# THE ROLES OF PRIOR RESIDENCE AND RELATIVE SIZE IN COMPETITION FOR SHELTER BY THE MALAYSIAN PRAWN, *MACROBRACHIUM ROSENBERGII*[1]

Behavorial dominance, territoriality, and their relationship to survival and population density have been the subject of extensive research (reviewed by Brown and Orians 1970; Itô 1970; Brown 1975). Generally dominance (behavioral) hierarchies imply some form of ranked order (reviewed by Marler and Hamilton 1966; Eibl-Eibesfeldt 1970; Itô 1970) whereby the alpha animal(s) has preferred access to food, shelter, or mates. Dominance may develop within a short time after an initial encounter (Dingle and Caldwell 1969), is partially controlled by differences in relative size (Marler and Hamilton 1966), and in some species is modified by relative location in space (Brown 1963). This latter modification is related to Noble's (1939) original concept of territory. Noble referred to territory as "any defended area." This area could serve as a "retreat" (in contrast to a sexual or nesting area) that "is occupied because it is familiar and defended because any newcomer is irritating to the resident."

Such space-related aggressive behavior has been reported in numerous animals (Brown and Orians 1970). Territorial behavior can be related to "defense" of 1) a breeding area (Buechner 1961; Watson 1964); 2) a renewable resource such as food (Stimson 1970); or 3) a physical shelter (Crane 1958; Reese 1964; Fielder 1965; Hughes 1966; Dingle and Caldwell 1969). Often the outcome of such a defensive action is exclusion of the intruder by the resident. Since this area is "familiar" to the resident and unfamiliar to the "newcomer," it follows that the resident has some type of advantage. This "prior resident effect" has been observed in a number of species (Braddock 1945, 1949; Miller 1958; Hughes 1966; Baird 1968; Dingle and Caldwell 1969; Selander 1970). Thus in many animals, spacing behavior is a powerful mechanism that can regulate resource utilization and influence distribution patterns.

Many of the above-mentioned studies and reviews dealt with animal populations in natural open systems subject to both immigration and emigration. In contrast, aquaculture systems are closed and deal with confined high-density populations. In the case of *Macrobrachium rosenbergii*, ponds are stocked with postlarvae, and harvesting of adults begins 9-12 mo later. The same space-related behavioral mechanisms observed in open systems may be operating in these high-density ponds. Circumstantial evidence indicates that this is occurring in ponds containing *M. rosenbergii*. Animals of the same age exhibit large variation in size at the end of several months of growth (Fujimura nad Okamoto 1970). Malecha (1977) reported that small *M. rosenbergii* can greatly increase their size when larger animals are absent. This has been called the "Bull Effect" by Fujimura and Okamoto (1970). Similar observations have been reported for carp (Nakamura and Kasahara 1955, 1961; Wohlfarth and Moav 1972), trout (Brown 1946), and salmon (Symons 1971). One hypothesis advanced by Nakamura and Kasahara (1961) is that the larger animals are outcompeting the smaller subordinates for food.

*Macrobrachium rosenbergii* is a large freshwater prawn. Its native distribution ranges from Pakistan to Papua, New Guinea, and Palau (Johnson 1960; McVey 1975). Usually it is found in fresh and brackish streams and pools. The eggs hatch near ocean waters, and the adults are found up to 200 km from the coast (Ling 1969). Generally males are thought to stay in upstream waters while the females undergo a seasonal migration, moving downstream and into brackish waters (Raman 1967). Relatively little is known of *M. rosenbergii's* behavioral ecology but Raman (1964) reported juveniles "hiding in crevices or among submerged plants along river banks." In order to understand how social behavior affects resource utilization by *M. rosenbergii*, three experiments were conducted in which shelter was the limiting resource, and relative size and prior residence were measured as variables.

## Methods

The three experiments consisted of: a prior resident experiment, a simultaneous introduction experiment, and a control experiment. The prior resident experiment was used to test for the role of prior residence and relative size in competition for shelter. The simultaneous introduction experiment tested for the role of relative size on competition in the absence of a "prior resident effect." The control experiment tested for the effect of handling and capture.

Water conditions were maintained via an air lift filter. The animals were fed a dry pellet diet approximately every other day (see diet #5, Balazs et al. 1973). A 12-12 photoperiod with one-half hour twilight lighting at "sunrise" and "sunset" was employed.

## Prior Resident Experiment

Earlier experiments revealed a form of shelter preference or selection operating in *M. rosenbergii* (Peebles 1977). The shelters used in this experiment were identical to those most frequently selected by animals in the earlier experiments. One shelter was placed in each experimental tank. A shelter consisted of six concrete bricks arranged into a double open ended square tunnel (19.3 · 19 ∨ 11.4 cm tall).

Refuge other than the shelter was eliminated by the use of oblong experimental tanks (137 ∖ 75 ∖ 92 cm deep) and the suspension of the air lift filters just below the water surface (the usual position for these filters was on the bottom). Water depth was 34 cm.

Adults from commercial ponds were placed in two separate holding tanks, where they were kept for no longer that 1 wk. Two animals were removed, one each from the separate holding tanks. Three body characteristics were measured: standard length (tip of telson to orbit of eye), and lengths of left and right chelae. The animals were tagged by means of a small plastic "bread bag twist-tie" that was color coded and tied around the tail. It took about 15 s to attach. Following tagging the two animals were placed separately in experimental tanks. Three observations were made before the introduction of the "immigrant" and four observations were made after the introduction. The preintroduction observations were made on the second, third, and seventh days after the animals were placed in their separate experimental tanks. There were three observations per animal, each lasting 3 min. After the preintroduction week a coin was flipped to determine which animal would be the immigrant. The immigrant was designated as the introduced specimen and was moved via a dip net from its tank to the resident's tank. The resident was the animal that was not moved from one experimental tank to another. The postintroduction observations were made on the day of introduction, and the second, third, and seventh days after introduction. The observation performed on the day of introduction was 15 min

and designed to monitor agonistic interactions associated with the initial encounters of the paired animals. The remaining three postintroduction observations were 3 min each and designed to record the animal's position within the tank. All observations were made between 1000 and 1530. Since these animals are nocturnal, movement and behavioral interactions were minimal during the daytime.

A total of 36 animals (18 immigrants, 18 residents) were used. Paired animals were of the same sex. This controlled for the possible confounding effect heterosexual courtship behavior might have on competition for shelter occupancy.

## Simultaneous Introduction Experiment

The treatment of the simultaneous introduction experiment differed from the prior resident experiment in four ways: 1) only males were used; 2) the animals were simultaneously introduced into the oblong tanks; 3) two additional body characteristics were measured (body weight and carapace length); and 4) the animals were not separately observed prior to introduction.

Fifteen trials were run employing a total of 15 pairs or 30 animals. Observations were made on the day of simultaneous introduction, and the second, third, and seventh days after introduction. The observation performed on the day of simultaneous introduction was 15 min and designed to monitor agonistic interactions associated with initial encounters of the paired animals. The remaining three postintroduction observations were 3 min each and designed to record the animal's position within the tank.

## Control Experiment

Eleven controls were run to test the effect of handling. Animals were selected, measured, tagged, and placed individually in experimental tanks. One week later the control was netted, held in the air, and reintroduced into the same experimental tank. Observations were made for the week before and the week after netting (mock immigration).

## Operational Definitions

Successful: an animal that was in a shelter at the end of the 7-day period following immigration.
Unsuccessful: an animal that was not in a shel-

ter at the end of a 7-day period following immigration.

Push: an aggressive act where one animal pushes one of its chelae against the body of another animal.

Nip: an aggressive act where one animal closes down the tips of its chela on the body part of another animal.

Tête-a-tête: a type of aggressive act characterized by a head to head confrontation with at least one nip or one push. The tête-a-tête appeared to be difficult enough in orientation from the push and the nip to be placed in a separate category. Further observation and analysis might not support this separation.

Shove: an aggressive act where one animal holds both chela forward and parallel while charging into the flanks of another animal.

Bout: an agonistic exchange between two animals where at least one aggressive act occurred. A bout was considered terminated when aggressive acts stopped or one animal moved away and was not chased. Bouts were measured in units of aggressive acts.

Bout length: the number of aggressive acts that occurred during a bout.

Body characteristics: standard length (centimeters), right and left chelae length (centimeters), weight (grams), and carapace length (centimeters).

Body size index: the number of body characteristics in which an animal was larger. It was derived as follows: animal A larger than animal B in standard length and right chela length, then A's body size index is two. In the Prior Resident Experiment three body characteristics were measured, thus the maximum body size index in this experiment was three. In the Simultaneous Introduction Experiment five body characteristics were measured, thus in this experiment the maximum body damage index was five.

### Results

#### Control Experiment

Ten out of 11 animals were in the shelter on every observation period before mock immigration. The remaining animal was in the shelter on one of the three observation periods. The same 10 were in the shelters on all observations following mock immigration, while the same remaining one was never observed in a shelter after immigration.

It was concluded that the act of netting had no effect on shelter use.

#### Prior Resident Experiment

Shelters were occupied on every observation by every animal during the preimmigration week. Following immigration all shelters were occupied on every observation period. On several occasions more than one animal was in a shelter during the first two observation periods following immigration. However, by the end of the week, observation period 4, one animal was in a shelter while the other was usually at the opposite end of the tank. When the data were examined by immigrant versus resident for shelter use over the 7-day period, an interesting change became apparent (Figure 1). On the day of immigration, residents were occupying shelter significantly more often than immigrants (Binomial Test, $P = 0.044$, Siegel 1956). By the second observation period and for the remaining two observations there were no significant differences between residents and immigrants in frequency of shelter use (Binomial Test: day 2 after immigration, $P = 1.0$, day 3, $P = 0.814$; day 7, $P = 0.814$).

Examining the data for the effect of size (Figure 2) revealed that successful animals were significantly larger than their unsuccessful paired
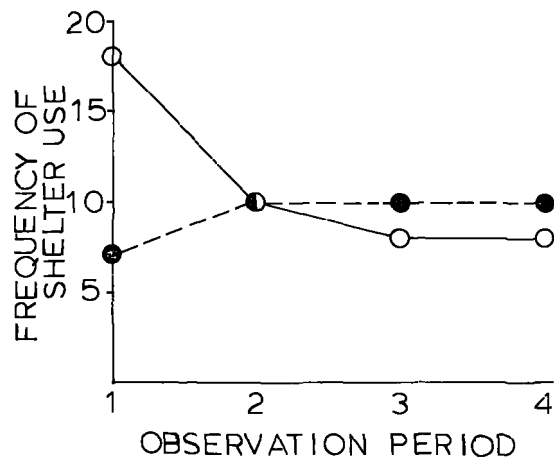


FIGURE 1.—Shelter usage by observation period for 18 pairs of *Macrobrachium rosenbergii*. The data from prior resident experiments are summed for the 18 pairs. During observation period 1, 18 residents (circles) and 7 immigrants (dots) were inside shelters. On observation period 1 there were seven cases of double occupancy; observation period 2, two cases; and observation period 3, none.
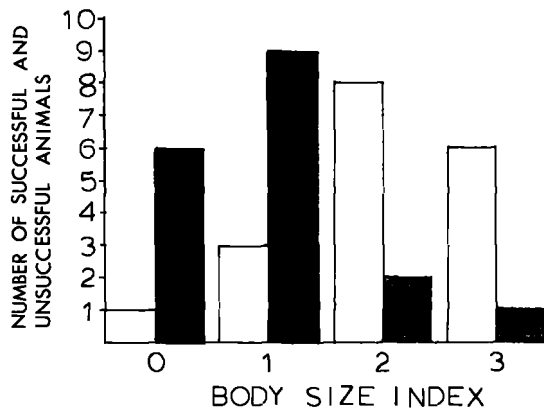
FIGURE 2.—Frequency of relative body size for successful (open bar) and unsuccessful (solid bar) prawns in the prior resident experiment. A body size index of one indicates one *Macrobrachium rosenbergii* was larger than the other in one body trait but smaller in the other two body traits.

partners (Kolmogorov-Smirnov Two Sample Test: $D$ max $= 11, n = 18, P = 0.01$).

## Simultaneous Introduction Experiment

A similar effect of size on shelter use was observed in the simultaneous introduction experiment (Figure 3; $r_s = 0.579, P < 0.001$). Once again larger animals used the shelters more often than their smaller partners.

Aggressive behavior was observed only on the day of introduction. The nip and push occurred
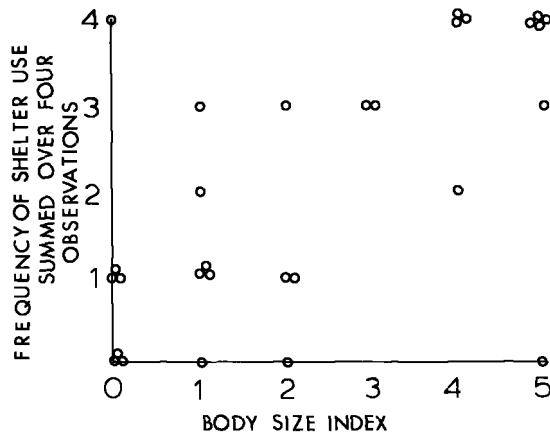


FIGURE 3.—Correlation between frequency of shelter use and body size index for *Macrobrachium rosenbergii*, from the simultaneous introduction experiment. A body size index of one indicates one animal was larger than the other in one body trait but smaller in the other four body traits.

more often than the shove or tête-a-tête (Figure 4). Generally aggressive interactions were limited to a few (one to three) bouts per 15 min (Figure 5), and these bouts were usually one or two aggressive acts long (Figure 6).

## Prior Resident Experiment by Simultaneous Introduction Experiment

A Kolmogorov-Smirnov chi-square approximation (Goodman 1954; Siegel 1956) revealed that animals of the simultaneous introduction experiment were more aggressive on the day of introduction than were animals in the prior resident experiment on the day of immigration ($\chi^2 = 15.54$, $P < 0.002$ for number of bouts/animal per 15-min period; $\chi^2 = 13.877$, $P < 0.002$ for number of ag-
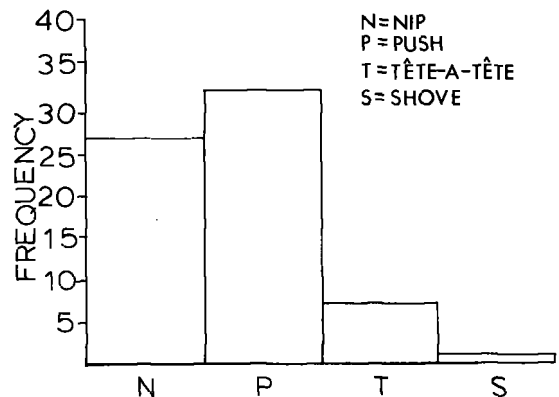


FIGURE 4.—Frequency by type of aggressive acts observed on the first day after introduction for the experiment on simultaneous *Macrobrachium rosenbergii* introduction. Frequency equals the number of aggressive acts by 17 animals.
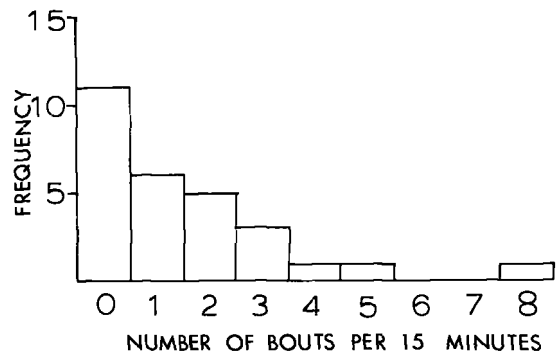


FIGURE 5.—Frequency of number of aggressive bouts per animal during the 15-min period of observation after simultaneous introduction of male *Macrobrachium rosenbergii* (14 pairs).
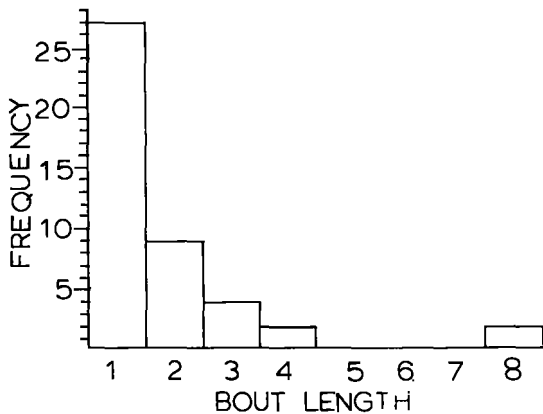
gressive acts/animal per 15-min period). Simultaneous introduction animals exhibited a total of 68 aggressive acts occurring in 43 bouts ($n$ = 28 animals), while the prawns from the prior resident experiment exhibited only five aggressive acts in five bouts ($n$ = 32 animals).

### Discussion

The results indicate that when *M. rosenbergii* compete for shelter at least three factors, relative size, prior residence, and length of time contestants are paired, play important roles in determining who occupies a shelter. It has long been recognized that in crustaceans relative size plays a large role in determining dominance (Allee and Douglas 1945; Bovbjerg 1953, 1956, 1960; Lowe 1956). More recent observations have confirmed the size/dominance relationship (Hughes 1966; Crane 1967; Griffin 1968; Hazlett 1968; Dingle and Caldwell 1969; Warner 1970; Rubenstein and Hazlett 1974; Jachowski 1974; Molenock 1976; Sinclair 1977). However, relative size does not appear equally important in all species (Hazlett and Estabrook 1974).

In prawns, relative size strongly influences the outcome of competition. When two prawns encounter one another in an area new to both, the larger animal usually has the advantage. Often these encounters are characterized by a limited series of pushes with one or the other chela. The function of the pushing might be threefold: 1) to test their opponent's weight (rest inertia), 2) to determine the opponent's molt state, and 3) to see if the opponent is capable of pushing back (has chelae). Other crustaceans appear to measure their opponent's physical strength by means of physical interactions involving the chelae (Griffin 1968; Schöne 1968). In *Cambarellus shufeldtii*, claw removal causes dominant animals to drop in rank (Lowe 1956). In *M. rosenbergii* deaths related to agonistic behavior usually occurred near ecdysis and often the first appendages lost during an agonistic encounter were the chelae (Peebles 1977).

Smaller animals have been observed successfully defending shelters from attempted occupation by larger congeners (Bovbjerg 1953; Griffin 1968; Sinclair 1977). This is related to the prior resident phenomenon and it is central to Nobel's (1939) definition of territory. Resident *M. rosenbergii*, regardless of their relative size, successfully retained their shelters. The mechanism the residents employed apparently was not limited to direct physical interaction. Immigrants and residents seldom fought. Generally immigrants were inactive upon placement into a tank housing a resident. The immigrant's aggressive behavior was well below its counterpart in the simultaneous introduction group. Only occasionally (Figure 1) did the immigrant seek out the shelter. This latter behavior is in direct contrast to the control group. A control group animal was usually back in its shelter within 1 min after reintroduction. Possibly an exocrine was an agent of communication between resident and immigrant prawns, since a novel environment did not inhibit exploration in animals of the simultaneous introduction experiment; and animals from the control experiment reintroduced into tanks contaminated with their own exocrines, rapidly entered their shelter.

The advantage conferred upon resident *M. rosenbergii* appears to disappear within a short period of time. The smaller resident can defend its shelter against intrusion for no longer than a few days (Figure 1). Apparently relative size can overcome the prior resident effect if resident and immigrant continue to encounter one another. Similar observations were reported by Lowe (1956). In the case of the *C. shufeldtii*, a dominance hierarchy was established before shelters were introduced. Dominant *C. shufeldtii* displaced subordinates from occupied shelters. In my experiments, *M. rosenbergii* first exhibited territoriality as determined by the presence of the prior resident effect. Territoriality then broke down, due to continued encounters, into simple dominance.

The important point addressed in this paper is not who wins or loses the encounter but which animal gains access to the resource. Investigators whose observations were limited to the first encounter might suggest that residents almost always outcompete intruders for shelter. However, I have shown that in a closed system the prior resident effect breaks down into simple size-related dominance. These results offer a behavioral explanation for the known and recognized bull effect in prawn aquaculture ponds. Larger animals have preferential access to food and shelter, two important resources which are often dispersed in a clumped or patchy fashion.

## Acknowledgments

## Literature Cited

ALLEE, W. C., AND M. B. DOUGLIS.
  1945. A dominance order in the hermit crab, *Pagurus longicarpus* Say. Ecology 26:411-412.
BALAZS, G. H., E. ROSS, AND C. C. BROOKS.
  1973. Preliminary studies on the preparation and feeding of crustacean diets. Aquaculture 2:369-377.
BAIRD, R. C.
  1968. Aggressive behavior and social organization in *Mollienesia latipinna* Le Sueur. Texas J. Sci. 20:157-176.
BOVBJERG, R. V.
  1953. Dominance order in the crayfish *Orconectes virilis* (Hagen). Physiol. Zool. 26:173-178.
  1956. Some factors affecting aggressive behavior in crayfish. Physiol. Zool. 29:127-136.
  1960. Behavioral ecology of the crab, *Pachygrapsus crassipes*. Ecology 41:668-672.
BRADDOCK, J. C.
  1945. Some aspects of the dominance-subordination relationship in the fish *Platypoecilus maculatus*. Physiol. Zool. 18:176-195.
  1949. The effect of prior residence upon dominance in the fish *Platypoecilus maculatus*. Physiol. Zool. 22:161-169.
BROWN, J. L.
  1963. Aggressiveness, dominance and social organization in the Stellar Jay. Condor 65:460-484.
  1975. The evolution of behavior. W. W. Norton & Co., N.Y., 761 p.

BROWN, J. L., AND G. H. ORIANS.
  1970. Spacing patterns in mobile animals. Annu. Rev. Ecol. Syst. 1:239-262.
BROWN, M. E.
  1946. The growth of brown trout (*Salmo Trutta* Linn.) I. Factors influencing the growth of trout fry. J. Exp. Biol. 22:118-129.
BUECHNER, H. K.
  1961. Territorial behavior in Uganda Kob. Science (Wash., D.C.) 133:698-699.
CRANE, J.
  1958. Aspects of social behavior in fiddler crabs, with special reference to *Uca maracoani* (Latreille). Zoologica (N.Y.) 43:113-130.
  1967. Combat and its ritualization in fiddler crabs (Ocypodidae) with special reference to *Uca rapax* (Smith). Zoologica (N.Y.) 52:49-76.
DINGLE, H., AND R. L. CALDWELL.
  1969. The aggressive and territorial behaviour of the mantis shrimp *Gonodactylus bredini* Manning (Crustacea: Stomatopoda). Behaviour 33:115-136.
EIBL-EIBESFELDT, I.
  1970. Ethology, the biology of behavior. Holt, Rinehart and Winston, N.Y., 530 p.
FIELDER, D. R.
  1965. A dominance order for shelter in the spiny lobster *Jasus lalandei* (H. Milne-Edwards). Behaviour 24:236-245.
FUJIMURA, T., AND H. OKAMOTO.
  1970. Notes on progress made in developing a mass culturing technique for *Macrobrachium rosenbergii* in Hawaii. Indo-Pacific Fisheries Council (FAO), Thailand.
GOODMAN, L. A.
  1954. Kolmogorov-Smirnov tests for psychological research. Psychol. Bull. 51:160-168.
GRIFFIN, D. J. G.
  1968. Social and maintenance behaviour in two Australian ocypodid crabs (Crustacea: Brachyura). J. Zool. (Lond.) 156:291-305.
HAZLETT, B. A.
  1968. Size relationship and aggressive behavior in the hermit crab *Clibanarius vittatus*. Z. Tierpsychol. 25:608-614.
HAZLETT, B. A., AND G. F. EASTBROOK.
  1974. Examination of agonistic behavior by character analysis. I. The spider crab *Microphrys bicornutus*. Behavior 48:131-144.
HUGHES, D. A.
  1966. Behavioural and ecological investigations of the crab *Ocypode ceratophthalmus* (Crustacea: Ocypodidae). J. Zool. (Lond.) 150:129-143.
ITÔ, Y.
  1970. Groups and family bonds in animals in relation to their habitat. *In* L. R. Aronson, E. Tobach, D. S. Lehrman, and J. S. Rosenblatt (editors), Development and evolution of behavior, p. 389-415. W. H. Freeman, San Franc.
JACHOWSKI, R. L.
  1974. Agonistic behavior of the blue crab, *Callinectus sapidus* Rathbun. Behaviour 50:232-253.
JOHNSON, D. S.
  1960. Some aspects of the distribution of freshwater organisms in the Indo-Pacific area, and their relevance to the validity of the concept of an Oriental region in

zoogeography. Proc. of the Centenary and Bicentenary Congress of Biology, Singapore, 1958, p. 170-181.

LING, S. W.
1969. The general biology and development of *Macrobrachium rosenbergii* (de Man). FAO Fish. Rep. 57:589-606.

LOWE, M. E.
1956. Dominance-subordinance relationships in the crawfish *Cambarellus shufeldtii*. Tulane Stud. Zool. 4:139-170.

MALECHA, S. R.
1977. Genetics and selective breeding of *M. rosenbergii*. *In* J. A. Hanson and H. L. Goodwin (editors), Shrimp and prawn farming in the Western Hemisphere, p. 328-355. Dowden, Hutchinson & Ross, Inc., Stroudsburg, Pa.

MARLER, P., AND W. J. HAMILTON III.
1966. Mechanisms of animal behavior. John Wiley & Sons, N.Y., 771 p.

MCVEY, J. P.
1975. New record of *Macrobrachium rosenbergii* (De Man) in the Palau Islands (Decapoda, Palaemonidae). Crustaceana 29:31-32.

MILLER, R. B.
1958. The rôle of competition in the mortality of hatchery trout. J. Fish. Res. Board Can. 15:27-45.

MOLENOCK, J.
1976. Agonistic interactions of the crab *Petrolisthes* (Crustacea, Anomura). Z. Tierpsychol. 41:277-294.

NAKAMURA, N., AND S. KASAHARA.
1955. A study on the phenomenon of the tobi-koi or shoot carp—I. On the earliest stage at which the shoot carp appears. Bull. Jpn. Soc. Sci. Fish. 21:73-76.
1961. A study on the phenomenon of the tobi-koi or shoot carp—IV. Effects of adding a small number of larger individuals to the experimental batches of carp fry and of culture density upon the occurrence of shoot carp. Bull. Jpn. Soc. Sci. Fish. 27:958-962.

NOBLE, G. K.
1939. The rôle of dominance in the social life of birds. Auk 56:263-273.

PEEBLES, J. B.
1977. Movement, dispersion and mortality in *Macrobrachium rosenbergii*. Ph.D. Thesis, University of Hawaii, Honolulu, 220 p.

RAMAN, K.
1964. On the location of a nursery ground of the giant prawn *Macrobrachium rosenbergii* (de Man). Curr. Sci. (India) 33:27-28.
1967. Observations on the fishery and biology of the giant freshwater prawn *Macrobrachium rosenbergii* de Man. *In* Symposium on Crustacea, Part I, p. 649-669 Mar. Biol. Assoc. India, Ernakulum.

REESE, E. S.
1964. Ethology and marine zoology. Oceanogr. Mar. Biol. Annu. Rev. 2:455-488.

RUBENSTEIN, D. I., AND B. A. HAZLETT.
1974. Examination of the agonistic behaviour of the crayfish *Orconectes virilis* by character analysis. Behaviour 50:193-216.

SCHÖNE, H.
1968. Agonistic and sexual display in aquatic and semiterrestrial brachyuran crabs. Am. Zool. 8:641-654.

SELANDER, R. K.
1970. Behavior and genetic variation in natural populations. Am. Zool. 10:53-66.

SIEGEL, S.
1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., N.Y., 312 p.

SINCLAIR, M. E.
1977. Agonistic behaviour of the stone crab, *Menippe mercenaria* (Say). Anim. Behav. 25:193-207.

STIMSON, J.
1970. Territorial behavior of the owl limpet, *Lottia gigantea*. Ecology 51:113-118.

SYMONS, P. E. K.
1971. Behavioural adjustment of population density to available food by juvenile Atlantic salmon. J. Anim. Ecol. 40:569-587.

WARNER, G. F.
1970. Behaviour of two species of grapsid crab during intraspecific encounters. Behaviour 36:9-19.

WATSON, A.
1964. Aggression and population regulation in red grouse. Nature (Lond.) 202:506-507.

WOHLFARTH, G. W., AND R. MOAV.
1972. The regression of weight gain on initial weight in carp. I. Methods and results. Aquaculture 1:7-28.

JOHN B. PEEBLES

*Hawaii Institute of Marine Biology*
*University of Hawaii*
*Kaneohe, HI 96744*

# PRINCIPAL SPAWNING AREAS AND TIMES OF MARINE FISHES, CAPE SABLE TO CAPE HATTERAS

The purpose of this compendium is to summarize spawning areas and seasons of the more abundant marine fishes of the continental shelf between Cape Sable, N.S., and Cape Hatteras, N.C., as an aid to the identification of fish eggs and larvae and planning and scheduling ichthyoplankton surveys. We have used the term "marine" to encompass fishes which spawn at sea (in contrast to estuarine spawners), although some of the species included spawn in both environments contingent on geographic location (e.g., winter flounder which spawn exclusively in estuaries in the Middle Atlantic Bight and offshore in the Gulf of Maine and Atlantic menhaden which spawn in estuaries along southern New England and in the New York Bight and offshore in the lower Middle Atlantic Bight and in the South Atlantic Bight).

The Gulf of Maine is defined as the oceanic bight bounded by Nantucket Shoals and Cape Cod on the west (long. 70°W) and Cape Sable on the east (long. 65°W) including Georges and Browns Banks and waters out to the 200-m contour (Colton 1964). The Middle Atlantic Bight is the area