Marine Biology 84: 83–91 (1984)

Marine Biology
International Journal on Life in Oceans and Coastal Waters

Effect of near-bottom currents on detection of bait by the abyssal grenadier fishes *Coryphaenoides* spp., recorded *in situ* with a video camera on a free vehicle

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Abstract

Free vehicles carrying bait, video cameras and current meters were deployed at three sites in the abyssal North Pacific Ocean in 1983 and 1984 (at depths of 3 800, 4 400 and 5 800 m). From the recovered video recordings, we analyzed responses of the abyssal grenadier fishes *Coryphaenoides* spp. to the bait, and, from the recovered current meters, we determined the velocities of the near-bottom tidal currents. The grenadiers consistently arrived at the camera within minutes after it landed (7.5 to 41 min, $N=9$ deployments), but the times of the first arrivals tended to increase within increasing distance from shore (which was correlated with increasing depth). Faster responses occurred near times of peak, as opposed to slack, current velocities. Behavioral observations suggest that grenadiers primarily use olfaction in locating the bait, because 75% of early arrivals came from down-current. Those coming from up-current typically did not appear to sense the bait until arriving down-current from it. A "wait" rather than "search" strategy is proposed for the use of food falls by these deep-sea scavengers.

Introduction

Mobile deep-sea scavengers such as fishes and amphipods are currently regarded as an important component of the deep-sea food web because of their supposed consumption and dispersion of large organic falls (e.g. Isaacs, 1969; Dayton and Hessler, 1972; Haedrich and Rowe, 1977). However, naturally-occurring organic falls are rarely observed in the abyss (Stockton and DeLaca, 1982), making it difficult or impossible to study how scavengers find and utilize them. Thus, "artificial" organic falls in the form of baited, free-vehicle traps and free-vehicle time-lapse cameras are used to attract scavengers for collection and observation (e.g. Hessler *et al.*, 1978; Thurston, 1979; Lampitt *et al.*, 1983).

Time-lapse photography has shown that grenadier fish and amphipods may arrive at bait within minutes after it contacts the seafloor (Dayton and Hessler, 1972; Isaacs and Schwartzlose, 1975; Hessler *et al.*, 1978). The rapid responses may reflect selection pressure for the quick localization and consumption of ostensibly rare and unpredictable food occurrences in an otherwise barren environment. Scavengers may typically be widely dispersed, as suggested by Dayton and Hessler (1972), but congregate rapidly at organic falls to insure themselves of an adequate meal. To achieve this, the scavengers must not only detect a food fall, but must proceed directly to it.

How grenadiers and amphipods find bait (or naturally-occurring organic falls) in abyssal darkness is not obvious. Studies using time-lapse photography suggest that near-bottom currents, which are tidal (Isaacs *et al.*, 1966; Wimbush and Munk, 1970), are important directional cues and may, by dispersing odor, provide a means for detection. For example, Thurston (1979) noted that virtually every amphipod seen approaching a baited camera in the North Atlantic did so from the down-current direction. Dayton and Hessler (1972) thought that polarized orientation of grenadiers as seen in their photographs suggested an orientation with the current, and Ingram and Hessler (1983) gave circumstantial evidence for the importance of near-bottom currents in the attraction of amphipods to bait. Isaacs and Schwartzlose (1975), Guennegan and Rannou (1979) and Lampitt *et al.* (1983) have suggested that the numbers of animals seen around bait at a given time may be related to the strength of the tidal current.

Near-bottom tidal currents could be of importance to scavengers in finding organic food falls, but their effects have not been specifically investigated. Here we report experiments designed and conducted to determine the importance of near-bottom tidal currents to grenadiers in finding artificial organic food falls in the abyss of the Pacific Ocean.

Materials and methods

Equipment

The study relied on the coordinated use of a free-vehicle video camera and recording system (FVV) and Savonius-type free-vehicle current meters (Isaacs *et al.,* 1966). The free-vehicle video was initially developed by M. Olsson and R. Merewether at the Scripps Institution of Oceanography, but has been significantly modified by M. Laver and J. Edelman of our laboratory. The system functions as a free-fall, baited camera, similar to those used by Isaacs and Schwartzlose (1975), Lampitt *et al.* (1983), and Lampitt and Burnham (1983). However, our system has greater analytical capabilities since it is programmable and records moving rather than still images. Components of the system include: a Panasonic (NV8420) video-cassette recorder mounted in a 43.2 cm benthos glass sphere, a Panasonic video camera (WV1650) housed in a windowed pressure case (11 cm o.d. × 32 cm), five (10.8 V, 35 W) projector lamps placed in a 25.4 cm benthos sphere, a rechargeable gel-cell battery (12 V, 76 A · h; Deep-Sea Power and Light Co., San Diego, California, USA), and a hydrophone.

The components are mounted in a trapezoidal-shaped frame (69 cm × 91 cm × 124 cm) made of fiberglass angle (4.6 cm × 4.6 cm × 0.64 cm), with the camera positioned to look down on the seafloor from slightly off center at an altitude of about 2.5 m. Approximately 4 m^2 of seafloor comprise the field-of-view (hereafter called the camera field). The instrument is connected in line to two 43.2 cm benthos spheres positioned 40 m above it, and free-vehicle mast flotation positioned 20 m above the spheres (Smith *et al.,* 1979). A v-shaped wire bridle below the fiberglass frame supports a precision time-release (Sessions and Marshall, 1971). (A full description of the FVV array and electronics may be found in Laver *et al.,* 1984.) The entire array is anchored to the seafloor by disposable ballast of 430 kg attached to the time-release. A cross (four 1 m lengths of PVC tube), with 10 cm incremental markings along each arm, is bolted to the ballast. The FVV is baited with Pacific mackerel (*Scomber japonica*). Two or three whole fish (each weighing about 0.5 kg) tied to the arms of the cross were used as bait in most deployments.

Experimental protocol

Tidal currents of the eastern Pacific Ocean are strongly semi-diurnal and dominated by the semi-diurnal lunar tidal component (Wimbush and Munk, 1970; Taft *et al.,* 1981). Data from current meters (K. Smith, unpublished data; Wimbush and Munk, 1970) indicate multiple daily maxima in current velocities at abyssal depths in the eastern North Pacific which may exceed 5.0 cm s^{-1}. Near the continent, four daily maxima are seen and appear to result from the twice daily ebb and flood of the semi-diurnal tides. With increasing distance offshore the number of obvious daily maxima decreases (K. Smith, unpublished data).

The FVV (baited) and current meters were deployed at three sites in the eastern and central North Pacific Ocean: Stations C, F, and CNP lying at 3 800, 4 400, and 5 800 m depth, respectively (Smith *et al.,* 1983). Increasing depth was correlated with distance from shore: Stations C, F, and CNP were respectively 315, 499, and 3 219 km west of San Diego, USA. All three stations were visited in March–April, 1984 and Stations C and CNP in October–November, 1983. Station CNP was also visited in June, 1983. The purpose of the cruise in March–April, 1984, was to measure the time required for grenadiers (*Coryphaenoides* spp.) to locate the baited FVV, and to determine how the time varied as a function of changes in velocities of near-bottom tidal currents. The emphasis was on measuring arrival times of the early-arriving fish, because near-bottom tidal currents perpetually change velocity and usually direction, and it is only in the first hour or so after landing that a clear picture of response patterns can be obtained. To achieve this, we adopted the following general protocol for the cruise of March–April, 1984.

We deployed two free-vehicle current meters within about one day of arriving on station. Current meters were suspended at 2 to 3 m above the bottom using the same general arrangement of ballast, flotation, and precision time-releases described for the FVV. The first, a short-term current meter, was recovered after 22 to 26 h, the records analyzed on board, and the times of peak and slack current velocities used to project the tidal cycle for the remaining station time. The second, a long-term current meter, remained on the bottom most of the time the station was occupied. Its purpose was to provide data on current velocities during periods when the FVV was also on the bottom. We have assumed that current velocities at the FVV agreed with those recorded simultaneously by the current meters, although the current meters and the FVV were generally separated by 3 to 9 km. This assumption is based on detailed surveys of bottom topography made with a multibeam echo-sounding system (Sea Beam) (Smith, unpublished data). At Stations C and CNP, the seafloor in the area of the deployments was relatively flat, with little relief interposing between the current meters and the FVV. The seafloor at Station F was more rugged, but there was still no significant relief interposing between the instruments.

The landings of the FVV were timed to coincide as nearly as possible with a time of peak or slack current in order to maximize expected differences in arrival times of grenadiers. Assuming an average descent rate of 52 m min^{-1}, we calculated the time required to reach the bottom and then deployed the FVV so that it arrived on the bottom near peak or slack current. Except for the first deployment (Station 119C) in which the system activated too late to record the landing, the FVV began recording at least 5 min before landing so the exact time of landing could be matched with the current data from the concurrent long-term current meter. (Time of landing at Station 119C was calculated from the average descent rate.) The FVV was programmed to record continuously for 95 min, and then for 2 min every 15 min thereafter. This partitioning of the normal 2 h recording time of VHS cassettes allowed recordings over a 4 h period on the bottom.

The FVV was deployed without regard to the tidal cycle during the cruises of 1983, but free-vehicle current meters were deployed concurrently with the FVV. For these 1983 deployments, the FVV was programmed to record for 2 or 3 min at 15 or 30 min intervals after arriving on the bottom, with the light extinguished between recording times. Video tapes made at Station CNP were used to eliminate the possibility that light has a positive or negative influence on the attraction of fish to the bait. We counted the number of fish present at the start and end of the recording (lighted) sequences directly from the video monitor and then compared the numbers statistically using the Wilcoxon signed-ranks test, testing the hypothesis that the numbers are equal.

Analysis

The following data were gathered whenever possible for each deployment of the FVV in March–April, 1984: the exact time of landing, elapsed time between landing and the arrival of the first 2 to 7 fish, swimming speeds of arriving fish, and the direction from which each fish came relative to the direction of current flow across the camera field. Direction of current flow was initially obtained (Station C) using a benthos current vane (with compass) placed within view of the video camera. The vane was eventually lost (Station C), requiring that current direction across the camera field be determined by viewing the drift of particles, and the clearing of the sediment cloud created when the FVV landed. This procedure worked well, except for a single deployment at the deepest station at low current velocities.

Elapsed time to the first arriving fish was compared when possible with the velocity of the near-bottom tidal current obtained from the long-term current meter. However, two of the long-term current meters were lost (Stations C and CNP). We have therefore estimated the velocity of the near-bottom currents at those stations when the FVV landed based on the projection of the tidal cycle, using data from the short-term current meter deployed at the same stations prior to the FVV deployments (cf. Fig. 1 A and B). The projections, however, do not give the exact current velocities occurring when the FVV landed. We use them here to show our timing of the FVV deployments with respect to the tidally-mediated changes in current velocities at stations where the long-term current meters were lost. Since landings of the FVV were timed to coincide with a time of either slack or peak current. differences in arrival times can qualitatively, if not quantitatively, be related to current velocity if the projections are accepted as a reasonable approximation of the true tidal cycle. Time intervals between consecutive arrivals were recorded and the mean interval determined for each deployment.

For the first four arrivals in the direction analysis, we noted the direction of their approach relative to the direction of current flow across the camera field and, when possible, their swimming speeds. Use of the first four arrivals was an *a posteriori* decision based on the completeness of arrival data for all deployments (Table 1). The approach direction is here defined as the reciprocal heading of the fish (i.e., the direction from which it came) relative to the current direction across the camera field. The direction is not given in degrees since that level of precision is beyond the capabilities of the present system. Rather, the reciprocal heading of each fish was assigned to one of eight equal divisions of a circle (spanning 45° each) surrounding an arbitrary current direction to which all deployments were standardized (Fig. 2). The distribution of approach directions around the circle was then tested for uniformity using chi-square. The use of eight divisions results in the minimum allowable expected frequency of four per cell, which conforms to the guidelines in Batschelet (1981).

We deployed the FVV once without bait on the March–April 1984 cruise to test whether the fish are attracted to the FVV by the light which was on continuously, or the sound of the landing. This was done in addition to our prior analysis of tapes from 1983 regarding the effect of the light.

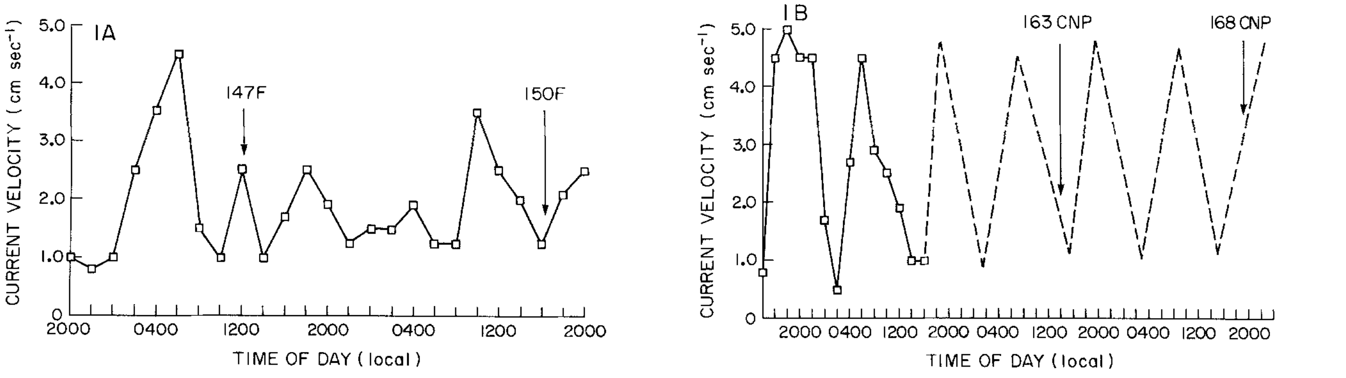

Fig. 1. Tidal current velocities vs time of day (hrs) at two Pacific Ocean Stations. (A) Data from long-term current meter at Station F (32°50.1′N; 124°09.9′W) (4 420 m) during neap tides between 9 and 10 April 1984; (B) data from short-term current meter (continuous line) and projection of tidal cycle (dashed line) at Station CNP (31°01.8′N; 159°00.0′W) (5 800 m) during spring tides between 18 and 21 April 1984. Arrows in (A) and (B) show times of landing of the free-vehicle video camera

An "arrival" is here defined as any fish entering the camera field (an area of about 4 m^2) for the first time and searching for the bait. Any fish seen just passing through the camera field was not so counted. This was observed in three separate deployments prior to a "first arrival". A fish was considered to be searching if it entered the camera field swimming close to the bottom and stayed until making contact with the bait. Cases where early arrivals remained in full view as more fish arrived resulted in the highest number of precisely determined arrival times. However, early arrivals sometimes moved out of and into view as other fish continued to arrive. In such cases, "new" arrivals were distinguished from "old" arrivals when feasible by noting the size differences of incoming individuals; the PVC cross was used as a reference scale for estimating fish length.

Results

Grenadiers were always the first fish seen and were numerically dominant around the bait. Prior sampling studies indicate that two abyssal species are present at Stations C and F, *Coryphaenoides armatus variabilis* and *C. yaquinae,* but only *C. yaquinae* is present at CNP (Wilson and Waples, 1983, 1984). Since *C. armatus variabilis* and *C. yaquinae* cannot be distinguished in the video tapes we hereafter refer to them collectively. An unidentified cusk eel (family Ophidiidae) of up to 1 m in length was seen in several video tapes at stations west of, but not including, Station C. A fish resembling this ophidiid was photographed at a bait drop (5 861 m) on the lip of the Philippine trench (Hessler *et al.,* 1978).

Grenadiers consistently arrived within minutes of the FVV landings (Table 1). The fastest arrival times of 7.5 and 7.8 min occurred at Station C in moderately fast currents of 3.6 and 4.0 cm s^{-1}, respectively, whereas the slowest time of 41 min occurred at Station CNP in a current estimated at $\leqq$ 3 cm s^{-1} (Table 1). Slowest arrival times at all three stations occurred when the FVV was deployed to coincide with slack current; however, confirmation of a landing during a slack current was made only at Station F. The time to the first arrival at Station F doubled when the current velocity dropped by one-half (Table 1).

No fish "arrived at" or investigated the unbaited FVV at Station 133C in 1 h of viewing (Table 1), although one grenadier passed through the camera field about 30 min after landing. The comparison of the numbers of fish present at the start and end of lighted sequences showed no significant differences ($p > 0.05$, Wilcoxon signed-ranks, two-tailed test, Tables 2 and 3) indicating that the fish are neither attracted to, nor repelled by, the light.

The mean interval of time between consecutive arrivals (up to the seventh) was variable within and between stations. It ranged from 0.7 to 5.7 min (Table 1). There is no correlation between the time elapsed until the first arrival and the mean time interval between subsequent arrivals ($p > 0.05$, Spearman rank test). Thus, quick first arrivals are not necessarily followed by short intervals between subsequent arrivals.

Fig. 2 shows the distribution of arrival directions of the first four arrivals of each deployment. The symbols indicate which of eight divisions of relative reciprocal headings (i.e., relative to the apparent current direction) the fish had when entering the camera field. Most of the first four arrivals (75%) were from down-current directions, heading generally into the current. Some, including two first arrivals, approached from an up-current direction. Arrival scenarios for four separate deployments (Fig. 3) show examples of this, where fish are seen entering the camera field (within minutes of landing) from opposite sides and with nearly diametrically-opposed headings.

Grenadiers arriving from down-current approached the bait directly, and were seen either gliding or swimming just above the bottom at less than 5 to 30 cm s^{-1}. They often bumped into the arms of the cross, or into the ballast itself, narrowly missing the bait before eventually locating

Table 1. *Coryphaenoides* spp. Summary of arrival times of grenadiers and current velocities for free-vehicle video (FVV) deployments. –: no data

Station	Depth (m)	Date of deploy-ment	Time (hrs) of landing (local)	Velocity of near-bottom currents at time of landing (cm s^{-1})	Times of first 7 consecutive arrivals (min after FVV landing) 1	2	3	4	5	6	7	Mean interval (min) between consecutive arrivals (± SE)
155 C	3 650	4. XI. 1983	13.40	3.6	7.5	8.0						ND
119 C	3 800	30. III. 1984	14.20	4.0	7.8	10.8	12.2	12.3	14.6	15.8	18.0	1.7±0.4
125 C	3 700	2. IV. 1984	12.50	≦2.5[b]	12.0	14.8	17.0	24.2	26.1			3.5 + 1.1
128 C	3 800	3. IV. 1984	13.25	≦2.5[b]	12.7	13.0	15.4	15.9	16.1	16.5	16.7	0.7±0.3
147 F	4 390	9. IV. 1984	11.55	2.5	13.9	14.1	15.0	17.2	18.6	19.3	19.4	0.9±0.3
150 F	4 550	10. IV. 1984	16.05	1.3	27.0	29.0	29.5	31.5	32.0	32.7		1.1±0.3
163 CNP	5 800	20. IV. 1984	14.05	≦3.0[b]	41.0	44.6	45.1					2.6±1.5
168 CNP	5 800	21. IV. 1984	18.55	≧3.0[b]	16.9	19.9	21.5	24.1	26.5			2.4±0.3
174 CNP	5 800	22. IV. 1984	22.05	≧3.0[b]	14.9	22.7	27.4	32.0				5.7±0.9
133 C[a]	3 790	5. IV. 1984	21.29	≦2.5[b]	No arrivals within 1 h after landing							

[a] Unbaited

[b] Estimated current velocities from a projection of tidal cycles at time of landing based on data from short-term current meters

Table 2. *Coryphaenoides* spp. Numbers of grenadiers within the field-of-view at start and end of lighted (2 min) sequences. Deployment at Station 142-CNP (5 650 m), June, 1983. $p > 0.05$, Wilcoxon signed-ranks test for H_0: number at start = number at end

	Sequence No.																												
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Time since landing of FVV (h)	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.25	4.5	4.75	5.0	5.25	5.5	5.75	6.0	6.25	6.5	6.75	7.0	7.25	7.5	7.75	8.0	8.25	8.5	8.75	9.0	9.25	9.75
No. at start	1	5	2	4	6	9	11	7	8	5	10	4	8	15	7	16	12	11	6	6	10	8	7	15	16	7	12	9	11
No. at end	0	4	3	2	7	8	10	7	6	4	9	6	10	11	8	12	10	10	10	12	8	7	10	9	12	11	10	12	12

Table 3. *Coryphaenoides* spp. Numbers of grenadiers within the field-of-view at start and end of lighted (2 or 3 min) sequences. Deployment at Station 116-CNP (5 500 m), October, 1983. $p > 0.05$, Wilcoxon signed-ranks test for H_0: number at start = number at end

	Sequence No.:																														
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Time since landing of FVV (h)	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5
No. at start	1	3	4	6	3	6	6	10	9	13	11	13	14	16	18	18	22	22	20	23	18	17	17	5	22	23	24	19	11	12	12
No. at end	1	2	4	6	6	3	10	8	10	7	13	19	14	17	19	18	21	16	20	15	15	16	26	20	21	21	23	16	12	11	11

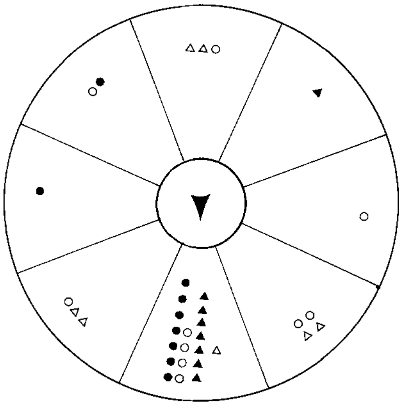

Fig. 2. *Coryphaenoides* spp. Distribution of arrival directions for the first 4 grenadiers arriving relative to current direction in nine deployments of the baited video camera. The circle is an imaginary circle around an arbitrary current direction (indicated by arrow) to which all current directions were standardized. The eight equal divisions represent ranges of directions from which the fish arrived relative to the current direction. Symbols show how many of the fish came from each of the eight categories of directions; positions of the symbols within each cell have no meaning. ●: First arrivals; ○: second arrivals; ▲: third arrivals; △: fourth arrivals. The null hypothesis that the distribution is uniform is rejected, $p < 0.05$ (chi-square)

it. Some fish appeared to lose interest in the bait after attempting a few bites since they wandered away then leisurely returned after a few minutes. This behavior was often repeated. When many fish were present, moving in and out was sometimes coordinated such that pulses of activity were observed. There would be a period when several fish were in view, followed by one in which few were seen. The pulses of activity were seen both when lighting was intermittent as in the deployments of 1983, and when the light was on continuously as in the deployments of 1984.

Grenadiers arriving from directions other than down-current generally did not go directly to the bait. Rather, they appeared to search for it, remaining close to the bottom and eventually arriving at a position approximately down-current from it, whereupon they turned and located it from the down-current direction (Fig. 3).

With increased numbers around the bait, many grenadiers were seen just "milling about", but higher off the bottom than those attempting to feed. Some swam straight-up toward, then past, the camera, but most remained down-current of the bait most of the time. No agonistic or aggressive behaviors were seen, although fish occasionally

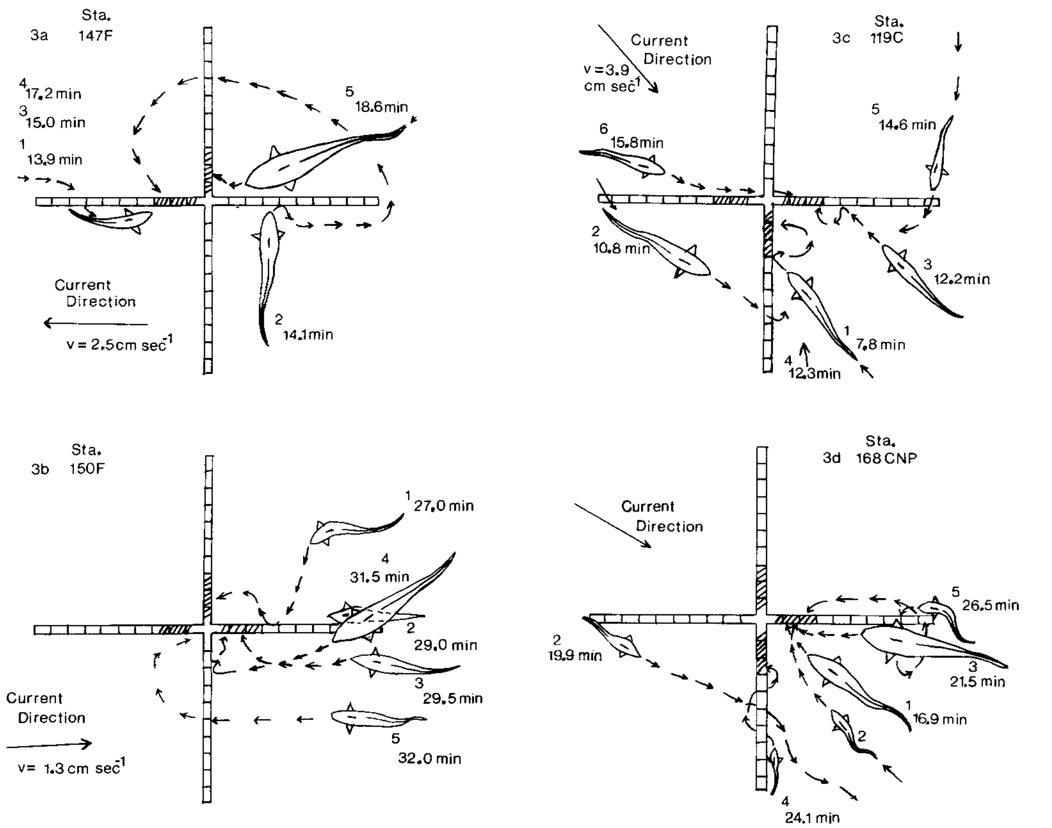

Fig. 3. *Coryphaenoides* spp. Arrival directions of grenadiers and paths followed to the bait or toward the bait for a variable number of arrivals in four separate deployments of the video camera. Diagrams represent top views of the area of the camera field: large crosses are cross-bars forming the reference grid, position of bait is shown as hatch marks near the center. Cross arms are marked at 10 cm intervals. Numbers indicate order of arrival of each fish represented, and time elapsed since landing is given below the numbers. Positions of fish show approximately their orientation and heading as they entered the camera field, dashed lines indicate approximate path followed to the bait, or in the direction toward it. Fish sizes are roughly to scale. Large arrow indicates current direction across grid (v = velocity). Ballast, wire bridle, and time release have been omitted

collided while swimming about. Although there were two or three separate bait parcels tied to the arms of the cross, several grenadiers would often congregate on one, while other parcels lay unmolested. Similar behavior was noted for amphipods by Hessler *et al.* (1978). Eventually, however, all of the bait is consumed even though several hours may be required (personal observations of long-term recordings).

Discussion

The initial attraction of abyssal grenadiers (*Coryphaenoides* spp.) to bait is consistently rapid, even between regions as different as those underlying the eutrophic California Current (Stations C and F) and the oligotrophic gyre of central North Pacific Ocean (Station CNP). The variability in response times could depend as much on the velocities of near-bottom tidal currents as on any inherent differences between species or regions, but the data collected here are insufficient for a two-way analysis of variance relating response times both with region and current velocity. Nevertheless, there is a trend in response times which should not be overlooked. Times to first arrivals tend to get longer in going from Station C (3 800 m) to Station CNP (5 800 m) (Table 1). Even so, the time scale over which first arrivals occur is minutes across all deployments, suggesting that the rates at which food falls are found (and presumably used) are similar at all abyssal depths across the eastern portion of the North Pacific Ocean.

Since the fish tended to approach the bait from down-current and did not converge at the unbaited "control" deployment, the dispersal of bait-odor by the current as opposed to sound of the impact or the light is apparently how most early-arriving fish detect organic falls. The average time until the first arrival at Station C was 10 min ($\pm$ 1.4 min, $N = 4$) after landing. Current flowing at about 2.4 m min^{-1} (4 cm s^{-1}) at Station C would not disperse the odor further than about 24 m in a single direction in 10 min. Similarly, the distance odor dispersed at Station F by the time of the first arrivals should have been about 21 m (147F) and 22 m (150F). The agreement between the estimated distances of odor dispersal at Station F is important, since in one case the current velocity and response time were both fast (147F), but in the other both were slow (150F).

The short-term current meter data at Station CNP showed velocities ranging from < 1 to 5 cm s^{-1} (Fig. 1B). Estimated velocities and the timing of our deployments with regard to the tidal cycle suggest that the odor would extend maximally to about 60 m on any deployment by the time of the first arrival. Fish using odor to detect and find bait, and arriving within the observed time spans, were probably within these respective distances when the FVV landed. These are certainly horizontal distances along the bottom, since Ingram and Hessler (1983) calculated that in the central North Pacific (5 808 m) it would take at least 48 h (four tidal cycles) for an odor plume to reach an altitude of 60 m, and at least 12 h to reach an altitude of 20 m. Grenadiers at Station CNP arrived at the bait in $\leqq$ 41 min (Table 1).

A relatively high density of abyssal fishes on the seafloor would account for the rapid localization of bait, since at any (random) locale where bait might fall, several fish would be nearby, capable of finding it quickly. Pearcy *et al.* (1982), using bottom trawls, estimated the density of *Coryphaenoides armatus variabilis* off the Oregon coast at 1.4 to 3.7 individuals 1 000 m^{-2}. The lowest value of 1.4 would predict (on average) one individual in an imaginary circle of about 18 m radius. Thus, on average, at least one individual would be expected to be within about 18 m of any random food fall. Distance from landing sites estimated for *C. armatus variabilis* at Stations C and F based on arrival times and current velocities are consistent with the density estimates of Pearcy *et al.* (1982) for that species. Similarly, Cohen and Pawson (1977) estimated the density of *C. armatus armatus* in the western North Atlantic Ocean at between 1.0 and 3.9 individuals 1 000 m^{-2} (2 300 to 2 800 m) based on phototransects using the submersible "Alvin".

The energetic strategy for the use of food falls at relatively high population densities might be to "wait" rather than "search", since searching has the disadvantage of expending energy with low probability of success, since it is likely a food fall would land close to another individual. "Search" models in which scavengers are envisioned as hovering or patrolling at significant altitudes ($\geqq$ 20 m) to increase the likelihood of finding carrion on the seafloor (Jumars and Gallagher, 1982) seem untenable, at least for grenadiers, in the light of present observations. The response times of first arrivals are far less than the amount of time required for an odor plume to rise to any appreciable height. Moreover, the fish appear to primarily track odor up-current along the bottom in most cases. When the fish arrive from directions other than down-current it is still along the bottom rather than headlong from above. A scavenger hovering at any appreciable altitude to detect (Jumars and Gallagher, 1982) or maintain a chemosensory overview (Ingram and Hessler, 1983) of food falls on the bottom would have little chance of arriving at the food before scavengers near the bottom and down-current from the fall. Except in the case of large falls requiring several hours to consume, hoverers probably could not arrive in sufficient time to benefit from a food fall unless they routinely track odor trails left in the water column as food materials fall to the seafloor. The ability to track such odor trails has been shown for a planktonic shrimp under laboratory conditions (Hamner and Hamner, 1977), but only after the shrimp contacts the trail by chance through normal swimming activity.

A "wait" strategy for the use of food falls requires only short-range searching in direct response to a stimulus, probably odor. Waiting, however, implies that near-by food falls are inevitable and therefore predictable over some temporal scale as yet unknown. If the most frequent food falls are of small but abundant pelagic organisms, such as squids and mid-water fishes found in the guts of *Coryphaenoides armatus* and other benthopelagic grenadiers (Haedrich and Henderson, 1974; Pearcy and Ambler, 1974), then they would appear to be consumed rapidly, probably in minutes. This would mean a relatively short residence time for most organic falls in the deep-sea regions investigated here. Fast consumption by an abundant population of scavengers would quickly remove evidence of organic falls even if occurring at a high rate. Thus, on the basis of existing data, one does not know whether food falls are rare or frequent events, and their importance in supplying benthopelagic scavengers remains an open question.

How grenadiers detect bait or naturally-occurring food falls, even if nearby, is still not completely explained by our findings. Our analysis of arrival directions shows the apparent importance of near-bottom tidal currents as directional cues and for dispersing odor. Still, some fish came quickly from up-current directions apparently without the benefit of odor dispersal in their direction. There are at least four possible explanations for up-current arrivals. (1) Fish entering the camera field from up-current initially approached the bait from down-current, but passed the FVV out-of-view, turned around once the odor was no longer detectable, then searched going with the current or perpendicular to it. (2) The fish detect sounds of feeding, or of stereotyped movements associated with feeding, of conspecifics at the bait and are attracted to it, as suggested by Smith and Baldwin (1984) for scavenging amphipods. (3) The fish can sense polarized movements of others toward the bait and follow in a manner suggested by Isaacs and Schwartzlose (1975). (4) The sediment stirred up as the FVV lands acts as high-density turbidity current propelled by the bow wave of the impact. It carries the odor of the bait some appreciable distance against the prevailing current where it is momentarily detected by a fish before the cloud is carried back down-current. The fish then searches for the source, going with the current. (Movement of the sediment cloud up-current then back down-current was observed in a few deployments.)

Although none of the above explanations can be eliminated as a means of detection, (1) and (4) seem most likely, since the behavior of the early-arriving fish once inside the camera field suggests that the bait has already been detected and is being searched for using olfaction. Fish arriving from up-current directions appear unable to locate the bait until reaching a position down-current from it. If arriving fish homed on sounds of movement or feeding of others at the bait, then one would expect them to go directly to it, irrespective of the prevailing current direction. Moreover, arrival directions should have a uniform circular distribution, since sounds would travel in all directions. Neither of these responses was observed. However, beyond the first seven or so arrivals, newcomers and their arrival directions are difficult to identify since many fish are arriving almost simultaneously, with many moving into and out of the camera field. Thus, it cannot be proved here that the circular distribution of arrival directions of late-arrivals, which may number twenty or more individuals, is the same as that of early-arrivals over the period required for complete consumption of a large food fall. Detection and localization through sounds (mechanoreception) might be important after a critical "noise level" is reached through increased numbers at the bait, in which case fish might arrive from all directions. Similarly, attraction by the sensing of polarized group-movements might follow after some number of individuals beyond the first few have converged at the bait.

Acknowledgements. We thank M. Laver and J. Edelman for technical help with the free-vehicle video and R. Baldwin for technical help with the current meters. The manuscript was improved by comments from R. R. Hessler, N. D. Holland, C. L. Ingram, R. H. Rosenblatt, W. L. Stockton, W. W. Wakefield, and an anonymous reviewer. The work was supported by NSF Grant OCE-81-17661 and a contract from Sandia laboratories.

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Date of final manuscript acceptance: September 21, 1984.
Communicated by N. D. Holland, La Jolla