Chapter 1

Directional Swimming Behavior Facilitates the Aggregation of Sea Nettles *Chrysaora fuscescens* Along the Monterey Bay Upwelling Shadow, Monterey Bay, California

Introduction

Ocean fronts have been known to science for over a century (Haeckel, 1893). These convergent features occur in surface waters, and are often marked by steep horizontal gradients in temperature and/or salinity over distances of tens of meters to kilometers. Intense biological activity is often associated with fronts (e.g. Haeckel, 1893; Beebe, 1926; Knauss, 1957). Recently, geographic, tidal and flow conditions that create frontal "lines in the sea" (*sensu* Yoder et al., 1994) have become better understood. Zooplankton aggregations are associated with fronts generated by tides (Pingree *et al.*, 1975; Franks and Chen, 1996) near headlands (Alldredge and Hamner, 1980), coral reefs (Wolanski *et al.*, 1989; Carleton *et al.*, 2001), and islands (Hamner and Hauri, 1981a). In addition, animal aggregations occur in association with frontal upwelling (Graham and Largier, 1997; Graham et al., 1992) and margins of eddies (DiGiacomo *et al.,* 2002). The contrast of temperature and chlorophyll reflectivity along fronts can be seen from satellites (DiGiacomo *et al*., 2002; Yoder *et al*., 1994). From the deck of ships, fronts can be highly visible, marked by lines of flotsam, seabirds, and fish.

Frontal zones often have both higher diversity and higher density of organisms compared to surrounding waters. Passive particles such as phytoplankton and fish and invertebrate eggs are concentrated along the front as one water mass is subducted under the other (Franks, 1992). Phytoplankton mechanically transported to the front reproduce rapidly due to higher nutrients from the colder waters meeting the warmer waters, which promote faster growth (Pingree *et al*., 1975; Owen, 1981; Le Fevre, 1986; Levasseur et al., 1992). Grazers are also advected to the front and sustained in turn by the rich source of food (Urban-Rich *et al*., 2001). A persistent front may consist of a wide array of planktivores, including larval fish (Govoni, 1993; Moser and Smith, 1993; Rissik, and Suthers, 1996), large planktivorous fishes (Clark and Nelson, 1997; Sims and Quayle, 1998; Wilson, 2004), seabirds (Durazo *et al*., 1998; Spear *et al.*, 2001; DiGiacomo et al., 2002), marine mammals (Baumgartner *et al*., 2001; Mendes *et al*., 2002), and gelatinous macrozooplankton (Purcell, 1985; Pages and Schnack-Schiel, 1996; Graham e*t al*., 2001).

Although the physical mechanisms of front formation are well understood, sampling intense patches of organisms at oceanic fronts over space and time has been difficult. If a fixed grid system is used to sample a non-fixed surface feature such as a front, plankton patches are dramatically under-sampled. While advection and buoyancy are sufficient for aggregation of non-swimming organisms at fronts, for most animals, behavior plays an important role in maintaining the aggregation. Although many planktonic species engage in vertical migrations that affect horizontal transport (Haury and Weihs, 1976; Sulkin, 1984; Young, 1995; Poulin *et al.*, 2002; Helfrich and Pineda, 2003), only a few studies have measured plankton behavior at fronts (Shanks, 1986; Epifanio, 1987).

This paucity of plankton behavioral studies at fronts may be due in part to the difficulty of making measurements at sea where there are no fixed reference points against which to make the measurements. The only practical solution is to take a large quantity of data around the front over short periods of time so as to build an accurate picture of the structure and dynamic nature of the feature while simultaneously measuring the abundance and behavior of the animal of interest. Thus, the front itself serves as the frame of reference in which distribution and behavior can be scored. Another complication to studying behavior lies in the traditional use of towed nets in plankton studies. The distribution of smaller plankton can be ascertained using nets, and some behavior can be inferred based on spatial and temporal differences in abundance when compared to physical oceanographic measurements taken simultaneously (e.g.; see Harris *et al.*, 2000; Shanks, 1986), but actual behavior cannot be measured directly by nets. Acoustics have been used to locate micronekton in conjunction with frontal measurements, yielding indirect behavioral information (e.g. Coyle and Hunt, 2000), however, many planktonic animals, particularly soft-bodied animals, are acoustically transparent. Further, owing to their delicate structure, gelatinous predators are virtually impossible to sample accurately with nets (Hamner *et al.*, 1975), where such sampling approaches result in animals being severely damaged beyond identification or dismembered, preventing meaningful quantification.

Also, many gelatinous predators such as scyphomedusae, ctenophores and salps tend to be larger in size, and this trait will often lead to under representation in tows using typically sized nets. Beebe (1935), first noted huge discrepancies between what he had caught in net tows and what he observed during bathysphere descents, remarking that net tows did not prepare him for the great abundance of medusae that he saw underwater. Hence only with *in situ* observations can one acquire robust data on abundance and behavior of large jellies. Many gelatinous zooplankton have swimming speeds greater than the velocities observed at many fronts (Mileikovsky, 1973), and it is probable that the intense aggregations of large jellyfish at fronts is due to their behavior (Hamner *et al.*, 1994). Larson (1992) observed that swarms of thimble jellies in Langmuir convergences maintained their position by upward swimming behavior. Perhaps the best way to accurately determine plankton behavior is by direct observations via use of remotely operated vehicles (Robison, 2004), manned submersibles (Youngbluth, 1989), or by blue-water scuba diving techniques (Hamner, 1975).

In this study, we quantify the density and behavior of large scyphomedusae near a front in Monterey Bay, California. The large-scale circulation within Monterey Bay is well know (Breaker and Broenkow, 1994; Graham and Largier, 1997), with counterclockwise flow in the northern part of the bay. Upwelling occurs north of Monterey Bay mainly between March and September, with colder, upwelled water transported southeast into Monterey Bay (Graham and Largier, 1997). This tongue of colder water sometimes contacts the coastline in the vicinity of Moss Landing Harbor where it then circulates northwest along the coast. The surface water is warmed as it moves west along shore until it eventually contacts the cold upwelled water entering the bay. This often occurs offshore of Santa Cruz where a strong convergent front is formed, trapping the mass of warmer water in the northeast corner of the Bay.

We observed jellies when they were most highly aggregated at night when the vertical migration of midwater micronekton occurs, accumulating most of the biomass in the water column above the thermocline. This creates intense vertical patchiness in addition to the horizontal patchiness generated at the surface convergence.

Materials and Methods

Two coordinated field efforts were required for this study. The first involved the characterization and location of frontal conditions in the bay during the daytime on August 23 and 24, 2000. The information gathered during these cruises was used to determine nighttime sampling involving in-water observations using a remotely operated vehicle (ROV).

Daytime Characterization

Daytime cruises were conducted with the Moss Landing vessel RV Ed Ricketts to physically characterize the northern portion of Monterey Bay. Vertical profiles were gathered using a Seabird SeaCat Profiler SBE 19 (unpumped) CTD (conductivity-temperature-depth) water profiler at approximately 1 km intervals along three transects beginning approximately two kilometers from shore and extending roughly 10-11 km in a south-southwest direction for a total of 32 casts along three transects (Figure 1-1). Data from transects 1 and 2 were gathered on August 23, 2000, and data from transect 3 was collected on August 24, 2000.

We also used a Guideline Minibat Towed Profiler 8820 housing an Applied Microsystems Ltd. Smart CTD, a SeaTech/WetLabs fluorometer, and a WetLabs C-Star transmissometer (Figure 1-1). This device was towed from the RV Ed Ricketts and directed via computer control in a surface-to-bottom oscillation. Upon completing the vertical casts along Transect 2, we returned to the beginning of the transect and began the Minibat deployment approximately 1 km south of the original starting point and completed the transect 1 km north of the original ending point. Thus, the Minibat transect covered an 8 km distance of Transect 2.

Seasave™ version 1.17 (Seabird Electronics) and SmartTalk™ version 1.10 (Applied Microsystems) were used to convert the raw data from the Seabird 9 profiler and Applied Microsystems™ CTD to tab-delimited format where further data reduction could be made using Microsoft Excel. The data were then imported into Tecplot version 7.5 (Amtec Company) where individual vertical casts along each transect were integrated into a two-dimensional temperature plot over depth and distance for each of the three transects. These plots were used to determine the location of any surface temperature discontinuity.

In-water Jellies Observations

In-water observations were made from the Monterey Bay Aquarium Research Institute research vessel RV Pt. Lobos via the ROV Ventana. On three consecutive nights (August 23-25, 2000) we reoccupied the daytime coordinates and deployed the ROV Ventana at sunset. Visualizing the location and orientation of the front during daylight hours was easy because the location of the steep temperature gradient seen in our transect profiles coincided with a prominent line of flotsam at the surface, but at night it was not possible to visualize the front. Nonetheless daytime coordinates permitted us to narrow our search area, aiding us in locating the front more quickly at night.

A high-definition digital video camera with a fisheye lens is fitted to the ROV Ventana. The digital video signal was transmitted through an umbilicus to a video recorder in the control room of the ship. A time stamp with latitude and longitude coordinates was streamed to an onboard computer, giving an exact position in time and space in coordination with the video feed. Simultaneously, physical data from the CTD, dissolved oxygen probe, and light transmissometer onboard the ROV Ventana, were streamed concurrently with the coordinate information. Video transects were 10 minutes long except for two of the transects on 24 August 2000, which were 20 minutes. Between 275 and 450 m of distance was sampled during the 10-minute transects while the two 20-minute transects were 540 and 700 m in length.

Video transects continued throughout the night and ended between 0200 and 0400 on the following morning, thus providing between seven and nine hours of raw video per sampling effort. On the first night, only two usable transects were recorded as much of the time was spent trying to relocate the front, which had shifted 2 km south of its daytime position (Figure 1-2). On the second night, three usable transects were recorded once the front was located. We were able to better predict the nighttime location of the front by the third night, when ten successful transects were made. All but two transects were carried out at the thermocline (approximately 10–12 m) or shallower. The two deeper transects were performed near the bottom in 22 and 26 m depth.

Video transects were extracted from 21 collective hours of video and annotated. Each transect was identified by the Julian day and order in which it was sampled (236, 237, and 238 correspond to August 23, 24, and 25, respectively) (Figure 1-2). Numerical counts, swimming orientation, and species type were scored in 15 second intervals along each transect. These data were combined with the physical data into a single database for analysis. Macrozooplankton abundances and physical variables were plotted over the distance of each transect. Student's t-tests compared the abundance of gelatinous animals on the cold versus warm sides of the front for each separate day. For angular orientation, a pair-wise Watson-Williams test compared the orientation of gelatinous animals along transects passing through cold and warm water.

Results

Daytime Characterization

Advanced Very High-Resolution Radiometry (AVHRR) satellite images prior to the study revealed that an upwelling event was occurring off of the Pt. Año Nuevo headland. The AVHRR image closest to the sampling dates with least cloud cover was from August 11, 2000 (CoastWatch West Coast Regional Node website, www.coastwatch.pfel.noaa.gov, Figure 1-3).

Interpolated vertical CTD profiles are shown in Figure 1-4. The starting point of each transect is shown on the right side of each plot, approximately 2 km from the coast and extending in a south-southwest direction. The thermocline was at 8-10 m for transects 1 and 2, and at 12 m for transect 3. At roughly 4.5 km into each transect, a flotsam line consisting of kelp, surf grass, anthropogenic materials, and a pinniped carcass, was observed oriented roughly perpendicular to our course heading.

It was possible to see approximately 5 meters into the water column from the deck of the RV Ed Ricketts. Sea nettles (*Chrysaora fuscescens*) and moon jellies (*Aurelia* sp.) were in the surface waters throughout the day, aggregating near flotsam lines and less abundant away from the slick. These jellies were counted off the port or starboard sides, whichever placed the sun at the back of the observer, thus giving a rough estimate of the density of large jellies along each transect (Figure 1-5). Sea conditions were considerably rougher on August 25, 2000 (transect 3) further outside the bay, where it was more difficult to observe jellies at the surface. All counts of jellies were normalized for distance. The greatest number of observed surface jellies on each of the transects occurred along fronts, with the largest density occurring at the surface slick crossing transect 1.

The line of debris at the 4.5 km mark coincided with the area of greatest horizontal temperature change in all three transects. Water clarity also declined in close proximity to the slick. The scales of each of the three plots in Figures 1-4 are not identical, where the color spectrum of each contains the extremes of only those data pertaining to the waters each represents. This allowed us to search for the zone of greatest discontinuity along each transect. Figure 1-6 shows sea surface temperature, where the surface values (the upper 1 m) of each vertical profile were integrated to better compare the three transects.

Data from the minibat transect were consistent with that obtained from the vertical CTD profiles (Figure 1-7), with a 10 m deep thermocline decreasing in intensity to the south. The greatest horizontal surface temperature gradient occurred at 4 km along the transect, corresponded with a surface chlorophyll maxima, and a decrease in light transmissivity near the slick at the 4 km mark.

In-water Jellies Observations

Each of the three transects crossed a front, although we concentrated our video sampling near transect 1 for several reasons. First, the intensity of the horizontal thermal gradient was strongest along the portion of the front crossing transect 1 (Figures 1-4 and 1-6). Second, the greatest density of large jellies occurring at the surface were seen along transect 1 in the vicinity of the front (Figure 1-5). Finally, the closer proximity of transect 1 to Moss Landing meant that the transit time would be less. This consideration was not just a matter of convenience. The Monterey upwelling shadow is wind-driven and shifts position if winds decrease or shift direction, and locating the front at night is often not possible. For example, CTD data from the ROV during all night transects showed that the surface thermal gradient had shifted from its daytime position, approximately 7 km from the northern coastline to a position 2 km further south at night.

On the first night, we did not find a front, although an abundance of jellies in the vicinity of the ship permitted us to gather useful data from two transects. Transect 236-1 was above the thermocline in a northward path, and was marked by temperature changes of almost 1 °C (Figure 1-8a). A total of 298 *C. fuscescens* were counted along the 475 m length. In one instance, at 300 m into the collection, 26 jellies were scored in 15-seconds. Virtually all of the jellies in this transect were oriented due north or slightly north-northeast. Transect 236-2 was carried out in a southward heading approximately 4 m below the thermocline and exhibited an unchanging temperature throughout the 302 m length (Figure 1-8b). Of 216 individual *C. fuscescens*, virtually all were oriented due south. The difference in swimming orientation of jellies in the two transects was highly significant (Watson-Williams, $N = 524$, $F_{0.05,1,N} = 4916.7$, $p < 0.00001$). The mean angle of jellies in transect 236-1 (above the thermocline) was 6.9^{o} while that of jellies along transect 236-2 (below the thermocline) was 171.7^{o}.

On the second night, we decided to commence operations between daytime CTD transects 1 and 2 (Figure 1-2). We located the front using the ship's temperature sensor, deployed the ROV and ran three transects in a southward direction beginning with the first one on the northern side of the front in the warmer water mass. Overall, fewer jellies were observed along the three video transects compared to the previous night. The first 20-minute transect (237-1) was above the thermocline where temperature fluctuations of 0.75 °C were seen throughout (Figure 1-8c), and most of the 108 jellies were swimming due south. Transect 237-2 was run 0.5 km south of the ending position of transect 237-1. This 10-minute transect was just above the thermocline (Figure 1-8d). Between 50 and 100 m along the transect, a dramatic drop in temperature of 1 °C was seen, thus indicating we had passed through the front. This temperature break was reflected by a drop in the number of observed jellies for the remainder of the transect distance. On the warm side of the front, 53 *C. fuscescens* were observed over the first 100 m of the transect, while 25 *C. fuscescens* were counted in the remaining 300 m on the cold side of the front. Jellies on the warm side were mostly oriented to the south, though there was a considerable number swimming east and west. On the cold side, many jellies were oriented north, although a sizeable number also were oriented to the east. A comparison of swimming direction of jellies on either side of the front was inconclusive because of the violation of the rule requiring unimodality in the data (Zar, 1999). However, a visual inspection of the angular plots suggests they might be different. Transect 237-3 was begun 1 km south of 237-2, and except for a spike in temperature half way into the collection, the temperature remained below 11.25 ^{o}C despite being above the thermocline (Figure 1-8e). Only 47 total jellies were scored along this 20-minute, 550-m long transect. These jellies showed a strong orientation to the north and northwest. In comparing the orientation of jellies from transects 237-1 (warm) and 237-3 (cold), a highly significant difference is revealed (Watson-Williams, $N = 155$, $F_{0.05,1,N} = 272.9$, $p < 0.00001$). The mean angle of the jellies on the warm side was 178.9^{o} while the mean angle on the cold side was 37.5^{o}.

We re-occupied the front on the third night and perform ten video transects to the east of transect 1 (Figure 1-2). All ten transects had much higher densities of jellies than the previous day, and were numerically more consistent with that of the first night. The ten transects fell into 4 categories. The first category (transects 238-4, 238-6, 238-7, and 238-9), includes transects completed at or slightly below the thermocline on the cold (south) side of the front (Figures 1-8f–i). Transect 238-6 was located 5 m below the thermocline and was 1 ^{o}C cooler than the other three transect which were very close to the thermocline. All jellies in these four samples were strongly oriented to the north with the number of jellies observed per transect ranging from 116 to 216. Generally less than 10 jellies were seen in any 15 second unit of time in these four transects, except in transect 238-7 where jellyfish numbers were greater than 10 per 15 seconds one third of the time, with 20 or more seen in two 15-second counts. Transects 238-4 and 238-9 were arrayed in an east-west fashion, parallel to the front and exhibited very little fluctuation in temperature down their lengths. In contrast, transects 238-6 and 238-7 were oriented north-south, perpendicular to the front. The latter two transects showed fluctuation in temperature of 0.5 ^{o}C down their lengths, likely related to small changes in depth that occurred simultaneously.

Transects 238-2 and 238-3 fall into the second category with both being recorded well above the thermocline on the warm side of the front (Figure 1-2; Figures 1-8j and 1-8k). The first was conducted perpendicular to the front (although it never completely crossed over it) and the second was parallel to the front. Transect 238-2 was ended at 10 minutes, although it was obvious from the CTD sensor on the ROV in retrospect that this transect had ended very near or in the front, as suggested by the slight drop in temperature at the end of the transect and difference in abundance of jellies in the two transects. Considerable numbers of jellies were recorded along transect 238-3, but not in transect 238-2, although on two occasions, more than 20 jellies were observed within a 15-second unit of time. The swimming orientation of jellies in transect 238-2 was strongly to the south while that of jellies along transect 238-3 showed a wider range of orientations.

Our third transect group (transects 238-1 and 238-8), were conducted above the thermocline and across the front (Figure 1-2; Figures 1-8l and 1-8m). Transect 238-1 began on the warm side of the front and extended to the south, crossing the front at 250 m along the course (Figure 1-8l). From 0 to 250 m, jellyfish became increasingly more numerous, with the highest density occurring at the front where the temperature dropped steeply from 12.0 ^{o}C to 11.25 ^{o}C within a 30 m distance. Beyond this point, the number of jellies decreased dramatically and remained lower along the rest of the transect. A similar pattern was seen in transect 238-8, where jelly densities became increasingly higher approaching the front and then decreased after crossing the front. This transect also had the highest densities of jellies of all the transects in the study, with the three highest counts being 42, 34, and 32 jellies scored over 15-second intervals (Figure 1-8m, note the greater y-axis in the abundance plot compared to all other plots). While the numbers of jellies occurring on the warm side of the front were much higher on average than those occurring on the cold side, it is important to note that the density of jellies on the cold side was considerably higher than seen in most other transects. A comparison of the number of jellies on the warm versus cold side of the front, normalized for distance, yielded a significant difference in both cases (transect 238-1, Student's t-test, $N = 293$, $p < 0.0001$; transect 238-8, Student's t-test, $N = 638$, $p < 0.0001$). A comparison of jellyfish swimming orientation on either side of the front for transect 238-1 was insignificant (Watson-Williams, $N = 243$, $F_{0.05,1,N} = 2.551$, $p = 0.1116$). On the warm side of transect 238-1, jellies were strongly oriented to the south (mean angle = 169.7^{o}), while half the jellies on the cold side were oriented south, the other half were evenly spread in other orientations (mean angle = 150.6^o). In comparing swimming orientation in transect 238-8, the jellies on the warm side were oriented differently than those on the cold side (Watson-Williams, N = 310, $F_{0.05,1,N}$ = 11.120, p = 0.0010). The spread of orientations on either side of the front appeared to be greater than in transects conducted only on the warm or cold side of the front. The direction in swimming behavior on the warm side showed a tendency to be oriented parallel to the front (mean angle = 72.7^o). A similar propensity of swimming orientation was seen on the cold side of the front (mean angle = 53.4^o), though this different was statistically significant.

Our last transect category (transects 238-5 and 238-10) were for transects only a few meters above the bottom, well below the thermocline. Transect 238-5 was conducted north of the front (at a similar latitude and longitude coordinate as transect 238-2), and transect 238-10 occurred south of the front. Both transects either began or ended approximately 300 m from the front and both were commenced in a southward direction. No temperature change was seen along the length of either transect, and the density of jellies was similar in both. Mean angle was 26.3^o for both transects 238-5 and 238-10.

A final comparison of overall abundance of jellies from the third night was conducted to establish overall differences in abundance and orientation of jellies throughout the study site with respect to temperature. All jellies counted in warm waters (>11.5 ^{o}C) were pooled and compared to those observed in colder waters (<11.5 ^{o}C). This analysis included transects 238-2, 238-3 and jellies from the warm portions of transects 238-1 and 238-8. The cold pool consisted of transects 238-4, 238-5, 238-6, 238-7, 238-9, 238-10, and jellies from the cold portions of transects 238-1 and 238-8.

Overall, a significantly greater density of jellies occurred in the warmer waters than in the colder waters (Student's t-test, $N = 288$ observations, $p < 0.00001$), and the orientation of jellies in the warmer waters (mean angle = 137.2^o) was highly statistically different from that of jellies in the colder waters (mean angle = 24.9^o) (Watson-Williams, $N = 1197$, $F_{0.05,1,N} = 804.265$, $p < 0.00001$).

Discussion

The satellite and CTD data demonstrate that a thermal front was present during our study. Satellite observations made prior to the field effort suggest that this front was the result of the entrainment of upwelled water into the bay forming an upwelling shadow (Figure 1-3) (Graham and Largier, 1997). Examinations of plankton distributions around this feature are few (Graham *et al.*, 1992), though others have investigated plankton aggregations in different capacities in Monterey Bay. For example, a comprehensive analysis was made of seasonal changes in plankton biomass in Monterey Bay as part of the California Cooperative Oceanic Fisheries Investigations studies (Baduini, 1997). Major changes in Monterey Bay plankton communities were shown to occur between seasons and years, particularly during periods of El Niño-Southern Oscillation warm-water events. A similar finding was described specifically for krill assemblages in Monterey Bay during the 1997-1999 El-Niño/La Niña cycle (Marinovic *et al.*, 2002). Also, plankton pulses associated with nourishment of Monterey Bay by seasonal upwelling events has also been investigated (Olivieri and Chavez, 2000).

However none of these investigations has quantified aggregations of large medusae around the upwelling front. In our study, we observed some 1,200 individual *C. fuscescens* medusae using an ROV. Had we used nets rather than the ROV, we would have under-sampled their abundance, and we would have collected no information on their behavior. Corroborative information for this claim are presented in the following chapter where eighteen vertical plankton hauls performed along the three transect during August 23 and 24, 2000, resulted in the capture of only two *C. fuscescens* and one *Aurelia* sp. Such a catch suggests a far less dense assemblage of large jellies than that shown in our surface and video ROV observations. Furthermore, the vertical tows with jellyfish had to be discarded and re-sampled since the presence of a large 7 m long, 20 kg jellyfish in the net made it impossible to retrieve the smaller species of zooplankton in the sample.

Chrysaora fuscescens showed a strong association with the inshore warmer water mass, and it was most abundant immediately at the front. From the Minibat towfish transect, we noted a concentration of phytoplankton higher than background levels in association with the zone of greatest discontinuity (Figure 1-7). This was confirmed by the drop in transmissivity along the same transect and was associated with a concentration of small zooplankton as much as two orders of magnitude higher than background levels (Chapter 2, this dissertation). Jellyfish are important predators in pelagic systems (Purcell, 1985), and we surmise that the high concentration of phytoplankton and small zooplankton at the front provides a ripe feeding opportunity for these large jellies.

These distributions appear to be actively maintained by the swimming behavior and directional orientation as observed using video data from the ROV. Swimming behavior of jellies results in aggregations (Omori and Hamner, 1982; Larson, 1992). Jellies respond to various stimuli in ways that elicit complex behavior, including sun (Mills and Goy, 1988), sun angle (Hamner *et al.*, 1994; Hamner and Hauri, 1981b), wind and waves (Shanks and Graham, 1987), escape responses to predators (Hansson and Kultima, 1995), and flow fields (Larson, 1992; Hamner and Schneider, 1986). Jellyfish aggregations have been reported near fronts (Pages and Schnack-Schiel, 1996), but no one has previously described how swimming behavior of jellies maintains their abundance at a front.

It is clear from the ROV video that jellies near or above the thermocline on the colder southern side of the front had a northward swimming orientation while those on the warmer northern side of the front exhibited a southward orientation. This behavioral response generates a concentration of jellies along the front. Those jellies that occurred immediately next to the front were more randomly oriented. Presumably, once the jellies encountered increased concentrations of food at the front, swimming behavior would maintain their position within the food concentration. This is consistent with experimental evidence that demonstrated a related species, *C. quinquecirrha*, was more likely to change direction more often in the presence of increased food (Matanoski *et al.*, 2001; and also see Bailey and Batty, 1983).

The swimming behavior of the jellies we observed was recorded at night, thus sunlight cannot explain the direction of swimming. Information on ocean currents was not collected, although this may be somehow related to the directional swimming we observed. For example, the front that passed through our study site was a buoyant convergence, and hence there was likely a difference within the flow field on either side of the front either in magnitude or direction. This may be why we observed jellyfish near the bottom, in the colder water mass, swimming in a northward orientation regardless of location. Transects 238-2 was located north of the front, but well beneath the warm water mass that characterized that side of the front. Observations along transect 238-2 resulting in similar abundances and identical swimming orientations to that of transect 238-10, which was recorded south of the front, but also near the bottom. Similar current direction and magnitude may explain the swimming orientation observed in the jellies in both of these transects. Nonetheless, it is not known if medusae can even sense differences in the direction of water flow.

The Monterey Bay front shifts constantly over meso-scale distances. However, large jellies apparently can swim well enough to track the movement of these fronts. Surface observations of jellies along the three daytime transects always resulted in the greatest density of animals at the convergence. Yet at night, although the location of the front had shifted south, the aggregation of jellies was still highest at the front. For smaller, less competent swimmers, passive advection may help maintain position along the front as it meanders, but our ROV video observations demonstrate that these jellies actively swim towards the front. Few studies have examined swimming speeds of *Chrysaora* sp. *in situ*, but some laboratory experiments indicate these jellies can sustain average speeds of 2 cm s^{-1} (Matanoski *et al.*, 2001), with similar swimming speeds for

Aurelia sp. (McHenry and Jed, 2003). These speeds are adequate to maintain aggregations near the front where horizontal flow velocities are generally slowest. Away from the front, the swimming orientation of jellyfish was strongly oriented to the north on the cold side and south on the warm side. In either case, this orientation is approximately perpendicular to the greatest flow, calculated previously at roughly 10 cm s^{-1} (Graham and Largier, 1997), further increasing the chance of encountering the highly productive front. This indicates how important behavior is in maintaining jellyfish aggregation (Omori and Hamner, 1982).

Figures

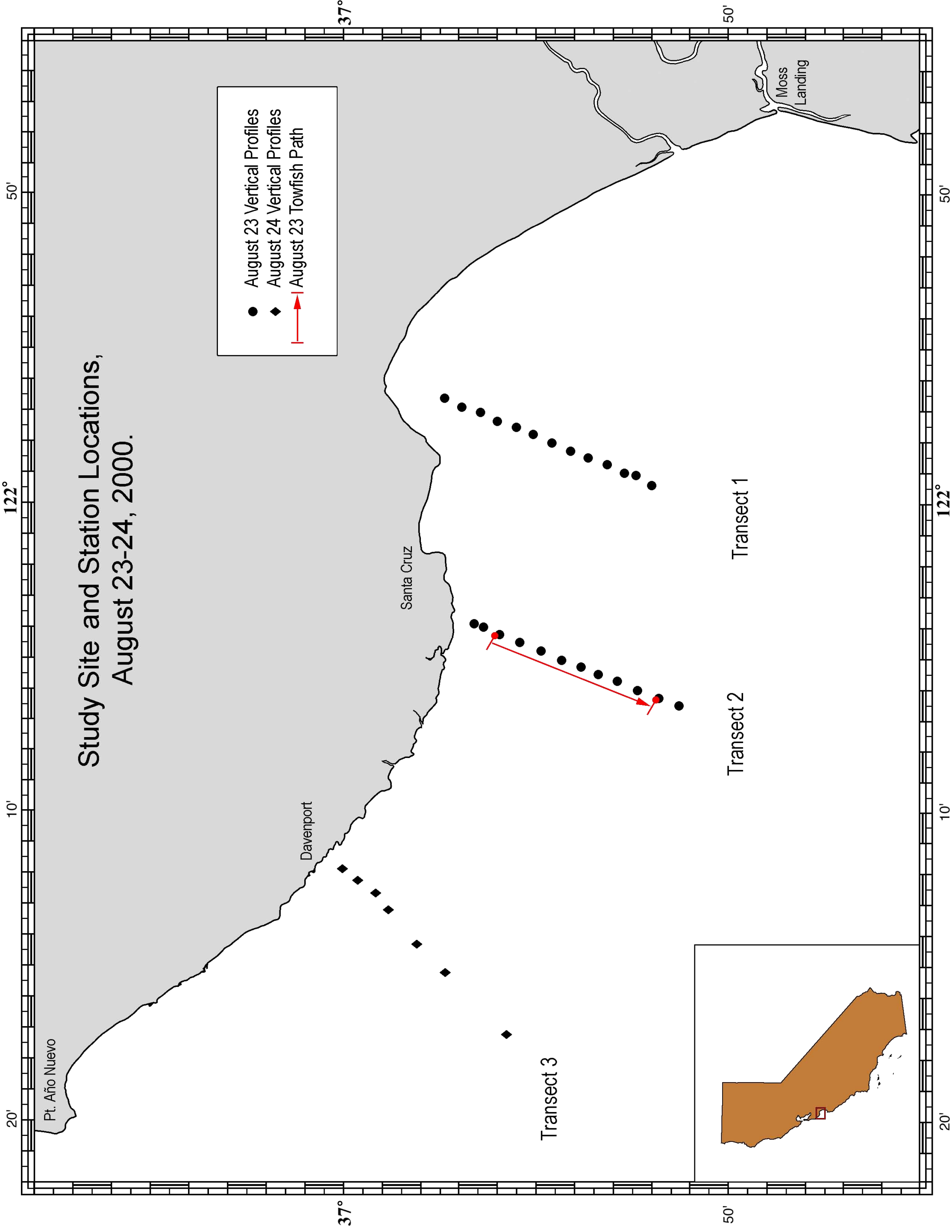

Figure 1-1. Station locations of daytime CTD vertical casts and towfish path, northern Monterey Bay, California. August 23-25, 2000.

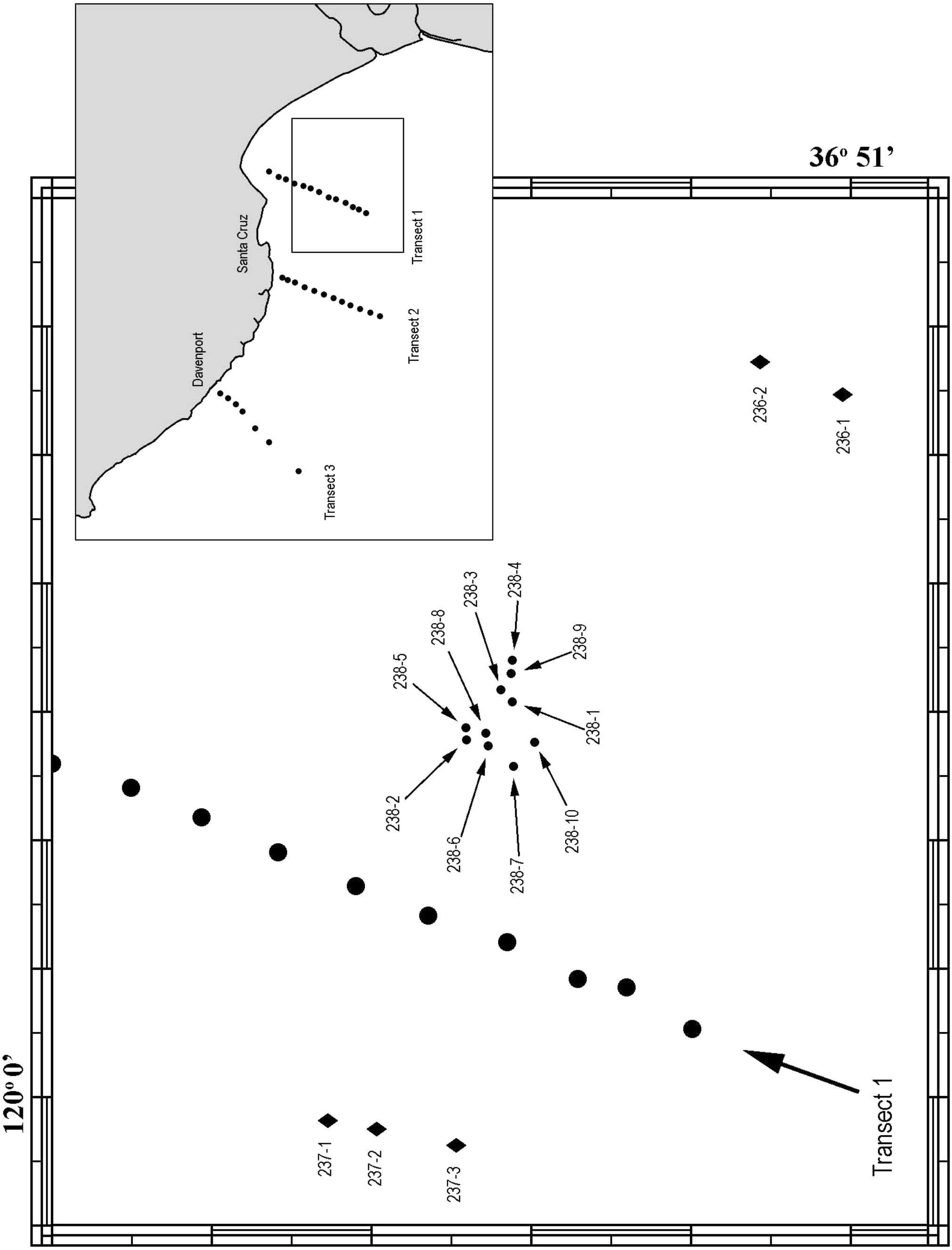

Figure 1-2. Station location for nighttime video transects designated by Julian day (23-25 August corresponds with 236-238) and transect order, northern Monterey Bay, California. August 23-25, 2000.

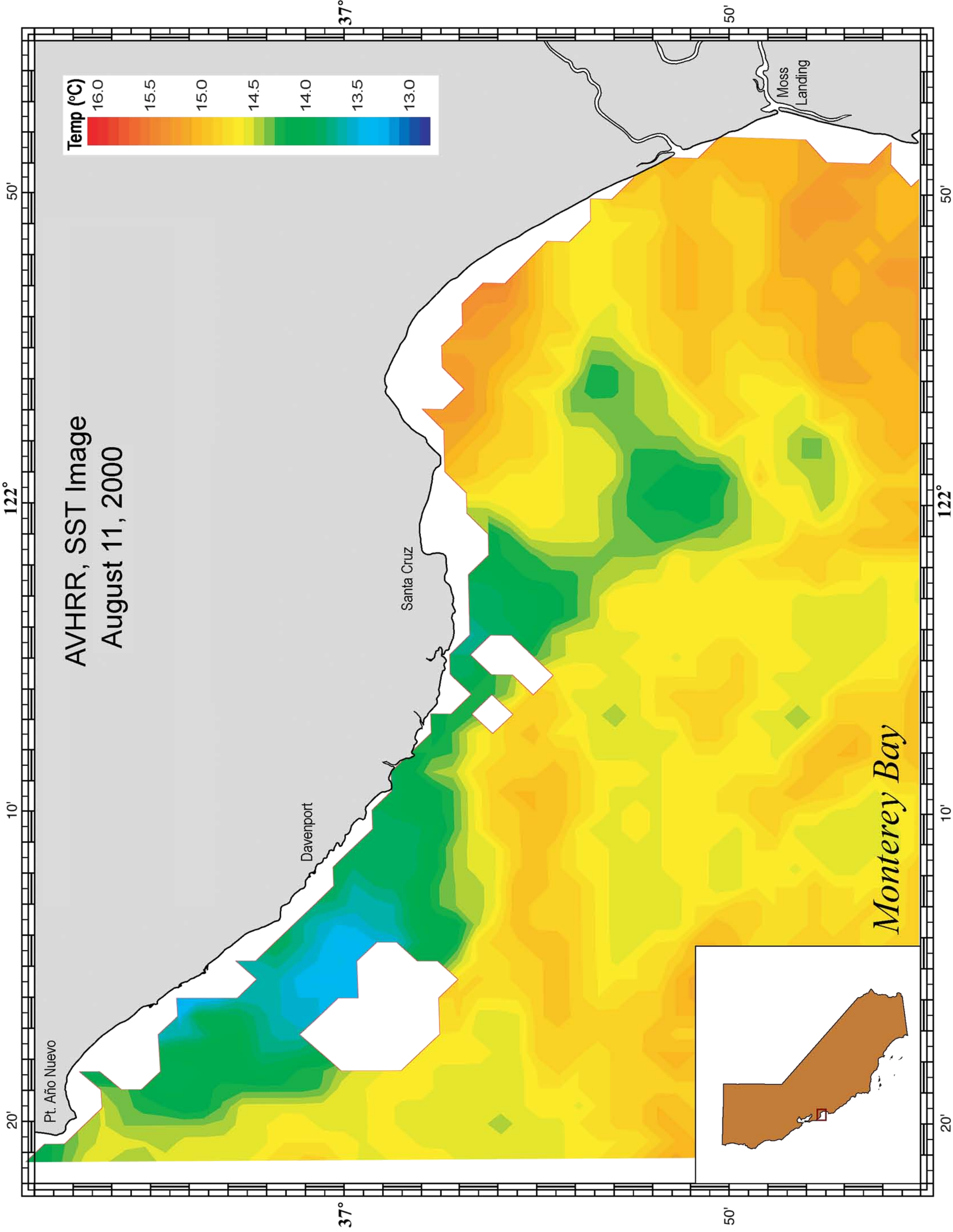

Figure 1-3. Advanced Very High Resolution Radiometry (AVHRR) sea surface temperature (SST) image from August 11, 2000. Data were obtained from the Coast Watch West Coast Regional Node website, www.coastwatch.pfel.noaa.gov.

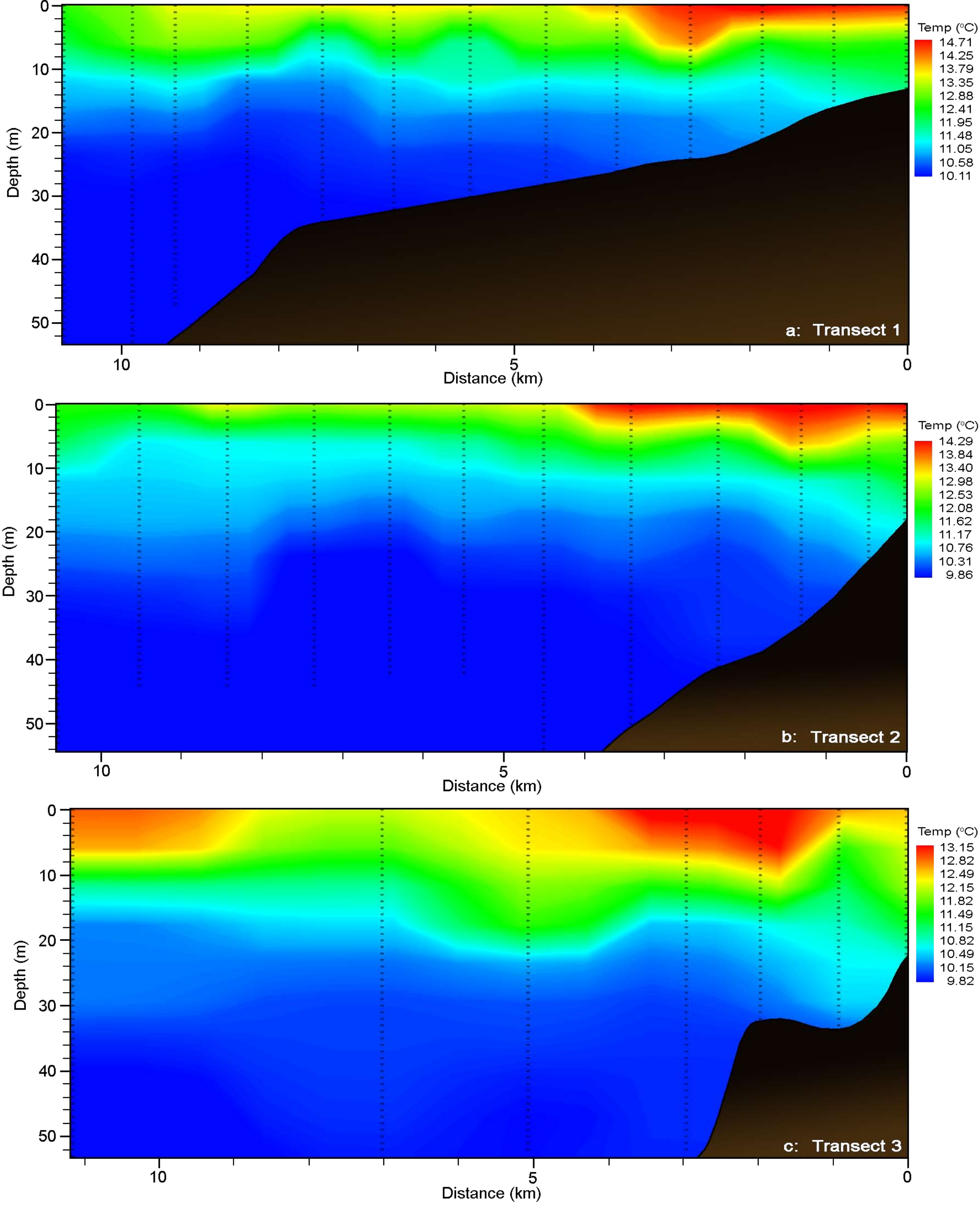

Figure 1-4. Integrated vertical temperature profiles along three transects with station locations depicted as vertical dotted lines, northern Monterey Bay, California. August 23-25, 2000.

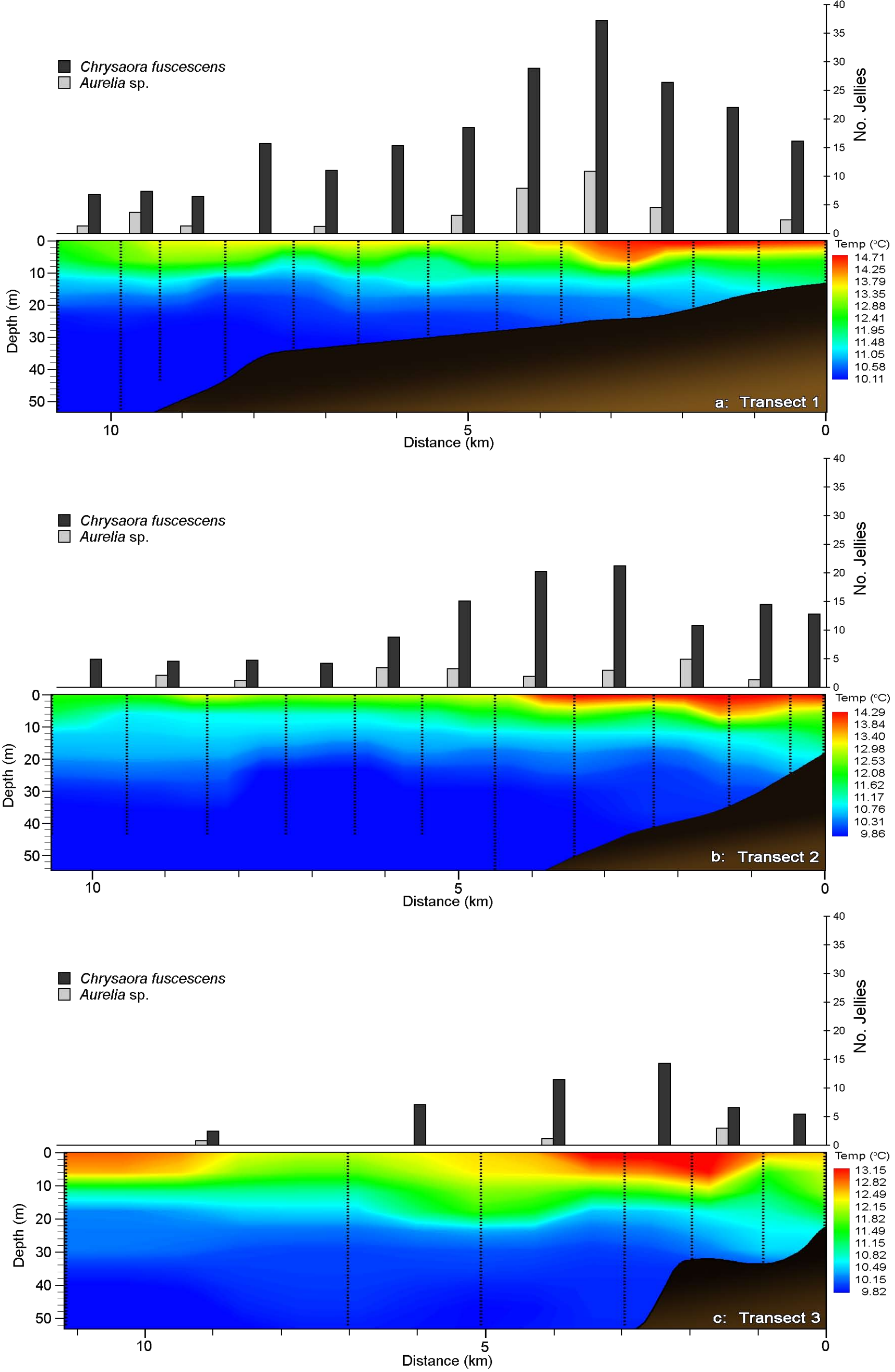

Figure 1-5. Abundance histograms of the scyphomedusae *Chrysaora fuscescens*, and *Aurelia* sp. along three transects with corresponding temperature profiles, northern Monterey Bay, California. August 23-25, 2000.

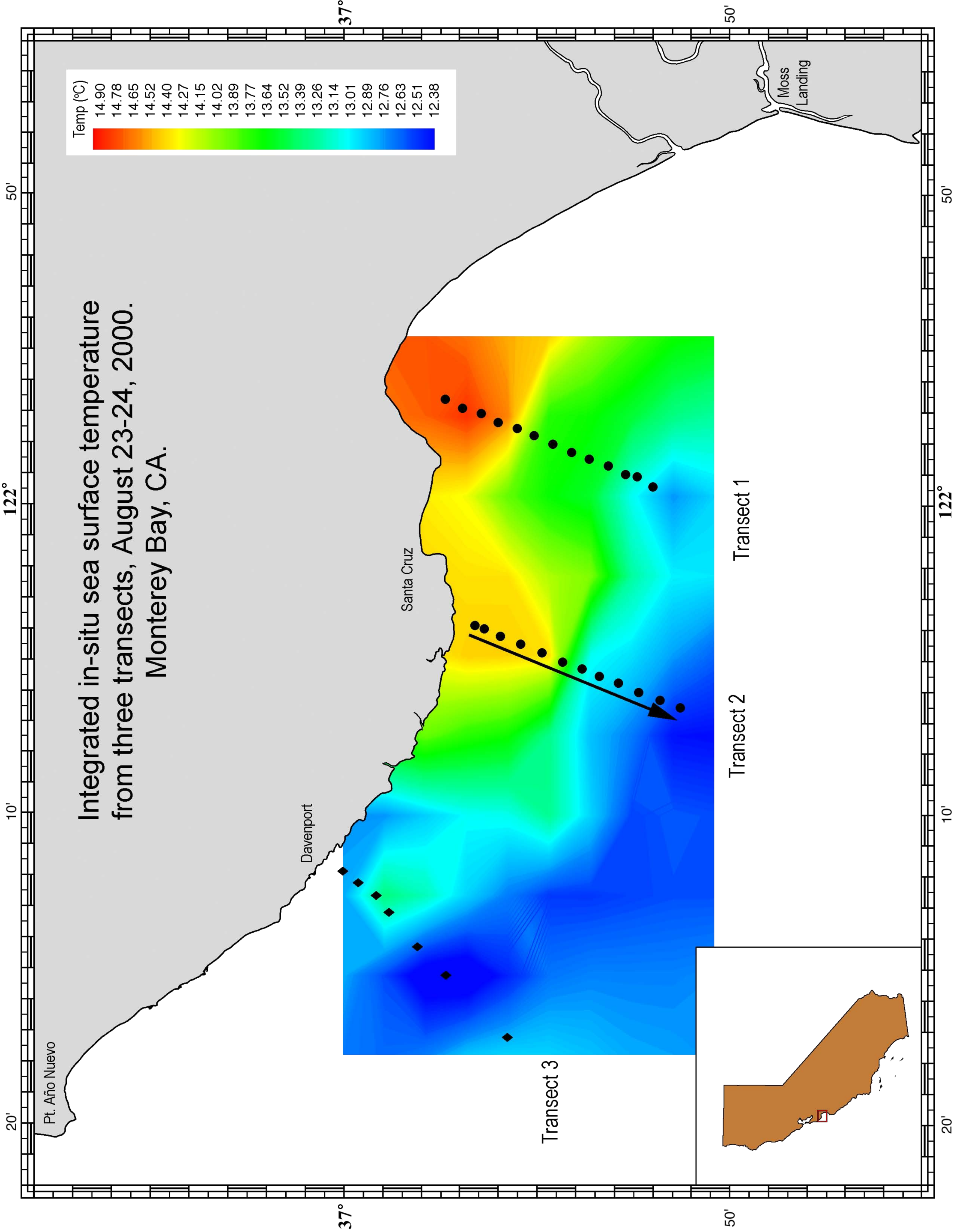

Figure 1-6. Integrated sea surface temperature interpolation from *in situ* surface readings along three transects in Monterey Bay, California. August 23-25, 2000.

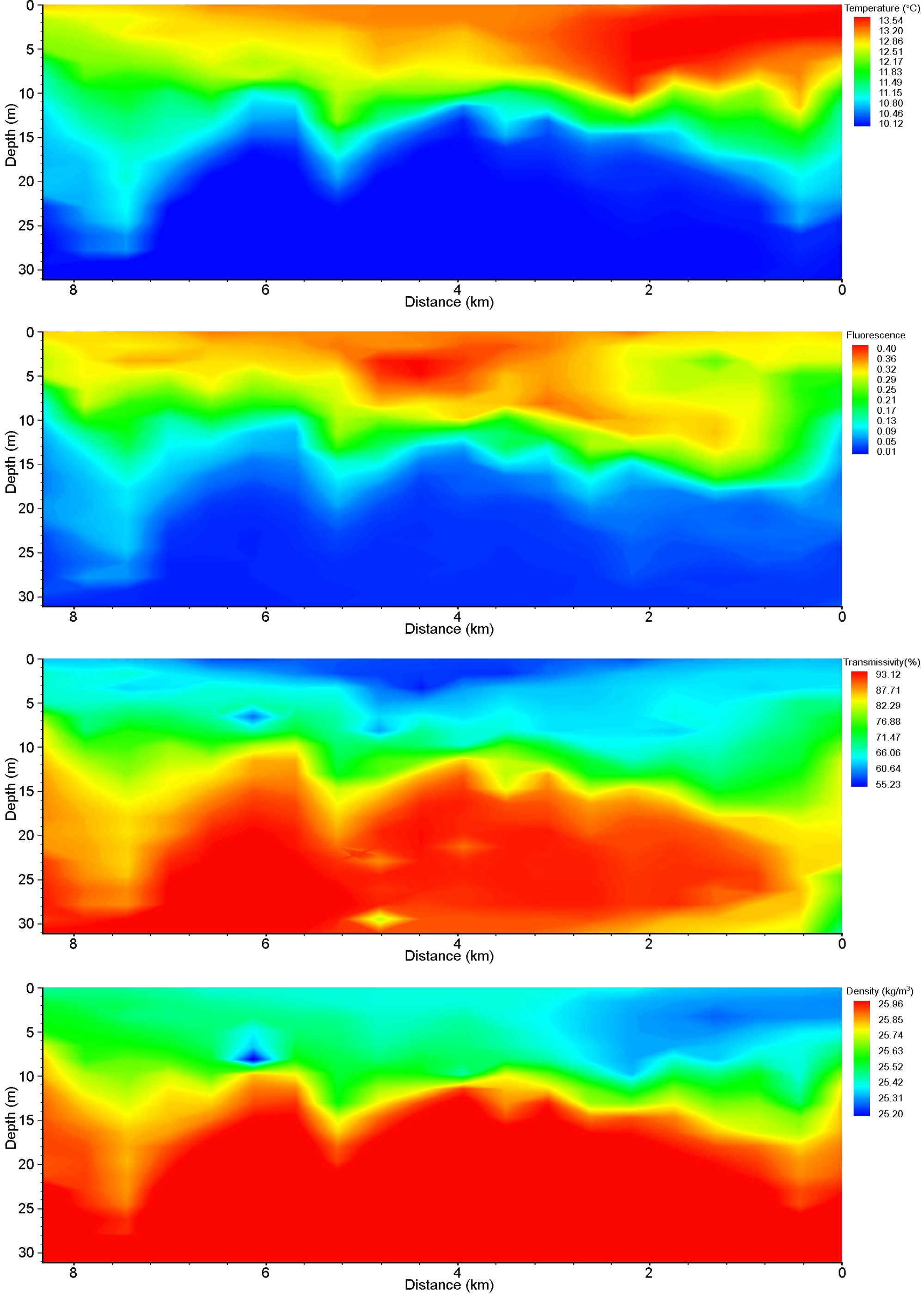

Figure 1-7. False color profiles of temperature, fluorescence, transmissivity and density along one transect on August 23, 2000, generated using an inverse-distance interpolation. A surface front was visible at 4 km along the transect.

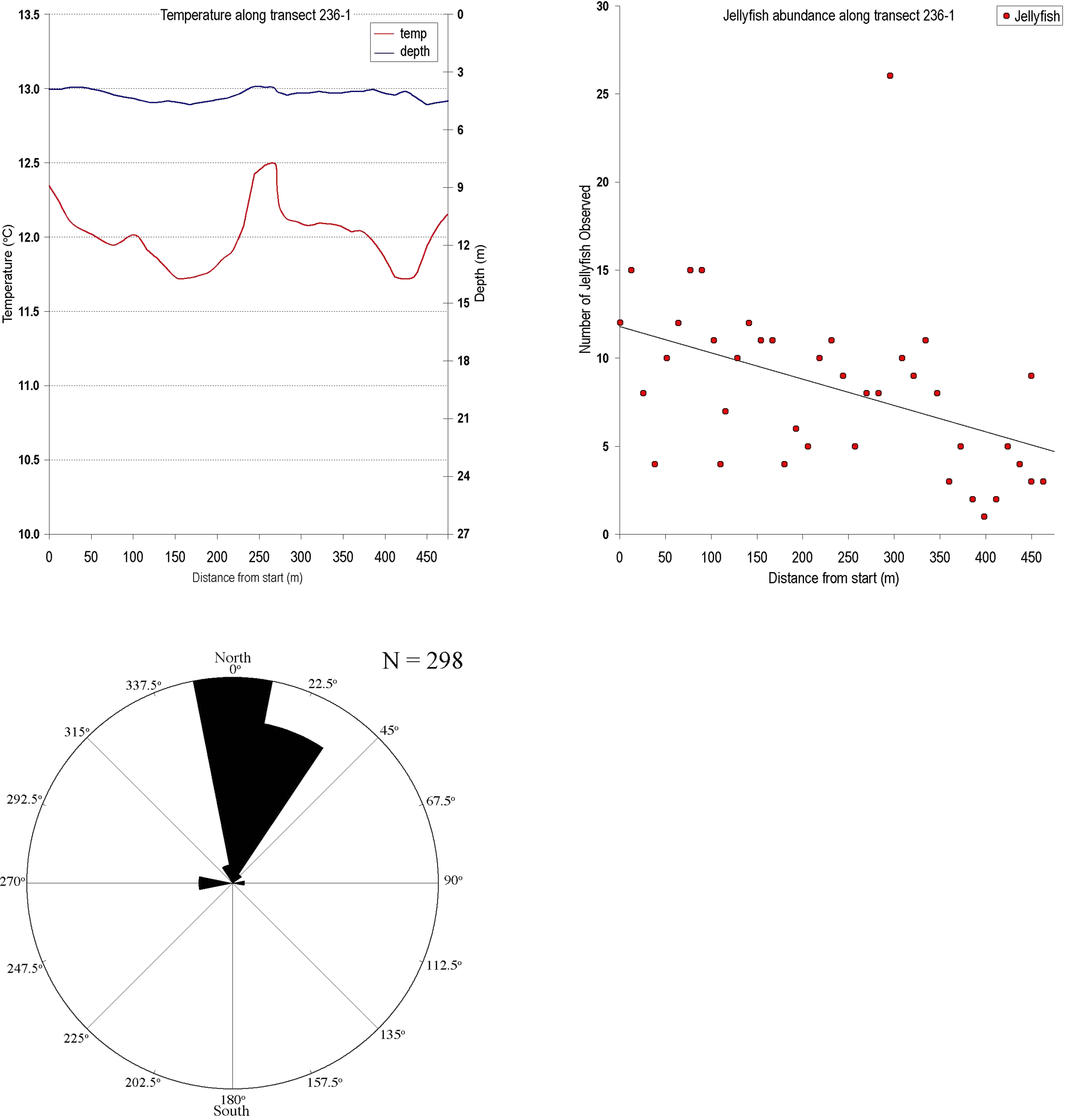

Figure 1-8a. ROV video transect 236-1 data including depth, temperature, *C. fuscescens* counts, and proportional swimming orientation. August 23-25, 2000.

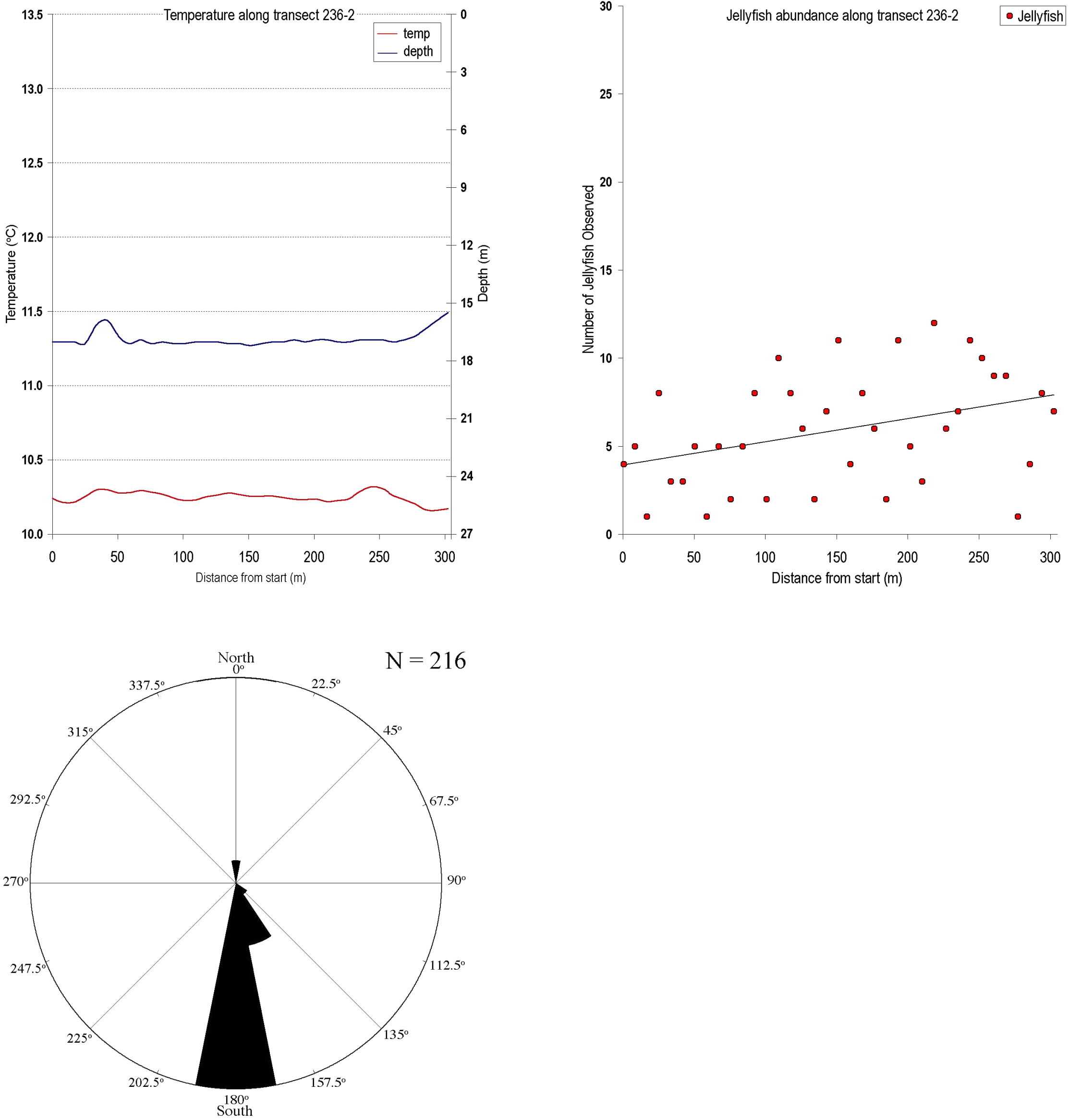

Figure 1-8b. ROV video transect 236-2 data including depth, temperature, *C. fuscescens* counts, and proportional swimming orientation. August 23-25, 2000.

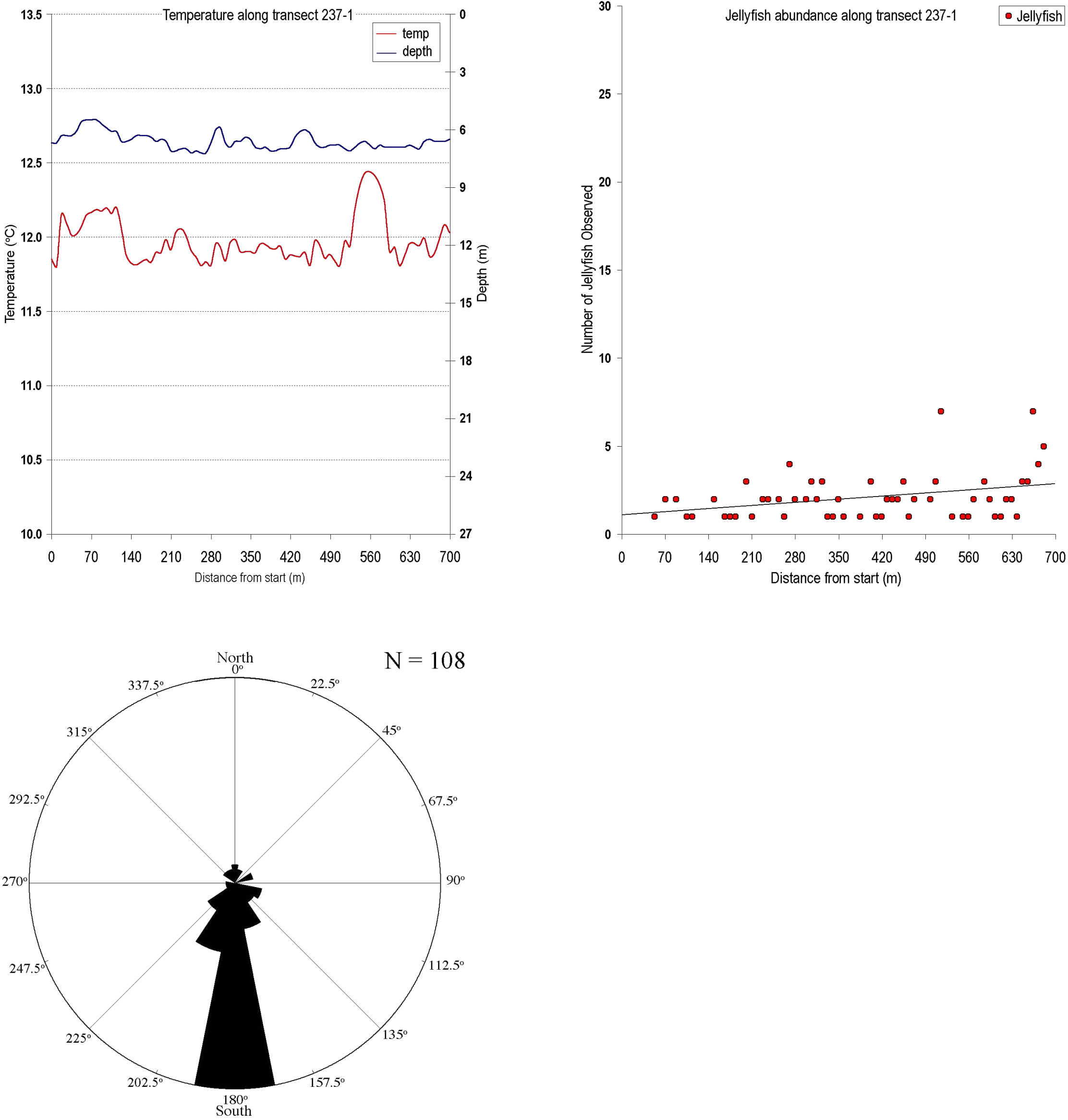

Figure 1-8c. ROV video transect 237-1 data including depth, temperature, *C. fuscescens* counts, and proportional swimming orientation. August 23-25, 2000.

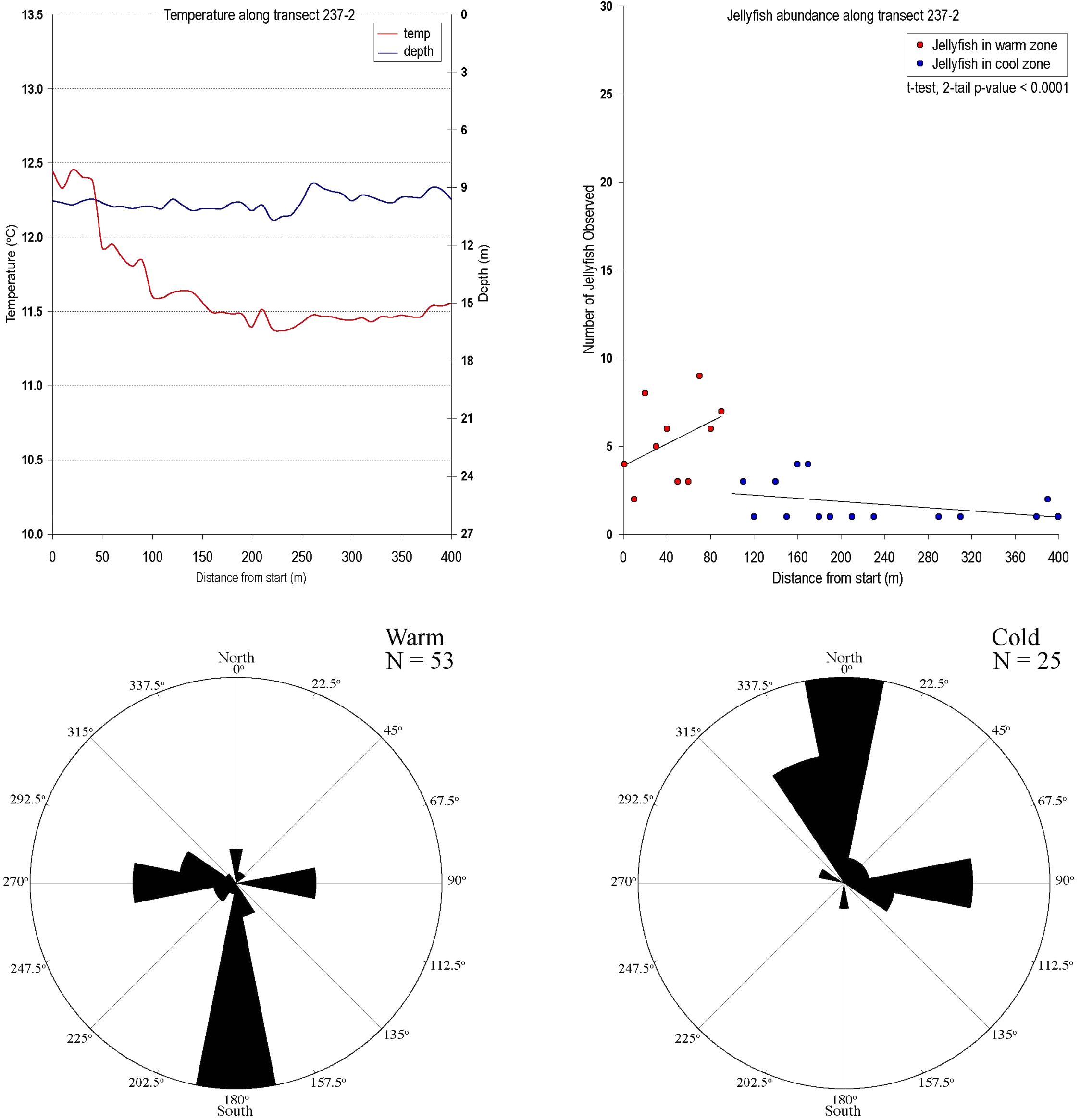

Figure 1-8d. ROV video transect 237-2 data including depth, temperature, *C. fuscescens* counts, and proportional swimming orientation. August 23-25, 2000.

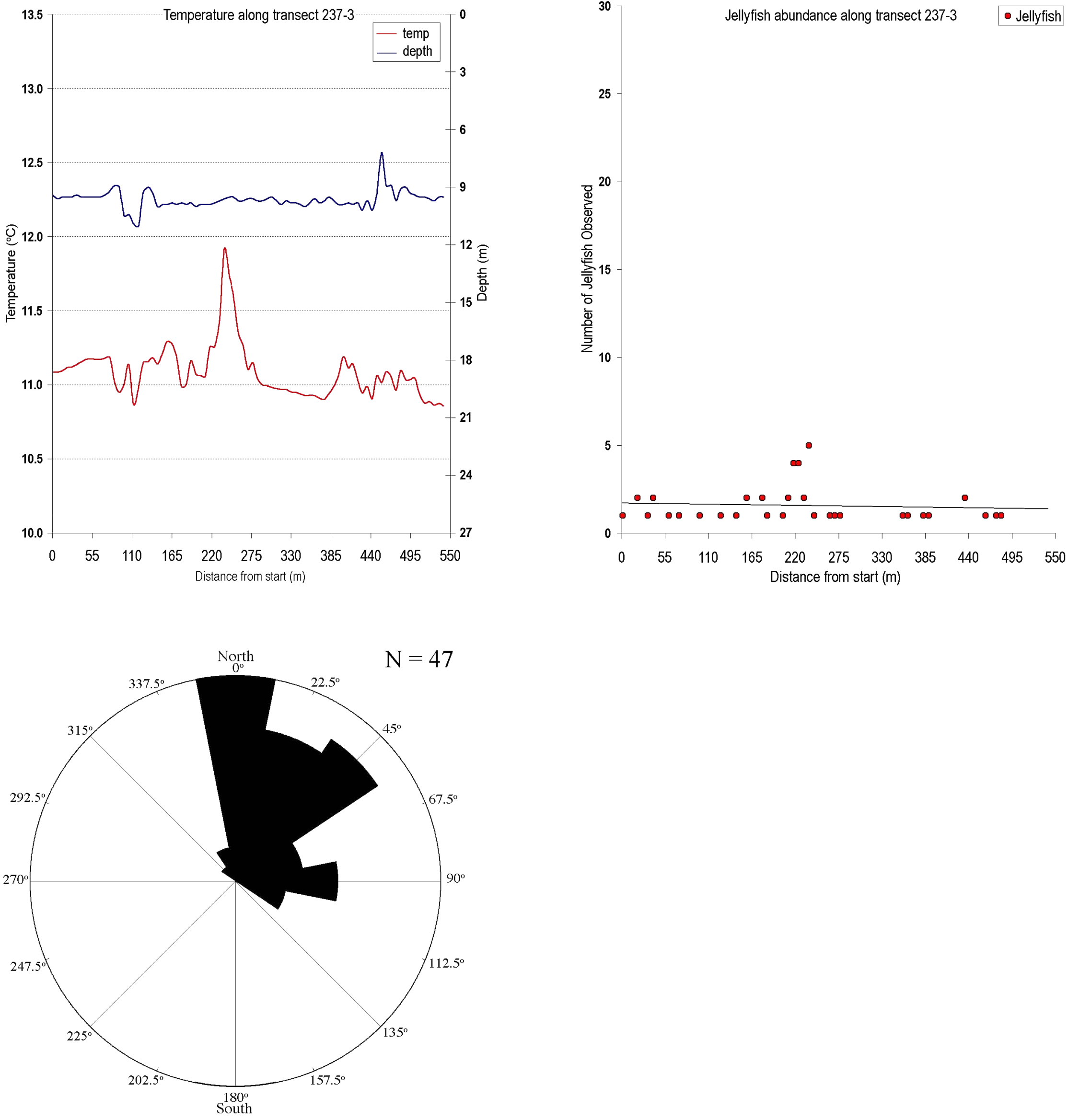

Figure 1-8e. ROV video transect 237-3 data including depth, temperature, *C. fuscescens* counts, and proportional swimming orientation. August 23-25, 2000.

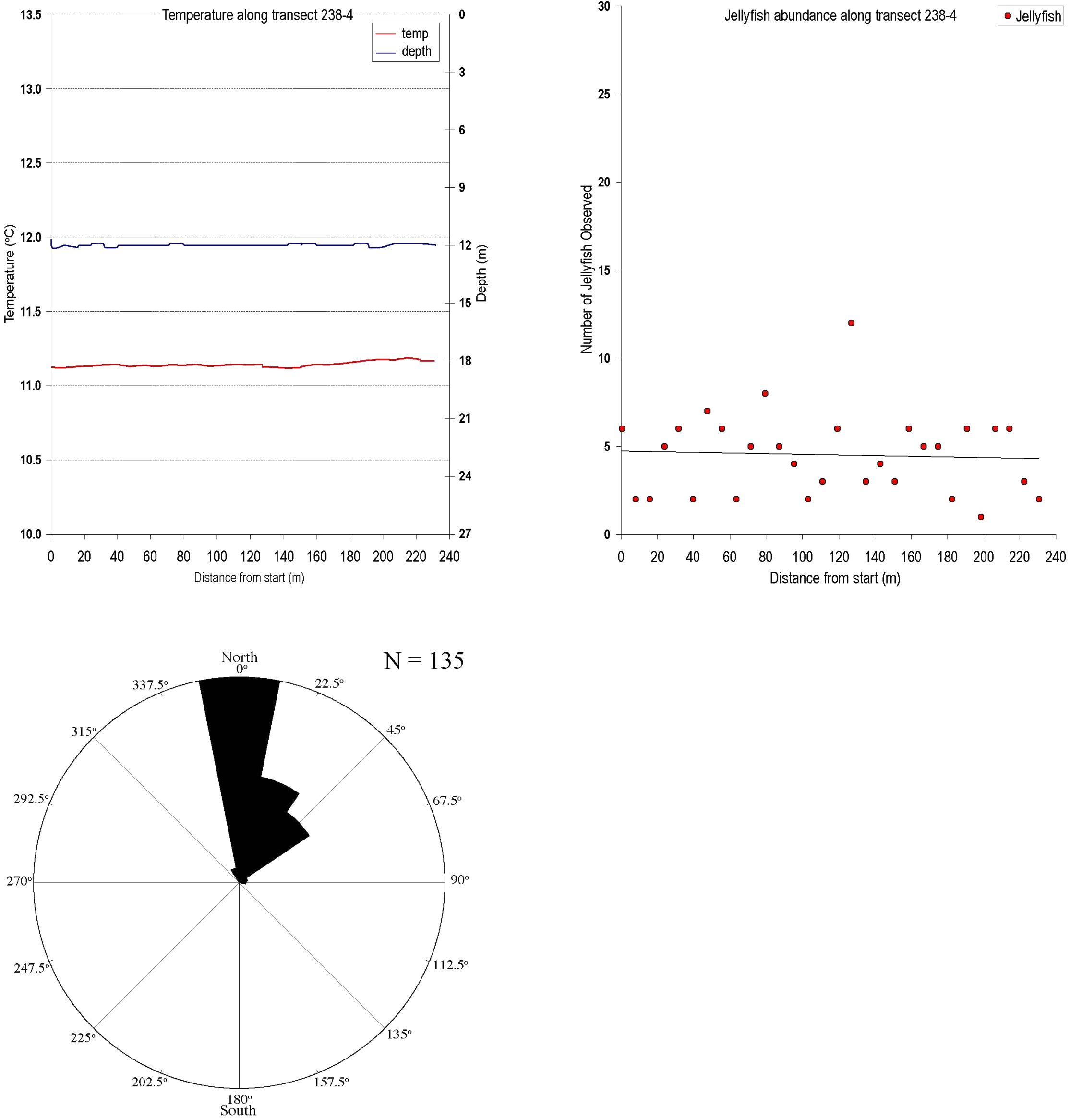

Figure 1-8f. ROV video transect 238-4 data including depth, temperature, *C. fuscescens* counts, and proportional swimming orientation. August 23-25, 2000.

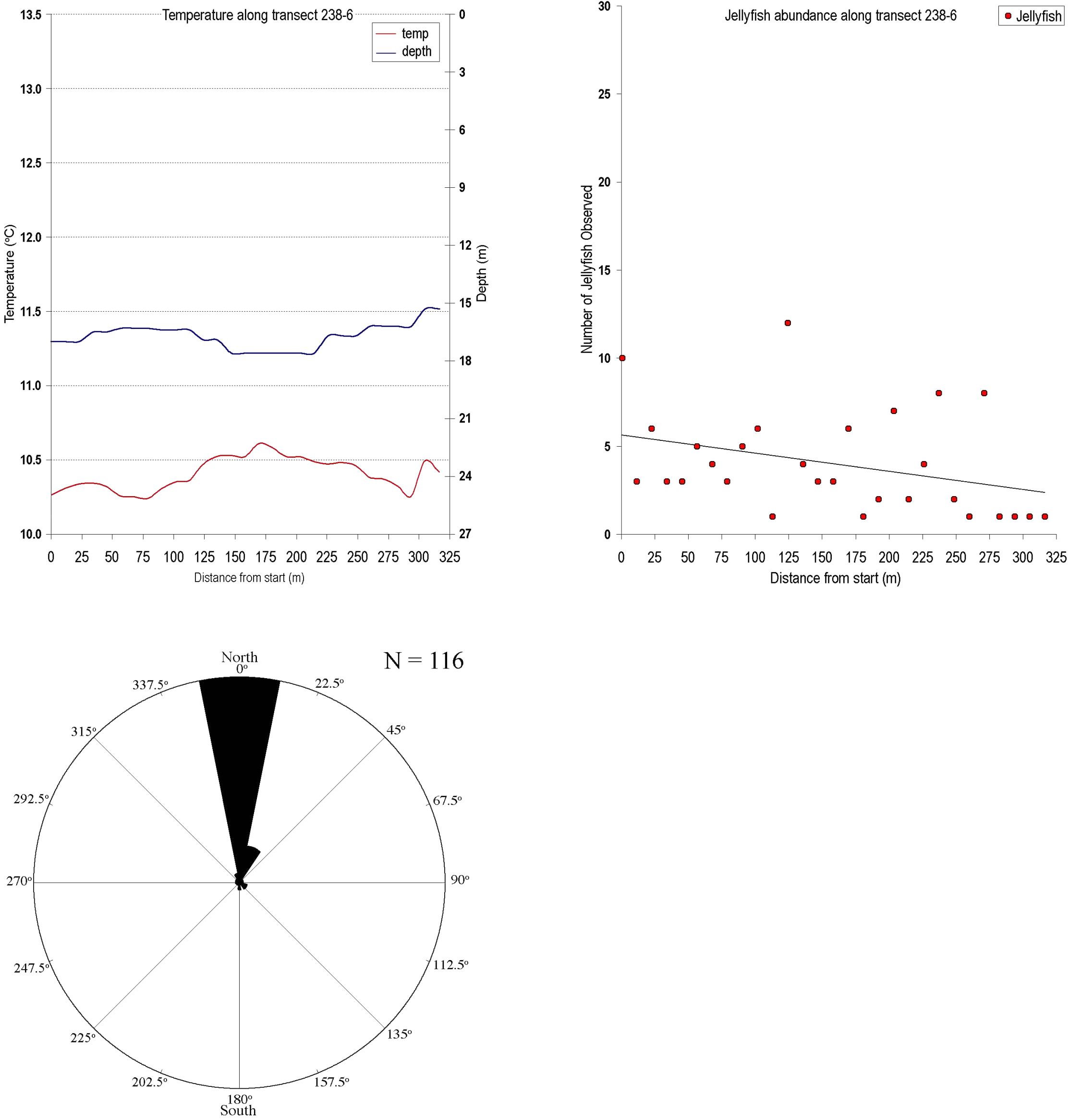

Figure 1-8g. ROV video transect 238-6 data including depth, temperature, *C. fuscescens* counts, and proportional swimming orientation. August 23-25, 2000.

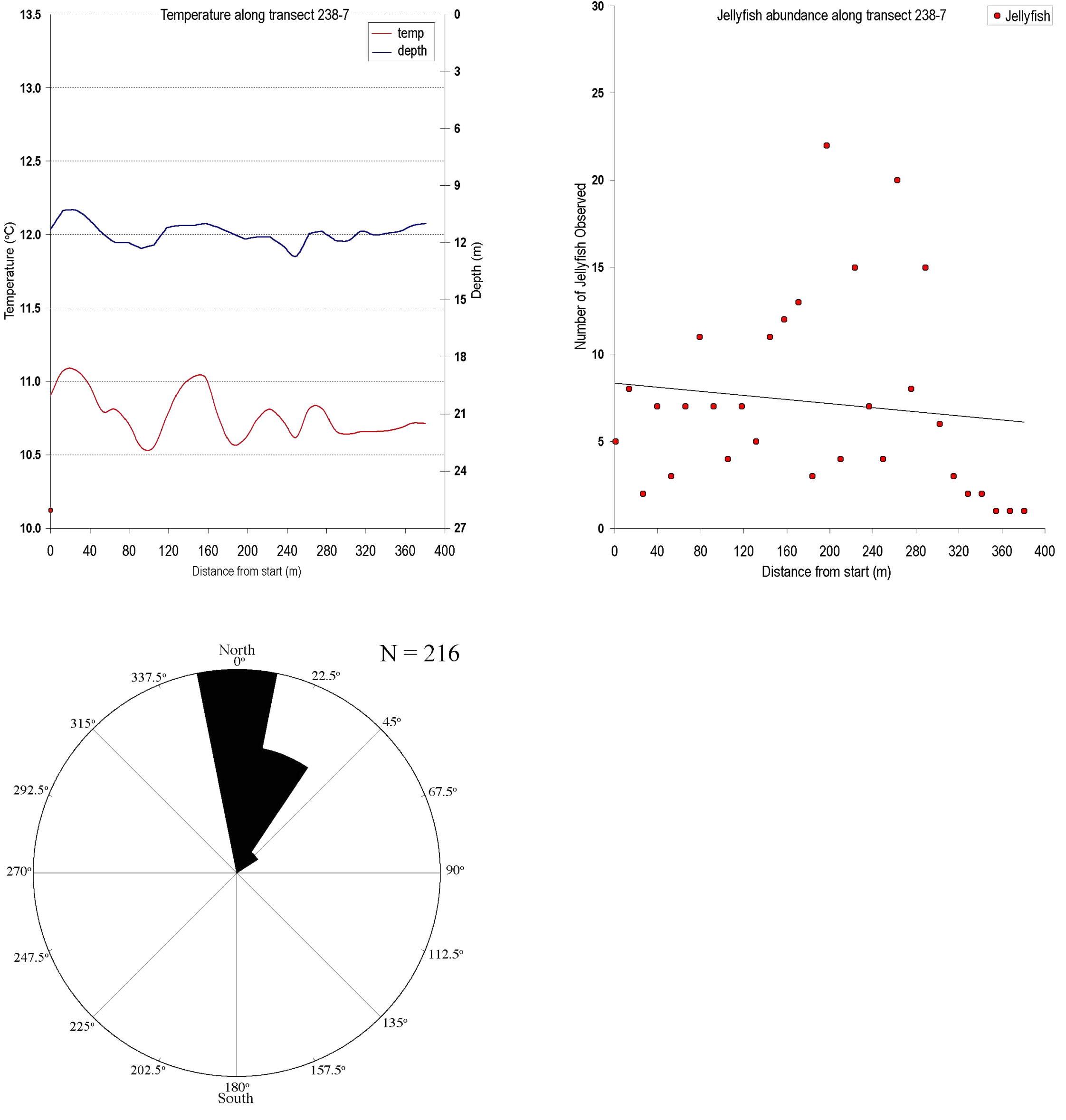

Figure 1-8h. ROV video transect 238-7 data including depth, temperature, *C. fuscescens* counts, and proportional swimming orientation. August 23-25, 2000.

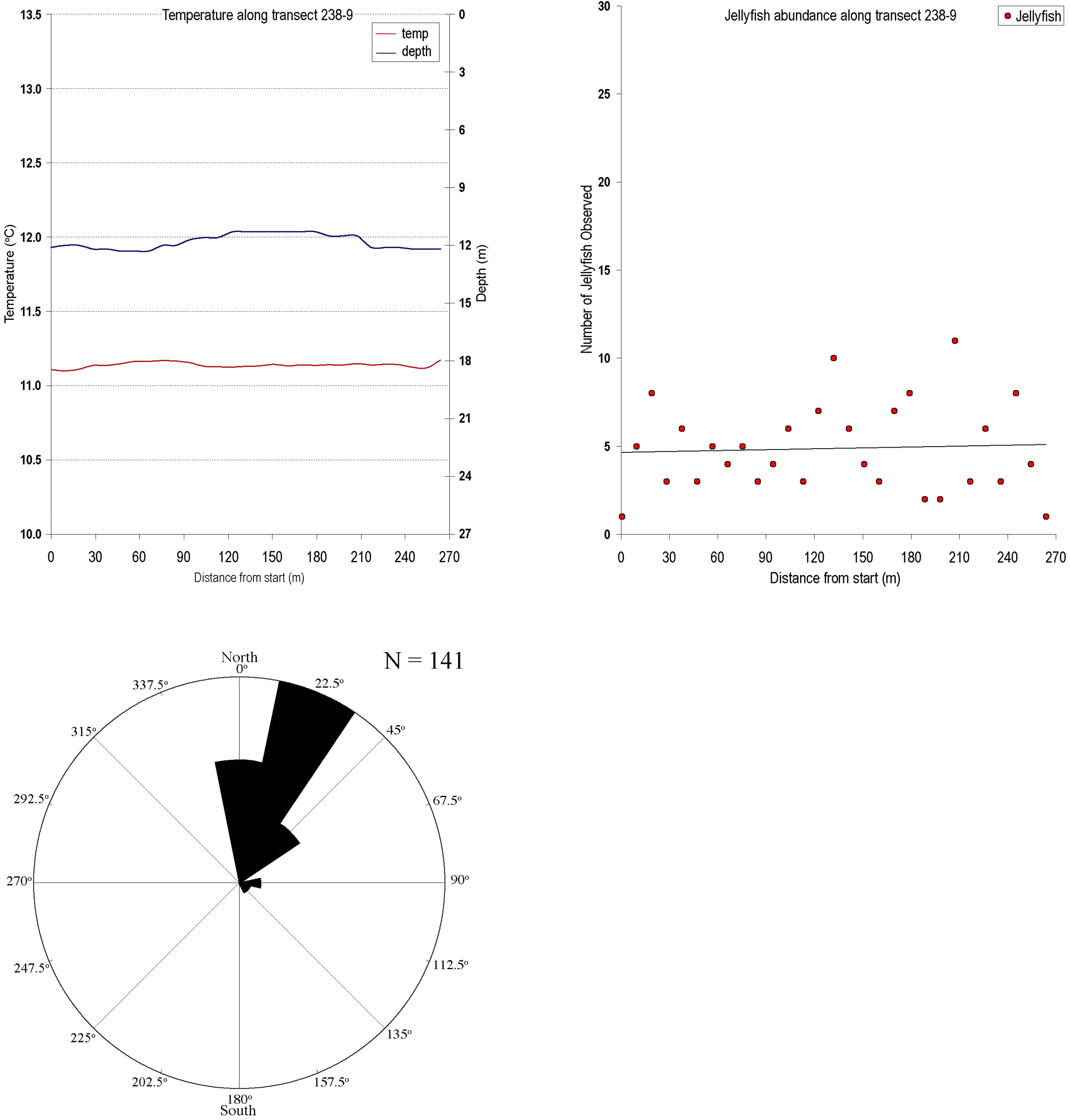

Figure 1-8i. ROV video transect 238-9 data including depth, temperature, *C. fuscescens* counts, and proportional swimming orientation. August 23-25, 2000.

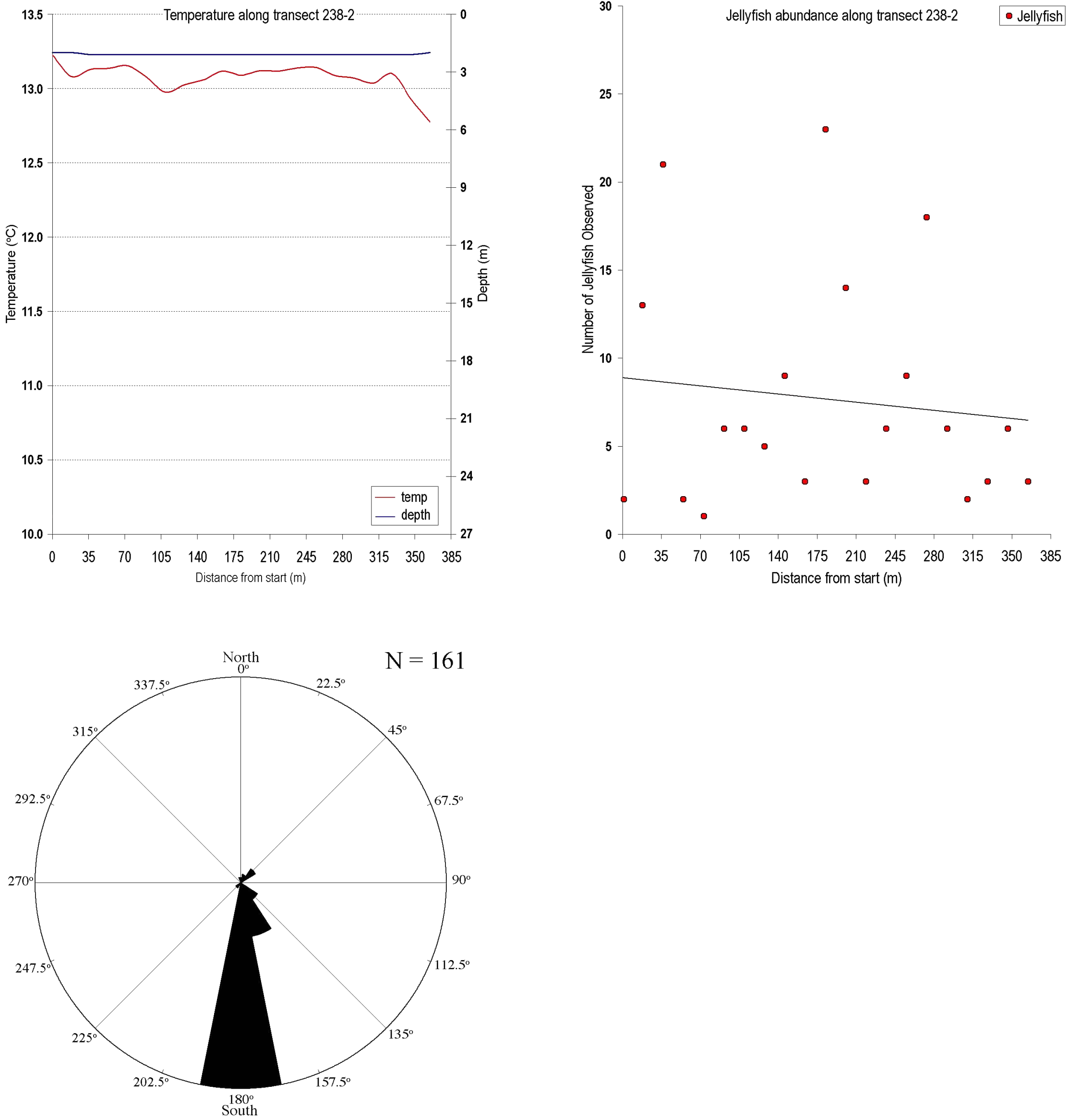

Figure 1-8j. ROV video transect 238-2 data including depth, temperature, *C. fuscescens* counts, and proportional swimming orientation. August 23-25, 2000.

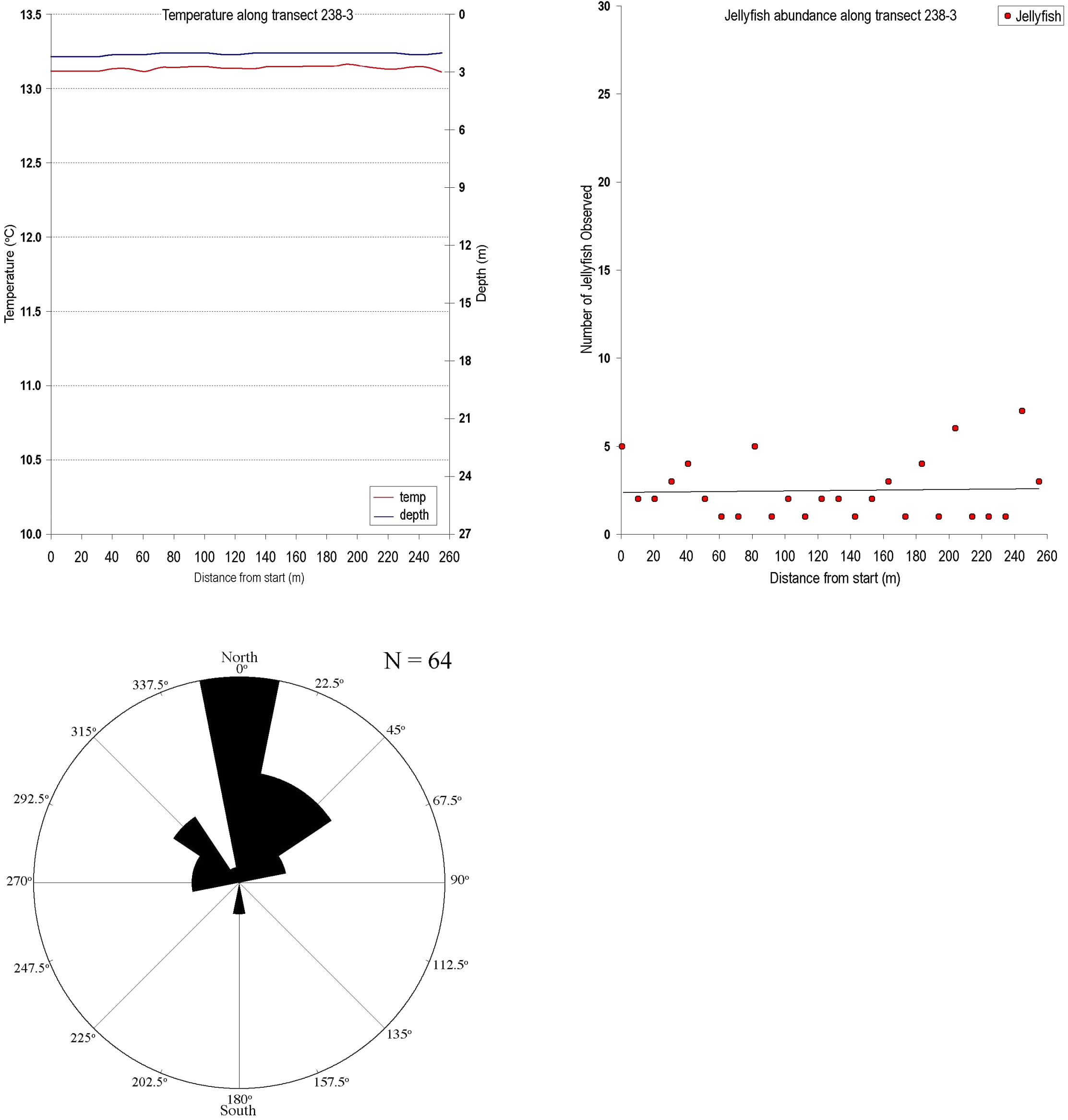

Figure 1-8k. ROV video transect 238-3 data including depth, temperature, *C. fuscescens* counts, and proportional swimming orientation. August 23-25, 2000.

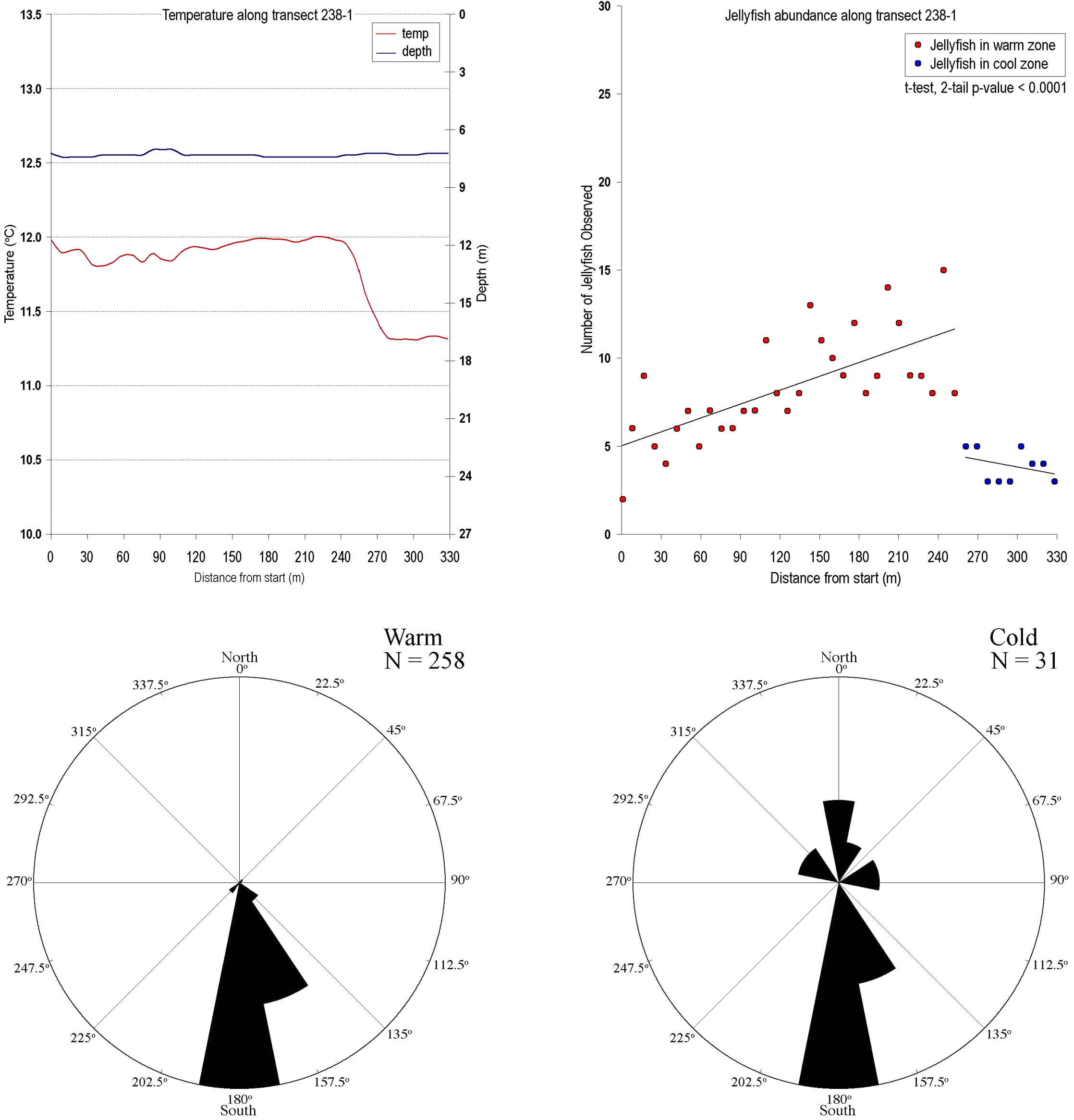

Figure 1-8l. ROV video transect 238-1 data including depth, temperature, *C. fuscescens* counts, and proportional swimming orientation. August 23-25, 2000.

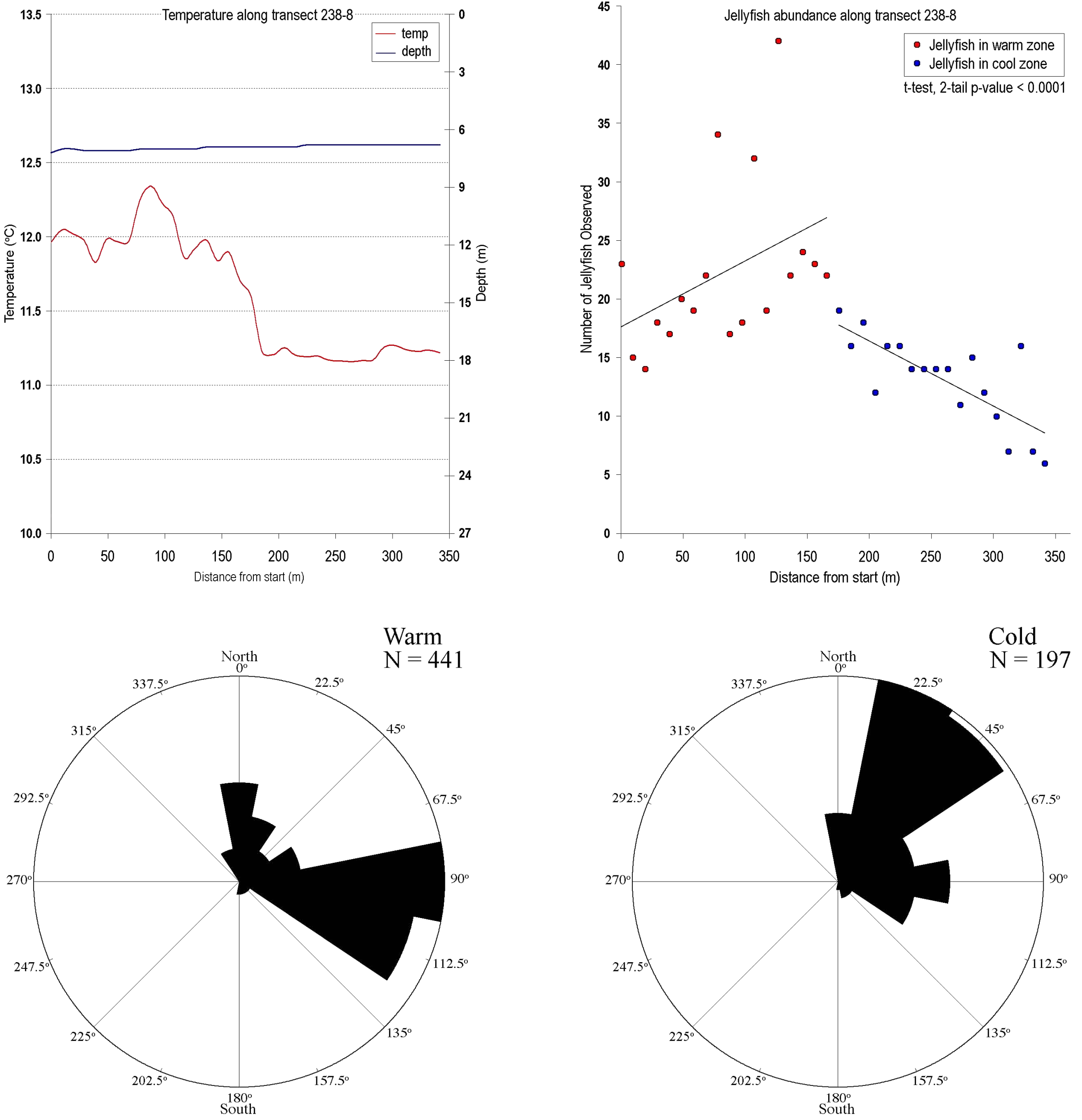

Figure 1-8m. ROV video transect 238-8 data including depth, temperature, *C. fuscescens* counts, and proportional swimming orientation. August 23-25, 2000.

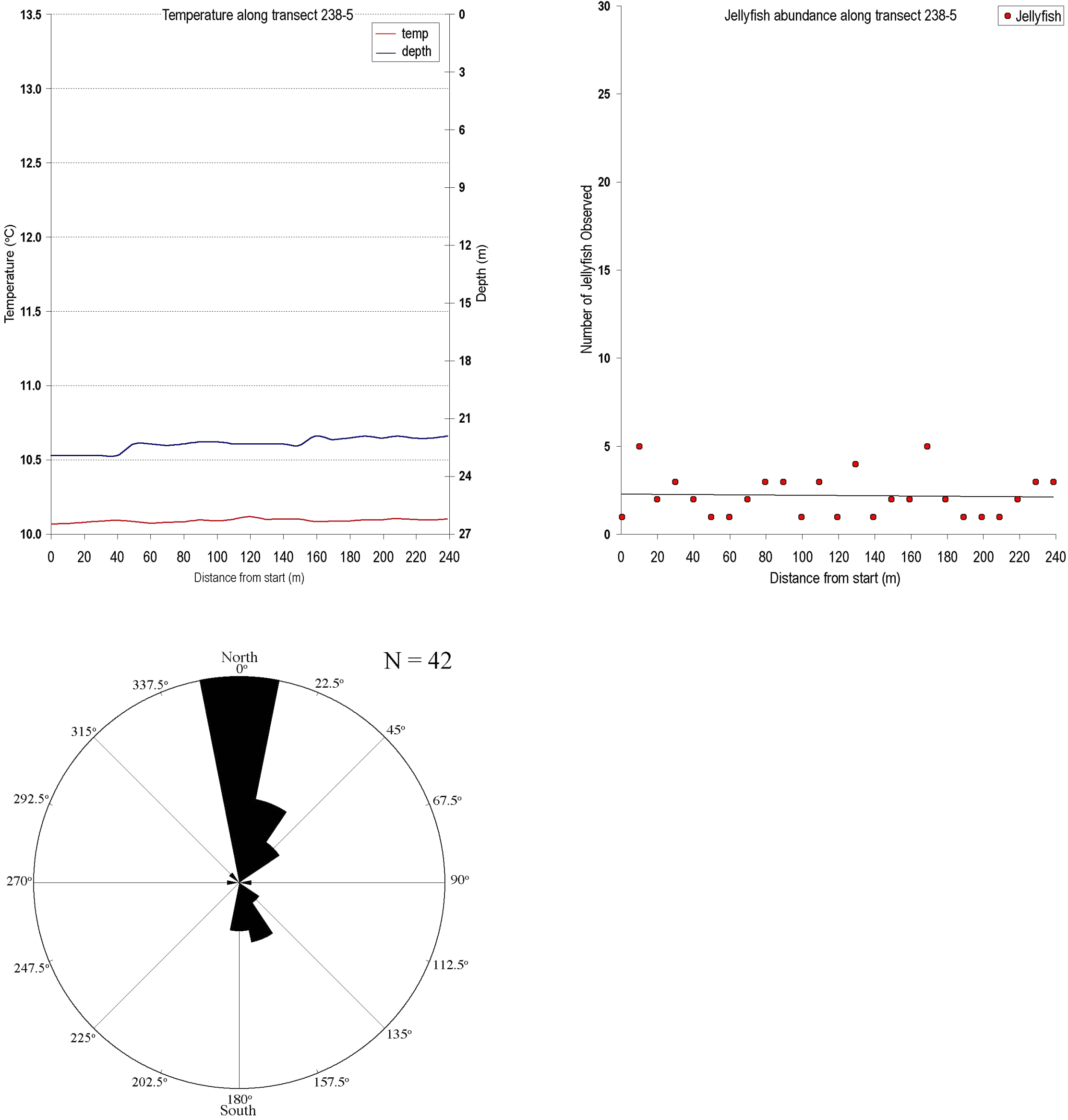

Figure 1-8n. ROV video transect 238-5 data including depth, temperature, *C. fuscescens* counts, and proportional swimming orientation. August 23-25, 2000.

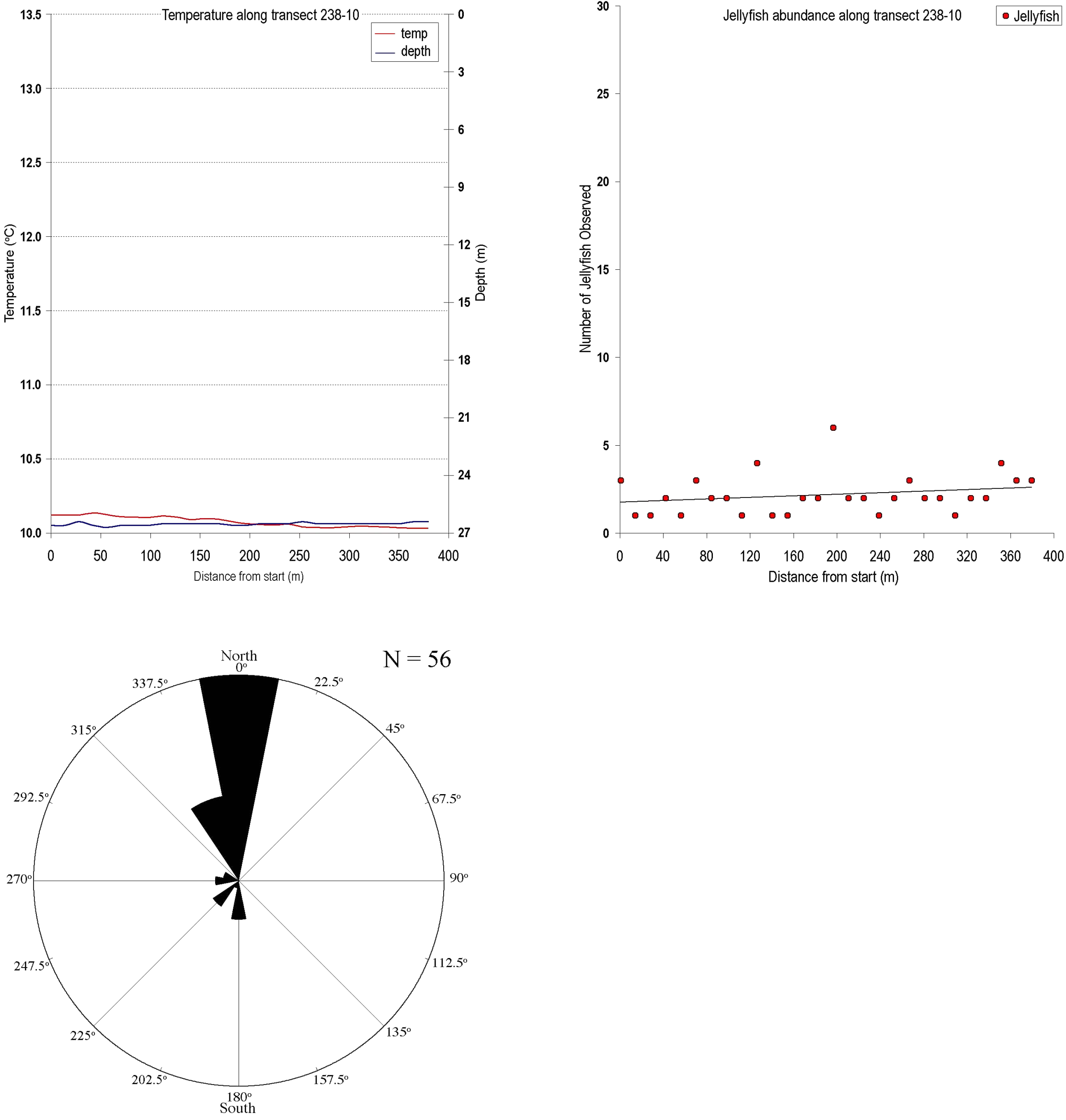

Figure 1-8o. ROV video transect 238-10 data including depth, temperature, *C. fuscescens* counts, and proportional swimming orientation. August 23-25, 2000.

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