

- fishes of the Sacramento-San Joaquin drainage system. IV. A review. Univ. Calif. Publ. Zool. 115:225-256.
- NETER, J., AND W. WASSERMAN.
1974. Applied linear statistical models. R. D. Irwin, Inc., Homewood, Ill., 842 p.
- REMINGTON, R. D., AND M. A. SCHORK.
1970. Statistics with applications to the biological and health sciences. Prentice-Hall, Inc., Englewood Cliffs, N.J., 418 p.
- SCOTT, W. B., AND E. J. CROSSMAN.
1973. Freshwater fishes of Canada. Fish. Res. Board Can., Ottawa, 966 p.
- SOKAL, R. R., AND F. J. ROHLF.
1981. Biometry: The principles and practice of statistics in biological research. W. H. Freeman, San Franc., 859 p.
- STEVENS, D. E.
1980. Factors affecting the striped bass fisheries of the west coast. In H. Clepper (editor), Proceedings of the Fifth Marine Recreational Fisheries Symposium, p. 15-28. Sport Fish. Inst., Wash., D.C.
- TESCH, F. W.
1968. Age and growth. In W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, p. 93-123. Blackwell Sci. Publ., Oxford.
- THORNDIKE, R. M.
1978. Correlation procedures for research. Gardner Press, Inc., N.Y., 78 p.
- WINDELL, J. T.
1968. Food analysis and rate of digestion. In W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, p. 197-203. Blackwell Sci. Publ., Oxford.

ROBERT A. DANIELS

New York State Museum
Biological Survey
Cultural Education Center, Room 3132
Albany, NY 12230

PETER B. MOYLE

Department of Wildlife and Fisheries Biology
University of California
Davis, CA 95616

LIFE HISTORY AND EXPLOITATION OF *MACROBRACHIUM FAUSTINUM* IN A TROPICAL HIGH-GRADIENT RIVER

Macrobrachium spp. are widely distributed in tropical freshwaters where they often support commercial or artisanal fisheries (Holthuis and Rosa 1965; Holthuis 1980). Studies of exploited *Macrobrachium* stocks have been carried out in large, low-gradient rivers in Liberia (Miller 1971), India (Rajyalakshmi and Ranadhir 1969), and the Philippines (Rasalan et al. 1969), but do not provide the bionomic information necessary for a quantitative assessment of the response of the stocks to exploitation. We know

of no such study of a wild population of *Macrobrachium* species.

Macrobrachium faustinum inhabits freshwaters throughout the Caribbean area and in Florida (Chace and Hobbs 1969). In Jamaica it is the most common, eurytopic, freshwater shrimp, inhabiting both slow-flowing rivers and marshes in low lying areas, and fast-flowing streams in hilly regions (Hunte 1978). In the former, *M. faustinum* supports trap fisheries; in the latter it is fished either by hand or by turning over stones and allowing the shrimps to be washed into baskets. Although this fishery is pursued part time by children and men after work, these and other shrimps from small rivers are an important dietary component in an area where protein is scarce and expensive. In this paper we describe the bionomics of *M. faustinum* in a high-gradient stream (Cane River, Jamaica), and assess the effects of fishing on yield and population fecundity.

Description of Study Area

Cane River (lat. 17°58'N, long. 76°44'W) flows into the Caribbean Sea on an exposed south shore (Fig. 1). There is no protected bay at the river mouth, and the estuary is small. Altitude at the source is about 650 m, total length about 10.2 km, overall mean width 2.3 m, and mean depth about 9.4 cm. The width and depth vary markedly with seasonal rainfall. Cane River is a characteristic high-gradient stream in Jamaica. The water is clear and fast-flowing with a high oxygen content and a rocky bottom devoid of macrovegetation. Mean oxygen concentration along the river was 8.5 mg/l, mean pH 7.3. Mean temperature at the extreme lower limit of the river was 25.4°C with a mean daily range of 8.6°C and a mean seasonal range of 4.2°C. Corresponding temperature values at the extreme upper limits were overall mean 21.7°C, mean daily range 3.7°C, and mean seasonal range 3.4°C. The river bed consisted of stones, pebbles, gravel, sand, and mud over rock.

Materials and Methods

Shrimps were collected using a combined Surber sampler (Moffett 1936; Surber 1936) and Box sampler (Berg 1938). It consisted of a square frame of 0.25 m² with four legs protruding 5 cm below the frame and 40 cm above it. Net (1 mm square mesh) enclosed the sampler on three sides. Flaps of net under all four sides of the frame served as a seal between the frame and the substrate. On the fourth (downstream) side, there was a detachable collecting net 80 cm long with a mouth 50 × 40 cm (1 mm square mesh).

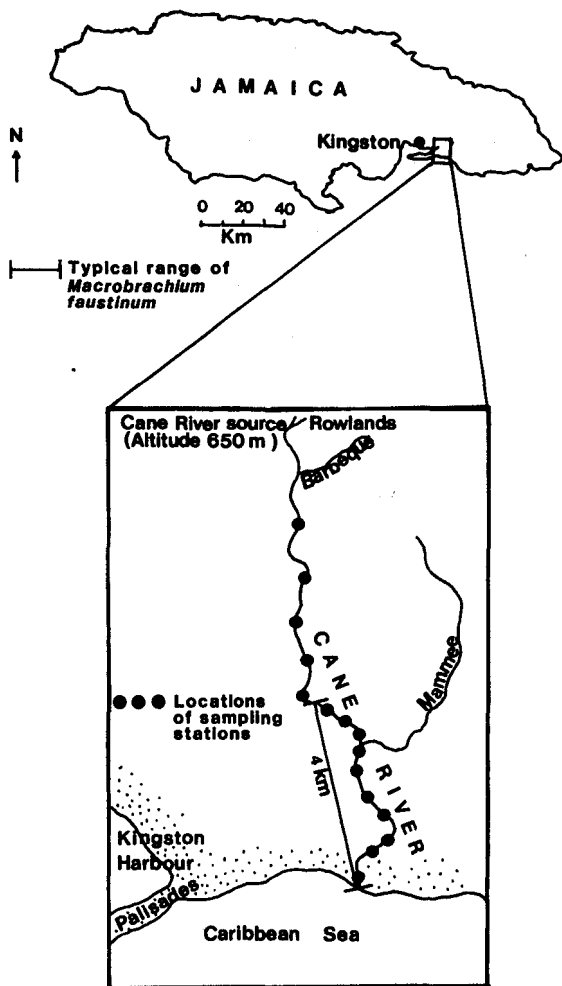


FIGURE 1.—Map of study area and its location in Cane River, Jamaica.

To sample, the legs were forced into the substrate and the net flaps pinned around by stones. The collecting net was attached to the frame, and its bottom side held firmly down by the operator's feet. All stones within the sample area were then removed and the shrimps swept into the collecting net by the current.

During a 20-mo period (February 1973–September 1974), 10 samples, randomly chosen, were taken monthly at each of 15 stations along the length of the river. Areas of the stream bed which were devoid of stones were not sampled since they were known to be without shrimps (Hunte 1976). Samples were taken during the day when the shrimps are inactive and hide under stones.

Each specimen of *M. faustinum* was sexed, and its

total length measured (from the tip of the rostrum to the tip of the telson) to the nearest 0.5 mm for adults and 0.1 mm for juveniles. Specimens subsampled from each month's catch were weighed to the nearest 10 mg for adults and the nearest 1 mg for juveniles. Growth and mortality were estimated from monthly length-frequency histograms.

The catch of fishermen was sampled opportunistically throughout the period of sampling in the river. On each occasion the shrimps in the catch were measured and the resulting length-frequency distribution converted to a catch curve using the age-length relationship.

Yield per recruit (Y/R) for various levels of fishing mortality (F) was estimated for males and females combined by the method of Thompson and Bell (Ricker 1975), using an APL algorithm (Rivard 1980). The parameters required for the input are b , age of the youngest age-group fished; m , age of the oldest age-group fished; w_i , weight (g) at age i ; r_i , the partial recruitment to fishing mortality at age i ; and M , the instantaneous rate of natural mortality. Then

$$Y/R = \sum_{i=b}^m w_i N_i F_i \frac{(1 - e^{-Z_i})}{Z_i},$$

where $F_i = r_i F$, $Z_i = F_i + M$, and $N_i = N_{i-1} e^{-Z_{i-1}}$. The sequence of N_i for each age-group in the fishery is calculated assuming $N_b = 1$.

The partial recruitment to fishery mortality (r_i) is the proportion of the fishing mortality which can be allocated to age-group i . These values increase throughout recruitment to a maximum of 1 for fully recruited age-groups. In this study r_i was estimated as the ratio of the proportions of age-group i in the catch and population survey, standardized to a maximum of 1 by dividing each ratio by the largest one (Winters 1978).

The number of eggs produced per female recruit (E/R) was estimated for various levels of fishing mortality.

$$E/R = \sum_{i=a}^m E_i N_i$$

where a is the age of first maturity for females and E_i is the number of eggs per female at age i . For postrecruits ($i > b$), N_i were as defined above for the estimation of Y/R . For prerecruits ($i < b$), N_i were backcalculated assuming $N_b = 1$, and $Z = M$. The number of eggs per female at each age was determined from the fecundity-length and age-length relationships.

Results

Cane River does not flow through to the sea for much of the year (January-August). As the larvae of *M. faustinum* must develop in the sea (Hunte 1980a, b), juveniles enter the river during a short period each year. Consequently, length-frequency histograms showed distinct modes which were useful for growth and mortality analyses (Fig. 2).

Juveniles entered the river between September 1973 and January 1974, and again in September 1974 (Fig. 2). The weighted mean time of entry of the 1973 cohort was in early December, and was assumed to be early December for all cohorts. At this time shrimps were about 3 mo of age. The peak of the breeding season is about 3 mo earlier (see Fig. 4). Larval development in the laboratory takes about 95 d (Hunte 1980a) after which the length of the juveniles (Hunte 1980b) is similar to that of juveniles entering the river.

Monthly growth for males and females (Fig. 3) was estimated from changes in mean length of cohorts (Fig. 2). Sex could not be distinguished before about 10 mo, when all members of a cohort are longer than 20 mm. Males grew slightly faster than females (Fig. 3).

The wet weight/length relationship for males was $\log W = 3.15 \log L - 2.02$, and for females $\log W = 3.23 \log L - 2.20$. The regression coefficients do not differ significantly, but are significantly >3 , indicating allometric growth ($b > 3$; for males $t = 2.64, P < 0.01$; for females, $t = 5.14, P < 0.001$).

Females composed 49% of adult shrimps caught (i.e., those >20 mm). This was not significantly different from a 1:1 sex ratio ($\chi^2 = 0.81, P > 0.25$).

No females smaller than 26 mm (about 9 mo old) bore eggs. This is therefore an estimate of the minimal size (age) at sexual maturity. Of the females in the 26-28 mm size class, 39% were berried, compared with 51% for all mature classes combined. This suggests that most females mature in the 26-28 mm size range, with little variation in size at sexual maturity.

Eggs were oval, about 0.54 by 0.42 mm when laid, and about 0.70 by 0.53 mm prior to hatching. Egg size was independent of female length. Eggs were counted on females carrying eggs in advanced developmental stages, and the fecundity/length relationship was $\log F = 3.52 \log L - 2.47$.

Monthly percentages of mature females carrying eggs (berried) showed that spawning was continuous but peaked between June and November (Fig. 4), just before or during the months of heaviest rainfall in Jamaica.

Total mortality for the *M. faustinum* stock is estimated from the decline in monthly catch of the four year classes sampled in this study (Fig. 5). The percentage contribution of each age-group to the fishermen's catch shows the age of first capture to be 16 mo and full recruitment to the fishery to be at 24 mo (Fig. 4). There is a distinct increase in mortality at, or just before, the age of complete recruitment. We estimate the instantaneous rate of natural mortality (M) as equal to the instantaneous rate of total mortality (Z) for the prerecruits (ages 5-15 mo). Fishing mortality (F) is taken as equal to $Z-M$ for the fully recruited age groups (25-34 mo). The estimates of M and F are 0.13 and 0.15, respectively, and the former is used in the estimation of Y/R .

The information used to calculate the partial recruitment values is given in Table 1. The ratios of proportion in catch to proportion in the survey indicate that F increases steadily with age and size. However, as there are relatively few individuals in the older age-groups, we felt it more appropriate to consider recruitment as complete at age 24 and to assign $r_i = 1$ to all older age-groups. Therefore, all values of r_i for $i < 24$ are relative to the catch survey ratio at age 24.

The relationship between Y/R and F (Fig. 6) appears to be asymptotic; therefore, no F for maximum yield could be computed. However, beyond an F of about 0.5 the returns in terms of Y/R for increased F are minimal. Both the mean weight of shrimp in the catch and the index of catch per unit effort change most rapidly at values of F less than about 0.5.

The relationship between fishing mortality and the number of ripe eggs produced per recruit shows that

TABLE 1.—The calculation of partial recruitment to fishing mortality at each age for *Macrobrachium faustinum* in Cane River, Jamaica.

Age (months)	Percent in catch	Percent in survey	Ratio catch/survey	R_i used in Y/R estimates
16	1.1	10.0	0.11	0.048
17	1.1	10.1	0.11	0.048
18	3.2	10.7	0.30	0.130
19	2.3	9.8	0.23	0.100
20	5.9	8.6	0.69	0.300
21	3.6	7.3	0.49	0.210
22	9.0	6.7	1.35	0.59
23	11.1	6.7	1.66	0.72
24	14.7	6.4	2.30	1
25	9.5	5.6	1.70	1
26	6.5	4.7	1.38	1
27	6.1	3.8	1.60	1
28	6.1	2.8	2.18	1
29	5.3	2.2	2.41	1
30	2.3	1.4	1.64	1
31	3.8	1.3	2.92	1
32	3.4	0.9	3.78	1
33	3.4	0.7	4.86	1
34	1.9	0.3	6.33	1

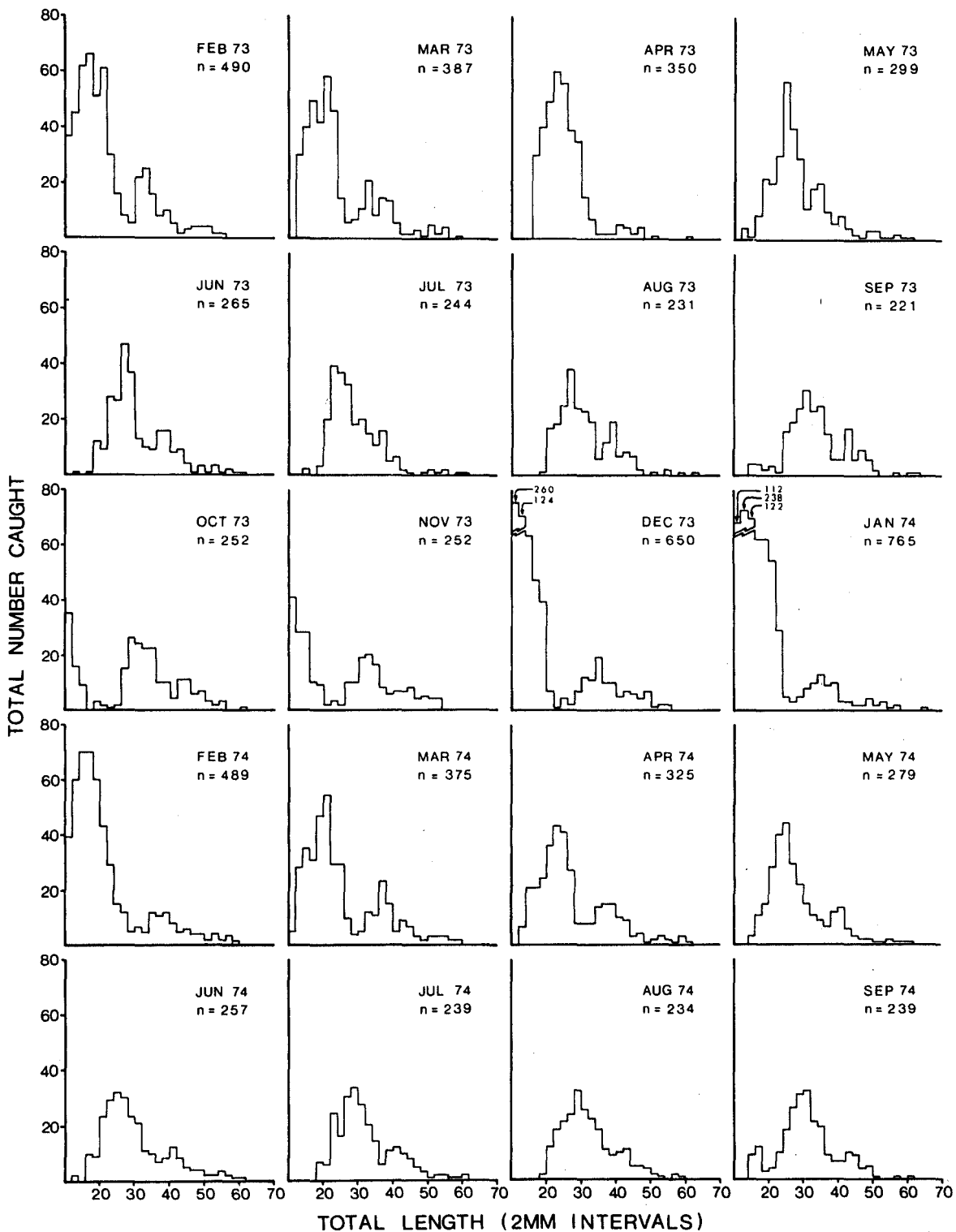


FIGURE 2.—Monthly length-frequency histograms for *Macrobrachium fastinum* in Cane River.

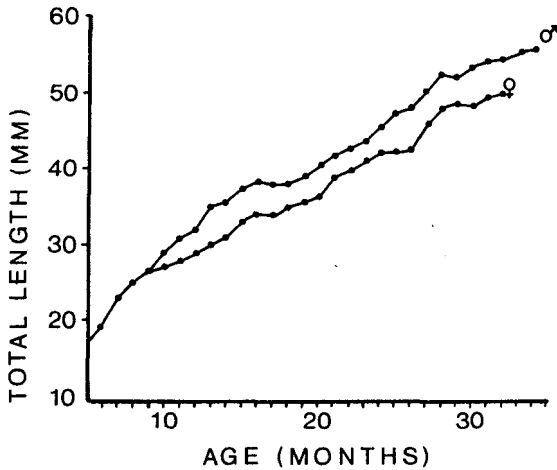


FIGURE 3.—Growth of *Macrobrachium faustinum* in Cane River.

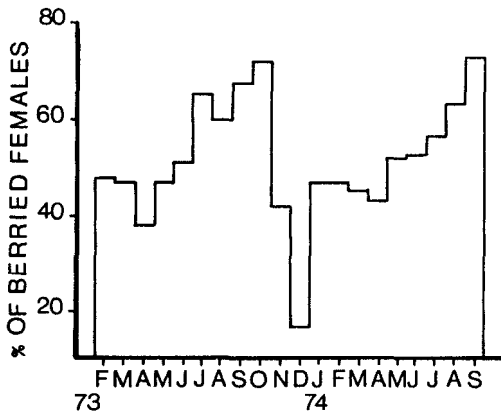


FIGURE 4.—Seasonal variation in the percentage of berried *Macrobrachium faustinum* in Cane River.

even at relatively high values of fishing mortality ($F \approx 2.0$) egg production is only 37% less than at $F = 0.1$ (Fig. 7).

Discussion

Macrobrachium faustinum and other small shrimps support important subsistence fisheries in the hilly regions of Jamaica and throughout the Caribbean. Management of a resource so widely and diffusely distributed throughout the countryside is difficult. Consequently, to assess the need for management it is important to have some understanding of the likely effects of increased exploitation on these shrimps.

The asymptotic relationship between Y/R and fishing mortality suggests that the shrimps are unlikely to be overfished from the viewpoint of optimal yield of biomass. At the present level of fishing mortality ($F = 0.15$) there would be substantial gains in yield from small increases in fishing effort (Fig. 6). However, sharp reductions in catch per unit effort and in the mean size of shrimp captured would be expected to accompany increased exploitation. *Macrobrachium faustinum* is already small, and we expect that, except in the event of extreme food shortage, the reduction in mean size and catch per unit

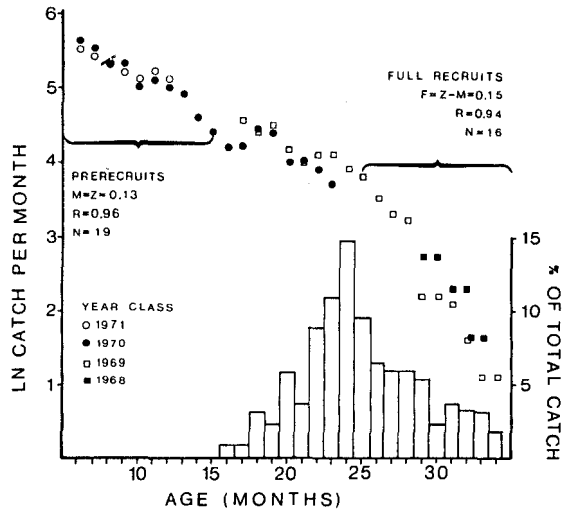


FIGURE 5.—Mortality of *Macrobrachium faustinum* in Cane River as indicated by decline in abundance of year classes (catch per month), and the age composition of the fisherman's catch (percent of total catch).

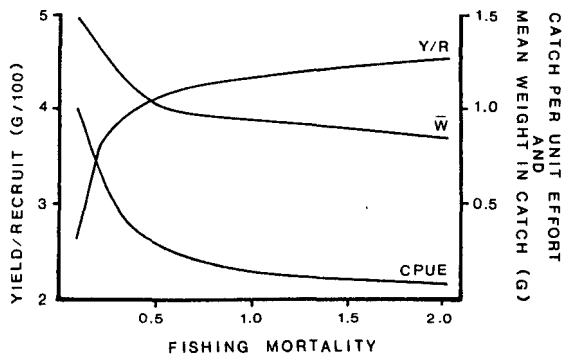


FIGURE 6.—The relationship of yield per recruit (Y/R), mean weight of shrimp caught (\bar{w}), and the index of catch per unit effort ($CPUE$) to fishing mortality for *Macrobrachium faustinum* in Cane River.

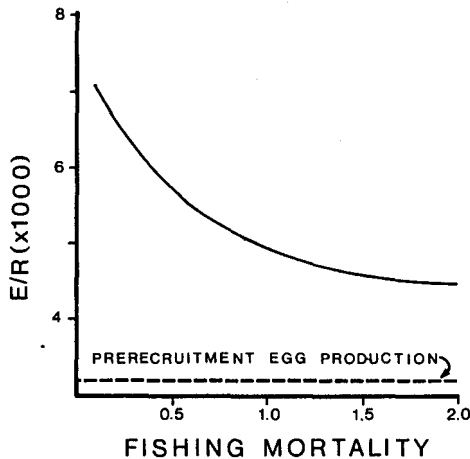


FIGURE 7.—The relationship between fishing mortality and the number of eggs produced per recruit for *Macrobrachium faustinum* in Cane River.

effort of shrimp will self-regulate the fishery. The low level of F suggests that this effect is currently operative.

Even though yield (growth) overfishing is unlikely, the possibility of recruitment overfishing (Cushing 1977) must be considered. This too is unlikely, because *M. faustinum* mature early and a high proportion of egg production takes place before recruitment to the fishery (Fig. 7).

Animals which are small, highly fecund, and mature early are to be expected in a habitat where density-independent mortality prevails and is not stronger and/or more variable for juveniles than for adults (see Stearns 1977). In the rainy season Cane River is subject to flash floods which cause high density-independent mortality of shrimps (Hunte 1976). This is almost certainly true of all high-gradient streams in the Caribbean and the shrimps which inhabit them would be expected to have life history characteristics similar to *M. faustinum*. It appears likely then that such species, many of which support significant subsistence fisheries, will be resistant to overexploitation and that regulatory management need not be considered.

Acknowledgments

This work was supported by an Alcan Junior Research Fellowship and a CIDA/NSERC Research Associateship to W. Hunte. We thank Pat Simpson and Susan Mahon for drafting the figures.

Literature Cited

- BERG, K.
1938. Studies on the bottom animals of Esrom Lake. *Konig Danske Vidensk. Selsk. Skr.* 8:1-255.
- CHACE, F. A., JR., AND H. H. HOBBS, JR.
1969. The freshwater and terrestrial decapod crustaceans of the West Indies with special reference to Dominica. *U.S. Natl. Mus. Bull.* 292, 258 p.
- CUSHING, D. H.
1977. The problems of stock and recruitment. In J. A. Gulland (editor), *Fish population dynamics*, p. 116-133. John Wiley & Sons, N.Y.
- HOLTHUIS, L. B.
1980. FAO species catalogue. Vol. 1. Shrimps and prawns of the world. *FAO Fish. Synop.* 125, 271 p.
- HOLTHUIS, L. B., AND H. ROSA, JR.
1965. List of species of shrimp and prawns of economic value. *FAO Fish. Tech. Pap.* 52, 21 p.
- HUNTE, W.
1976. Biological studies of freshwater shrimps (Atyidae and Palaemonidae) in Jamaica. Ph.D. Thesis, University of the West Indies, Jamaica, 379 p.
1978. The distribution of freshwater shrimps (Atyidae and Palaemonidae) in Jamaica. *Zool. J. Linn. Soc.* 64:135-150.
1980a. The larval development of the shrimp *Macrobrachium faustinum* reared at the laboratory. *Caribb. J. Sci.* 15(3-4):49-68.
1980b. The laboratory rearing of larvae of the shrimp *Macrobrachium faustinum*. *Caribb. J. Sci.* 16:57-62.
- MILLER, G. C.
1971. Commercial fishery and biology of the freshwater shrimp, *Macrobrachium*, in the Lower St. Paul River, Liberia, 1952-53. *U.S. Dep. Commer., Natl. Mar. Fish. Serv., Spec. Sci. Rep. Fish.* 626, 13 p.
- MOFFETT, J. W.
1936. A quantitative study of the bottom fauna in some Utah streams variously affected by erosion. *Bull. Univ. Utah* 26:1-32.
- RAJYALAKSHMI, T., AND M. RANADHIR.
1969. The commercial prawn *Macrobrachium malcolmsonii* (H. Milne-Edwards) of the River Godavary, a discussion of the trend and characteristics of the population during 1963-1966. *FAO Fish. Rep.* 3(57):903-921.
- RASALAN, S. D., M. N. DELMENDO, AND T. G. REYES.
1969. Some observations on the biology of the freshwater prawn *Macrobrachium lanceifrons* (Dana), with notes on the fishery. *FAO Fish. Rep.* 3(57):923-933.
- RICKER, W. E.
1975. Computation and interpretation of biological statistics of fish populations. *Fish. Res. Board Can., Bull.* 191, 382 p.
- RIVARD, D. E.
1980. APL programs for stock assessment. *Can. Tech. Rep. Fish. Aquat. Sci.* 953, 103 p.
- STEARNS, S. C.
1977. The evolution of life history traits: A critique of the theory and a review of the data. *Annu. Rev. Ecol. Syst.* 8:145-171.
- SURBER, E. W.
1936. Rainbow trout and bottom fauna production in one mile of stream. *Trans. Am. Fish. Soc.* 66:193-202.
- WINTERS, G. H.
1978. Production, mortality, and sustainable yield of North-

WAYNE HUNTE

Bellairs Research Institute of McGill University
St. James, Barbados, West Indies

ROBIN MAHON

Marine Fish Division
Fisheries Research Branch
Department of Fisheries and Oceans
P.O. Box 1006, Dartmouth
Nova Scotia, B2Y 4A2 Canada

INCIDENTAL CATCH OF HARBOR PORPOISE, *PHOCOENA* *PHOCOENA* (L.), IN HERRING WEIRS IN CHARLOTTE COUNTY, NEW BRUNSWICK, CANADA

In this report we examine the indirect exploitation of harbor porpoises, *Phocoena phocoena*, by the weir fishery for herring (*Clupea harengus*) in Charlotte County, New Brunswick, in the lower Bay of Fundy. This fishery is of considerable economic importance to the region; the landed value averaged 2.2 million dollars annually from 1974 to 1979 (table 11 in Iles 1979). Although herring constitute 50% of the harbor porpoise diet (Smith and Gaskin 1974), the level of competition and conflict between *P. phocoena* and the fishery is unknown.

The harbor porpoise is taken accidentally by several commercial fisheries throughout the world (Mitchell 1975), including a pound net fishery in Denmark (Andersen 1974) similar to the weir fishery of eastern Canada. In Canadian waters, harbor porpoises have been caught frequently in Newfoundland cod traps (Sergeant and Fisher 1957) and an unknown number are killed annually in gill nets in the Gulf of St. Lawrence (Laurin 1976). In addition to the indirect catch in the Bay of Fundy, harbor porpoises have been hunted for food and oil by native people and fishing families from at least the 19th century to the present (Gilpin 1878; Leighton 1937; Prescott et al. 1981). An unknown number of animals were also used as mink food in the 1950s (Fisher and Harrison 1970).

As part of a continuing study of *P. phocoena*, we had the opportunity to examine 48 specimens trapped in herring weirs since 1969. Eleven were tagged or equipped with radio-telemetry packs and released (Gaskin et al. 1975). The remainder were routinely autopsied and ages of 30 specimens were estimated

from dentinal growth layers (Gaskin and Blair 1977).

Since no formal reporting system exists, we attempted to assess the annual rate of entrapment by mailing questionnaires to all 214 members of the Fundy Weir Fishermen Association in 1980. A total of 49 questionnaires were returned, of which 36 (16.8%) were of a usable nature.

Specimens Examined from Herring Weirs

The 48 harbor porpoises examined between 1969 and 1982 consisted of 22 females and 26 males. Harbor porpoises became trapped in weirs from May to December with the majority (36) taken in July and August. Ages ranged from 0 to 8 yr, with a disproportionate number of 1-yr-old animals. Over half (52%) of the aged sample ($n = 25$) taken from 1969 to 1973 consisted of 1-yr-old harbor porpoises, while yearlings constituted only 18.9% of a sample of 95 animals collected by shotgun from the free-ranging population during the same time period (Fig. 1).

This catch bias may be a consequence of the inexperience of 1-yr-old harbor porpoises in echolocation, navigation, and prey capture. *Phocoena phocoena* has a lactation period of only 8 mo (Gaskin et al. 1981), short in comparison with other odontocete species. Brodie (1969) suggested that prolonged lactation in odontocetes is attributable to the

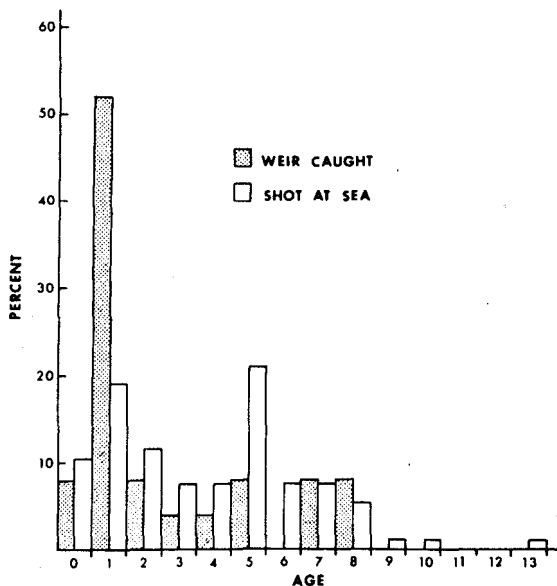


FIGURE 1.—Frequency histogram of age classes (estimated from dentinal growth layers) of harbor porpoises collected in the Bay of Fundy, 1969-73, expressed as percentage of totals captured by two methods: Weir-caught ($n = 25$) and shot at sea ($n = 95$).