# VERTICAL MIGRATION AND ITS EFFECT ON DISPERSAL OF PENAEID SHRIMP LARVAE IN THE GULF OF CARPENTARIA, AUSTRALIA

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## ABSTRACT

Penaeid shrimp larvae in the Gulf of Carpentaria, Australia, sampled over discrete depths and time intervals showed a day-night pattern of vertical distribution. The magnitude of the migrations increased with larval development. The patterns of vertical distribution were variable and depended strongly on light penetration. Vertical migratory behavior of larvae was linked to currents at various depths. Daily and fortnightly extrapolations of larval displacement showed that vertical migration generally enhanced horizontal advection but the distances and directions were dependent on the current regime and the vertical distribution pattern. It was estimated that larvae could be advected from 70 to 100 km, far enough to traverse the distance from the known spawning grounds to estuarine nursery grounds. Results of this short-term study indicate that differential advection on a seasonal scale may be responsible for the temporal and spatial recruitment patterns of postlarvae observed in the Gulf of Carpentaria.

Vertical migration is widespread among marine and freshwater Crustacea (Russell 1925; Bainbridge 1961). The migration is often periodic and can vary from diurnal and tidal through to seasonal and ontogenetic periodicity. Almost as diverse as the organisms involved are the probable environmental cues that elicit the response and adaptive advantages attributed to this behavior (Bainbridge 1961; Enright 1977; Pearre 1979). Undoubtedly animals have adopted vertical migratory behavior for a variety of immediate and long-term biological advantages (Vinogradov 1968).

Most of the adaptive advantages of vertical migration that have been suggested usually apply to animals that live in relatively deep water with temperature, pressure, light, food, and predator abundance gradients. Shallow-water holoplanktonic and meroplanktonic animals also undergo vertical migrations, however. Because the vertically migrating animal is exposed to different current regimes at different depths (Hardy 1936, 1953), the behavior has been invoked to aid maintenance of position within estuaries (Bousfield 1955; Graham 1972; Weinstein et al. 1980; Wooldridge and Erasmus 1980) and on continental shelves (Walford 1938). It has also been suggested that timed vertical migration enhances horizontal displacement up an estuary (Carriker 1951; Wood and Hargis 1971; Sandifer 1975; Bigford 1979; Sulkin et al. 1980), alongshore (Longhurst 1968; Efford 1970), or onshore (Woodmansee 1966; Penn 1975; Rimmer and Phillips 1979), often against the prevailing currents. In no instance, however, have these mechanisms been demonstrated by monitoring both the vertical behavior and the in situ current regimes simultaneously.

Dispersal, during the pelagic larval phase, is the most likely mechanism that brings postlarval and juvenile penaeid shrimp into shallow-water coastal and estuarine nursery areas from their offshore spawning grounds (Kirkegaard 1975). Evidence of vertical migration of penaeid larvae, which might enhance the onshore movement, is mixed and inconclusive. In the study by Eldred et al. (1965) the larval vertical distribution patterns were variable between species, but appeared to be consistent in the study by Temple and Fischer (1965). A change in behavior from photopositive to photonegative with development was reported by Racek (1959), while a gradual increase in vertical migratory ability, without a phase change, has been seen in other studies (Temple and Fischer 1965; Jones et al. 1970). Most noticeable have been the variable patterns in vertical distribution with varying environmental conditions in studies with repeated sampling (Temple and Fischer 1965; Jones et al. 1970). Nevertheless, based on an idealized larval

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behavior and limited knowledge of current regimes, Penn (1975) hypothesized that larvae of *Penaeus latisulcatus*, off Western Australia, were capable of moving onshore against prevailing currents during certain times of the year.

In this study I attempted to test Penn's (1975) hypothesis by intensively sampling the changes in vertical distribution of penaeid larvae while simultaneously monitoring currents and other environmental parameters in the water column. I hoped to gain insight into the following: the ontogeny of vertical migratory behavior, the environmental factors that control the larval behavior, the current regimes and how they change with depth, and the advective consequences to the larvae resulting from vertical migration through this variable current field.

Staples (1979), studying the postlarvae of *Penaeus merguiensis* in the Gulf of Carpentaria, found discrete temporal and spatial patterns of postlarval recruitment into the rivers around the gulf. These patterns could not be explained entirely by the distribution of adults and the timing of spawning. He proposed that the temporal and spatial patterns of recruitment were caused by the different fates of larvae arising from two peaks of spawning (spring and autumn). While seasonal changes in the direction of larval advection were suggested, little was known about current regimes in the gulf (Cresswell 1971) and nothing known about how these currents would affect the distance and direction of penaeid larval dispersal. This study was, therefore, intended to provide insight into the mechanisms and pathways of larval dispersal and to help explain the variable timing and magnitude of postlarval recruitment.

## MATERIALS AND METHODS

Discrete depth sampling was conducted repeatedly at two locations (Fig. 1) during survey cruises in the Gulf of Carpentaria (Rothlisberg and Jackson 1982). These locations were <30 m in depth and close to known concentrations of adult penaeid shrimp. The ship was anchored on station and a 7.6 cm (3 in) centrifugal pump (Fig. 2), driven by a 6 kW (8 hp) aircooled gasoline engine, was used to pump water from depth. The end of the 10.2 cm (4 in) intake hose was clamped to a weighted wire fed through a meter block. The full length of the hose, in 9.2 m (30 ft) quick coupled lengths, was deployed, regardless of the sampling depth, to prevent variable friction effects. Water from the pump was discharged through a 7.6 cm (3 in) diameter hose tangentially into a drum (spinner) mounted on a tripod. Upon loss of velocity the water drained gently through a 56 cm diameter plankton net (142 μm mesh) suspended beneath the spinner. The outlet hose was coupled to the spinner in such a manner that it could be inserted and withdrawn quickly to allow precisely timed pumping intervals. The pumping rate (up to 1,000 l/min) was monitored with timed fills of a container of known volume.

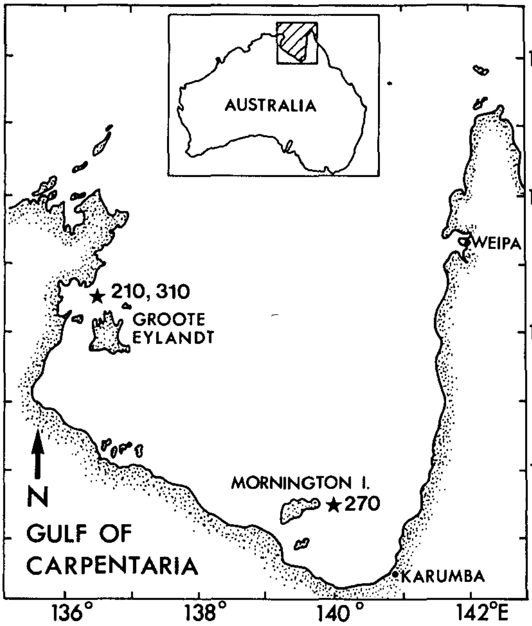

FIGURE 1.—Station numbers and locations for discrete depth sampling (stars) in the Gulf of Carpentaria, Australia.

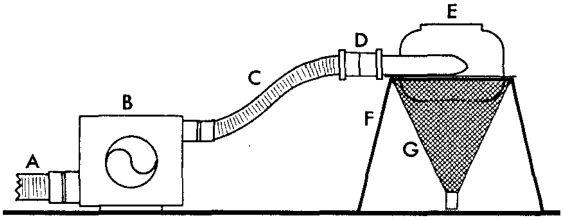

FIGURE 2.—Schematic of pump, water discharge, and filtering system: A) 10.2 cm (4 in) intake hose; B) 7.6 cm (3 in) self-priming centrifugal pump with 6 kW (8 hp) gasoline engine; C) 7.6 cm (3 in) outlet hose; D) quick coupling; E) spinner drum; F) tripod; G) 142 μm mesh plankton net.

The water column was divided into four strata, and the inlet placed at the center of the stratum. The pump was brought to speed, the outlet hose inserted in the spinner, and the stratum sampled for a 15-min interval. After 15 min the outlet hose was quickly withdrawn, the pump speed reduced, and the hose inlet lowered to the next stratum for 5 min of flushing before the next 15-min sample was taken. The four strata were therefore sampled in a 75-min pumping series which was initiated every 2 h and continued for 24-36 h.

At the same time that the pump inlet was being deployed astern on the main wire, a Lerici current meter (Frassetto 1967), modified for deck readout of current velocity, was deployed amidship on the hydrographic wire. Fifteen-minute records at each depth stratum were obtained simultaneously with plankton samples. All current meter records were annotated on a strip chart recorder in the deck readout unit.

To link the vertical distribution of the shrimp larvae to the current vectors at depth, the median level of larval vertical distribution was calculated (Cronin and Forward 1979) for each of the larval substages at each 4-h time interval and assigned to one of the four depth strata. The intermediate (2-h) larval distributions were interpolated from the 4-h time series. The current vectors for each 2-h time interval, associated with the depth stratum (levels 1-4) to which the median larval depth corresponded, were added progressively over 24 h for each larval substage (Fig. 7b, c). In addition to the median larva, three other hypothetical behavior patterns were modelled: 1) a nonmigratory surface dwelling animal; 2) a nonmigratory near-bottom dwelling animal; and 3) a larva (12:12 larva, Figs. 7, 8, 9) that followed the behavior pattern dictated by Penn's (1975) hypothesis, i.e., it moved the full height of the water column on a strict 12:12 day: night cycle for the entire length of the larval life.

A photometer, with both deck and submersible cells, was used to measure the ambient and submarine irradiance ($\mu W/cm^2$). Irradiance levels were recorded at 2 m intervals at the start of every 2-h pumping series during daylight. The meter was not sensitive enough to record variable levels of moonlight or starlight. Temperature profiles were obtained with both a bathythermograph and water sampled from the pump outlet.

Plankton biomass (settled volume) from discrete depth samples was obtained by settling the fixed sample (10% formaldehyde, sodium tetraborate buffer) for 4 h in Imhoff cones (Rothlisberg and Jackson 1982). The samples were then transferred to 2% 2-phenoxy ethanol for preservation and subsequent microscopic examination. For economy and expediency, only every other sampling series (4-h) was examined. No subsampling scheme was employed. Numbers of larvae in each sample were standardized to numbers per cubic meter based on the calibrated pumping rates.

## RESULTS

### Ontogeny of Vertical Migration

From sampling done on 22 and 23 March 1977 north of Groote Eylandt (Station 210), early larvae (zoeal stages 1-3) were seen to move up into the water column only at night (Fig. 3). This movement was very limited and rarely extended more than one-half the distance to the surface. By day they were almost totally restricted to the bottom stratum of the water column sampled. The mysis stages extended the range of their nighttime excursions to the full water column without completely abandoning the lower part of the water column at night. They too returned almost completely to the bottom stratum by day. Postlarval numbers in the samples were too few to make generalizations, but they did appear to

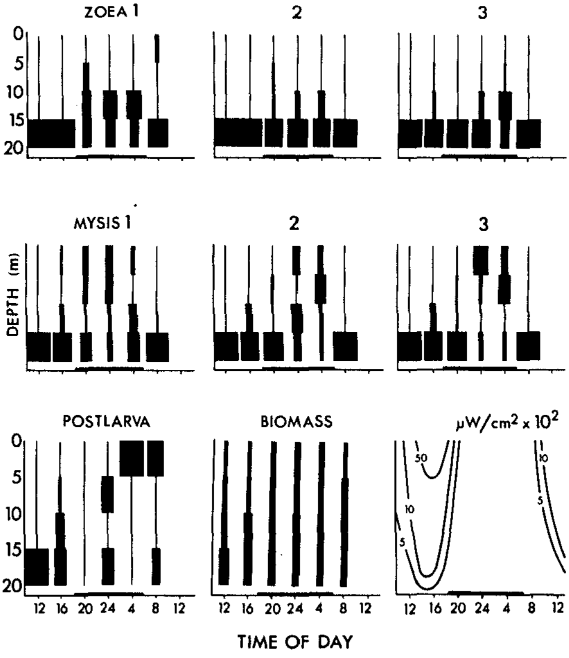

FIGURE 3.—Relative larval abundance (percent) by substage and depth stratum, vertical distribution of settled plankton volume (percent), and vertical profiles of submarine irradiance ($\mu W/cm^2$) for 22-23 March 1977 at Station 210 north of Groote Eylandt. The dark horizontal bar indicates night.

extend the mysis pattern further by almost completely abandoning the lower parts of the water column by night but still returning by day.

## Variations in the Pattern of Vertical Distribution

High light penetration was characteristic of the station occupied on 22 and 23 March 1977 (Fig. 3). Conditions were calm, isothermal, and clear with a secchi disc depth of 16 m in the 22 m water column and penetration of the 1,000 $\mu$W/cm$^2$ isolume to 20 m. Under these conditions, movement of the larvae away from the deepest stratum occurred only at night and almost all stages (first zoea (Z1) through third mysis (M3)) returned to the bottom stratum during daylight.

On 6 and 7 May 1977 (Station 310), though sea state and wind conditions were comparable with the previous sampling session, increased turbidity limited the 1,000 $\mu$W/cm$^2$ isolume penetration to only 10 m or about half of the water column (Fig. 4). This change in light penetration paralleled marked changes in the vertical distribution of all larval stages. During daylight, early larval stages (zoea 1-3) were not confined to the bottom stratum. The day-night differences in vertical distribution, though present, were less distinct than in the previous case, and these early larval stages were seen even at the surface at night. The day-night pattern for mysis stage larvae was even less distinct. Though spread throughout the water column, they appeared to be slightly more concentrated at or near the surface at night. Postlarval (PL) numbers were again low, and they were near the surface during the entire diel period. They were more abundant in the surface stratum during the night.

At the station east of Mornington Island on 27 and 28 March 1977 (Station 270) the wind and sea conditions were extremely calm but light penetration was even more diminished than in the previous two cases. On this occasion the 1,000 $\mu$W/cm$^2$ isolume penetrated only about one-third of the water column (Fig. 5). Further changes in the patterns of larval distribution were seen. Early larval stages were concentrated in the middle two depth strata with nighttime movements to the surface. The mysis stage larvae were also predominantly in the middle part of

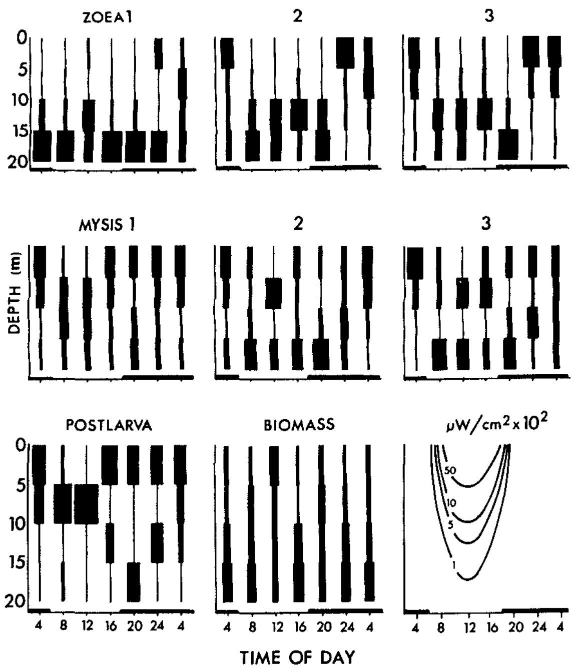

FIGURE 4.—Relative larval abundance (percent) by substage and depth stratum, vertical distribution of settled plankton volume (percent), and vertical profiles of submarine irradiance ($\mu$W/cm$^2$) for 6-7 May 1977 at Station 310 north of Groote Eylandt. The dark horizontal bar indicates night.

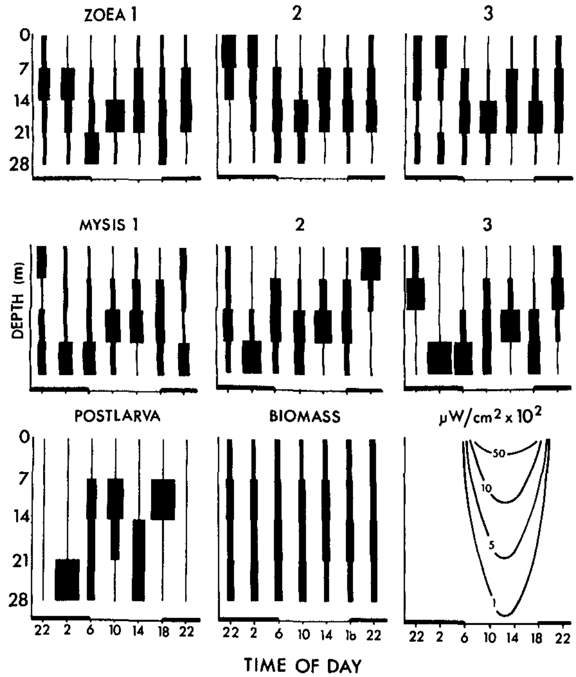

FIGURE 5.—Relative larval abundance (percent) by substage and depth stratum, vertical distribution of settled plankton volume (percent), and vertical profiles of submarine irradiance ($\mu$W/cm$^2$) for 27-28 March 1977 at Station 270 east of Mornington Island. The dark horizontal bar indicates night.

the water column by day but spread out to both the surface and the bottom strata at night. Again the postlarval numbers were low and little day-night patterning was evident. No postlarvae were caught at any time in the surface stratum and were near the bottom both day and night.

Of concern was possible day-night variation in larval abundance due to avoidance of the inlet hose and/or larval distribution outside the range of the sampler. Of particular concern was the possibility that during the day larvae were on or near the bottom below the hose inlet at its lowest extent. To test statistically for a temporal variation in larval abundance, the larval numbers were initially combined over all depths within a sampling time interval and then a square root transformation was applied. A sine curve was fitted to estimate gradual rather than abrupt day-night changes in larval numbers. Postlarval numbers were too low to include in the analysis. Time alone was highly significant for the total number of larvae and significant at lower levels for three of six larval substages (Table 1). The high level of significance of the station-time interaction for all but the Z2 larvae indicates that the small diel variation in abundance was variable between sampling occasions. Inspection of the data showed that the peak abundances varied by stage, location, and time of day and that there was no systematic difference in catchability which would bias the interpretation of the diurnal patterns shown previously.

To add confidence to the diagrammatic interpretation (Figs. 3-5), further analysis, using an arc-sine transformation of the proportional larval abundances by depth also, showed that the abundances at the four depth strata were quite variable from one date to the next. This was indicated by the high degree of significance of the station effects at almost all depths (Table 2). The abundances of larvae in the surface stratum (level 1) showed the most consistent relationship with time of day, with larvae rarely at the surface by day, on any cruise, and increasing in abundance at the surface by night. Further, the station-time interaction at depth (e.g., level 3) was significant for most larval stages and substages, indicating a high degree of station-to-station variation in the depth of peak abundance.

TABLE 1.—Summary of analysis of variance of larval abundance. A square root transformation was applied to all data pooled within each time increment over all four depths.

| | F-ratios | | | |
|---|---|---|---|---|
| Stage/ substage | Station (2, 11 df) | Time (2, 11 df) | Station-time interaction (4, 11 df) | Error mean square |
| Zoea | 9.98** | 4.92* | 4.89* | 2.6519 |
| Mysis | 32.04*** | 3.58+ | 4.82* | 1.6531 |
| Total | 56.63*** | 18.03*** | 10.75*** | 1.0528 |
| Z1 | 6.21* | 1.98 | 6.31** | 0.8505 |
| Z2 | 11.86** | 4.86* | 2.89+ | 1.4859 |
| Z3 | 11.49** | 4.81* | 8.33** | 1.0520 |
| M1 | 33.30*** | 2.94+ | 3.49* | 1.8837 |
| M2 | 25.72*** | 1.66 | 13.65*** | 0.2452 |
| M3 | 40.68*** | 0.13 | 12.88*** | 0.2976 |

***P<0.001, **P<0.01, *P<0.05, + 0.05<P<0.10.

TABLE 2.—Summary of analysis of variance of proportional larval abundance at four discrete depths. An arc-sine transformation was applied to the percentages.

| | | F-ratios | | | |
|---|---|---|---|---|---|
| Stage/ sub- stage | Level | Station (2, 11 df) | Time (2, 11 df) | Station-time interaction (4, 11 df) | Error mean square |
| Zoea | 1 | 7.53** | 5.29* | 2.56+ | 0.03293 |
| | 2 | 17.01*** | 0.72 | 2.15 | 0.02167 |
| | 3 | 4.56* | 0.60 | 6.49** | 0.02906 |
| | 4 | 22.68*** | 2.31 | 2.10 | 0.04125 |
| Mysis | 1 | 7.33* | 16.11*** | 0.76 | 0.02179 |
| | 2 | 10.55** | 1.94 | 8.46** | 0.01277 |
| | 3 | 7.68** | 2.58 | 3.35+ | 0.01925 |
| | 4 | 14.89*** | 1.25 | 9.27** | 0.03075 |
| Z1 | 1 | 1.25 | 0.13 | 2.10 | 0.03876 |
| | 2 | 10.61** | 0.78 | 0.91 | 0.04839 |
| | 3 | 3.84+ | 0.59 | 7.31** | 0.03953 |
| | 4 | 12.74** | 2.12 | 3.27+ | 0.05937 |
| Z2 | 1 | 6.65* | 7.42** | 2.23 | 0.04838 |
| | 2 | 17.53** | 0.46 | 1.59 | 0.02760 |
| | 3 | 8.85** | 1.03 | 5.56* | 0.03270 |
| | 4 | 30.46*** | 3.48+ | 0.97 | 0.05877 |
| Z3 | 1 | 11.05** | 6.43* | 2.38 | 0.3573 |
| | 2 | 9.99** | 0.27 | 1.09 | 0.03112 |
| | 3 | 4.03* | 1.89 | 4.10* | 0.04522 |
| | 4 | 14.00*** | 0.47 | 1.22 | 0.09720 |
| M1 | 1 | 9.13** | 16.15** | 0.35 | 0.01989 |
| | 2 | 13.82*** | 0.27 | 5.78** | 0.01714 |
| | 3 | 4.26* | 1.90 | 3.39* | 0.02365 |
| | 4 | 40.92*** | 2.24 | 21.86*** | 0.01289 |
| M2 | 1 | 2.50 | 4.97* | 1.11 | 0.06961 |
| | 2 | 2.06 | 0.34 | 1.07 | 0.08163 |
| | 3 | 3.31+ | 0.20 | 3.02+ | 0.05118 |
| | 4 | 5.70* | 1.06 | 2.44 | 0.10437 |
| M3 | 1 | 4.85* | 9.31** | 0.80 | 0.05065 |
| | 2 | 1.21 | 0.16 | 2.27 | 0.09051 |
| | 3 | 3.74+ | 1.01 | 9.24** | 0.03211 |
| | 4 | 2.22 | 1.51 | 2.13 | 0.16646 |

***P<0.001, **P<0.01, *P<0.05, + 0.05<P<0.10.

## Consequences of Vertical Migration

At the two sampling locations in the Gulf of Carpentaria, the currents were dominated by a tidal component as seen in the individual current vectors, represented by the mean speed and direction for the 15-min sampling periods (Fig. 6). Detailed analyses of these records, however, were complicated by three factors: 1) time lag between sampling surface and bottom strata; 2) short-term wind events; and 3) anomalous current vectors at depth. At most sampling times, current speed and direction changed with depth. Although the speed usually decreased with depth (e.g., Fig. 6a, 0200; 6c, 2200), an increase was noted on some occasions, especially around the time of slack water (e.g., Fig. 6a, 1200; 6b, 0000). This apparent increase is believed to be an artifact of the time lag in sampling with the migrating current meter. Short-term wind events can also be detected at the surface stratum (Fig. 6b, 2.5 m; 1800-2200). Time lag and wind events alone, however, cannot explain all the variation in the current vectors. Other anomalous current vectors at depth (e.g., Fig. 6a, 1000, 17.5 m; 0800, 7.5 m) represent short-term nontidal perturbations of unknown origin.

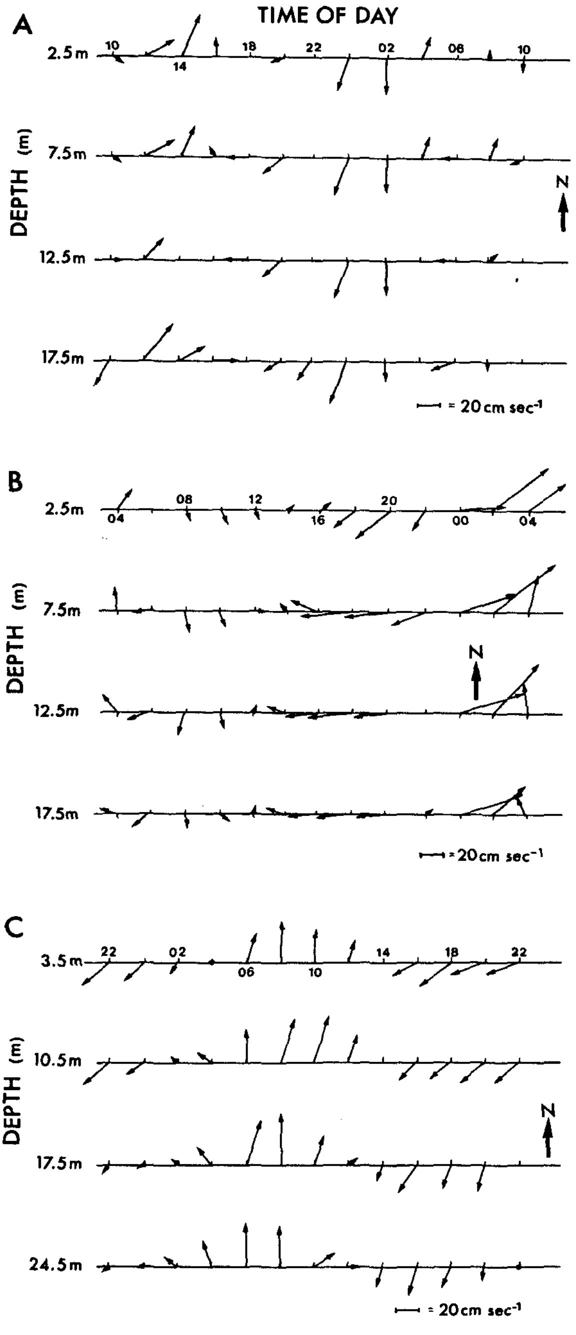

FIGURE 6.—Mean 2-h current vectors at four depths and three stations: A) Station 210, 22-23 March 1977 north of Groote Eylandt; B) Station 310, 6-7 May 1977 north of Groote Eylandt; C) Station 270, 27-28 March 1977 east of Mornington Island.

Over the 24-h sampling period at Station 210, the net displacement (measured as a straight line from the origin to the end of the progressive vector) was quite variable for migratory and nonmigratory animals. Surface-dwelling animals would have been displaced to the northwest, near-bottom dwelling ones to the south, and the 12:12 larva almost due west. The net drift of the 12:12 larva was considerably less than either of the nonmigratory animals. The larval movements (Fig. 7b, c) based on sampled vertical distributions would have closely paralleled the bottom currents in this case because so much of their time was spent in the lower parts of the water column. The slight differences in displacement direction and distance between substages reflect the differences in depth distribution. Because of their wider excursions, the postlarvae were exposed to more of a mixture of the bottom and surface currents and therefore approached the 12:12 larva in direction of advection during that larval stage. To calculate an approximate total displacement over the whole of the larval phase, the 24-h picture was extrapolated by making several assumptions. Firstly, the larval life span was set at 14 d with 2 d for each larval substage (Z1, Z2, Z3, M1, M2, M3, PL). Secondly, within each substage the same vertical migratory behavior prevailed on both days. Thirdly, the current regime, seen during the 24-h sampling period, was constant over the 14-d larval life. By doubling the length of the daily resultant vectors for each larval substage and adding them progressively, the 2-wk displacement is approximated (Fig. 7d). The calculation of absolute distances is not precise because of the nature of the assumptions, especially the third. The period of sampling was, however, between neap and spring tides so the tidal currents would have been moderate and a reasonable approximation of mean velocities over the tidal cycle. Under these criteria, the median larva would have been displaced about 69 km (37 nmi), the 12:12 larva 25 km (13 nmi),

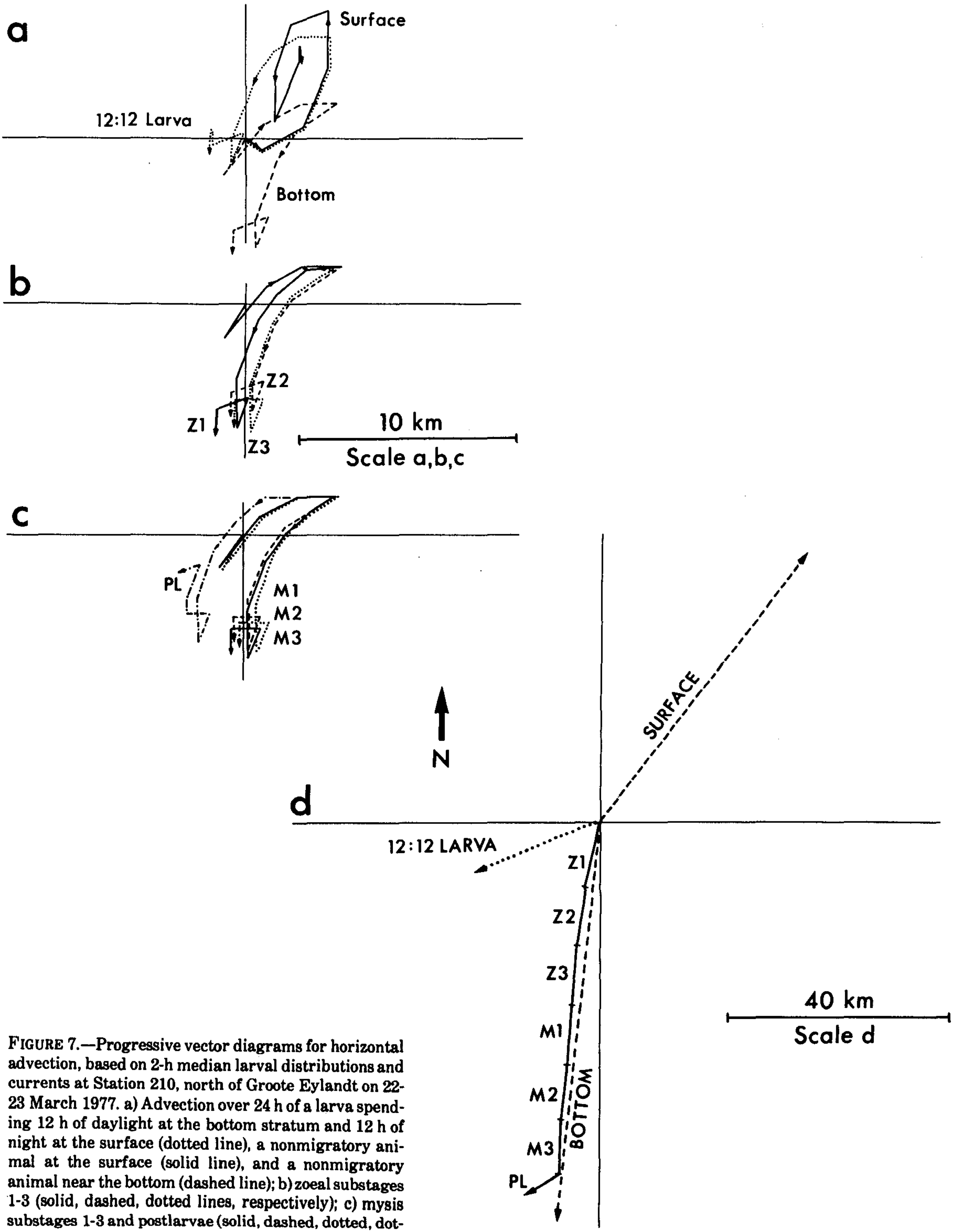

FIGURE 7.—Progressive vector diagrams for horizontal advection, based on 2-h median larval distributions and currents at Station 210, north of Groote Eylandt on 22-23 March 1977. a) Advection over 24 h of a larva spending 12 h of daylight at the bottom stratum and 12 h of night at the surface (dotted line), a nonmigratory animal at the surface (solid line), and a nonmigratory animal near the bottom (dashed line); b) zoeal substages 1-3 (solid, dashed, dotted lines, respectively); c) mysis substages 1-3 and postlarvae (solid, dashed, dotted, dot-dashed lines, respectively); d) 14-d extrapolation of daily resultant vectors: nonmigratory surface (dashed line); nonmigratory bottom (dashed line); 12:12 surface bottom larva (dotted line); median larva (solid line).

and the surface and near bottom nonmigratory animals 62 km (34 nmi) and 72 km (39 nmi), respectively. The larvae were displaced to the southwest from the sampling station north of Groote Eylandt. This trajectory would have taken them in the general direction of Groote Eylandt or the coastal rivers in the Limmen Bight, southwest of Groote Eylandt. Greater distances could be attained if the pelagic postlarval stage was maintained through several instars before metamorphosing to the benthic-living juvenile shrimp.

Procedures for approximating displacement distance and direction on the other two sampling occasions were similar but the resultant displacements were quite different because of the different vertical distribution patterns seen on each occasion. At Station 310, north of Groote Eylandt, submarine irradiance was reduced and the vertical distribution of the larval substages was more varied (Fig. 4). Consequently, the horizontal displacements of individual larval substages (Fig. 8b, c), though dominated by the bottom currents (Fig. 6b), were quite varied. The hypothetical 2-wk displacement was again in the same direction as the bottom current (Fig. 8d), but the distance was enhanced by the fact that larvae were further off the bottom in their nightly excursions for slightly higher proportions of the time. Total horizontal displacement over the 2-wk larval period, up to and including 2 d of postlarval life, would be about 75 km (40 nmi). The direction of advection of the median larva in this case is to the northwest. The 12:12 larva would have been displaced seawards to the central Gulf of Carpentaria.

Analysis of the larval migratory patterns (Fig. 5) and the current regime (Fig. 6c) at Station 270 east of Mornington Island showed yet another pattern of displacement (Fig. 9). Here, because there were large numbers of larvae in the upper part of the water column both night and day, the displacement would have been in the direction of the surface currents (Fig. 9a, b, c). Slight deflection away from the surface direction was seen in older larvae (M1-PL) as more of them moved into the lower part of the water column (Fig. 9d). The displacement distance over the 2-wk period would have been 98 km (53 nmi). All advection was to the west, with the 12:12 larva going to the southwest towards the coast and the median larva heading west-northwest, away from the coast, in the general direction of the surface currents.

## DISCUSSION

While it is widely thought that changes in light intensity are the primary environmental cues that initiate and control the diel vertical migrations in aquatic animals (Ringelberg 1964; Thorson 1964; Boden and Kampa 1967; Hutchinson 1967; Segal 1970; Buchanan and Haney 1980), there have been cases in which the timing of the migration was not strictly in phase with changes in light intensity, possibly because of changes in subsurface light and/or feeding history and strategy of the animals (Enright and Honegger 1977; Bohrer 1980). In shallow-water coastal environments, factors affecting light penetration and therefore vertical distribution of animals are numerous and subject to rapid change. Turbulence with concomitant turbidity caused by both wind and tidally induced currents, river and coastal runoff, and rapid phytoplankton growth would be the more significant causes of light reduction. It is these short-term changes in submarine irradiance that are probably responsible for some of the conflicting reports about whether or not penaeid larvae migrate vertically.

The first mention of differential vertical distribution of penaeid larvae is by Racek (1959), sampling off the eastern Australian coast. His sampling was not strictly stratified, he published no supportive data, and the conclusions are probably drawn from a combination of field and laboratory observations. He stated that nauplii as well as first and second protozoeae (= zoeae) were strongly attracted to bright light. I saw no evidence of this in our field collections but have observed it under artificially high light intensities in the laboratory. There may be some threshold light intensity at which point penaeid larvae shift their behavior from photonegative to photopositive similar to that described for the larvae of *Uca pugilator* (Herrnkind 1968). From his field sampling, Racek found that late protozoeae and early mysis stages rose to the surface at night and sunk to lower strata during daylight. The vertical distribution of late mysis and postlarvae were not mentioned in Racek's brief account.

In the study by Eldred et al. (1965), the day-night pattern of vertical distribution was neither persistent within nor consistent among genera. For *Penaeus duorarum* only postlarvae were discussed. Pooled samples were dealt with, so little information about station-to-station variation

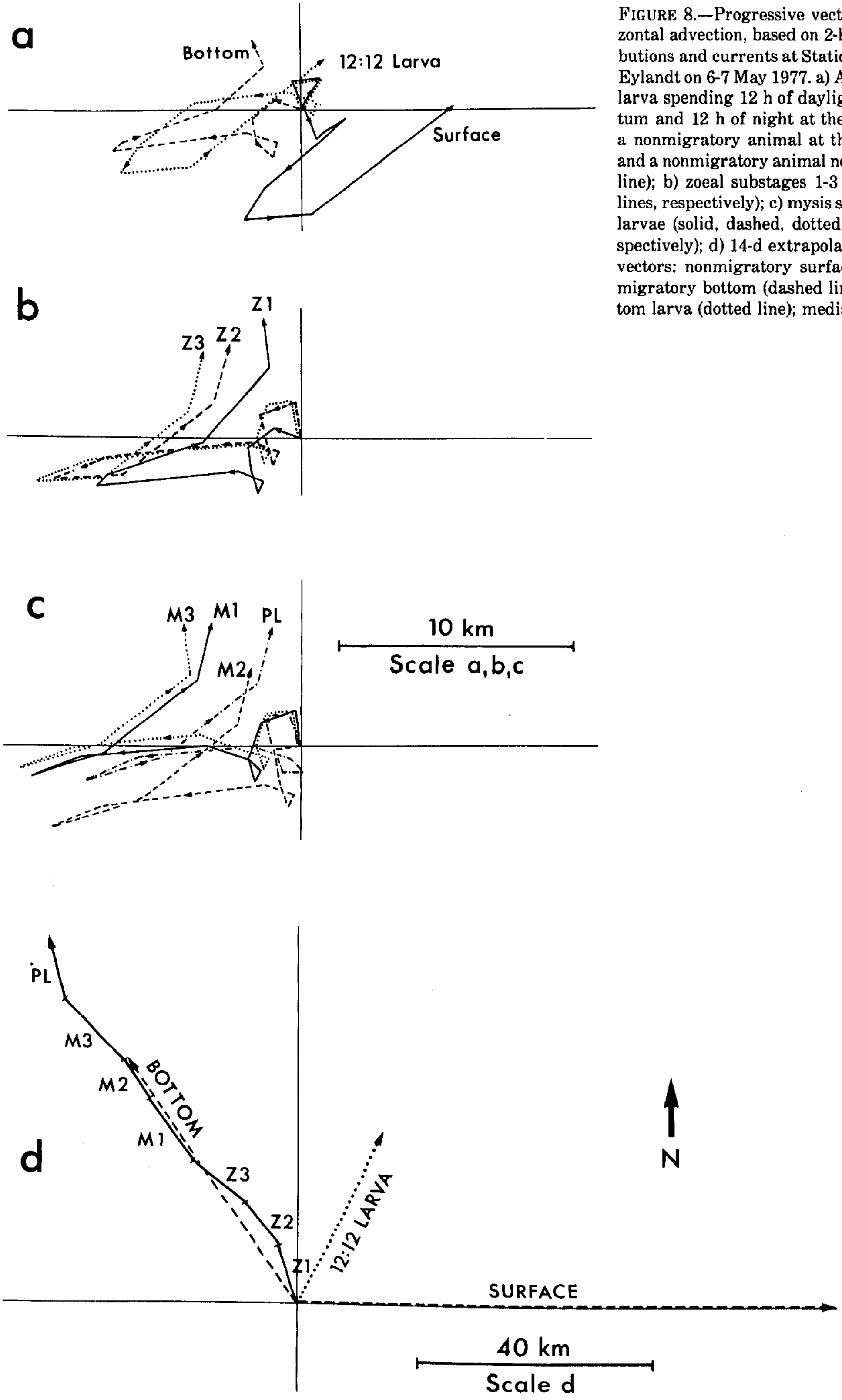

FIGURE 8.—Progressive vector diagrams for horizontal advection, based on 2-h median larval distributions and currents at Station 310, north of Groote Eylandt on 6-7 May 1977. a) Advection over 24 h of a larva spending 12 h of daylight at the bottom stratum and 12 h of night at the surface (dotted line), a nonmigratory animal at the surface (solid line), and a nonmigratory animal near the bottom (dashed line); b) zoeal substages 1-3 (solid, dashed, dotted lines, respectively); c) mysis substages 1-3 and postlarvae (solid, dashed, dotted, dot-dashed lines, respectively); d) 14-d extrapolation of daily resultant vectors: nonmigratory surface (dashed line); nonmigratory bottom (dashed line); 12:12 surface bottom larva (dotted line); median larva (solid line).

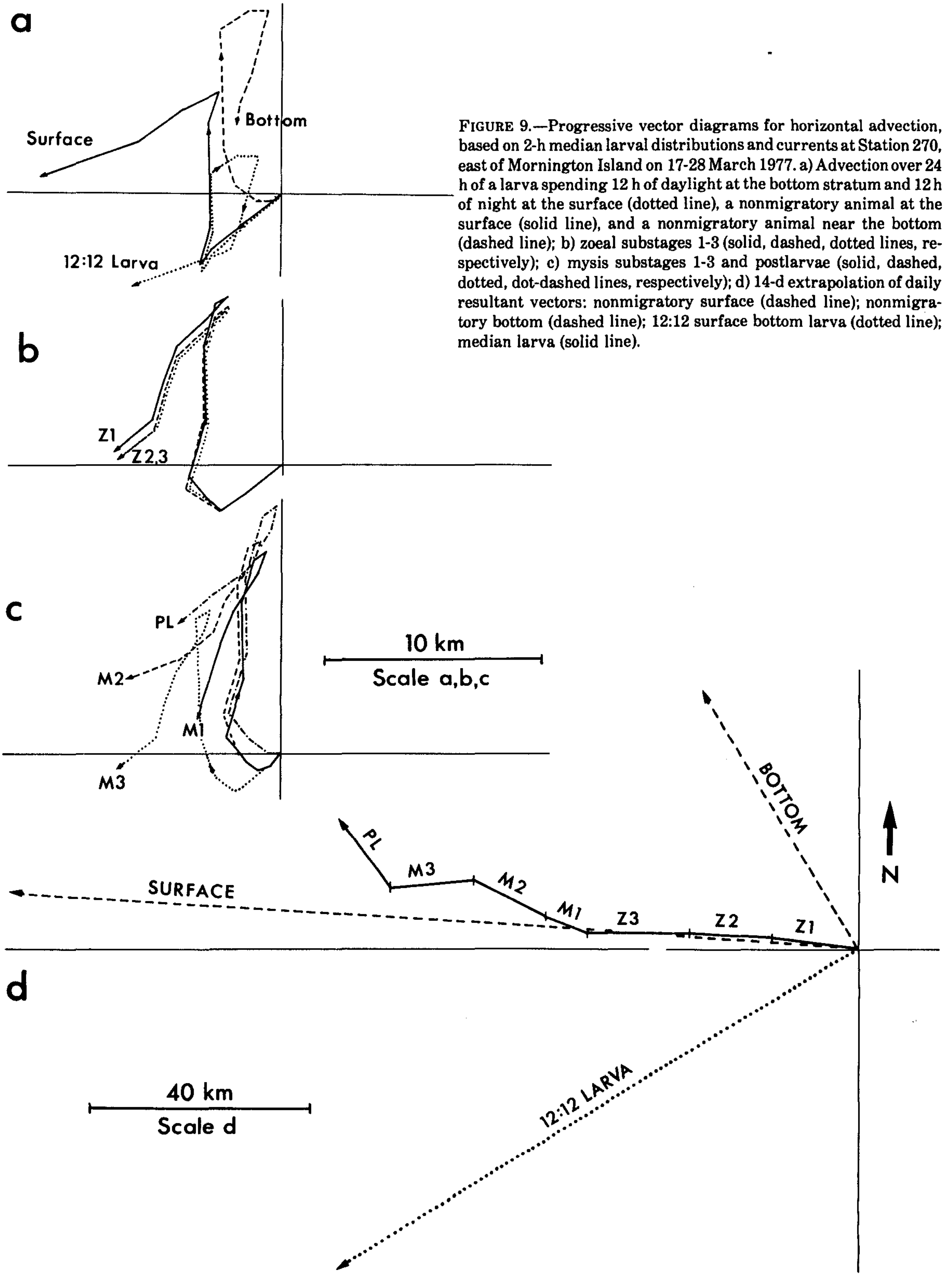

FIGURE 9.—Progressive vector diagrams for horizontal advection, based on 2-h median larval distributions and currents at Station 270, east of Mornington Island on 17-28 March 1977. a) Advection over 24 h of a larva spending 12 h of daylight at the bottom stratum and 12 h of night at the surface (dotted line), a nonmigratory animal at the surface (solid line), and a nonmigratory animal near the bottom (dashed line); b) zoeal substages 1-3 (solid, dashed, dotted lines, respectively); c) mysis substages 1-3 and postlarvae (solid, dashed, dotted, dot-dashed lines, respectively); d) 14-d extrapolation of daily resultant vectors: nonmigratory surface (dashed line); nonmigratory bottom (dashed line); 12:12 surface bottom larva (dotted line); median larva (solid line).

can be obtained. The broad picture based on percentages indicated that more postlarvae occurred at the surface than near the bottom during daylight while more were near the bottom at night. The actual locations were not given but were probably pooled observations of a number of nearshore stations. Thus, the possibility exists that these postlarvae, close to nearshore nursery grounds and sampled mostly on flood tides, were in a tidally induced behavior pattern that has been shown for the postlarvae of *P. duorarum* (Hughes 1969a, b), *P. aztecus* (St. Amant et al. 1966), *P. plebejus* (Young and Carpenter 1977), and *P. merguiensis* (Munro 1975; Staples 1980). The zoeal and mysis-stage larvae of *Trachypenaeus* and *Sicyonia* were also sampled in the Eldred et al. (1965) study. These early larvae (all stages pooled) showed a marked increase in abundance near the bottom during the day and slightly increased abundances at the surface at night. In their summaries, no larval distributions with intermediate depths and times were shown. In the Gulf of Carpentaria there are at least eight genera represented: *Penaeus, Metapenaeus, Atypopenaeus, Parapenaeopsis, Trachypenaeus, Metapenaeopsis, Solenocera,* and *Eusicyonia.* When generic resolution was applied to the present series of samples, no changes in the patterns emerged, but the numbers of larvae available for each analysis decreased. It therefore seemed reasonable to analyze the pooled samples since it appeared the behavioral patterns were family-wide.

Temple and Fischer (1965) were the first to show clear patterns of vertical distribution by penaeid larvae. They too were sampling mixed genera of penaeids (*Penaeus, Trachypenaeus, Sicyonia,* and *Solenocera*). Using discrete depth sampling nets, they showed some increase in migratory ability with the development of the larval stages, as well as the variable patterns seen on different sampling occasions. They did not measure light penetration and attributed the variations of larval distribution to differing conditions of water column structure and stability, as characterized by the presence or absence of a thermocline. The same degree of variation in vertical migratory patterns was seen in this study under isothermal conditions, in calm to slight seas. Therefore, turbulence seemed to be of minimal importance in explaining the differences in distribution patterns. However, even under near uniform wind and sea conditions, light penetration in the shallow coastal stations was quite variable and this variation was reflected in larval behavior. It therefore appears that light penetration is the dominant environmental variable affecting larval behavior. There is little doubt, under conditions of strong vertical mixing in shallow water, that both turbulence and the concomitant increase in turbidity would result in a mixed vertical distribution. Temple and Fischer (1965) also believed that there was evidence for a reversal of vertical distribution with growth from zoeal to postlarval stage. Their summary figure (fig. 3, p. 62) is not convincing and again may be biased by the change in behavior of postlarvae to a tidally dominated one used to enter coastal estuaries (Temple and Fischer 1965). In the Gulf of Carpentaria sampling, there was no evidence of a reversal with development, but these samples were taken well offshore so a tidal-coastal behavior pattern cued by salinity or pressure differences was probably not in evidence.

Only one other study of larval penaeid vertical migration has been undertaken; Jones et al. (1970) sampled *P. duorarum* larvae off southern Florida. Summary figures of pooled data also show the ontogenetic change in vertical migratory ability of the larvae, as well as variability in the patterns between sampling periods. No environmental data are provided to help explain the difference.

All these studies (Racek 1959; Eldred et al. 1965; Temple and Fischer 1965; Jones et al. 1970) were undertaken to help explain how the vertical distribution of penaeid larvae affects dispersal from offshore spawning grounds to nearshore or estuarine nursery grounds. None of the studies, however, was able to explain the variable results encountered, and furthermore, the currents that would be responsible for this onshore movement were not measured. Penn (1975) attempted to overcome these deficiencies by using an idealized larval behavior, one which required all larvae to move the full height of the water column from the surface to the bottom on a strict night-day cycle (12:12 larva in Figs. 7, 8, 9). This, however, did not allow for differential larval abilities and/or environmentally induced variations in behavior. Furthermore, because of the lack of in situ current recordings, he used differences in predicted tide heights to calculate residual flows. Penn found, even with these constraints, a general mechanism by which larvae could be transported farther inshore at night than offshore during the day, against the prevailing currents between March and August, the main period of postlarval recruitment in Shark Bay, Western Australia. Penn proposed that during a larval life lasting 2-4 wk the larvae would be displaced 30-80 km before becoming postlarvae at which time they would migrate more actively using a tidal cue. In the present study the 12:12 larva that behaved in a manner dictated by Penn's (1975) scheme seldom travelled in the same direction or distance as the median larva (Figs. 7, 8, 9). This is largely because these larvae did not utilize the full water column over all their larval life even under ideal conditions and that subtle changes in environmental factors changed the patterns of vertical distribution of all larval stages quite markedly.

With more detailed information on larval distribution and its causes, realistic dispersal distances and directions are even more dependent upon detailed knowledge of current speeds and direction at depth. In the present study there were shortcomings in assessing both short-term and long-term in situ current regimes. The migratory current meter used gave some indication of variation of speed and duration of currents but is probably biased by sampling technique and influenced, at times, by short-term wind events and short-term nontidal pertubations. Furthermore there were errors introduced by deploying the meter from a moored vessel. A certain amount of oscillation in current direction appeared during periods of low current velocity when the ship would swing on its anchor. This was overcome to some extent by using both a bow and stern anchor. The most serious shortcoming, however, is the robustness of the extrapolation from the 24-h record to the entire larval life of about 14 d. At best this would only be an approximation of the distance and direction of advection of median larva.

The distances estimated by extrapolation (ca. 70-100 km) are large enough to transport the larvae from the farthest known offshore commercial concentrations of adult penaeid shrimp in the Gulf of Carpentaria (Lucas et al. 1979) to their nearshore and estuarine nursery grounds. This range of advection is greater than that estimated by Penn (1975) even though in this study only a 2-wk larval life was used as opposed to a 4-wk period in his. The 2-wk period seems more realistic at ambient Gulf of Carpentaria temperatures (unpubl. data; Cook and Murphy 1969; Mock and Murphy 1971). This period still allows for one to two postlarval intermolts before settlement. It is suggested that the advection of the larvae limits the offshore adult distribution of those species of penaeid shrimp in the Gulf of Carpentaria that rely on nearshore or estuarine habitats for juvenile nursery grounds. There are no apparent depth or substrate limitations that would restrict the adult distribution to a coastal zone <100 km wide.

Whether or not differential larval advection can account for the large-scale temporal and spatial patterns of postlarval recruitment seen in the Gulf of Carpentaria (Staples 1979) is still open to speculation. There is some evidence from this study of offshore transport of larvae in March (Fig. 9d) at a time when large numbers of ripe female shrimp are present in the commercial fishery in the southeastern corner of the Gulf of Carpentaria. It may be this offshore advection of larvae that explains the subsequent low level of postlarval recruitment in the following weeks into the coastal rivers of this region of the Gulf of Carpentaria (Staples 1980). The short-term sampling of currents in the present study is not capable of annotating the long-term seasonal effects of tropical wind regimes and the long-term progression of tidal phase. Long-term monitoring and modelling of tidal and wind driven currents (Church and Forbes 1981; Forbes and Church in press) in the Gulf of Carpentaria has recently been completed and will be used to overcome this shortcoming of the present study. It is also likely that a better understanding of short-term meteorological events at critical times in the larval life history would help explain the year-to-year variation seen in the strength of postlarval recruitment in individual rivers around the gulf (Staples 1979) and the subsequent commercial catch (Lucas et al. 1979).

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