

ASSESSMENT OF MORTALITY IN AN OFFSHORE POPULATION OF QUEEN CONCH, *STROMBUS GIGAS* L., IN SOUTHWEST PUERTO RICO

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ABSTRACT

A Jolly-Seber multiple tag-recapture experiment was conducted for 2 years on a queen conch population offshore of La Parguera, Puerto Rico in order to estimate mortality rates. Over 2,000 individuals were tagged in 9 sampling periods spaced at 3-month intervals from August 1983 to August 1985. The occurrence of fishing in half the intervals allowed estimates to be made of both fishing and natural mortality rates. Fishing mortality averaged 1.14 over the study period. An upper limit of natural mortality including effects of emigration, was estimated to be 1.53. Assuming random diffusion, emigration was estimated and subtracted from the above yielding a corrected value of natural mortality of 1.05.

The queen conch, *Strombus gigas*, is one of the most valuable fishery resources of the Caribbean. Under heavy fishing pressure, stocks throughout the region have declined (Brownell and Stevely 1981), and the need for management has become increasingly obvious. Ideally, management decisions should be based on a firm understanding of queen conch biology, stock dynamics, and rates of exploitation. Estimates of natural and fishing mortality rates are fundamental to understanding the dynamics of exploited populations and are prerequisites of many stock assessment techniques, e.g., yield-per-recruit analysis (Beverton and Holt 1957).

All previous reports of natural mortality rate in queen conch populations have been made using only juveniles (Alcolado 1976; Baisre and Paez 1981; Wood and Olsen 1983; Berg 1976). There are two primary reasons for this: 1) populations where adult queen conch are not fished have not been studied or assessed, thus mortality estimates would include losses due to fishing as well as from natural causes; 2) estimates derived from length-frequency analysis cannot be made for adults because growth in length ceases at the onset of sexual maturity. These past estimates of natural mortality rate have all been high, ranging between 1.0 and 4.0, depending upon the age-group studied, except those of Wood and Olsen (1983) who reported values of 0.19 and 0.04 between ages 1 and 2 and ages 2 and 3, respectively. Thus, there is a dichotomy among reported val-

ues. Intuitively, it is difficult to predict whether high or low values of natural mortality rate should be expected. A low value of natural mortality rate, comparable to that of Wood and Olsen, might be expected for *S. gigas* because, in general, natural mortality is inversely related to size (Ursin 1967; Peterson and Wroblewski 1984; Blueweiss et al. 1978; Pauly 1980) and other large mollusks, from temperate areas, have typically low values of natural mortality. However, natural mortality should also be significantly related to temperature, both directly and through growth-rate mediated effects (Pauly 1979, 1980). Thus, higher values should be expected in tropical species. A casual literature review revealed only one estimate of natural mortality (M) in tropical mollusks for comparative purposes: $M = 3.66$ for the aplysiid gastropod *Dolabella auricularia* from the Philippines (Pauly and Calumpong 1984).

In the present study, rate of mortality was estimated for an offshore queen conch population spanning a wide size range and including both juveniles and adults. The Jolly-Seber multiple tag-recapture method was used. Separate estimates were made during periods of fishing and nonfishing, thus allowing partitioning of mortality into its fishing and natural components.

METHODS

The study area was located in southwest Puerto Rico, 7 km south of La Parguera (Fig. 1). The area has a uniform depth of 17 m and consists of a broad, patchy sand and macroalgal plain with oc-

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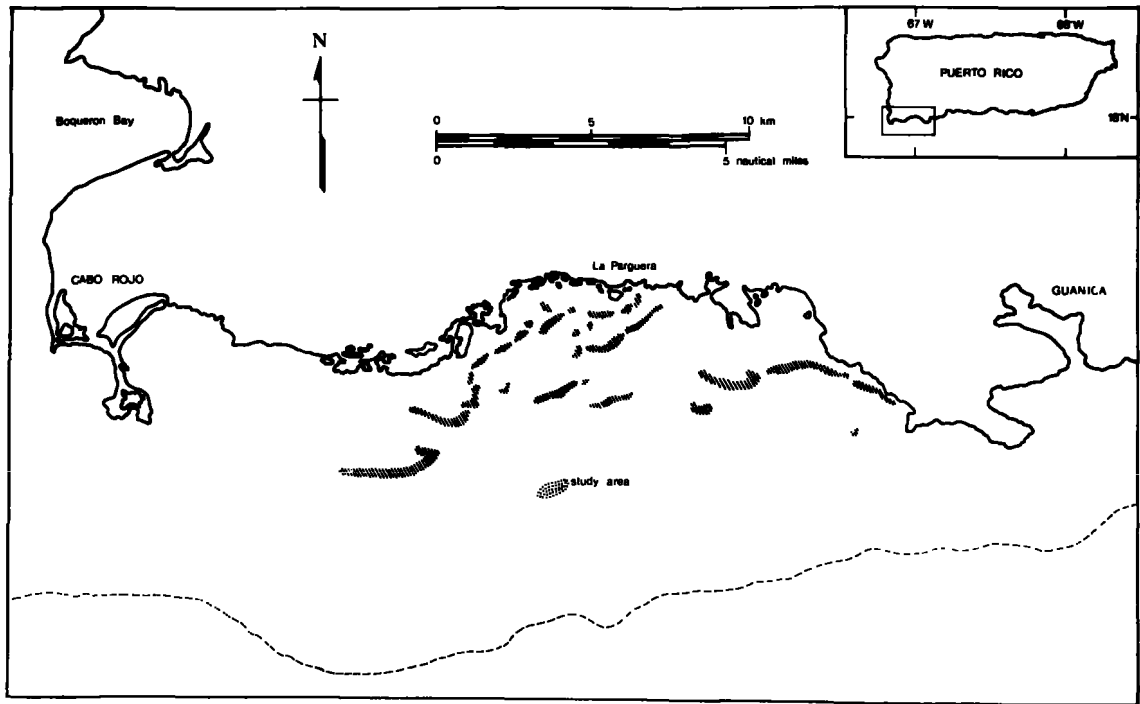


FIGURE 1.—Location of the queen conch study area (stippled) off La Parguera, Puerto Rico. Dashed line is the edge of the insular shelf. Shaded areas are emergent coral reefs.

casional patch reefs. The total study area is estimated to be 0.4 km², although for the first two periods sampling was limited to approximately the eastern 50% of the area.

Sampling occurred quarterly, generally in the latter half of August, November, February, and May, resulting in 9 sampling periods spanning 2 years from August 1983 to August 1985. Sampling during each period was conducted in the following manner. The area was surveyed by scuba divers and all data were collected in situ. Attempts were made to locate a minimum of 200 individuals. The maximum number was variable and subject to limits on queen conch density, the time dedicated to sampling (generally 3 weeks), and the weather during that time. During each period a two-stage haphazard sampling plan was used. Dive sites were located haphazardly throughout the full range of the study area, and the bottom covered during each dive was a function of direction and distance travelled, which also were determined haphazardly.

All queen conchs were tagged, when initially encountered, and measured for siphonal length to the nearest 1 mm using calipers. In addition,

adults, defined by the presence of a flared shell-lip, were measured for lip-thickness in a similar manner. Tags consisted of 4.5 cm strips of Dymo² label tape, upon which a unique identification number was embossed. They were tied around the shell spire with nylon line (Fig. 2). The spines characteristic of queen conch shells held the tag firmly in place. Upon subsequent sightings tag number was recorded and shell dimensions re-measured.

During the 2-yr study period, casual assessments were made of fishing activity in the area. This was easy to do routinely as fishermen were willing to return tags from fished shells, and the presence of newly fished, empty shells on the bottom (left behind after meat extraction) was obvious after fishing had occurred. When encountered, tag numbers of these shells were recorded.

Data analysis used the Jolly-Seber method. The theory and practical mechanics of the method are presented in detail by Seber (1982: Section 5.1). It is valid for open populations where the effects of

²Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

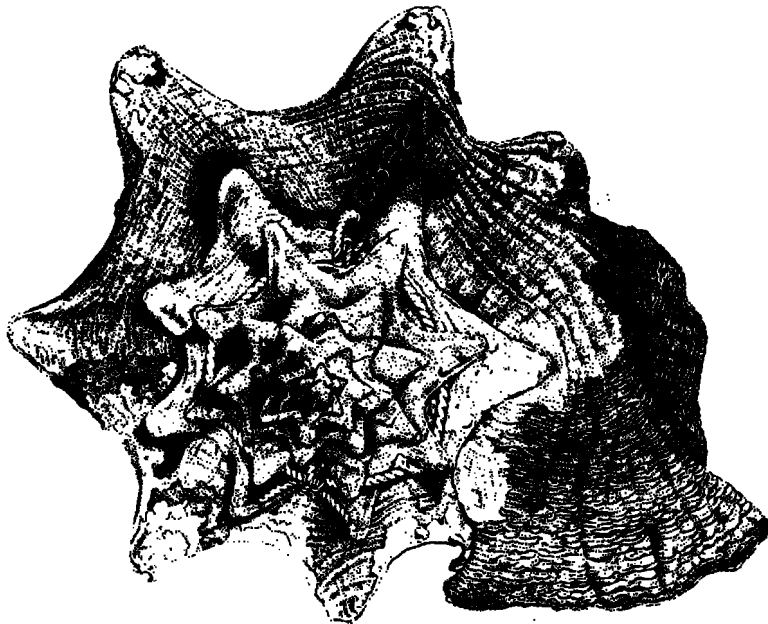


FIGURE 2.—Posterior view of adult *Strombus gigas* with numbered tag tied around the shell spire.

mortality, emigration, and recruitment can be significant between sampling periods. The assumptions of the method and their relation to the present sampling design are presented in the Discussion.

RESULTS

Over 2,000 individual queen conchs were tagged, spanning a range from 9 cm to 28 cm in length. Adult queen conchs averaged 24 cm in

length and represented between 22% and 59% of sample populations, varying due to fishing activity and juvenile recruitment.

Tag return data are given in Tables 1 and 2 according to the methods in Seber (1982), with the results of the analysis given in Table 3. At any given time, roughly one-quarter of the population in the study area was tagged (Table 3, col. 2). Note the effect of increasing the sampling area at time 3 had on the estimate of abundance (*N*) at that time and on the estimates of survival (*S*) and

TABLE 1.—Tabulation of the number of queen conchs caught in the *i*th sample last caught in the *h*th sample (after Seber 1982). *i* and *h* designate sampling periods; *n_i* = number of conchs caught in the *i*th sample; *R_i* = number of conchs released at the *i*th sample; *r_h* = total number of conchs recaptured, last caught in the *h*th sample; *m_i* = number of conchs recaptured in the *i*th sample.

<i>i</i>	1	2	3	4	5	6	7	8	9	Total
<i>n_i</i>	424	196	275	228	352	375	262	231	227	
<i>R_i</i>	424	196	275	228	352	375	262	231	—	(<i>r_h</i>)
<i>h</i>										
1		42	28	19	22	8	1	0	0	120
2			18	7	17	6	0	0	0	48
3				10	9	2	0	2	0	23
4					40	14	5	1	1	61
5						76	22	3	2	103
6							37	13	4	54
7								35	22	57
8									36	36
<i>m_i</i>	0	42	46	36	88	106	65	54	65	

TABLE 2.—Tabulation of the number of queen conchs caught in the i th sample last caught in or before the h th sample (after Seber 1982). i and h designate sampling periods. z_i = number of different individuals caught before the i th sample which were not caught in the i th sample, but were caught subsequently, and is equal to the sum across the row excluding the diagonal element.

i	1	2	3	4	5	6	7	8	9	Total
h										
1		42	28	19	22	8	1	0	0	$z_2 = 78$
2			46	26	39	14	1	0	0	$z_3 = 80$
3				36	48	16	1	2	0	$z_4 = 67$
4					88	30	6	3	1	$z_5 = 40$
5						106	28	6	3	$z_6 = 37$
6							65	19	7	$z_7 = 26$
7								54	29	$z_8 = 29$
8									65	

TABLE 3.—Population estimates for queen conch derived from the Jolly-Seber multiple mark-recapture analysis. M/N = proportion of marked conchs in the population just before sample i ; N = population abundance just before sample i with standard deviation $\hat{\sigma}(N/N)$ and coefficient of variation $\hat{\sigma}/N$; S = proportion surviving from the i th to $(i + 1)$ th sample with standard deviation $\hat{\sigma}(S)$ and coefficient of variation $\hat{\sigma}/S$; B = number of new individuals joining the population between the i th and $(i + 1)$ th sample with standard deviation $\hat{\sigma}(B)$ and coefficient of variation $\hat{\sigma}/B$.

i	M/N	N	$\hat{\sigma}(N/N)$	$\hat{\sigma}/N$	S	$\hat{\sigma}(S)$	$\hat{\sigma}/S$	B	$\hat{\sigma}(B)$	$\hat{\sigma}/B$
1	—	—	—	—	0.8387	0.1196	0.1426	—	—	—
2	0.214	1,629	310	0.1905	1.8956	0.4474	0.2360	2,585	1,017	0.393
3	0.167	5,673	1,437	0.2532	0.2372	0.0535	0.2257	409	324	0.792
4	0.158	1,754	341	0.1946	0.4706	0.0626	0.1330	62	148	2.398
5	0.250	888	106	0.1191	0.7359	0.1096	0.1490	608	136	0.223
6	0.283	1,261	196	0.1557	0.2913	0.0493	0.1692	361	89	0.246
7	0.248	729	117	0.1602	0.6208	0.1202	0.1937	542	152	0.280
8	0.234	995	205	0.2059	—	—	—	—	—	—
9	0.286	—	—	—	—	—	—	—	—	—

recruitment (B) between times 2 and 3. These figures are obviously unrealistic (e.g., survival cannot be greater than one) and are not considered in any subsequent analysis or discussion.

Survival rates of queen conch varied from 0.839 to 0.237 with coefficients of variation varying from 13.3% to 22.5%. Intensive fishing was known to have occurred in the study area between samples 3 and 4, and 6 and 7. Fishing also occurred between samples 7 and 8, but to a much lesser degree. In the former two periods estimated survival rates were the lowest found: 0.237 and 0.293, respectively. Survival estimates from all other periods represent the effects of only natural mortality and emigration. The average of these 3 values is 0.6817. This would correspond to an instantaneous rate of natural mortality per 3-mo period of 0.3832 [$= -\ln(1 - S)$] if no emigration occurred. Assuming the effects of emigration are constant between sampling periods, estimates of instantaneous fishing mortality can be obtained by subtracting the average value of instantaneous natural mortality (which includes any emigration effect) from instantaneous total mortality for periods of known fishing activity. For sam-

pling periods 3-4, 6-7, and 7-8, the instantaneous rates of fishing mortality per 3-mo period were, respectively, 1.056, 0.845, and 0.0935. Dividing the sum of these by the total time period for which mortality estimates are available (1.75 year) results in an estimate of the annual instantaneous fishing mortality rate (F) for the population in the study area of 1.14 between August 1983 and May 1985.

On an annual basis, the apparent instantaneous rate of natural mortality for queen conch is 1.533. However, this overestimates true natural mortality because permanent emigration was known to occur, and it was not possible to precisely quantify the effects of emigration on the basis of these data (see Discussion). The estimate does provide an upper bound on the value of natural mortality.

DISCUSSION

Model Assumptions

Principal assumptions of the Jolly-Seber method are that sampling is random, with catch-

ability equal for all individuals, that rates of survival are equal for all individuals, and that tag loss is negligible. No field study can hope to manipulate the environment to such a degree that all assumptions are perfectly met. Thus, potential deviations from these assumptions must be considered and their significance and resulting implications assessed (Begon 1983). Presented below is a review of each assumption. Based on known or suspected aspects of the biology and ecology of queen conch, potential problems with respect to each assumption are raised. Each potential problem is then considered in light of the specifics of the present study, and an attempt is made to assess its significance, if any. Finally, consideration is given to the robustness of Jolly-Seber estimates. In general, it will be shown that deviations from Jolly-Seber assumptions, if present, would be small and have little impact, and in addition, the Jolly-Seber method is robust to such deviations.

In the present study, sampling was conducted on an areal basis. Although sampling was not truly random (i.e., with areas predetermined in a random fashion), dive sites were spread throughout the study area and chosen without prior reference to, or knowledge of, the specific nature of the habitat or conch density in the immediate area. The two stage sampling design employed allowed every section of the study area to have an equal probability of being covered. The assumption of equal catchability is the more important property here, and there were several points where potential departures from this assumption could have arisen. Queen conchs usually showed a distinct clustered distribution. Within a cluster all individuals were felt to have an equal probability of capture, regardless of size. However, large queen conchs were easier to see at a distance. This would affect capture probabilities if distinct size groups characterized clusters; thus, clusters of large queen conchs would be noticed more frequently. While it was thought that there existed areas differentially characterized by the abundance of juveniles and adults, these areas generally occurred on a larger scale than typically covered on a dive. The random allocation of dive sites, then, should have minimized any effect of this heterogeneity. The tendency of very small queen conchs to remain buried is a second factor potentially affecting catchability. Thus, a small tagged queen conch (<13 cm) might have a reduced probability of recapture until it grows large enough to be exposed most of the time. However, only a very

small fraction of queen conchs sampled would have been affected by this. By the time the animals are large enough to be sampled in significant numbers, they will, by the time of next sampling, have grown to a size where burial is not a problem; thus recapture would not be affected. In sum, for the size range sampled, it is thought that departures from the assumption of equal catchability are small, if present. Pollock and Mann (1983) and Carothers (1973) have both found Jolly-Seber estimates of survival to be robust against heterogeneity of capture probabilities.

Mortality of queen conch could have been dependent upon mark status if tags attracted predators. There is no direct evidence (e.g., observations or signs of predators or predation during tagging periods) to indicate that this problem occurred, implying that it did not. Tags quickly fouled with macroalgae and were subsequently impossible for divers to see at any distance. Thus, any tag attraction effect could only occur immediately after initial tagging. As such, the problem is thought to be negligible. Departures from equal probability of survival may have occurred owing to size related processes, but not to a serious degree. Natural mortality is thought to decrease with age, with the effect being predominant among small juveniles (Appeldoorn in press a, b). However, the majority of queen conchs sampled here were large juveniles and adults, which should have had similar survival probabilities. Although fishermen usually take all sizes of queen conchs found, large conchs should have suffered a greater mortality because generally fishermen will not dive in an area unless conchs are visible (i.e., large) from the surface or on shallow test dives. Thus, areas predominantly characterized by small queen conchs should have been undersampled by fishermen. Again, the potential effect of this is offset because the majority of conchs were large. Also, only a portion of the small queen conchs were from areas particularly characterized by such individuals. Lastly, rate of dispersion is also a function of size (Hesse 1979; Appeldoorn and Ballantine 1983), so the emigration component of survival could have been higher for larger individuals. This, to some degree, would counter the size-mortality trend, with the effect being predominant among small juveniles. As such, the effect here should also have been minor. In sum, there is no reason to suspect substantial departures from the assumption of equal probability of survival, and if survival is independent of mark status and probability of

capture is independent of age, Jolly-Seber survival estimates are not greatly affected by age-dependent mortality (Seber 1982).

There are methods available for determining age-dependent mortality rates from Jolly-Seber data (Pollock 1981; Pollock and Mann 1983). Queen conchs, however, are difficult to age (Appeldoorn 1987). Length groups could be used, but these would have to be defined narrowly so that all individuals could grow into the next largest size group within the 3 months between sampling periods, thereby reducing sample sizes within length groups to impractical levels. Data pooled over time would have forced confounding of natural and fishing mortality effects, which was deemed undesirable.

Tags were held securely in place because spines on the queen conch shell spire prevented tie lines from slipping off, and they became more secure over time due to fouling. Numbers remained readable throughout the 2-yr period. In only those individuals with poor spine development could the tag be lost, and then only within the short time prior to fouling. These included some very small juveniles (<12 cm) and a few very old queen conchs where spines had been eroded. The total number of such potential cases was exceedingly small and is, therefore considered negligible.

Estimation of Emigration and Natural Mortality

Permanent emigration of queen conch was known to occur. Reports from fishermen placed some individuals as much as 9 km away from the study area, although the time this took is unknown. The degree of emigration needs to be accounted for if a more accurate estimate of natural mortality is to be obtained. Emigration can occur by either of two dispersion processes: random diffusion, and directed migration or drift. Seasonal migrations are expected in late fall and early spring based on other studies (Hesse 1979; Appeldoorn 1985), although the expected distance travelled is unknown. However, no evidence of such migration is apparent in the data for either mortality or recruitment. Possible reasons for this are 1) the mortality component is confounded by fishing effects thereby masking seasonal trends, 2) Jolly-Seber estimates of B are typically imprecise (Seber 1982), and 3) sampling periods were too few and inopportune placed. Since the data do not support the occurrence of significant drift, at least to the point where it can be partitioned from

diffusion, the degree of emigration was estimated by analyzing diffusion only.

Skellam (1951) presented a two-dimensional diffusion model which can predict the proportion of a population (P_t) outside the area of radius (ρ_t) in a given time (t) if the average distance travelled (ϵ) per unit time (Δt) is known. Assuming no mortality or birth, the equation is

$$P_t = \exp[-(\rho_t^2)/(t \cdot \epsilon^2/\Delta t)]$$

To estimate emigration an average value of ϵ is needed. Dispersal ability in *Strombus* is related to size (Hesse 1979; Miller 1972; Appeldoorn and Ballantine 1983). Specifically, if total movement is expressed solely as diffusion, the data of Hesse (1979) from a 1.5-mo period encompassing episodes of both diffusion and drift indicated that adults travelled twice as fast as "maturing" queen conchs (adults with thin lips or very large juveniles) and three times as fast as juveniles. Hesse (1979) recorded adults to move commonly 50-100 m/day, but no average figure was given, and it is assumed that rates less than this were also common. Clifton et al. (1970) tracked one group of adult queen conchs at 45-55 m/day over several days. Given these rates, a value of 50 m/day seems a reasonable estimate of ϵ for adults, averaging higher values during migration with lower values at other times. The La Parguera population consists of both juveniles and adults, so this value needs to be adjusted downward accordingly. Since the majority of queen conchs were old juveniles or young adults, an average stage of "maturing" can be assumed, and a value of ϵ , one half that for adults, would be most appropriate, i.e., $\epsilon = 25$ m/day. If it is assumed that the 0.4 km² study area is a circle of radius ca. 350 m, then in one sampling period (90 days) 11.2% of the population would be expected to emigrate. This results in an instantaneous rate of annual emigration equal to 0.481. Subtracting this from the estimate of natural mortality plus emigration (1.533) yields a corrected estimate of natural mortality rate at 1.05.

This value of natural mortality rate is lower, but consistent with values reported by Alcolado (1976), Berg (1976), and Baisre and Paez (1981), which might be expected since their estimates were limited to juveniles. However, it is still much greater than those reported by Wood and Olsen (1983). Hoenig (1983) presented empirical equations predicting mortality rate on the basis of oldest known age, which can be used for com-

parative purposes. Given a maximum life span of 7 years (Wefer and Killingley 1980) the predicted mortality rate is 0.72, a result compatible with the above estimate of natural mortality rate considering the variability associated with each estimate.

Status of the Fishery

The value of fishing mortality (F) relative to natural mortality (M) indicates that the La Parguera *S. gigas* population is intensely exploited. Gulland's (1971) calculation of $F = M$ at the point of maximum sustainable yield (MSY) would indicate, allowing for variability in the estimates, that the population was being fished at or above F_{MSY} at this time. However, Francis (1974) has shown that this relationship does not always hold, and Caddy and Csirke (1983) stated that tropical species in particular, already characterized by high levels of natural mortality, would be more likely to be overfished according to this formula. Using this conservative approach, a diagnosis of overfishing seems warranted. Since the study area is representative of that portion of the offshore La Parguera shelf supporting queen conch fishing, in terms of habitat, conch density, and general fishing activity, these results should have general relevance.

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