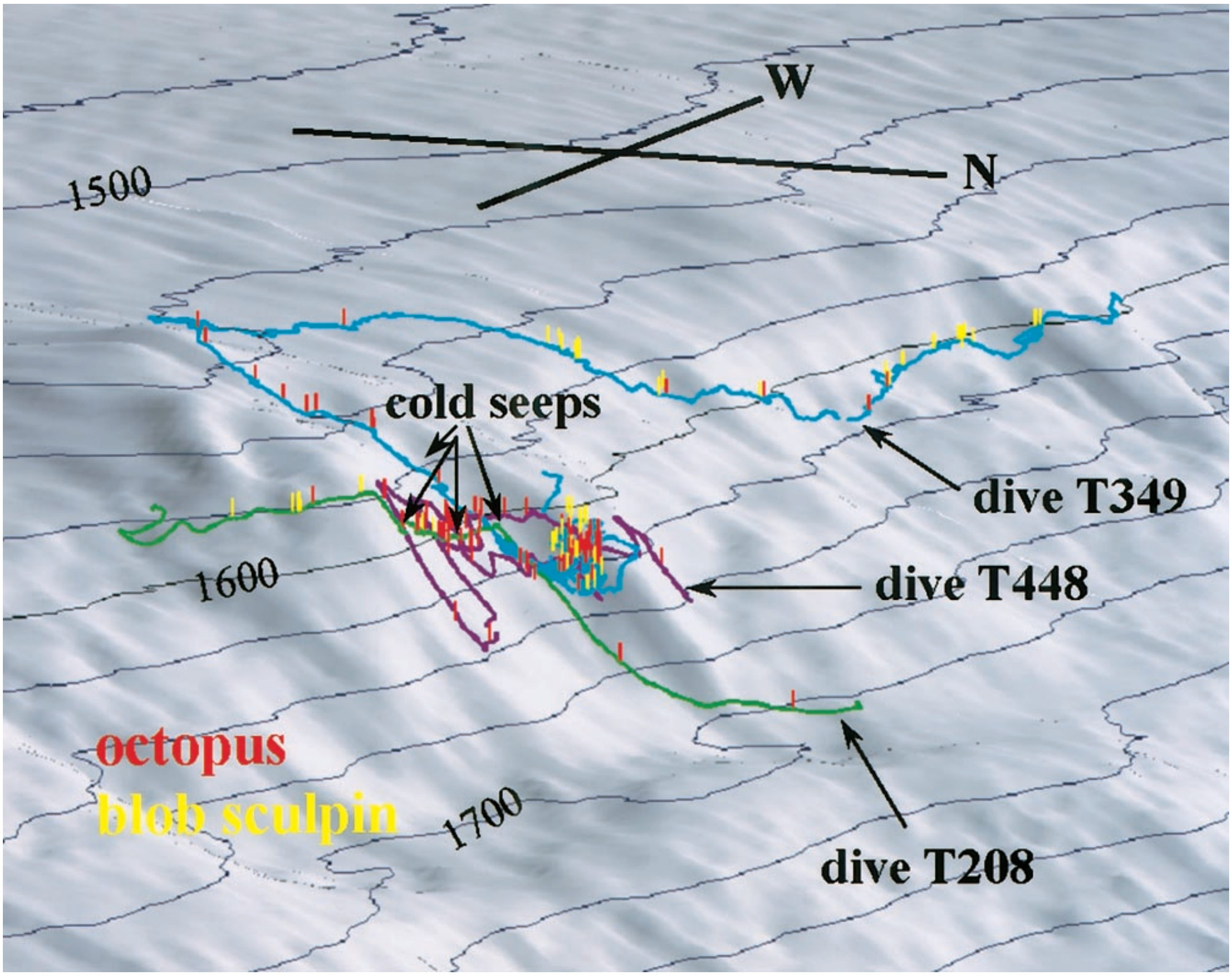

Figure 4. Three-dimensional sunshaded map of dive tracks and locations of all sightings of blob sculpin, octopus, and cold seeps at Site 1. Contours are in meters. Mapping information was generated as for Figure 1. The compass is also a scale bar with each arm equivalent to 500 m. Note that, due to the typical perspective of a three-dimensional rendering, the apparent distances for each axis are not equal.

correlate with the highest temperature anomalies. Therefore, we conclude that cold seeps do not benefit these animals physically, but they may provide a food source that could play a role in the location of the animal aggregations.

In addition, elevated currents may influence site selection by brooding aggregations. All blob sculpin and most octopus were observed near the ridge crest where exposure to elevated currents is likely (1, 3, 20). As on seamount crests, abundant suspension feeders such as brisingid sea stars, tunicates, gorgonians, and venus flytrap anemones were found at the crest of the Gorda Escarpment, providing evidence of accelerated current speeds. Some shallow-living sculpins have a strong preference for nesting sites that are exposed to the current; this exposure aids in gas exchange and waste removal and accelerates embryogenesis (21, 22). At Site 1, where oxygen concentrations are very low, enhanced water movement may be required to deliver adequate oxygen for embryogenesis. A reduction in the need to ventilate or fan the eggs could be an energetic benefit to the adults. In addition, benthic egg brooding and hatching implies a demersal larval/juvenile phase (23). Bottom currents in the deep sea are generally low, so these organisms may take advantage of intensified currents at this site to enhance the dispersal of larvae or juveniles within the demersal habitat.

At one time the deep sea was thought to be a sparsely populated and homogenous environment (1). Today, dense localized communities such as the chemosynthetic communities of hydrothermal vents and methane cold seeps (2) and the suspension-feeding communities of seamounts (3) are well known. Our study site on the Gorda Escarpment is another unique type of biological hot spot in the deep sea. The site is connected to the continental margin but topographically exhibits characteristics of a seamount environment. In addition, small cold seeps are present. We hypothesize that the local topography interacting with the physical and geologic setting has created a localized reproductive hot spot in the deep sea utilized by at least two very different animals.

This information has several important implications. The reproductive hot spot on the Gorda Escarpment (and future sites determined to be similar) might qualify as an area to be protected from fishing. The protection of habitats associated with vulnerable life stages, notably spawning aggregations, is a main objective of marine reserves (24). Our study site could be threatened by commercial trawling and long-lining operations. In the last two decades, the world has seen a rapid development of deep-sea fisheries to depths of 2000 m, and currently fishers regularly operate at depths of 1000 m off of the west coast of the United States (25). From an ecological perspective, our findings contribute to our understanding of habitat heterogeneity within the broader deep-sea ecosystem as well as providing sites where scientists can predictably observe reproductive biology in deep-sea animals, a prospect that is exciting for the study of these elusive species.

Acknowledgments

Special thanks to Linda Kuhnz, Kyra Schlining, Susan Von Thun, and Kris Walz for video annotation. Dan Davis provided helpful advice and software for measuring egg and nest sizes from video framegrabs. We are indebted to Dave Clague, Robert Young, and Jenny Paduan for their assistance with dive T448. Janet Voight also provided assistance on that dive and helped to confirm the octopus identity. Bob Vrijenhoek was the principal investigator on dives T349 and T351. Thanks to the pilots of the ROV *Tiburon* and the crew of the RV *Western Flyer*. Thanks to Jim Barry, Brad Seibel, Bruce Robison, and Greg Cailliet for discussion and comments. Waldo Wakefield, Eric Hochberg, and an anonymous reviewer provided valuable insight and revisions. Dives T348, T350, and T352 were funded by a grant from the National Undersea Research Program awarded to Robert Duncan (Oregon State University). J. C. Drazen was supported by a postdoctoral fellowship from MBARI.

Literature Cited

1. **Gage, J. D., and P. A. Tyler. 1991.** *Deep-Sea Biology: a Natural History of Organisms at the Deep-Sea Floor.* Cambridge University Press, Cambridge.
2. **Tunnicliffe, V., A. G. McArthur, and D. McHugh. 1998.** A biogeographical perspective of the deep-sea hydrothermal vent fauna. *Adv. Mar. Biol.* **34:** 353–442.
3. **Genin, A., P. K. Dayton, P. F. Lonsdale, and F. N. Spiess. 1986.** Corals on seamount peaks provide evidence of current acceleration over deep-sea topography. *Nature* **322:** 59–61.
4. **Van Dover, C. L., C. R. German, K. G. Speer, L. M. Parson, and R. C. Vrijenhoek. 2002.** Evolution and biogeography of deep-sea vent and seep invertebrates. *Science* **295:** 1253–1258.
5. **Wilson, R. R., Jr., and R. S. Kaufmann. 1987.** Seamount biota and biogeography. Pp. 355–377 in *Seamounts, Islands, and Atolls,* B.H. Keating, P. Fryer, R. Batiza, and G.W. Boehlert, eds. Geophysical Monograph 43, American Geophysical Union, Washington DC.
6. **Domeier, M. L., and P. L. Colin. 1997.** Tropical reef fish spawning aggregations: defined and reviewed. *Bull. Mar. Sci.* **60:** 698–726.
7. **Pankhurst, N. W. 1988.** Spawning dynamics of orange roughy, *Hoplostethus atlanticus*, in mid-slope waters of New Zealand. *Environ. Biol. Fishes* **21:** 101–116.
8. **Voight, J. R., and A. J. Grehan. 2000.** Egg brooding by deep-sea octopuses in the North Pacific Ocean. *Biol. Bull.* **198:** 94–100.
9. **Young, C. M., P. A. Tyler, J. L. Cameron, and S. G. Rumrill. 1992.** Seasonal breeding aggregations in low-density populations of the bathyal echinoid *Stylocidaris lineata. Mar. Biol.* **113:** 603–612.
10. **Stakes, D. S., A. M. Trehu, S. K. Goffredi, T. H. Naehr, and R. A. Duncan. 2002.** Mass wasting, methane venting, and biological communities on the Mendocino transform fault. *Geology* **30:** 407–410.
11. **Smith, C., and R. J. Wootton. 1995.** The costs of parental care in teleost fishes. *Rev. Fish Biol. Fish.* **5:** 7–22.
12. **Silverberg, N., H. M. Edenborn, G. Ouellet, and P. Beland. 1987.** Direct evidence of a mesopelagic fish, *Melanostigma atlanticum* (Zoarcidae) spawning within bottom sediments. *Environ. Biol. Fishes* **20:** 195–202.
13. **Stein, D. L. 1980.** Aspects of reproduction of liparid fishes from the continental slope and abyssal plain off Oregon, with notes on growth. *Copeia* 687–699.
14. **Mead, G. W., E. Bertelsen, and D. M. Cohen. 1964.** Reproduction among deep-sea fishes. *Deep-Sea Res.* **11:** 569–596.
15. **Merrett, N., and R. L. Haedrich. 1997.** *Deep-Sea Demersal Fish and Fisheries.* Chapman and Hall, London.
16. **Haedrich, R. L. 1997.** Distribution and population ecology. Pp. 79–114 in *Deep-Sea Fishes,* D. J. Randall and A. P. Farrell, eds. Academic Press, San Diego.
17. **Grassle, J. F., H. L. Sanders, R. R. Hessler, G. T. Rowe, and T. McLellan. 1975.** Pattern and zonation: a study of the bathyal megafauna using the research submersible *Alvin. Deep-Sea Res.* **22:** 457–481.
18. **Billett, D. S. M., and B. Hansen. 1982.** Abyssal aggregations of *Kolga hyalina* Danielssen and Koren (Echinodermata: Holothurioidea) in the Northeast Atlantic Ocean: a preliminary report. *Deep-Sea Res.* **29:** 799–818.
19. **Tyler, P. A., C. M. Young, D. S. M. Billett, and L. A. Giles. 1992.** Pairing behaviour, reproduction and diet in the deep-sea holothurian genus *Paroriza* (Holothuroidea: Synallactidae). *J. Mar. Biol. Assoc. UK* **72:** 447–462.
20. **Fock, H., F. Uiblein, F. Koster, and H. von Westernhagen. 2002.** Biodiversity and species-environment relationships of the demersal fish assemblage at the Great Meteor Seamount (subtropical NE Atlantic), sampled by different trawls. *Mar. Biol.* **141:** 185–199.
21. **DeMartini, E. E. 1978.** Spatial aspects of reproduction in buffalo sculpin, *Enophrys bison. Environ. Biol. Fishes* **3:** 331–336.
22. **DeMartini, E. E., and B. G. Patten. 1979.** Egg guarding and reproductive biology of the red Irish lord, *Hemilepidotus hemilepidotus* (Tilesius). *Syesis* **12:** 41–55.
23. **Hochberg, F. G., M. Nixon, and R. B. Toll. 1992.** Order Octopoda Leach, 1818. Pp. 213–280 in *"Larval" and Juvenile Cephalopods: A Manual for Their Identification,* M. J. Sweeney, C. F. E. Roper, K. M. Mangold, M. R. Clarke, and S. v. Boletzky, eds. Smithsonian Contributions to Zoology 513, Smithsonian Institution Press, Washington, DC.
24. **Roberts, C. M., S. Andelman, G. Branch, R. H. Bustamante, J. C. Castilla, J. Dugan, B. S. Halpern, K. D. Lafferty, H. Leslie, and J. Lubchenco. 2003.** Ecological criteria for evaluating candidate sites for marine reserves. *Ecol. Appl.* **13:** S199–214.

25. **National Research Council. 2002.** *Effects of Trawling and Dredging on Seafloor Habitat.* National Academy Press, Washington, DC.
26. **Matarese, A. C., and D. L. Stein. 1980.** Additional records of the sculpin *Psychrolutes phrictus* in the eastern Bering Sea and off Oregon. *Fish. Bull.* **78:** 169–171.
27. **Alton, M. S. 1972.** Characteristics of the demersal fish fauna inhabiting the outer continental shelf and slope off the northern Oregon coast. Pp. 583–634 in *The Columbia River Estuary and Adjacent Ocean Waters,* A. T. Pruter and D. L. Alverson, eds. University of Washington Press, Seattle.
28. **Collins, M. A., C. Yau, L. Allcock, and M. H. Thurston. 2001.** Distribution of deep-water benthic and bentho-pelagic cephalopods from the north-east Atlantic. *J. Mar. Biol. Assoc. UK* **81:** 105–117.
29. **Wakefield, W. W. 1990.** Patterns in the distribution of demersal fishes on the upper continental slope off central California with studies on the role of ontogenetic vertical migration in particle flux. Ph.D. dissertation, Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA.
30. **Davis, D. L., and C. H. Pilskaln. 1993.** Measurements with underwater video: camera field width calibration and structured light. *Mar. Technol. Soc. J.* **26:** 13–19.