

NOTES

A PRELIMINARY INVESTIGATION OF THE STOCK STRUCTURE OF THE DOLPHIN, *CORYPHAENA HIPPURUS*, IN THE WESTERN CENTRAL ATLANTIC

Dolphin, *Coryphaena hippurus*, are fast swimming, migratory, pelagic fish, which support commercial and sport fisheries throughout the western central Atlantic (Erdman 1956; Zaneveld 1961; Beardsley 1967; Rose and Hassler 1969; Sacchi et al. 1981; Olsen and Wood 1982). In terms of weight and revenue, they are the most important large pelagic fish landed by the commercial fisheries in the south-eastern Caribbean (Mahon et al. 1981). In the north-west, they are the most important sport fish, being taken on more trips and in greater numbers by charter boats in Florida (Ellis 1957; Iversen 1962) and in North Carolina (Hassler and Hogarth 1977; Rose and Hassler 1969) than any other species. Rapid expansion of the dolphin fishery fleets is currently underway in the eastern Caribbean, but the biological data necessary for management have not been gathered. For example, we remain ignorant of the number and distribution of stocks of *C. hippurus* in the western central Atlantic.

Regional dolphin fisheries are markedly seasonal and this presumably results from migration; but migration patterns remain largely unknown (Palko et al. 1982). However, Beardsley (1967) believed that dolphin migrate northwards during spring and summer, and Gibbs and Collette (1959) suggested that the spring abundance of *C. hippurus* in the Caribbean may be a prespawning migration, mostly by females. A preliminary survey of regional catch records indicates a staggering of the peak fishing seasons, which supports the assumption that migration is large-scale (Hunte and Mahon 1982).

In the present paper, we take three approaches to our investigation of *C. hippurus* in the western central Atlantic: 1) We use commercial and sport fishing data from several countries to examine seasonality and size structure of catch throughout the region; 2) we compare growth, age/size at sexual maturity, fecundity, and egg size of dolphin from different parts of the region; 3) we use electrophoretic techniques to compare dolphin sampled from Miami and Barbados, two widely spaced fisheries in the region. Electrophoretic techniques, combined with histo-

chemical staining for isozymes, are now widely recognized as a useful tool for examining genetic affinities between fish stocks (Iwata 1975; Allendorf 1979; McGlade 1981; Ihssen et al. 1981; Ferris et al. 1982). By these means, we address the question of whether the dolphin fisheries in the western central Atlantic exploit a single stock migrating through the region or distinct units located in geographically contiguous areas. Resolution of this question will affect the extent to which individual territories should expand their dolphin fisheries, will determine whether management programs need be regional or territory-specific, and will identify which territories need to collaborate for joint management of stocks.

Methods

Dolphin monthly catch data, recorded by commercial or sport fisheries, were obtained either by letter, personal visit to fisheries departments, and/or published literature (Table 1). The catch data, recorded as numbers, weights, catch per day or per boat, and over time periods of 1 to 12 years, were standardized and plotted as percentages of total annual catch landed each month. Where more than 1 year's data were available, the average catch each month was calculated.

Tissue samples for the electrophoretic survey were collected off Barbados between December 1982 and March 1983, and off Miami in May and June 1983. Samples of eye, heart, liver, gonad, and white muscle were taken from a total of 1,669 freshly landed dolphin and were deep frozen for later analysis. A survey of 22 enzymes encoded by 55 presumptive loci was conducted to identify polymorphic enzyme systems. The allelic frequencies of the highly polymorphic isocitrate dehydrogenase, Idh-2, locus were compared in Miami and Barbados dolphin. The horizontal starch gel electrophoresis methodology follows that of May et al. (1979) and McGlade et al. (1983). Allelic nomenclature follows that of Allendorf and Utter (1979).

Life history data were obtained from the literature, from records of length and weight of specimens caught in the Bahamas, Bermuda, and North Carolina, and from our own studies of 624 dolphin landed during the peak of the sport fishery in Miami and 3,126 dolphin landed by the commercial fishery in Barbados.

TABLE 1.—Countries from which catch data on the dolphin, *Coryphaena hippurus*, were obtained, with the data source for each country.

Territory	Data source	Time period	Territory	Data source	Time period
Curacao	Zaneveld (1961)	1957-58	Puerto Rico	Erdman (1956)	1951-56
Grenada	J. Finlay, Fisheries Officer, Ministry of Agriculture, National Resources and Industrial Development, St. George's, Grenada.	1981-83		O. Munoz-Roure, Executive Director, Caribbean Fisheries Management Council, Hato Rey, Puerto Rico.	
St. Vincent	K. Morris, Fisheries Officer, Ministry of Agriculture and Fisheries, Kingstown, St. Vincent.	1975-81	Bahamas	P. Major, Fisheries Biologist, Ministry of Agriculture, Fisheries, and Local Government, Nassau, Bahamas.	1976, 1978
Barbados	R. Hastings and P. McConney, Fisheries Officers, Fisheries Division, Bay Street, Bridgetown, Barbados.	1973-82	Florida	A. Jones, Fisheries Scientist, Southeast Fisheries Center, NMFS, NOAA, Miami, Florida.	1970-80
St. Lucia	P. Murray, Fisheries Biologist, Ministry of Agriculture, Lands, Fisheries, and Cooperatives, Fisheries Division, Castries, St. Lucia.	1978, 1980-82	Georgia	A. Jones, see Florida	1971-79
Martinique and Guadeloupe	Sacchi et al. (1981)	1980	South Carolina	A. Jones, see Florida	1978-79
Virgin Isles	R. Wood, Fisheries Biologist, Department of Conservation and Cultural Affairs, Division of Fish and Wildlife, St. Thomas, Virgin Islands.	1967-78	North Carolina	A. Jones, see Florida	1976-80
	Olsen and Wood (1982)			Manooch and Laws (1979)	1977
				Rose and Hassler (1969)	1961
			Bermuda	B. Luckhurst, Fisheries Officer, Ministry of Fisheries and Agriculture, Naval Base, Southampton, Bermuda.	1973-80

RESULTS AND DISCUSSION

Seasonality and Size Structure of Catch

The seasonality of dolphin catch in 14 territories is shown in Figure 1. Martinique and Guadeloupe supplied no data, but information was given on the duration and peak of the dolphin season. It should be noted that the U.S. Virgin Islands is the only territory with a distinctly bimodal catch pattern.

The peak months of catch in each territory are superimposed on a map of the western central Atlantic in Figure 2. Grenada peak catch is in February/March; Barbados, St. Vincent, and St. Lucia in March/April; Martinique and Guadeloupe in April; and the Virgin Islands in April/May, giving the Virgin Islands their first and largest annual peak. This pattern of catch seasonality is suggestive of a stock (subsequently called the southern stock) moving northwest through the island arc. If the stock then turned west and moved past Puerto Rico, we would expect peak catch there to be between June, July, and August; but this is when Puerto Rico catches the least dolphin (see Figure 1). We therefore suggest that, on leaving the Virgin Islands, the stock moves northeasterly into the Atlantic, completing a circuit and returning to Grenada by February/March of the following year. This implies that there is a sec-

ond stock (subsequently called the northern stock) located in the northwest region of the western central Atlantic. It occurs near Puerto Rico between December and February. It next moves northwesterly past the Bahamas in April/May, Florida and Georgia in May/June, South and North Carolina in June/July, and Bermuda in July/August. It then completes its circuit by passing through the Virgin Islands, giving that territory its second and smaller peak in November and returning to Puerto Rico by December/February.

The mean size of fish caught in five territories during peak fishing season is shown in Figure 3, and the size structure of the catch throughout the fishing season in Barbados is shown in Figure 4. The data are consistent with the migration circuits proposed. In the northern stock, small presumably young-of-the-year fish are predominant during the summer when the stock is near Florida, North Carolina, and Bermuda. The mean size taken by the sport fishery in Florida is 1.69 kg; in North Carolina, where they occur 1 mo later, it is 2.92 kg; and in Bermuda, where they occur 2 mo later, it is 3.85 kg. These differences presumably reflect growth within the cohort. The largest fish are taken by Puerto Rico, where Erdman (1956) reported that dolphin up to 23 kg in weight occur during the peak winter fishing season, and by the Bahamas where the mean weight during the peak fishing months is 6.45 kg. This suggests

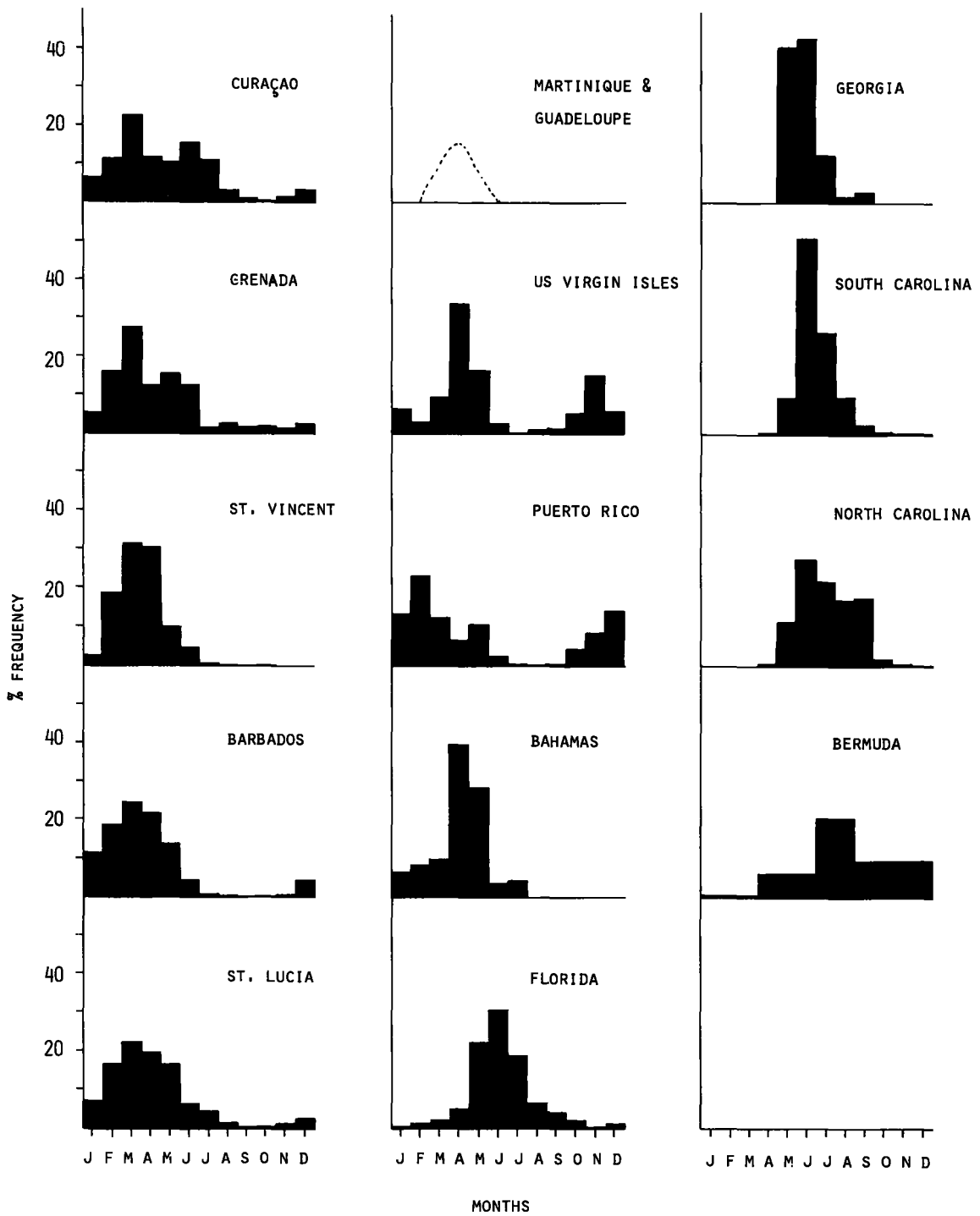


FIGURE 1.—Seasonality of the dolphin, *Coryphaena hippurus* fisheries in the western central Atlantic, shown in geographical order from south to north. Note that raw catch data were not available from Martinique and Guadeloupe, but the duration of season and peak month were known.

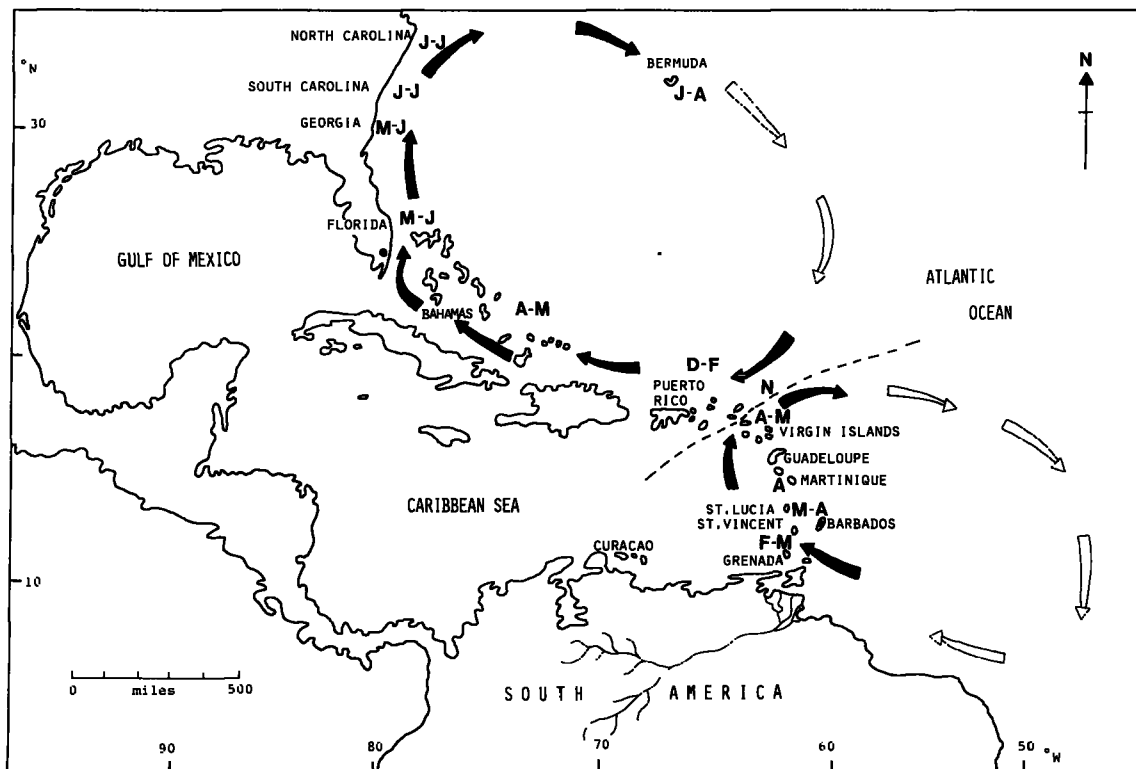


FIGURE 2.—Months of peak catch of the dolphin, *Coryphaena hippurus*, and proposed migration circuits for northern and southern dolphin stocks in the western central Atlantic. Letter symbols (e.g., A-M) indicate months of peak catch. **➔** indicate proposed migration. **➡** indicate proposed migration where catch data were not available. • indicate locations from which samples for electrophoresis were collected.

continued growth of the cohort as it leaves Bermuda and returns southwards into the northern Caribbean for the winter. Note that since dolphins are serial spawners and since fecundity is proportional to size (Beardsley 1967; Oxenford and Hunte in press), most spawning by a cohort will occur when the dolphins comprising it are large. For the northern dolphin, this would be when the stock is near Puerto Rico, i.e., at the southeastern or up-current limit of their range. Peak spawning near Puerto Rico is reported to occur in early spring (Erdman 1976) and presumably produces the small young-of-the-year fish caught near Florida during the summer.

The size structure of dolphin caught at Barbados (Fig. 4) is consistent with the proposed migration for the southern stock. In February, the main cohort is composed of fish about 5½ mo old with a mean standard length of 812.24 mm. Growth within this cohort occurs throughout the fishing season to June, when the average fish size is 1,007.83 mm SL (Oxenford and Hunte 1983). After this, abundance drops sharply (Fig. 1) as the cohort leaves Barbados

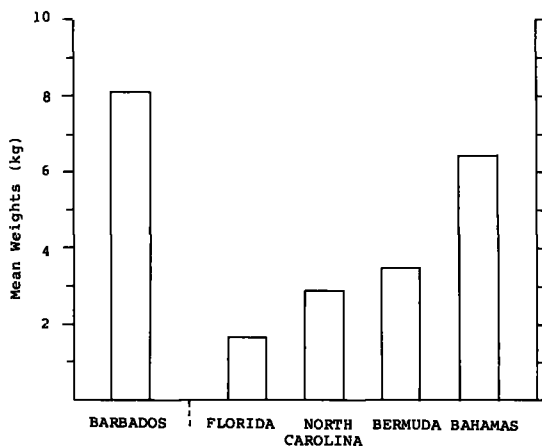


FIGURE 3.—Mean weights of individuals of the dolphin, *Coryphaena hippurus*, landed during peak fishing seasons at five locations in the western central Atlantic.

migrating northwards. During early summer (June/July) and early autumn (October), the presence of

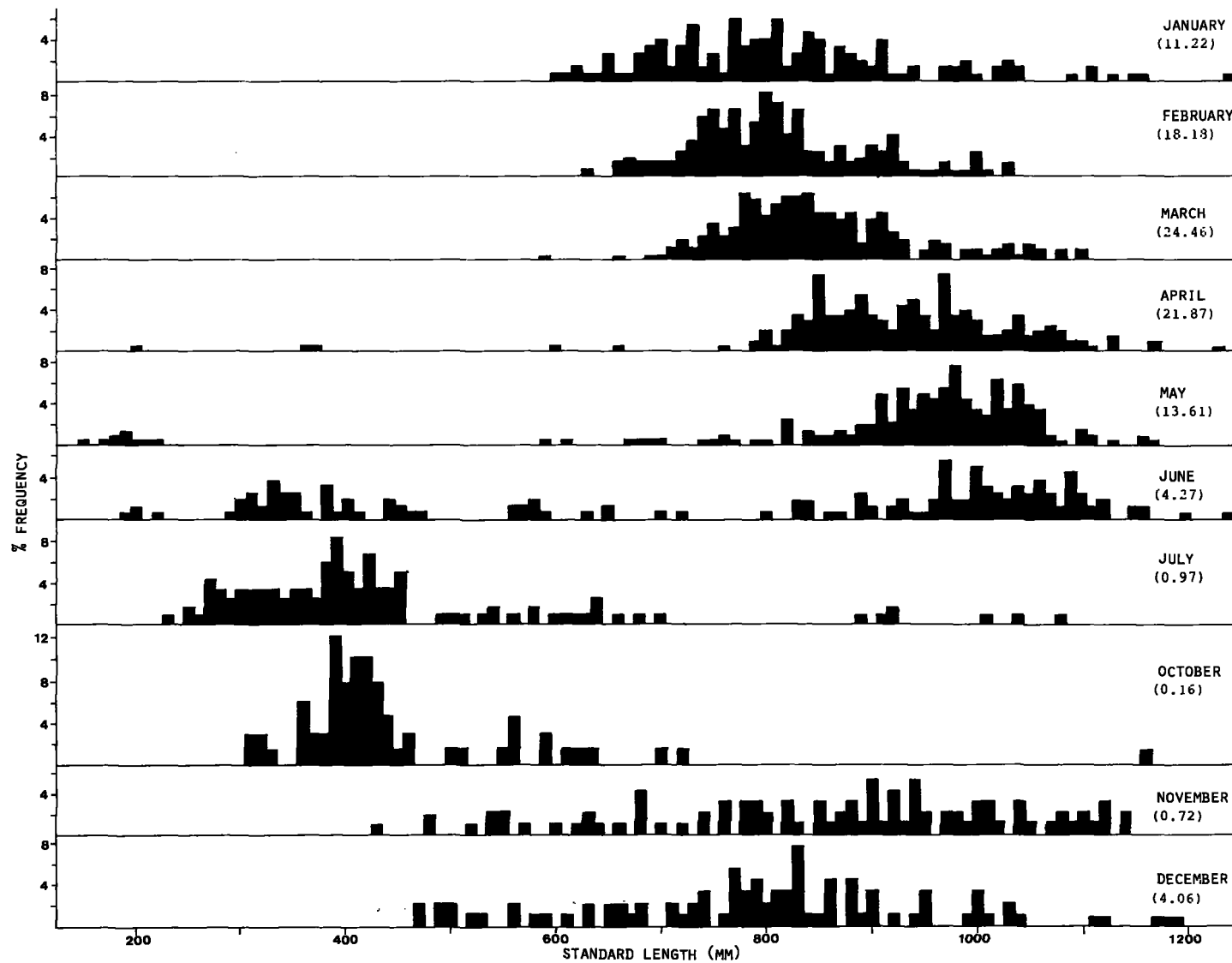


FIGURE 4.—The size-structure of the dolphin, *Coryphaena hippurus*, landed by the Barbados commercial fishery over 10 mo. The values in parentheses are the percentage of total annual catch by weight landed each month.

a few very small dolphin (<2% of the annual catch by weight), landed as bycatch of the flying fish fishery (see Figure 4), indicates the arrival of the first of the young-of-the-year group, with a few very large mature adults from the previous year. Note that many of these young-of-the-year are already mature on reaching Barbados in November, and all are ripe by the time the cohort leaves Barbados in June. Note too, that aging of the cohort (Oxenford

and Hunte 1983) suggests that the cohort was spawned between September and January, when the parent stock would be towards the southeastern, up-current extreme of the proposed migration circuit.

Life History Comparisons

Data on life history parameters of dolphin from northern and southern circuits are summarized in

TABLE 2.—Life history characteristics of the dolphin *Coryphaena hippurus* in the western central Atlantic.

Life history characteristics		Location	Data Source
Northern area:			
Average 1st year growth rate (mm SL/d)	≈ 1.64 ≈ 1.82	N. Carolina Florida	Rose and Hassler (1968) Beardsley (1967)
Length-weight relationship in the form $y = ax^b$ (y is weight (kg) x is SL (mm))	Males: $y = 0.05 \times 10^{-6} x^{2.75}$ $y \approx 1.45 \times 10^{-7} x^{2.58}$ Females: $y = 1.27 \times 10^{-7} x^{2.59}$ $y \approx 5.75 \times 10^{-8} x^{2.71}$	N. Carolina Florida	Rose and Hassler (1968) Beardsley (1967, fig. 7)
Fecundity-length relationship in the form $y = ax^b$ (y is mature egg numbers x is FL (mm))	$y \approx 2.52 \times 10^{-4} x^{3.12}$	N. Carolina Florida	Rose and Hassler (1968) Beardsley (1967, fig. 7)
Size at first maturity (mm SL)	Males: 393 Females 324	Florida	Beardsley (1967)
Age at first maturity (months)	≈ 6-7	Florida	Beardsley (1967)
Mature egg size range (mm diameter)	1-1.7	Florida	Beardsley (1967, fig. 9)
Mean mature egg size (mm diameter)	1.3	N. Carolina	Hassler and Rainville (1975)
Spawning season	Extended	Atlantic Florida Current	Shcherbachev (1973) Fahay (1975) Johnson (1978) Gibbs and Collette (1959) Beardsley (1967)
Age structure (% which are <2 yr)	96 98	N. Carolina Florida	Rose and Hassler (1968) Beardsley (1967)
Southern area:			
Average 1st year growth rate (mm SL/d)	≈ 4.17	Barbados	Oxenford and Hunte (1983)
Length-weight relationship in the form $y = ax^b$ (y is weight (kg) x is SL (mm))	Males: $y = 1.24 \times 10^{-8} x^{2.84}$ Females: $y = 2.22 \times 10^{-8} x^{2.84}$	Barbados	Oxenford and Hunte (in press)
Fecundity-length relationship in the form $y = ax^b$ (y is mature egg numbers x is FL (mm))	$y = 2.7 \times 10^{-6} x^{3.67}$	Barbados	this study
Size at first maturity (mm SL)	Males: 735 Females: 610	Barbados	this study
Age at first maturity (months)	≈ 4	Barbados	this study
Mature egg size range (mm diameter)	0.86-1.00	Barbados	this study
Mean mature egg size (mm diameter)	0.97	Barbados	this study
Spawning season	Extended	Barbados	this study
Age structure (% which are <2 yr)	100	Barbados	Oxenford and Hunte (1983)

Table 2 and are not supportive of a single stock hypothesis. Dolphin in Barbados waters appear to grow faster (Oxenford and Hunte 1983) than those in North Carolina (Rose and Hassler 1968) and Florida (Beardsley 1967). Note that scale annuli are found in northern dolphin but not in southern dolphin; a difference supportive of the assertion that the two groups are distinct. Beardsley (1967) suggested that the formation of the dolphin scale annuli at Florida was correlated with the temperature reduction occurring in the Florida Current during winter.

Dolphin from Barbados are larger but younger at first sexual maturity than those from Florida. Fecundity increases with fish size in both groups, but Florida dolphin have higher fecundity at size than Barbados dolphin (Oxenford and Hunte in press). Mature eggs taken from Florida and North Carolina dolphin are apparently larger than those from Barbados dolphin. Intraspecific variation in egg size is seldom environmental and is typically a function of fish age (Bagenal 1971; Kazakov 1981). Mature egg size does not increase with fish size/age for Barbados dolphin (linear regression, $r = 0.353$ $b = 0.0001$). Therefore, assuming that the differences observed in egg size of southern and northern dolphin do not result merely from differences in investigators' methodologies, they are suggestive of separate stocks as shown for different spawning groups of herring (Blaxter and Hempel 1963; Cushing 1967) and sockeye salmon (Foerster 1968; Bagenal 1971).

Electrophoretic Comparisons

In the electrophoretic survey, 55 presumptive loci could be consistently scored. Of these, 39 were fixed

for the same alleles in both samples, and a further 12 were close to fixation. Two isocitrate dehydrogenase loci (Idh-2,3) and two esterase loci (Est-1,2) had alternate alleles at a frequency >0.05 , i.e. were significantly polymorphic.

Seven phenotypes were observed at the Idh-2 locus expressed in heart tissue (Fig. 5). The pattern of activity at this locus is typical of an active dimeric enzyme with disomic inheritance (Darnall and Klotz 1972; Kirpichnikov 1981) and four alleles with relative mobilities to 100, 123, 86, and 68. Thus, putative genotypes could be assigned to the observed phenotypes as indicated in Figure 5, and allelic frequencies calculated (Table 3). Unequivocal assignation of genotypes to the phenotypes, observed at the remaining polymorphic loci, was not possible in the absence of inheritance data, since the loci have alleles with overlapping mobilities. Idh-3 and Idh-2, expressed together in liver tissue, both have alleles with relative mobilities to 100, 123, and 86, and although the asymmetrically banded phenotypes could be easily read, the presence of a null allele at Idh-3 meant that certain phenotypes could have been produced by a number of different genotypes. Est-1 and Est-2 share all or some of four alleles, but the banding intensity ratios of individual phenotypes could not be determined. Hence, assignation of genotypes to phenotypes at these loci was not possible. In summary, only the Idh-2 locus, expressed independently from Idh-3 in heart tissue, was considered suitable for a comparison of Miami and Barbados dolphin.

The frequencies of alleles at Idh-2 differed significantly in the two populations (chi-square 2×4 contingency test: $\chi^2 = 12.725$, $df = (r - 1)(C - 1) = 3$, $0.01 > P > 0.0005$; Table 3). Note that the varia-

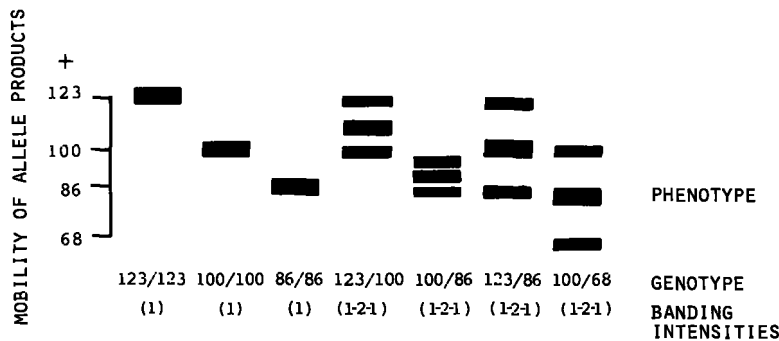


FIGURE 5.—A starch-gel zymogram of the dimeric enzyme isocitric dehydrogenase, showing the phenotypes observed and putative genotypes at the Idh-2 locus in heart extracts of the dolphin, *Coryphaena hippurus*, from the western central Atlantic. Values in parentheses are ratios of allele products.

TABLE 3.—Observed allelic frequencies (obs. freq.) and number (obs. no.) of alleles at the Idh-2 locus in heart tissue of the dolphin, *Coryphaena hippurus*, from Miami and Barbados. Expected values (exp. no.) refer to the number expected if the samples do not differ.

Sample location	No. of fish	Alleles			
		68	86	100	123
Miami	obs. freq.	0.0009	0.3154	0.6660	0.0176
	obs. no.	1	340	718	19
	exp. no.	(0.47)	(304.14)	(751.56)	(21.83)
Barbados	obs. freq.	0.0000	0.2521	0.7253	0.0226
	obs. no.	0	301	866	27
	exp. no.	(0.53)	(336.86)	(832.44)	(24.17)

tion observed at Idh-2 did not differ from that predicted under Hardy-Weinberg equilibrium for either population (chi-square goodness of fit: for Barbados, $\chi^2 = 6.337$, $df = 3$, $0.25 > P > 0.1$; for Miami, $\chi^2 = 9.9145$, $df = 6$, $0.25 > P > 0.1$; Table 4).

The differences in life history traits of Miami and Barbados dolphin could in principle be environmental. The genetic differences observed at the Idh-2 locus suggest that there may be little gene flow between the northern and southern groups; but could in theory result from a regional cline. The primary evidence supporting our suggestion of more than one dolphin stock in the western central Atlantic is there-

fore the seasonality of catch data and the mean size of dolphin landed in each territory. Taken together, the three data sets certainly suggest that the assumption of a single stock may be unjustified. Efforts should now be made to test the two stock hypothesis proposed and to investigate the possible presence of additional dolphin stocks, particularly in the western Caribbean Sea and in the Gulf of Mexico.

Acknowledgments

This project was supported by an Inter-University Council (British Council) grant to Hazel Oxenford, a University of the West Indies research grant to Wayne Hunte and a Manuel Noreiga Morales Science Prize from the Organization of American States to Wayne Hunte. The electrophoresis was carried out at the Bedford Institute of Oceanography, Dartmouth, Nova Scotia, with technical supervision by J. McGlade, and C. Annand, and with technical assistance from D. Beanlands. We thank C. Limouzy for collecting specimens in Miami, R. Mahon for assistance in compiling regional catch records, and J. Horrocks and J. Marsden for comments on the manuscript. Cooperation of fisheries officers and fisheries biologists in the region is gratefully acknowledged.

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TABLE 4.—The number of each phenotype observed (obs.) at the Idh-2 locus in heart tissue of the dolphin, *Coryphaena hippurus*, from Barbados and Miami. Expected values (exp.) refer to the numbers expected if the populations are in Hardy-Weinberg equilibrium.

Putative genotype for Idh-2	Sample location	Sample location	
		Barbados (n = 597)	Miami (n = 539)
86/86	obs.	47	64
	exp.	(37.94)	(53.62)
100/86	obs.	199	205
	exp.	(218.31)	(226.46)
100/100	obs.	325	251
	exp.	(314.05)	(239.11)
100/123	obs.	17	10
	exp.	(19.58)	(12.65)
123/123	obs.	1	1
	exp.	(0.31)	(0.17)
123/86	obs.	8	7
	exp.	(6.81)	(5.99)
68/68	obs.	—	0
	exp.	—	(0.00)
100/68	obs.	—	1
	exp.	—	(0.67)
123/68	obs.	—	0
	exp.	—	(0.02)
86/68	obs.	—	0
	exp.	—	(0.32)

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