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A study of possible "reef effects" caused by a long-term time-lapse camera in the deep North Pacific

M.F. Vardaro[a,c,*], D. Parmley[b], K.L. Smith Jr.[c]

[a]*Scripps Institution of Oceanography, University of California at San Diego, 9500 Gilman Drive, La Jolla, CA 92093-0208, USA*
[b]*Torrey Pines Institute for Molecular Studies, 3550 General Atomics Court 2-129, San Diego, CA 92121-1122, USA*
[c]*Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, CA 95039-9644, USA*

Abstract

The aggregation response of fish populations following the addition of artificial structures to seafloor habitats has been well documented in shallow-water reefs and at deeper structures such as oil extraction platforms. A long-term time-lapse camera was deployed for 27 four-month deployment periods at 4100 m in the eastern North Pacific to study abyssal megafauna activity and surface–benthos connections. The unique time-series data set provided by this research presented an opportunity to examine how deep-sea benthopelagic fish and epibenthic megafauna populations were affected by an isolated artificial structure and whether animal surveys at this site were biased by aggregation behavior. Counts were taken of benthopelagic grenadiers, *Coryphaenoides* spp., observed per week as well as numbers of the epibenthic echinoid *Echinocrepis rostrata*. No significant correlation ($r_s = -0.39$; $p = 0.11$) was found between the duration of deployment (in weeks) and the average number of *Coryphaenoides* observed at the site. There was also no evidence of associative behavior around the time-lapse camera by *E. rostrata* ($r_s = -0.32$; $p = 0.19$). The results of our study suggest that abyssal fish and epibenthic megafauna do not aggregate around artificial structures and that long-term time-lapse camera studies should not be impacted by aggregation response behaviors.
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1. Introduction

Associative behavior is the aggregation of different species at a single structure or topographic area not driven solely by the incentive of prey species or small-scale habitat requirements (Fréon and Dagorn, 2000). Such behavior has been observed in many pelagic fish species, most notably tuna (Fréon and Dagorn, 2000; Parin and Fedoryako, 1999; Uda, 1933). The attraction of assemblages to natural or artificial structures has not been completely explained, although many competing hypotheses have been proposed. For example, structures and topographic highs could serve as shelter from predators (Soemarto, 1960), a means for predators to concentrate smaller prey species

(Kojima, 1956), a spatial reference point to aid navigation in the open ocean (Klima and Wickham, 1971), or a meeting point for members of the same species to associate and form larger schools (Dagorn and Fréon, 1999). The practical implication of the "reef effect" is a localized increase in the density and activity of fish and invertebrate species, potentially leading to inflated counts of local population size during censuses.

Shallow-water platforms and artificial reefs can be colonized by invertebrates and fish within days (Golani and Diamant, 1999). Longer-term observations show that colonization rates gradually increase over periods of months, finally leveling off at a stable population at around 6–8 months, although densities and species compositions can vary over yearly time scales (Relini et al., 2002). Artificial reefs also appear to be sites of increased reproductive success, rather than simply concentrating the surrounding populations around a single structure (Stephens and Pondella, 2002). Deep-sea colonization rates by invertebrates are much lower (Beaulieu, 2001; Grassle, 1977; Smith and Hessler, 1987) and populations are more diffuse (Rex, 1981), making long time-series measurements vital to the study of deep ocean habitats. The unique properties of deep-water environments (lack of downwelling light, low population densities, reduced food supply, etc.) allow testing of the various rationales for aggregation behavior by removing many of the variables that have been used to explain associative behavior in shallow-water environments.

Fifteen years of hourly photographs taken with a time-lapse camera system were analyzed to evaluate the impact of aggregation effects on counts of fish and epibenthic invertebrates at an abyssal site in the eastern North Pacific (Station M; 34′50′N, 123″00′W; 4100 m depth). The camera system was deployed at 4100 m for 4-month periods almost continually since 1989, providing a long time-series record of biological activity on and near the seafloor. We hypothesized that the numbers of mobile animals observed by the time-lapse camera would increase significantly over the deployment period. Here we examine the observations and the possible effects of the camera system on the animal populations at the site over intervals of weeks to months.

2. Materials and methods

The time-lapse camera system (Fig. 1) was first deployed at Station M in 1989 (Smith et al., 1993),

and has since collected 27 time-lapse image data sets of approximately 4 months each. Station M lies in the eastern North Pacific and is subject to strong seasonal pulses of surface productivity (Smith et al., 1992). The seafloor at 4100 m has very little topographic relief (<100 m over 1600 km^2) and is composed of silty-clay sediment with seasonal deposits of flocculent phytodetritus. Currents near the seafloor average 3.8 cm s^{-1}, can reach a maximum of 18.2 cm s^{-1} and flow to the south during periods of highest current speeds and towards the north and west during the periods of low current speeds (Beaulieu and Baldwin, 1998). Time-lapse photography has revealed abundant evidence of bioturbation and other epifaunal activity at the site in the form of numerous trails, furrows and mounds that can be centimeters to meters across (Smith et al., 1993). No organisms or features taller than glass sponge stalks, $\sim$10–20 cm in height (Beaulieu, 2001), were observed during any time-lapse deployment.

The camera took one still photograph of the seafloor every hour and the film was recovered and the equipment redeployed during maintenance cruises three times a year. The time-lapse camera consists of a Benthos 377 camera mounted on a titanium frame at an angle of $31°$ from horizontal with the lens $\sim$2 m above the seafloor. The camera is equipped with a 28-mm Nikonos lens, providing angular coverage of $50°$ in the horizontal and $35°$ in the vertical plane, and holds 400 ft of 35-mm color-negative film (Fuji, Type 8514, 500 ASA). Up to 3500 images can be collected in 4.6 months. Two 400-W-s strobes, one mounted on either side of the camera housing, illuminate approximately 20 m^2 of the seafloor beginning at a distance of 1.8 m from the camera frame and extending approximately 6.5 m from the base of the camera frame (see Smith et al. 1993 for a more complete description of the time-lapse camera). The entire camera frame was examined after each recovery to identify any encrusting animals and remove any other biofouling. However, the time-lapse camera system returned to the surface after a 4-month deployment with no visible encrusting growths or attached organisms.

The oblique photographs taken by the time-lapse camera (Fig. 2) were analyzed using a perspective-grid method (Wakefield and Genin, 1987; Wolf, 1983). Each image was projected onto a flat surface and digitized with a Science Accessories Corp.® electronic digitizer interfaced with a computer. Fish and the echinoid *Echinocrepis* that appeared in the
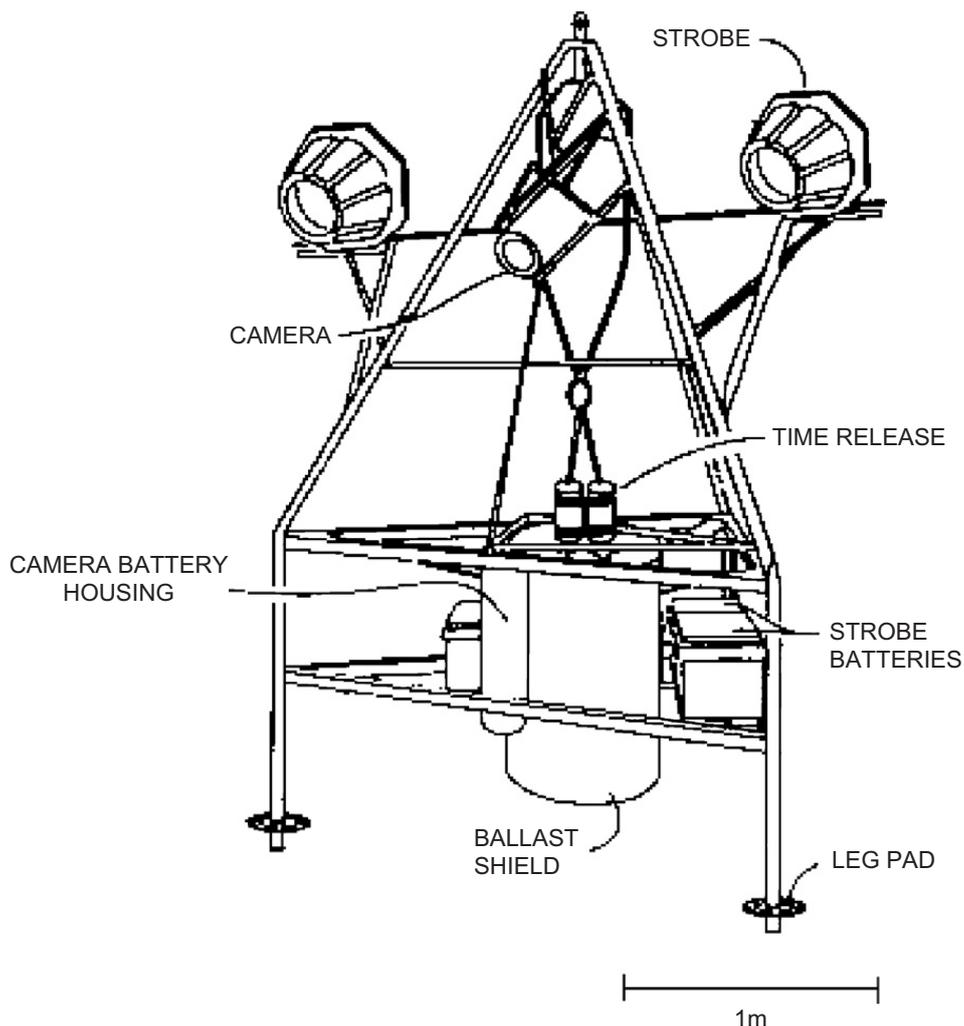
Fig. 1. The time-lapse camera deployed at Station M (adapted from Smith et al., 1993).

time-lapse record were tentatively identified based on appearance, apparent behavior and species geographic range. The presence and relative orientation (swimming or on the seafloor) of individual fish and echinoids observed in the photographic record were digitally recorded and entered into a spreadsheet. Each appearance of an animal in the time-lapse record was counted separately, as there was no practical way to distinguish individuals that may have appeared in multiple frames.

Statistical analyses of the data were performed to determine if there was a positive correlation between the numbers of fish seen at the deployment site and the number of weeks the time-lapse camera was on the seafloor. A weekly time interval was chosen to maximize the number of animals included while retaining sufficient resolution to see changes over time. The numbers of fish seen during each week (168 frames) of the camera deployment were summed, and these weekly sums were then averaged for the entire time series to provide a mean number of animals observed during each week of deployment time. A non-parametric Spearman correlation was run on the summed weekly data from each 4-month deployment. A separate Spearman correlation was run on the combined average weekly data from all of the camera deployments. The same tests were then run on the numbers of echinoids seen over the time-lapse camera deployment period.

3. Results

A total of 1406 fishes and 178 *Echinocrepis* echinoids were observed during the entire time-lapse record, which was composed of 27, 4-month deployments over 15 years (Table 1). The most abundant fish species on and near the seafloor were grenadier fish ($n = 1337$), either *Coryphaenoides*

Fig. 2. A single frame from the long time-series photographic record collected at Station M using a time-lapse camera. A fish (*Coryphaenoides* spp.) can be seen in the right foreground; also visible are epibenthic fauna including several hexactinellid sponge "stalks" which extend from the sediment surface. The viewing area is approximately $20\,\text{m}^2$.

armatus or *Coryphaenoides yaquinae*. These species are indistinguishable in photographic images (D. Bailey, personal communication), and both are common scavenging predators in the deep North Pacific (Priede et al., 1990). Other fishes observed included *Bathysaurus* sp. ($n = 61$; probably *B. mollis*, based on the depth and North Pacific location of the deployment site) and an unidentified species, most likely an Alepocephalid, *Conocara salmoneum* or *Alepocephalus tenobrosus* (J. Drazen, personal communication). Because 95.1% of the individuals observed in the time-lapse record were *Coryphaenoides* species, only *Coryphaenoides* were included in the statistical analysis. Roughly seven times as many *Coryphaenoides* individuals were photographed while swimming ($n = 1176$) than while foraging on the seafloor ($n = 161$), which was inferred from the distinctive head-down tilted posture (Sakurai and Kido, 1992) and possible contact with the sediment surface (Fig. 3). No direct feeding activity was observed.

Only one of the individual deployments, Station 2411 (Table 1), showed a significant correlation between deployment time and the number of *Coryphaenoides* observed ($r_s = -0.57$; $p < 0.05$). None of the data from the other individual deployment periods exhibited significant correlations, either positive or negative. No significant correlation was found between the duration of the time-lapse camera deployment (in weeks) and the number of *Coryphaenoides* per week during all 27 deployments ($r_s = -0.06$; $p = 0.25$) or the combined average number per week ($r_s = -0.39$; $p = 0.11$) observed at the site (Fig. 4a).

A conspicuous mobile epibenthic megafaunal species at Station M, the echinoid *Echinocrepis rostrata*, also did not show evidence of associative behavior around structures. Weekly totals of the number of individual *E. rostrata* observed were obtained in a manner similar to the fish data. Only two of the individual deployments, Stations 612 ($r_s = -0.54$; $p = 0.05$) and 2022 ($r_s = 0.62$;

Table 1
Time-lapse camera deployments and correlations between weekly fish numbers (*Coryphaenoides* spp.) and Echinoid numbers (*Echinocrepis rostrata*) over the deployment period

Station	No. of frames	Deploy date (MM/DD/YY)	Recovery date (MM/DD/YY)	Days deployed	Fish observed	Fish Spearman correlation	*E. rostrata* observed	*E. rostrata* Spearman correlation
223	2773	10/29/1989	02/22/1990	116	63	$r_s = 0.15$; $p = 0.59$	3	$r_s = -0.05$; $p = 0.84$
323	2999	02/23/1990	06/28/1990	125	35	$r_s = -0.10$; $p = 0.70$	4	$r_s = 0.17$; $p = 0.51$
448	2801	06/29/1990	10/24/1990	117	72	$r_s = -0.43$; $p = 0.10$	4	$r_s = -0.19$; $p = 0.49$
612	2927	02/22/1991	06/22/1991	122	43	$r_s = 0.20$; $p = 0.50$	3	**$r_s = -0.54$; $p = 0.05$**[a]
715	718	06/23/1991	07/23/1991	30	16	$r_s = 0.32$; $p = 0.68$	0	N/A
1616	3422	02/22/1993	07/15/1993	143	43	$r_s = 0.30$; $p = 0.22$	5	$r_s = 0.18$; $p = 0.48$
1707	2664	07/17/1993	11/05/1993	111	42	$r_s = -0.02$; $p = 0.96$	7	$r_s = -0.38$; $p = 0.16$
2022	3085	06/18/1994	10/25/1994	129	52	$r_s = -0.06$; $p = 0.81$	5	**$r_s = 0.62$; $p = 0.01$**[a]
2311	2760	10/26/1994	02/18/1995	115	61	$r_s = -0.42$; $p = 0.09$	10	$r_s = -0.01$; $p = 0.98$
2411	2533	02/18/1995	06/04/1995	106	51	**$r_s = -0.57$; $p = 0.02$**[a]	6	$r_s = 0.02$; $p = 0.95$
2612	2533	06/04/1995	11/18/1995	106	65	$r_s = 0.29$; $p = 0.24$	6	$r_s = 0.28$; $p = 0.24$
2718	1789	11/18/1995	02/01/1996	75	23	$r_s = 0.21$; $p = 0.53$	6	$r_s = 0.36$; $p = 0.28$
2918	2922	02/01/1996	06/03/1996	122	56	$r_s = 0.21$; $p = 0.41$	2	$r_s = -0.19$; $p = 0.47$
3027	3086	06/03/1996	10/10/1996	129	66	$r_s = -0.28$; $p = 0.27$	4	$r_s = -0.41$; $p = 0.12$
3301	3934	11/11/1996	04/24/1997	164	51	$r_s = -0.24$; $p = 0.34$	4	$r_s = 0.33$; $p = 0.17$
3408	2972	04/24/1998	08/31/1998	124	70	$r_s = 0.12$; $p = 0.65$	4	$r_s = -0.44$; $p = 0.07$
3510	2629	08/31/1998	12/19/1998	110	43	$r_s = -0.20$; $p = 0.46$	13	$r_s = 0.01$; $p = 0.97$
3708	3143	06/16/2001	10/25/2001	131	41	$r_s = 0.17$; $p = 0.49$	0	N/A
3822	2850	10/26/2001	02/23/2002	119	42	$r_s = 0.25$; $p = 0.34$	7	$r_s = 0.09$; $p = 0.74$
3909	2532	02/24/2002	06/10/2002	106	44	$r_s = 0.02$; $p = 0.95$	6	$r_s = -0.42$; $p = 0.12$
4010	2012	06/11/2002	09/09/2002	84	49	$r_s = -0.51$; $p = 0.08$	0	N/A
4211	3141	10/12/2003	02/26/2004	131	68	$r_s = 0.46$; $p = 0.06$	22	$r_s = 0.17$; $p = 0.48$
4302	2444	02/27/2004	07/30/2004	102	46	$r_s = -0.20$; $p = 0.47$	1	$r_s = -0.43$; $p = 0.11$
4407	2107	08/01/2004	10/27/2004	88	47	$r_s = -0.14$; $p = 0.65$	10	$r_s = 0.41$; $p = 0.16$
4512	2856	10/29/2004	02/23/2005	119	66	$r_s = -0.18$; $p = 0.48$	12	$r_s = 0.29$; $p = 0.26$
4609	2729	02/24/2005	06/14/2005	114	37	$r_s = 0.08$; $p = 0.76$	16	$r_s = -0.34$; $p = 0.20$
4806	3108	11/14/2005	8/15/2006	130	57	$r_s = 0.24$; $p = 0.34$	18	$r_s = -0.18$; $p = 0.47$

[a]Results in bold denote a significant correlation.

$p = 0.01$), exhibited significant correlations between deployment time and the weekly number of *Echinocrepis* echinoids observed. A separate Spearman test of the data from all 27 deployments showed no correlation between the duration of deployment and the total number of animals observed per week ($r_s = -0.02$; $p = 0.67$). The weekly numbers were then averaged together to find the mean number of animals seen per week post-deployment (Fig. 4b). No positive correlation between the duration of deployment of the time-lapse camera and the average weekly number of *E. rostrata* echinoids observed over that period was found ($r_s = -0.32$; $p = 0.19$).

4. Discussion

The results indicate no aggregations of *Coryphaenoides* spp. or *E. rostrata* within the 20 m^2 field-of-view of the time-lapse camera system at Station M. The absence of any sustained aggregation could be explained by the reduced numbers of megafauna at abyssal depths, the open structure of the camera frame, the length of deployment, or deep-sea animal behavior. The low density of prey and food falls on the abyssal plain (Rex, 1981; Smith and Baco, 2003) requires most active predators to move constantly, possibly negating sustained aggregation behavior around structures (Armstrong et al., 1992; Childress, 1995; Collins et al., 1998; Priede et al., 1994). Some studies have found evidence of schooling in deep-sea fish, but nearly all of these aggregations occurred on seamounts, deep-sea coral reefs or in association with spawning behavior, and all were in waters shallower than 4100 m (Drazen et al., 2003; Gunn et al., 1989; Husebø et al., 2002; Krieger and Wing, 2002; Pankhurst, 1988; Rogers, 1994). Seamounts, reefs and large rock outcroppings are theorized to attract fish aggregations for a number of reasons. Currents concentrate plankton, particulate organic matter and other food sources around these structures, the hard substrate provides a surface
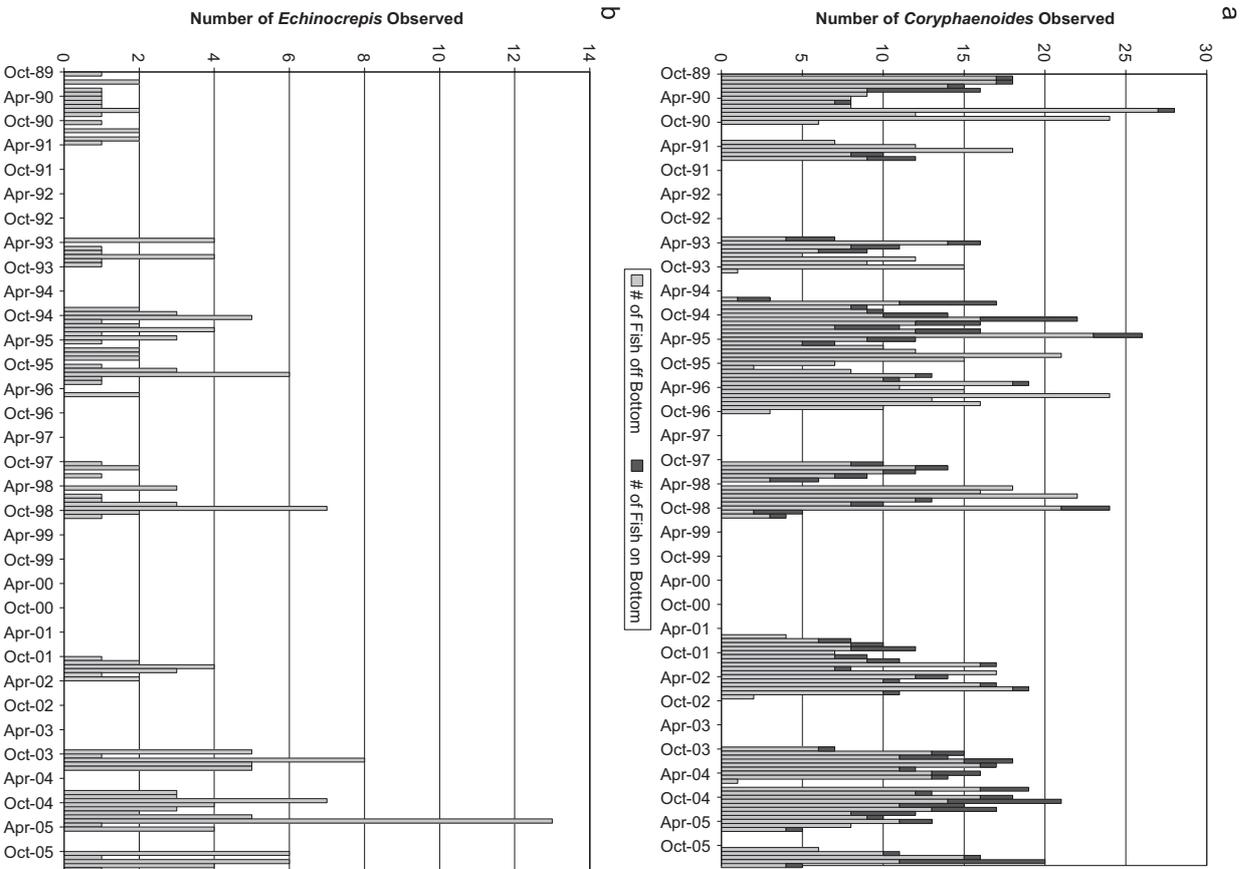
Fig. 3. Chart of monthly abundance of *Coryphaenoides* fish (a) and *Echinocrepis* echinoids (b) at Station M over the 15-year seasonal deployment period, with periodic gaps due to equipment failure or ship unavailability.
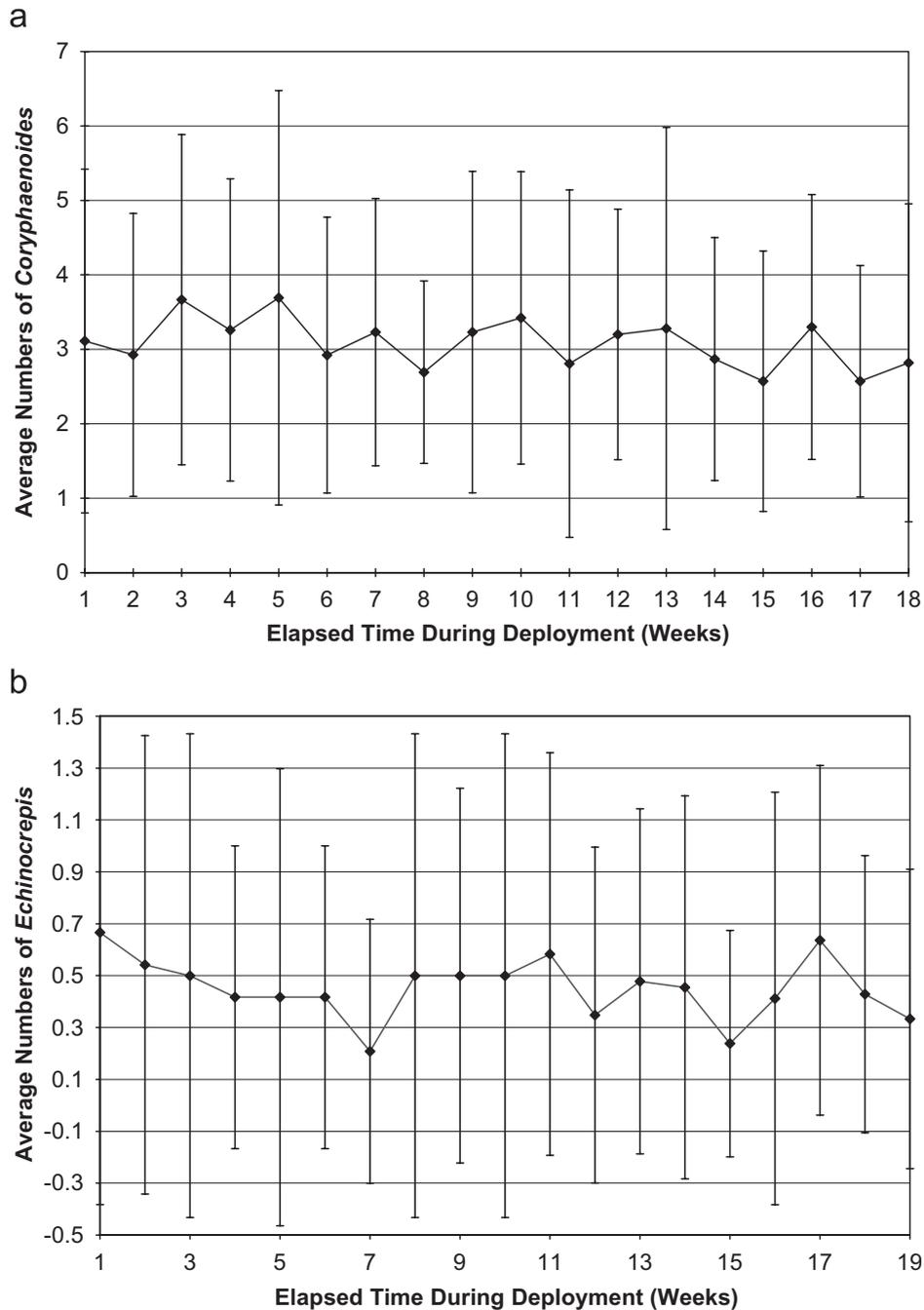
Fig. 4. Average *Coryphaenoides* fish (a) and *Echinocrepis* echinoid (b) abundance at Station M over the deployment period of the time-lapse camera system. The number of animals seen in the photo images was averaged over every week after the camera was deployed for all 27 deployments. No positive correlation was found between deployment time and numbers of near-seafloor *Coryphaenoides* ($r_s = -0.37$; $p = 0.14$) or *Echinocrepis* ($r_s = -0.32$; $p = 0.19$). Error bars indicate the standard deviation.

for egg attachment or for colonization by epifaunal invertebrates that could serve as potential prey and the complex surfaces of seamounts and coral reefs can serve as shelter from predators. Conversely, fish and echinoids inhabiting the abyssal plain may not possess any instinctual need for shelter, and the relatively open structure of the time-lapse camera reduces its potential attractiveness as an attachment

point for eggs or epifaunal invertebrates. While currents at Station M are usually weak compared to currents in slope and seamount habitats, they have been recorded at speeds of nearly 20 cm s^{-1} (Beaulieu and Baldwin, 1998), which is strong enough to cause significant turbulence around a solid object on the seafloor and lift particulate matter into the water column. However, the open

structure of the camera frame provides little resistance to bottom currents, resulting in less trapping of particulate matter.

The lack of epifauna attached to the time-lapse camera frame following a deployment suggests that it does not provide habitat for potential prey animals such as bivalves, crustaceans and other organisms often observed attached to shallower water systems. Such faunal assemblages would supply substrate and a food source sufficient to support larger animals that could eventually result in the attraction of bathypelagic predatory fish. The enrichment of the seafloor by fecal pellets and other detritus secondary to colonization of the frame might then attract deposit-feeding epibenthic megafauna. However, the 4-month deployment time of the time-lapse camera could be insufficient to allow the settlement and growth of attached species. There may be a longer time lag between the deployment of a deep-sea structure, subsequent colonization by epifaunal invertebrates and ensuing aggregation than was observed during these experiments. Shallow-water artificial reefs and other structures can have a noticeable effect on the local community within a period of 1 week (Davis et al., 1982), but deep-sea structures do not appear to attract concentrations of encrusting fauna at speeds or in numbers comparable to hard surfaces located in shallower waters (Beaulieu, 2001; Grassle, 1977; Smith and Hessler, 1987). Surveys of shipwrecks in deep water (Husebø et al., 2002) and of drums of radioactive waste that were sunk in 914–1829 m of water off the Farallon Islands in the 1970s (Columbo and Kendig, 1990; Schell and Sugai, 1980) indicate that deep-sea structures do eventually support elevated local fish and invertebrate populations. Much longer deployments of deep-sea equipment platforms might provide adequate time for the attachment and development of abyssal sessile species.

Mobile epibenthic megafauna represent another potential food source that could attract predatory fish to seafloor structures. Abyssal megafaunal animals such as the echinoid *Echinocrepis* are known to occur in distributions ranging from near-random to patchy across the eastern North Pacific seafloor (Lauerman and Kaufmann, 1998; Lauerman et al., 1996). Large breeding aggregations of echinoids and holothurians have been observed in the deep-sea in several locations worldwide (Billett and Hansen, 1982; Young et al., 1992). However, these distribution patterns appear to be related to the arrival of sinking detrital aggregates and other food sources rather than the presence of natural or artificial structures on the seafloor. Although aggregations of mobile benthic megafauna are often seen in the vicinity of shallow-water artificial reefs (Fabi et al., 2002) and seamounts (Probert et al., 1997), the time-lapse camera data from Station M have provided no evidence of aggregation around structures at abyssal depths. If hard substrate suitable for attachment or shelter is a limiting resource in the deep sea (Drazen et al., 2003; Voight and Grehan, 2000), rapid colonization and aggregation around artificial structures such as the time-lapse camera would be expected. Again, the deployment period of the time-lapse camera system may be insufficient to allow for local increases in the numbers of mobile epibenthic megafauna.

Some studies suggest that deep-sea fish such as *Coryphaenoides* do exhibit schooling behavior near the seafloor on the edge of the continental shelf, at depths greater than 1000 m (Nero et al., 1997), which may act to confuse the sensory field of a potential predator or to utilize the combined search ability of the entire school to find prey (Auster et al., 1992). However, the utility of fixed structures as shelter from predators (Soemarto, 1960) appears to be reduced in the abyss because of the low population density and rare occurrence of large predators (Rex, 1981). Although bioluminescence triggered by contact with a structure could provide a point of reference for organisms able to detect light, the adaptive advantages of using structures as navigational tools or meeting points (Klima and Wickham, 1971) may be obviated by the lack of downwelling light and relatively featureless mud bottom at Station M. The absence of sunlight also removes the need for shade (Damant, 1921; Helfman, 1981), which is another possible cause of shallow-water aggregation around structures. The ability of an individual to locate a potential mate may be enhanced by aggregation behavior around objects in shallow-water or open-ocean environments (Dagorn and Fréon, 1999). However, the possible increased mating success conferred by a stationary aggregation is likely outweighed in the deep sea by the corresponding decrease in time that could be devoted to food finding behavior. The importance of constant motion is supported by the fact that seven times as many *Coryphaenoides* were photographed while swimming than while foraging in contact with the seafloor.

The time-lapse camera is fixed at an oblique angle that views an area approximately 1.8 m from the base of the camera frame, so no information is gathered on the faunal populations within the structure or outside of the camera's field of view. Nevertheless, any localized aggregations of animals around the camera frame should be reflected in an increase in activity within the field of view of the camera as well. Grenadiers, for example, tend to swim actively while remaining relatively close to the seafloor (Priede et al., 1990). Although the study took place at one site in a limited area of the North Pacific, the results may be representative of similar water depths with comparable fish and epifaunal populations. For example, a 6-month baited time-lapse camera deployment in the NE Atlantic at a depth of 2710 m drew large aggregations of *C. armatus* over the first 15 days, which rapidly diminished to less than three individuals per frame and then to single, infrequently seen, individuals by 45 days (Kemp et al., 2006). This experiment became an unbaited camera platform for several months in the deep Atlantic and the downward-looking camera recorded no fish aggregation in and around the frame, despite the residual presence of the bait carcass and a small population of scavenging crustaceans.

The apparent lack of aggregation behavior around the time-lapse camera in the deep North Pacific has significant implications for the study of abyssal populations. Many pelagic and shallow-water fish and invertebrate species congregate around natural and artificial structures, and deep-sea predatory species have been observed to briefly gather around baited camera platforms (Kemp et al., 2006; Priede et al., 1991, 2002). However, it appears that artificial structures alone do not cause significant associative behavior in abyssal fish or detritus-feeding echinoids around the time-lapse camera. Although more study is warranted on the effects of deployments longer than 4 months, long-term time-lapse photography remains a useful tool in studying the "undisturbed" ecology of the abyssal plain.

Acknowledgments

References

Armstrong, J.D., Bagley, P., Priede, I.G., 1992. Photographic and acoustic tracking observations of the behaviour of the grenadier *Coryphaenoides* (*Nematonurus*) *armatus*, the eel *Synaphobranchus bathybius*, and other abyssal demersal fish in the North Atlantic Ocean. Marine Biology 112, 535–544.

Auster, P.J., Griswold, C.A., Youngbluth, M.J., Bailey, G., 1992. Aggregations of myctophid fishes with other pelagic fauna. Environmental Biology of Fishes 39, 133–139.

Beaulieu, S.E., 2001. Colonization of habitat islands in the deep sea: recruitment to glass sponge stalks. Deep-Sea Research I 48, 1121–1137.

Beaulieu, S., Baldwin, R., 1998. Temporal variability in currents and the benthic boundary layer at an abyssal station off central California. Deep-Sea Research II 45, 587–615.

Billett, D.S.M., Hansen, B., 1982. Abyssal aggregations of *Kolga hyalina* Danielssen and Koren (Echinodermata: Holothurioidea) in the Northeast Atlantic Ocean: a preliminary report. Deep-Sea Research 29 (7a), 799–818.

Childress, J.J., 1995. Are there physiological and biochemical adaptations of metabolism in deep-sea animals? Trends in Ecology and Evolution 10 (1), 30–36.

Collins, M.A., Priede, I.G., Addison, S., Smith, A., Bagley, P.M., 1998. Acoustic tracking of the dispersal of organic matter by scavenging fishes in the deep-sea. Hydrobiologia 371/372, 181–186.

Columbo, P., Kendig, M.W., 1990. Analysis and evaluation of a radioactive waste package retrieved from the Farallon Islands 900-meter disposal site. Department of Nuclear Energy, Brookhaven National Laboratory, Upton, NY, p. 65.

Dagorn, L., Fréon, P., 1999. Tropical tuna associated with floating objects: a simulation study of the meeting point hypothesis. Canadian Journal of Fishing and Aquatic Science 56, 984–993.

Damant, G.C.C., 1921. Illumination of plankton. Nature 108, 42–43.

Davis, N., VanBlaricom, G.R., Dayton, P.K., 1982. Man-made structures on marine sediments: effects on adjacent benthic communities. Marine Biology 70, 295–303.

Drazen, J.C., Goffredi, S.K., Schlining, B., Stakes, D.S., 2003. Aggregations of egg-brooding deep-sea fish and cephalopods on the Gorda Escarpment: a reproductive hot spot. Biological Bulletin 205, 1–7.

Fabi, G., Luccarini, F., Panfili, M., Solustri, C., Spagnolo, A., 2002. Effects of an artificial reef on the surrounding soft-bottom community (central Adriatic Sea). ICES Journal of Marine Science 59, S343–S349.

Fréon, P., Dagorn, L., 2000. Review of fish associative behaviour: toward a generalisation of the meeting point hypothesis. Reviews in Fish Biology and Fisheries 10, 183–207.

Golani, D., Diamant, A., 1999. Fish colonization of an artificial reef in the Gulf of Elat, northern Red Sea. Environmental Biology of Fishes 54, 275–282.

Grassle, J.F., 1977. Slow recolonisation of deep-sea sediment. Nature 265, 618–619.

Gunn, J.S., Bruce, B.D., Furlani, D.M., Thresher, R.E., Blaber, S.J.M., 1989. Timing and location of spawning of blue grenadier, *Macruronus novaezelandiae* (Teleostei: Merlucciidae), in Australian coastal waters. Australian Journal of Marine and Freshwater Research 40, 97–112.

Helfman, G.S., 1981. The advantage to fishes of hovering in shade. Copeia 2, 392–400.

Husebø, Å., Nøttestad, L., Fosså, J.H., Furevik, D.M., Jørgensen, S.B., 2002. Distribution and abundance of fish in deep-sea coral habitats. Hydrobiologia 471, 91–99.

Kemp, K.M., Jamieson, A.J., Bagley, P.M., McGrath, H., Bailey, D.M., Collins, M.A., Priede, I.G., 2006. Consumption of large bathyal food fall, a six-month study in the NE Atlantic. Marine Ecology Progress Series 310, 65–76.

Klima, E.F., Wickham, D.A., 1971. Attraction of coastal pelagic fishes with artificial structures. Transactions of American Fishing Society 1, 86–99.

Kojima, S., 1956. Fishing for dolphins in the western part of the Japan Sea. II. Why do the fish take shelter under floating materials? Bulletin on Japanese Society of Scientific Fishing 21 (10), 1049–1052.

Krieger, K.J., Wing, B.L., 2002. Megafauna associations with deepwater corals (*Primnoa* spp.) in the Gulf of Alaska. Hydrobiologia 471, 83–90.

Lauerman, L.M.L., Kaufmann, R.S., 1998. Deep-sea epibenthic echinoderms and a temporally varying food supply: results from a one year time series in the NE Pacific. Deep-Sea Research II 45, 817–842.

Lauerman, L.M.L., Kaufmann, R.S., Smith Jr., K.L., 1996. Distribution and abundance of epibenthic megafauna at a long time-series station in the abyssal northeast Pacific. Deep-Sea Research I 43 (7), 107–1103.

Nero, R.W., Thompson, C.H., Love, R.H., 1997. Abyssopelagic grenadiers: the probable cause of low frequency sound scattering at great depths off the Oregon and California coasts. Deep-Sea Research I 44 (4), 627–645.

Pankhurst, N.W., 1988. Spawning dynamics of orange roughy, *Hoplostethus atlanticus*, in mid-slope waters of New Zealand. Environmental Biology of Fishes 21 (2), 101–116.

Parin, N.V., Fedoryako, B.I., 1999. Pelagic fish communities around floating objects in the open ocean. In: Scott, M.D., Bayliff, W.H., Lennert-Cody, C.E., Schaefer, K.M. (Eds.), Proceedings of the International Workshop on the Ecology and Fisheries for Tunas Associated with Floating Objects, 11–13 February 1992. Inter-American Tropical Tuna Commission Special Report 11. La Jolla, CA, pp. 447–458.

Priede, I.G., Smith Jr., K.L., Armstrong, J.D., 1990. Foraging behaviour of abyssal grenadier fish: inferences from acoustic tagging and tracking in the North Pacific Ocean. Deep-Sea Research 37, 81–101.

Priede, I.G., Bagley, P., Armstrong, J.D., Smith, K.L., Merrett, N.R., 1991. Direct measurement of active dispersal of foodfalls by abyssal demersal fishes. Nature 351, 647–649.

Priede, I.G., Bagley, P.M., Smith Jr., K.L., 1994. Seasonal change in activity of abyssal demersal scavenging grenadiers *Coryphaenoides* (*Nematonurus*) *armatus* in the eastern North Pacific Ocean. Limnology and Oceanography 39 (2), 279–285.

Priede, I.G., Deary, A.R., Bailey, D.M., Smith Jr., K.L., 2002. Low activity and seasonal change in population size structure of grenadiers in the oligotrophic abyssal central North Pacific Ocean. Journal of Fish Biology 63, 187–196.

Probert, P.K., McKnight, D.G., Grove, S.L., 1997. Benthic invertebrate bycatch from a deep-water trawl fishery, Chatham Rise, New Zealand. Aquatic Conservation: Marine and Freshwater Ecosystems 7, 27–40.

Relini, G., Relini, M., Torchia, G., Palandri, G., 2002. Ten years of censuses of fish fauna on the Loano artificial reef. ICES Journal of Marine Science 59, S132–S137.

Rex, M.A., 1981. Community structure in the deep-sea benthos. Annual Reviews on Ecological System 12, 331–353.

Rogers, A.D., 1994. The biology of seamounts. Advances in Marine Biology 30, 305–350.

Sakurai, Y., Kido, K., 1992. Feeding behavior of *Careproctus rastrinus* (Liparididae) in captivity. Japanese Journal of Ichthyology 39, 110–113.

Schell, W.R., Sugai, S., 1980. Radionuclides at the US radioactive waste disposal Site near the Farallon Islands. Health Physics 39 (3), 475–496.

Smith, C.R., Baco, A.R., 2003. Ecology of whale falls at the deep-sea floor. Oceanography and Marine Biology: An Annual Review 41, 311–354.

Smith, C.R., Hessler, R.R., 1987. Colonization and succession in deep-sea ecosystems. Trends in Ecology and Evolution 2 (12), 359–363.

Smith Jr., K.L., Baldwin, R.J., Williams, P.M., 1992. Reconciling particulate organic carbon flux and sediment community oxygen consumption in the deep North Pacific. Nature 359, 313–316.

Smith Jr., K.L., Kaufmann, R.S., Wakefield, W.W., 1993. Mobile megafaunal activity monitored with a time-lapse camera in the abyssal North Pacific. Deep-Sea Research I 40 (11/12), 2307–2324.

Soemarto, 1960. Fish behaviour with special reference to pelagic schooling species: Lajang (*Decapterus* spp.). Eighth Proceedings of Indo-Pacific Fisheries Council 3, 89–93.

Stephens II, J., Pondella, D., 2002. Larval productivity of a mature artificial reef: the ichthyoplankton of King Harbor, California, 1974–1997. ICES Journal of Marine Science 59, S51–S58.

Uda, M., 1933. Types of skipjack schools and their fishing qualities. Bulletin on Japanese Society of Scientific Fishing 2 (3), 107–111.

Voight, J.R., Grehan, A.J., 2000. Egg brooding by deep-sea octopuses in the North Pacific Ocean. Biological Bulletin 198, 94–100.

Wakefield, W.W., Genin, A., 1987. The use of a Canadian (perspective) grid in deep-sea photography. Deep-Sea Research 34, 469–478.

Wolf, P.R., 1983. Elements of Photogrammetry: With Air Photo Interpretation and Remote Sensing. McGraw-Hill, New York.

Young, C.M., Tyler, P.M., Cameron, J.L., Rumrill, S.G., 1992. Seasonal breeding aggregations in low-density populations of the bathyal echinoid *Stylocidaris lineata*. Marine Biology 113, 603–612.