Factors affecting the immigration of postlarval penaeid shrimp into a Mexican lagoon system

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ABSTRACT

Penaeus californiensis, P. brevirostris, P. vannamei and *P. stylirostris* occur in western Mexico, and all breed in the sea. *P. californiensis* is the dominant species in commercial catches from the sea and *P. vannamei* from coastal lagoons. The paper summarizes observations on the laboratory behaviour of postlarvae of these species and on their distribution in relation to environmental factors in the channel (estero) linking Huizache Lagoon to the sea. This estero, which is about 10 km long, is at a lower salinity than the sea only from July to November. The net tidal flow in the estero is lagoonward from February to July and seaward in August to January.

In the laboratory, postlarvae of all species selected lower salinities than those to which they had been acclimated, and older postlarvae selected lower salinities than younger ones. *P. vannamei* selected lower salinities than the other species. Estero water was selected rather than sea water of a similar salinity by the two species tested. Postlarvae did not consistently swim with or against currents. There was no evidence that their direction of swimming was influenced by changes in light, salinity or the type of water or by endogenous factors.

The depth distribution of postlarvae in the estero showed no consistent correlation with the absolute or relative salinity or temperature for any species. On the other hand, postlarvae showed a marked tendency to leave the bottom layers with the tidal flood, and this tendency was most consistently shown by *P. vannamei*. At the seaward end of the estero, postlarvae showed minimum concentrations in May increasing to a maximum in September, with *P. vannamei* usually dominant. Only the first part of this increase (in June and July) penetrated as far as the lagoon in large numbers. Passive drift with the flood tide probably provides the chief mechanism of immigration. The failure of most postlarvae to reach the lagoon after July was chiefly due to a reversal of the net current.

The vast surplus of postlarvae of *P. vannamei* recorded at the seaward end of the estero in August to November 1977 probably occurs in most years and in many esteros. It provides a potential source of small shrimps for rearing in captivity on a commercial scale. Their removal at that time of year would have little effect on recruitment to the lagoon fishery.

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RÉSUMÉ

Facteurs intervenant dans les migrations de la mer vers un système lagunaire mexicain de postlarves de crevettes pénéides.

Penaeus californiensis, P. brevirostris, P. vannamei et *P. stylirostris* existent sur les côtes Ouest du Mexique. Toutes ces espèces se reproduisent en mer. *P. californiensis* est la plus abondante dans les pêches commerciales marines, alors que dans les prises lagunaires c'est *P. vannamei* qui domine. Cette note est un résumé des observations faites en laboratoire, sur le comportement des postlarves de ces espèces, ainsi que leur distribution en fonction des facteurs environnants du canal (estero) qui relie la lagune de Huizache à la mer. Celui-ci fait 10 km de long, et il est caractérisé par une eau à salinité plus basse que celle de la mer de juillet à novembre. Dans l'« estero », de février à juillet, le flux de marée a une direction lagunaire, tandis que d'août à janvier il est de sens contraire, c'est-à-dire vers la mer.

En laboratoire, les postlarves de toutes ces espèces ont préféré des salinités plus faibles que celles auxquelles elles ont été adaptées. Contrairement aux plus jeunes, les postlarves les plus âgées ont choisi les plus basses salinités. Par rapport aux autres espèces, *P. vannamei* a préféré les plus faibles salinités. A salinité presque identique enfin, les deux espèces testées ont choisi l'eau de l'« estero » plutôt que celle de la mer. Par ailleurs, les postlarves ne se sont déplacées ni avec ni contre les courants. En outre, il n'y a aucune preuve certaine que le sens de leur déplacement ait été influencé par un changement de lumière, de salinité ou par la nature de l'eau ou des facteurs endogènes.

Dans l'« estero », pour chaque espèce, nous n'avons pu déceler aucune corrélation entre la profondeur de répartition des postlarves et une salinité ou une température absolues ou relatives. D'autre part, il y a une tendance très nette chez les postlarves à quitter le fond lors du flux de marée, en particulier chez *P. vannamei*. A l'extrémité marine de l'« estero », en mai, il y a une concentration minimum des postlarves ; elle croît et atteint un maximum en septembre, avec *P. vannamei* habituellement dominante. Seules les postlarves de la première phase de cet accroissement (juin-juillet) pénètrent très loin dans la lagune et en grande quantité. Le transport passif dû aux flux de marée serait le principal responsable du mécanisme des migrations. L'échec de la plupart des postlarves à atteindre la lagune après juillet est dû essentiellement à l'inversion du sens du courant.

L'excédent énorme de postlarves de *P. vannamei* observé dans l'extrémité marine de l'« estero » d'août à novembre 1977, se produit sans doute tous les ans et dans plusieurs « esteros ». Il est une source potentielle de jeunes crevettes pour élevage en captivité à une échelle commerciale. Leur enlèvement à cette époque de l'année n'aurait que peu d'effet sur le recrutement dans la pêcherie de la lagune.

INTRODUCTION

The coastal waters of Sinaloa, western Mexico, support breeding populations of four species of *Penaeus* : *P. californiensis* (Holmes), *P. brevirostris* Kingsley, *P. vannamei* Boone and *P. stylirostris* Stimpson. The commercial catch from the sea is dominated by *P. californiensis* at all seasons. Fishing in the lagoons is mostly from September to December, and sub-adults of *P. vannamei* make up the bulk of this catch. It is known that shrimps enter the lagoons as postlarvae, but unanswered questions concern the relative importance of passive drift and active migration, the physical and chemical factors involved and the reactions of postlarvae to them. In an attempt to answer these questions, this paper summarizes and brings together laboratory observations on the behaviour of postlarvae and field investigations into the distribution of postlarvae and environmental factors in the approaches to the lagoons. The authors were particularly interested in interspecific differences which may help to explain the relative success of *P. vannamei* as a lagoon species.

The laboratory work is described in much greater detail by Mair (1979 b ; 1980) and the field work by Watkins (1980).

PHYSICAL AND HYDROGRAPHIC BACKGROUND

The Caimanero-Huizache lagoon system, where the field investigations took place, is shown in Figure 1. Rain falls mostly in July-September, and the figure shows the lagoons at their maximum extent, in September. Before the onset of the rains, Caimanero may occupy less than half and Huizache about a quarter of the area shown and the internal link between the lagoons is then usually dry. The outer limits of the system are marked by the rivers Baluarte and Presidio, and winding « esteros » connect the rivers to the lagoons. « Tapos », used in the fishery for sub-adult shrimp (Edwards, 1978), are situated near the seaward and landward ends of the esteros linking the lagoons to the river mouths. These are the most accessible parts of the esteros and they were used as sampling stations in the present work. The original mouth of the River Presidio (Fig. 1 : Boca de Baron) was blocked by a sand-bar throughout the period of
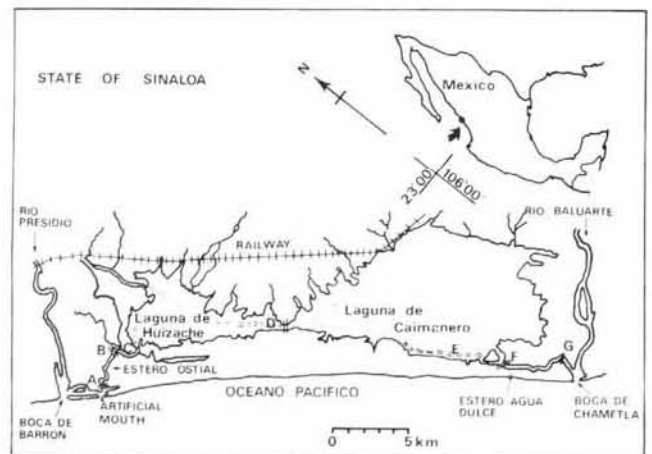

Figure 1
The Caimanero-Huizache lagoon system.

the investigations, but the artificial mouth was open except from 10 April-5 May 1977 and 23 March-4 July 1978. It was re-opened each year with earth moving equipment. The level of the lagoons rises with the rains and the mean level of the nearby Pacific also fluctuates seasonally. As a result, mean sea level is higher than lagoon level from February to July, and the net tidal flow (except when blocked by sand-banks) is from the sea to the lagoons during these months. Esteros Ostial and Agua Dulce are at a lower salinity than the sea from July to November of each year.

IDENTIFICATION OF POSTLARVAE

Any work on specific differences in the behaviour and distribution of postlarvae was obviously dependent on their identification. It was found that living postlarvae could be divided into four groups on the basis of their chromatophore patterns and rostral lengths. Correlation with the adults was achieved by rearing representatives of each group. The

distinctive characters of the four species of postlarvae are described by Mair (1979 a).

The lengths of planktonic postlarvae encountered were: *P. vannamei* 5.0-7.0 mm, *P. stylirostris* 6.0-7.5 mm, *P. californiensis* 7.0-10.0 mm, *P. brevirostris* 8.0-11.5 mm.

LABORATORY EXPERIMENTS

Tests were made on the ability of postlarvae of the four species to select between waters of different salinity and between waters of different origin, and some observations were made on their swimming ability and behaviour in currents.

Salinity

The apparatus for observations on salinity preferences was based on that used by Keiser and Aldrich (1973). It consisted of two tall tanks of clear perspex, each 220 cm × 10 cm × 10 cm, mounted parallel to each other and at an angle of 25° to the horizontal (Fig. 2). Behind each was a fluorescent light tube, 235 cm long, wrapped in red cellophane. This produced uniform red illumination in each tank, just sufficient to see the postlarvae in them. Ten horizontal lines, 5 cm apart, were marked on the front of each tank. Water of different salinities was prepared from aquarium salt and fresh water. In most experiments the bottom 10 cm of one tank was filled with water of salinity 56 ‰; the 5-cm layers above this were successively filled with water of salinity 49, 42, 35, 28, 21, 14, 7 and 0 ‰ respectively. The other tank was usually used as a control, with water of uniform salinity equal to that in which the postlarvae had been living either in the sea or in acclimation tanks. Postlarvae were released in the gradient at this same salinity (natural or acclimated) and at the same level in the control tank, using a device similar to that described by Keiser and Aldrich (1973). Salinity gradients were checked before and after each experiment by siphoning a small volume of water from each level. Neither the introduction of postlarvae nor their subsequent movements caused any measurable change.
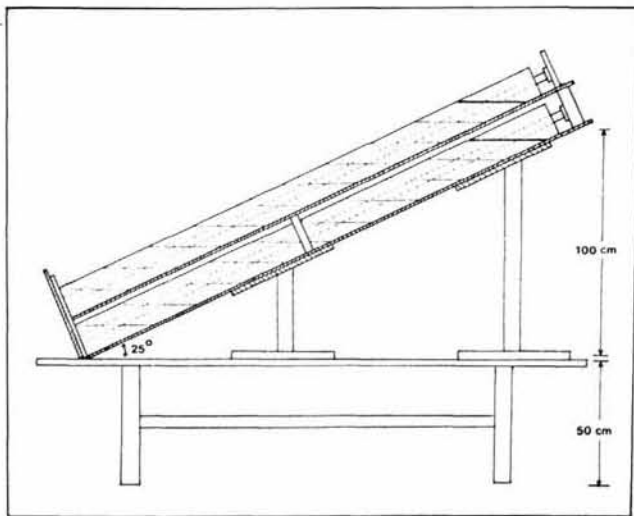

Figure 2
Salinity gradient apparatus.

Many tests were made on postlarvae of *P. californiensis* and *P. vannamei*, some starting on the day after capture, others after keeping the postlarvae in the laboratory for 10 days at a salinity of either 35 or 10 ‰. While in the laboratory the postlarvae were fed on *Artemia* nauplii and they moulted at intervals of 2-4 days. Figure 3 shows a typical set of results for recently captured postlarvae of *P. californiensis* and
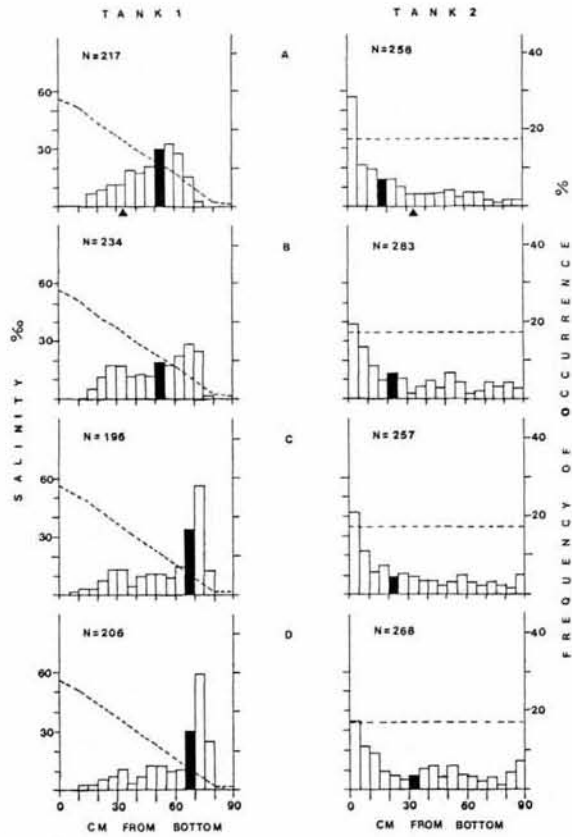

Figure 3
Distribution of postlarvae of P. californiensis *(mean length 7.9 mm) in salinity gradient (tank 1) and control (tank 2). T = 30 °C. Specimens collected 17.X.77, experiment 18-19.X.77. Arrow in A marks level at which specimens were introduced. A, mean of hourly distributions after 1-6 h; B, 7-12 h; C, 13-18 h; D, 19-24 h. N, mean number counted. Black bar = median.*
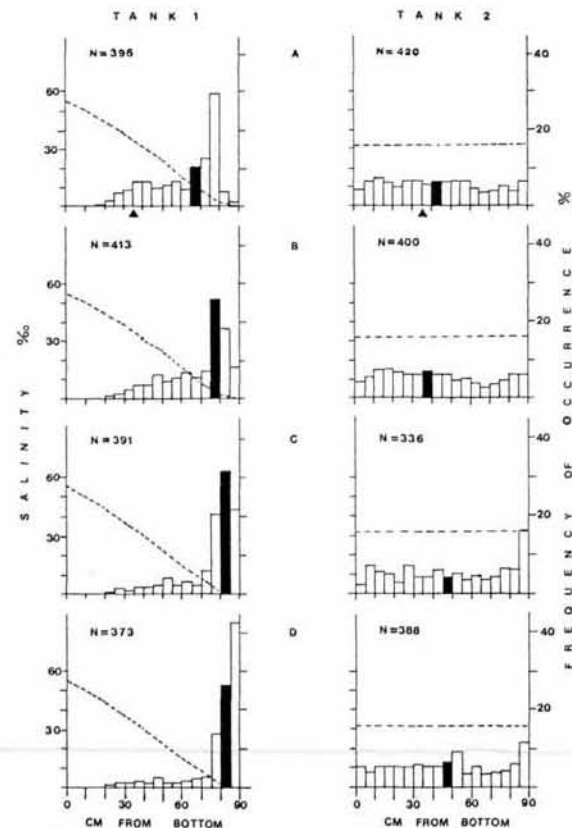

Figure 4
Distribution of postlarvae of P. vannamei *(mean length 5.7 mm) in salinity gradient (tank 1) and control (tank 2). T = 31 °C. Specimens collected 27.IX.78; experiment 28-29.IX.78. Symbols as in Figure 3.*

Table

Ranges of median values of salinities selected by postlarvae of the four species of Penaeus. *Tests were commenced within 24 h of capture, and some were repeated after 10 days in the laboratory at a known salinity. * marks result from one experiment only.*

		Range of salinity preference (‰)	
	Recently caught	After 10 days acclimation to	
		35 ‰	10 ‰
P. vannamei	1-8	3-6	2-3
P. stylirostris	32-35*	5-7*	–
P. californiensis	9-26	10-19	3-8
P. brevirostris	15-22	10-14*	–

Figure 4 for *P. vannamei*. Variations in the number counted (N) at different times during an experiment reflect the difficulty of counting moving animals in a dim light. Only sporadic supplies of postlarvae of *P. brevirostris* and *P. stylirostris* were available, and considerably fewer experiments were made on these species. Results for all species are summarized in the Table.

Both *P. californiensis* and *P. vannamei* selected lower salinities than those in which they had been captured or in which they had been held in captivity. The selected salinity tended to be lower in the older postlarvae, which had been held in the laboratory for 10 days, and was lowest in those which had been held at 10 ‰. *P. vannamei* selected lower salinities than *P. californiensis* with the same history of acclimation. Both species showed a tendency to move to lower salinities during the course of a 24 h experiment. In control experiments, postlarvae of *P. californiensis* showed a tendency to frequent the bottom of the tank whatever the salinity. The same tendency was shown by postlarvae of *P. vannamei* in a uniform salinity of 10 ‰ but not at 35 ‰. In the few experiments with postlarvae of *P. brevirostris*, this species showed similar salinity preferences to those of *P. californiensis* and an even stronger tendency to frequent the bottom of the tank in control experiments. Postlarvae of *P. stylirostris* were used in only two experiments. The majority of recently caught specimens selected salinities similar to those of the sea, but older postlarvae, which had been held for 10 days at 35 ‰, selected much lower salinities (see Table).

Waters of different origin

The apparatus used for experiments on salinity preferences was also used to test the ability of postlarvae to distinguish between water from an estero and water from the sea. It was filled with three layers of water of different salinity, each 30 cm deep. The bottom layer in both tanks contained water of salinity 50 ‰, made up with sea-water and aquarium salt. The salinities in the other two layers did not exceed 30 ‰ and differed by 5 ‰. In one tank the middle layer contained diluted sea-water, the top layer estero water. In the other tank the middle layer was estero water, the top layer sea-water with a further addition of fresh-water.

With both *P. californiensis* and *P. brevirostris*, more post-larvae frequented the layer of estero water than the layer of sea-water, irrespective of which was at the lower salinity. A typical example is shown in Figure 5. There was no opportunity to apply this test to postlarvae of the other two species.

Swimming

Observations on the swimming behaviour of postlarvae were made in the circular canal between two perspex cylinders of diameter 26 and 16 cm respectively, filled to a depth of 20 cm. A current of approximately 5 cm/sec. was produced by electrically driven paddles, which moved round the canal. The water could be changed during an experiment. Most of the experimental animals were postlarvae of *P. californiensis*.
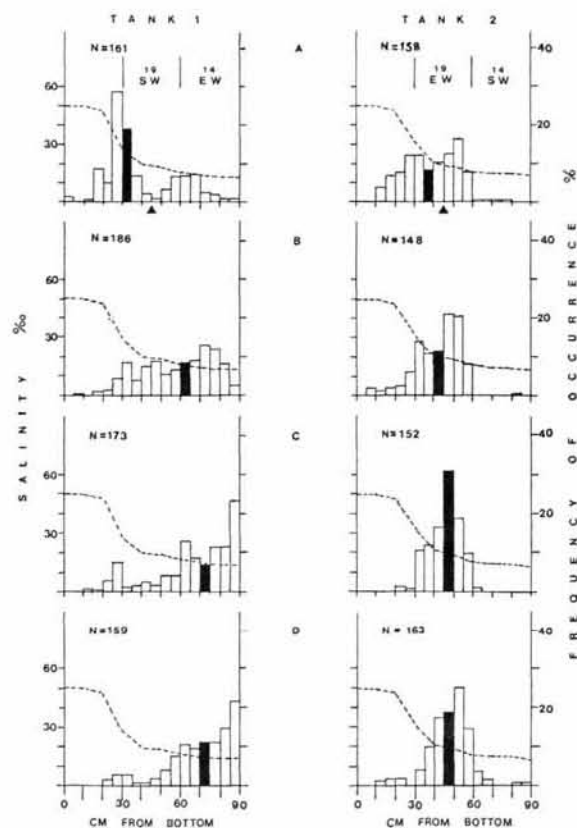

Figure 5

Distribution of postlarvae of P. californiensis *(mean length 7.7 mm) in a water preference experiment. T = 29 °C. Specimens collected 4.VIII.78 ; experiment 4-5.VIII.78. SW, sea-water ; EW, estero water (the salinity of each of these layers is also given). Other symbols as in Figure 3.*

Postlarvae were observed swimming at speeds up to about 10 cm/sec, but swimming was not always continuous and there was frequent passive sinking. In some experiments the majority of postlarvae swam upstream, but in others the numbers swimming upstream and downstream were similar. In one experiment rather more postlarvae were observed swimming in low intensity red light than in bright white light, but in another similar experiment there was no significant difference. No general change in the direction of swimming was produced by changing from red to white light, gradually reducing the salinity or gradually substituting estero water for sea-water. Observations under constant conditions provided no evidence of endogenous changes in the direction of swimming, but monitoring with an infra-red beam showed that there is an endogenous rhythm of swimming activity, with more movement at night.

FIELD INVESTIGATIONS

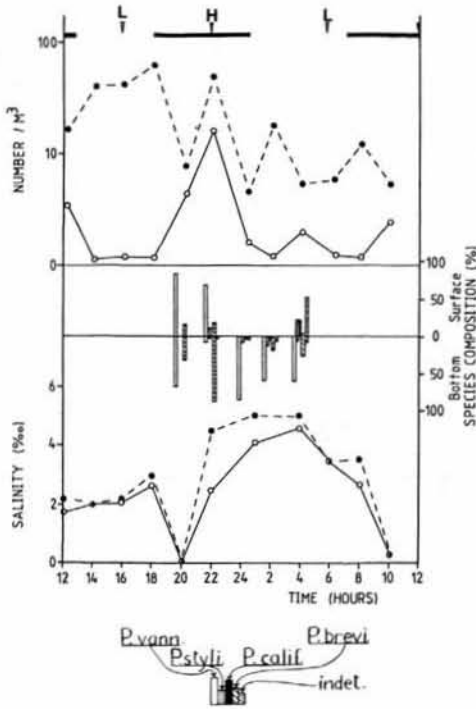Results reported here relate to collections of postlarvae taken at intervals throughout 1977 and 1978 at Tapo

Figure 6

Postlarvae and environmental factors at Tapo Botadero on 2-3.VIII.77. From top : times of high (H) and low (L) tide ; periods of flow towards lagoon (black bar) ; concentrations of postlarvae at surface (O——O) and bottom (●- - -●) ; species composition ; salinities at surface and bottom ; key to species of postlarvae.

Figure 8

Mean concentrations of postlarvae at Tapo Botadero (seaward end of estero) and Tapo Ostial (lagoonward end of estero) between May 1977 and April 1978.

Botadero (*A* in Fig. 1) and Tapo Ostial (*B*), both on Estero Ostial. Details of these collections and of a comparable series from Estero Agua Dulce are given by Watkins (1980). On each occasion near-surface and near-bottom samples were taken at 2 h intervals throughout 24 h, using plankton nets with flow meters. The direction of water flow and surface and bottom temperatures and salinities were taken at the same intervals, and times of high and low water were noted. Typical examples of results are shown in Figures 6 and 7. It should be noted that concentrations of postlarvae are shown on a logarithmic scale.

A consistent feature of all results was the rise in numbers of postlarvae at the surface during the period of flow towards the lagoons, reaching a peak about the time of high water. This surface peak appeared to be quite independent of fluctuations in salinity or temperature. The species composition at Tapo Botadero (at the seaward end of the estero) was usually mixed, with *P. vannamei* the most common
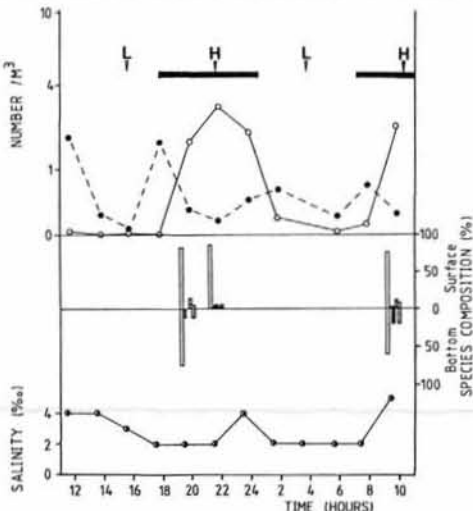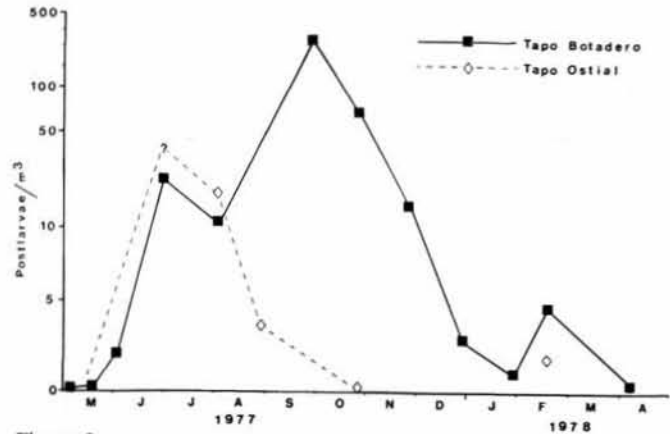

Figure 7

Postlarvae and environmental factors at Tapo Ostial on 17-18.VIII.78. Explanation as for Figure 6.

species, while at Tapo Ostial the dominance of *P. vannamei* was more marked. Figure 6 provides an example in which most of the postlarvae of *P. vannamei* rose in the water column at high tide while most of the *P. brevirostris* remained near the bottom. On some other occasions postlarvae of all species rose towards the surface at high water, but the phenomenon was shown most consistently by *P. vannamei* and it usually affected a greater percentage of the population than for the other species.

Figure 8 gives the concentrations of postlarvae (again on a logarithmic scale) at the seaward and lagoonward ends of Estero Ostial from the opening of the connection to the sea in May 1977 to its closure in April 1978 (see Physical and Hydrographic Background). Figure 9 gives the species composition for the three most common species at the same stations over the same period. Each point on each of these figures gives a mean for all samples taken on either or both sides of the tapo in question at each sampling period. Many more samples were taken at Tapo Botadero than at Tapo Ostial. No samples were taken at Tapo Ostial in late June 1977, and the point marked " ? " (Fig. 8) is an estimate based largely on samples taken after the opening of the channel to the sea in the following year. While no precise value can be given for this point, there is no doubt that the opening of the channel to the sea in 1977 was followed by a rapid rise in the concentrations of postlarvae in late May and June which affected the whole length of the estero.

Apart from minor fluctuations, there was a general increase in concentrations of postlarvae at the seaward end of the estero from May until late September, then a steady fall over the next few months. Numbers of postlarvae at the lagoonward end of the estero reached high levels in June and July, then plunged in August and September while concentrations at the seaward end were still shooting upwards.

Tapo Botadero was « closed » from mid August 1977 until the following January, by the insertion of screens of approximately 1 cm mesh to prevent the migration of large shrimps. Whenever comparative samples were taken, concentrations of postlarvae on the lagoonward side of the closed tapo were between a quarter and a half those on the seaward side.

When the channel to the sea was opened in May, the initial influx of postlarvae was dominated by *P. californiensis* (Fig. 9). However, the percentage of this species fell rapidly as numbers of *P. vannamei* and *P. brevirostris* increased. The increase in the relative numbers of *P. vannamei* continued until October, but the peak of *P. brevirostris* was in early August. Whenever data were available, the percentage of *P. vannamei* was appreciably higher at the lagoonward end of the estero than at the seaward end, while the reverse was true for both *P. californiensis* and *P. brevirostris*.
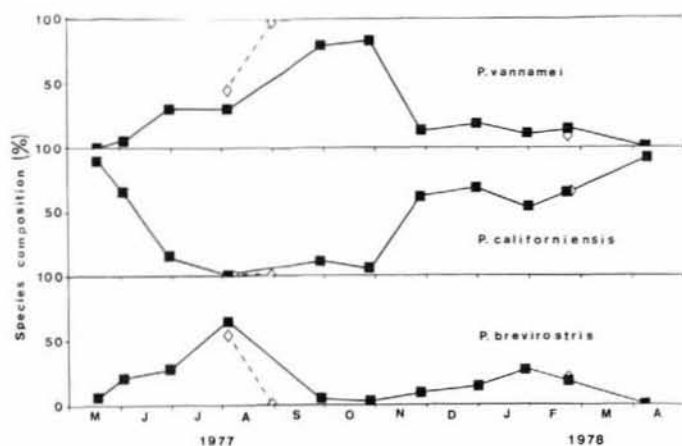
Figure 9

Mean percentages of the three most common species of postlarvae at Tapo Botadero and occasional samples at Tapo Ostial between May 1977 and April 1978. Symbols for tapos as in Figure 8.

DISCUSSION

It is clear that postlarvae of *P. vannamei* reach Huizache Lagoon in far greater numbers than postlarvae of other species. In 1977 the main influx was in June and July. The pattern is probably similar in all years when satisfactory recruitment takes place and in other lagoon systems in the same area. The policy of the fishery cooperatives in trying to open a channel from Estero Ostial to the sea in May seems fully justified, but in some years there is insufficient river flow at this time of year to keep it open.

The ability of postlarvae to select water of reduced salinity and with a « taste » of lagoons was demonstrated in the laboratory. Selection of water with these qualities may play an important part in enabling postlarvae to congregate near river mouths, but it seems quite inadequate to explain their further immigration into the esteros and lagoons. The lowest salinities and the highest concentrations of terrigenous material would be encountered in outflowing water at river mouths, and the swimming powers of postlarvae seem inadequate to make headway against such an outflow, even if the correct orientation could be maintained. Furthermore, the species which migrates into the esteros and lagoons in the greatest numbers is *P. vannamei*. Its postlarvae are, on average, smaller than those of the other species and are, therefore, probably the weakest swimmers. The situation is further complicated by the fact that the esteros are at a higher salinity than the sea in June, when the main influx of postlarvae begins, and at a lower salinity in July, when the influx continues.

The tendency, particularly marked in *P. vannamei*, for postlarvae to rise towards the surface on a rising tide and sink again as the tide falls, probably provides the main behavioural mechanism of immigration from river mouth to lagoon. In the Gulf of Mexico, *P. duorarum* also tends to leave the bottom as the tide rises (Jones *et al.*, 1970 ; Roessler, Rehrer, 1971), but this species seems to show much more consistent responses than *P. vannamei* to changes in salinity (Hughes, 1969 *a, b*). The capacity to rise in the water column on a rising tide is probably important to postlarvae of other species of Penaeidae and to a wide range of other forms with limited swimming powers which migrate into estuaries and lagoons. Upward swimming in all these

species could well be triggered by rising pressures, which animals on or near the bottom would experience during a rising tide. A number of species are known to respond to pressure changes of the magnitude which would be associated with tidal rise and fall (Knight Jones, Morgan, 1966). It is, however, difficult to see what stimulus correlated with falling water levels or reversal of flow could initiate the return to the bottom of animals swimming in the upper layers.

In 1977, concentrations of postlarvae at the seaward end of Estero Ostial rose from May until September. Concentrations were probably similar throughout the estero from May to July, but they fell rapidly at the lagoonward end in August and remained low in the following months. The screens, which were inserted in Tapo Botadero in August to prevent the seaward migration of larger shrimps, apparently caused an appreciable reduction in the number of postlarvae passing this point in the opposite direction. After the insertion of the screens, concentrations on the lagoonward side of the barrier averaged about 1/3 of those on the seaward side. This, however, is comparatively trivial in relation to the reduction of at least a hundredfold between Tapo Botadero and Tapo Ostial in September and October. The major factor which prevented all but a few postlarvae penetrating to the lagoonward end of the estero in the autumn months was almost certainly the annual change in the relative levels of the sea and the lagoon and the consequent reversal in the net flow in the estero. In May-July the sea was higher and the net flow was towards the lagoon ; in August and succeeding months the lagoon was higher and the net flow was towards the sea. This seaward net flow did not prevent further massive immigration of postlarvae from the sea to the seaward end of the estero in August and September, but only a very small proportion reached the lagoonward end or the lagoon itself. Those that did penetrate the length of the estero were nearly all *P. vannamei*.

Some of the postlarvae from the great concentration at the seaward end of Estero Ostial in September must have developed into the sub-adult shrimps fished at Tapo Botadero later in the year. This, however, could account for only a very small proportion, and there must have been a vast surplus of postlarvae. Samples taken in Estero Agua Dulce (Fig. 1) showed that the situation in the approaches to Caimanero Lagoon was similar (Watkins, 1980), and comparable conditions probably prevailed in other lagoon systems in the region. *P. vannamei* is obviously well adapted to the shallow waters and variable conditions experienced in lagoons. These same adaptations are likely to make it a particularly suitable species for farming. If this proves to be so, the surplus of postlarvae at the seaward end of Sinaloan esteros in August - November could provide a stock for transplanting. Their removal in these months would have little effect on recruitment to the lagoon fisheries.

REFERENCES

Edwards R. R C., 1978. The fishery and fisheries biology of penaeid shrimp on the Pacific coast of Mexico, *Oceanogr. Mar. Biol. Ann. Rev.*, **16**, 145-180.

Hughes D. A., 1969 *a*. On the mechanisms underlying tide-associated movements of *Penaeus duorarum* Burkenroad, *FAO Fish Rep.*, **57**, 3, 867-874.

Hughes D. A., 1969 *b*. Responses to salinity change as a tidal transport mechanism of pink shrimp, *Penaeus duorarum, Biol. Bull. (Woods Hole)*, **136**, 43-53.

Jones A. C., Dimitriou D. E., Ewald J. J., Tweedy J. H., 1970. Distribution of early development stages of pink shrimp, *Penaeus duorarum*, in Florida waters, *Bull. Mar. Sci.*, **20**, 634-661.

Keiser R. K., Aldrich D. V., 1973. A gradient apparatus for the study of salinity preference of small benthic and free swimming organisms, *Contr. Mar. Sci.*, **17**, 153-162.

Knight-Jones E. W., Morgan E., 1966. Responses of marine animals to changes in hydrostatic pressure, *Oceanogr. Mar. Biol. Ann. Rev.*, **4**, 267-299.

Mair J. Mc D., 1979 *a*. The identification of postlarvae of four species of *Penaeus* (Crustacea : Decapoda) from the Pacific coast of Mexico, *J. Zool., Lond.*, **188**, 347-351.

Mair J. Mc D., 1979 *b*. Identification and behaviour of postlarval penaeid shrimp from west Mexico, *Ph. D. Thesis, Univ. Liverpool*, 93 p.

Mair J. Mc D., 1980. Salinity and water type preferences of four species of postlarval shrimp *(Penaeus)* from west Mexico, *J. Exp. Mar. Biol. Ecol.*, **45**, 69-82.

Roessler M. A., Rehrer R. G., 1971. Relation of catches of postlarval pink shrimp in Everglades National Park, Florida, to commercial catches on the Tortugas grounds, *Bull. Mar. Sci.*, **24**, 791-805.

Watkins J. L., 1980. The immigration of postlarval penaeid shrimp into a lagoon system on the Pacific coast of Mexico, *Ph. D. Thesis, Univ. Liverpool*, 99 p.