Migration of the Dolphin (<u>Coryphaena hippurus</u>) and its Implications for Fisheries Management in the Western Central Atlantic

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ABSTRACT

Regional differences in the seasonality of catch data were used to investigate migration and stock structure of the dolphin <u>Coryphaena hippurus</u> in the Western Central Atlantic. The data suggest at least two dolphin stocks in the region, one southeast and the other northwest of the Virgin Islands. The southern stock travels through the Windward Island chain from Grenada in February/March, northwards to the Virgin Islands by April/May, and then may begin a return migration southeastwards in the Atlantic. The northern stock occurs near Puerto Rico in January/February, and travel northwards up to North Carolina by June/July, and return via Bermuda in July/August, and are once more in the region of the Virgin Islands and Puerto Rico by winter. Changes in mean size of dolphin caught regionally are consistent with the migration circuits proposed. The two-stock hypothesis is supported by the observation that southern dolphin grow faster, attain sexual maturity at a larger size, have lower fecundity at size, and have smaller eggs than northern dolphin. An electrophoretic survey of dolphin from Miami and Barbados indicated a significant difference in allele frequencies of the two populations at the IDH-2 locus in heart extracts, and in phenotypic frequencies at the IDH-2,3 loci in liver extracts. The implications of the proposed migration circuits for regional fisheries revolve around the possibilities for increased exploitation and the need for cooperative managment programs for dolphin stocks.

INTRODUCTION

Dolphin (<u>Coryphaena hippurus</u>) are migratory, oceanic, epipelagic fish, often found associated with flotsam. They support commerical and sport fisheries throughout the Western Central Atlantic (Erdman, 1956; Zaneveld, 1961; Beardsley, 1967; Rose and Hassler, 1969; Sacchi et al., 1981; Mahon et al., 1982; 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 southeast Caribbean (Mahon et al., 1982). In the region to the northwest of the Virgin Islands, dolphin are the most important sport fish, being taken on more trips and in greater numbers by charter boats in Florida (Ellis, 1957), and in North Carolina (see Hassler and Hogarth 1977, Rose and Hassler 1969) than any other species.

Extensive technical development and expansion of the pelagic fishing fleet is currently underway in Barbados and neighboring islands. This is disturbing, given our ignorance of the stock structure and potential yield of C. hippurus in the western Central Atlantic.

The seasonality of regional dolphin fisheries is suggestive of migration, but there are no published data on its pattern or extent. However, Beardsley (1967) suggested that migration is northwards during spring and summer, and Gibbs and Collette (1959) believed that the spring abundance of C. hippurus in the Caribbean resulted from a pre-spawning migration, mostly by females. Tagging programs are expensive, and only 3 dolphin tagged in the region have been recaptured (see Rose and Hassler, 1968).

For this paper, we have gathered dolphin catch data from many territories in the region and examined the seasonality of catch in an attempt to trace possible migration circuits. This has been supplemented by comparisons of life history data and electrophoretic analysis of dolphin from the southern and northern extremes of the region. Electrophoretic techniques in combination with histochemical staining are now used routinely for examining genetic differences between fish stocks (Iwata, 1975; Johnson and Beardsley, 1975; Kristiansson and McIntyre, 1976; Allendorf, 1979; McGlade, 1981; Philipps et al., 1983; Ihssen et al, 1981; Ferris, 1982; Kornfield et al, 1982). Clarification of the stock structure of dolphin will affect the extent to which individual territories should expand their fisheries, will determine whether management programs need be regional or territory-specific, and will identify which territories need collaborate with which as regards stock management.

MATERIAL AND METHODS

Monthly catch data for dolphin were obtained from several territories in the Western Central Atlantic, either by letter, personal visit to fisheries departments and/or published literature (Table 1). The catch data, which had been recorded as numbers, weights, catch per day or per boat and over time periods of 1 to 12 years, were standardised and plotted to display seasonality of catch. Where more than one year's data were available, the average catch each month was calculated. Monthly catches are presented as percentages of annual totals.

Dolphin 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 general survey of 22 enzymes encoded by 55 presumptive loci was conducted to identify polymorphic enzyme systems. The pheontypic and genotypic frequencies of two highly polymorphic enzymes, isocitrate dehydrogenase (IDH) and esterase (EST), were compared for differences between the two samples. 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 several territories, and from our own studies of 624 dolphin landed during the peak of the sport fishery in Miami and 3126 specimens landed by the commercial fishery in Barbados.

RESULTS

Catch Seasonality.--Seasonality of the dolphin fisheries is presented in geographical order from south to north in Figure 1. Moving north, peak months occur progressively later in the year; from February/March at Grenada to June/July at North Carolina (Figure 1). Two central countries, the Virgin Islands and Puerto Rico, have fishing seasons which disrupt the otherwise smooth staggering of peak months northwards. The Virgin Islands have a bimodal season with peaks in November and April/May, and in Puerto Rico, peak catch occurs from December to February. Moreover, Bermuda, lying slightly south of North Carolina but approximately 850 miles into the Atlantic, has the latest dolphin season with a peak in July/August.

Spawning.--The general concensus from the literature is that dolphin have an extended spawning season and that at least some spawning takes place year-round (Gibbs and Collette, 1959; Beardsley, 1967; Shcherbachev, 1973; Fahay, 1975; Palko et al., 1982). Near Florida, spawning occurs at the beginning of the fishing season (January-March) and again at the end (July-September). At Barbados, nearly ripe, ripe and spent fish are found throughout the fishing season, ie. from November to July, with the greatest proportion of ripe and spent fish occurring toward the end of the season (Table 2). It should be noted that the Barbados fishery primarily exploits a single cohort (see Figure 2), and otolith rings (see Oxenford and Hunte, 1983) indicate that the cohort is spawned between September and January, when dolphin are essentially absent from Barbadian waters (see Figure 1).

Dolphin appear to be multiple spawners (Beardsley, 1967; Johnson, 1978). At Barbados, this is supported by the occurrence of three size-groups of eggs in the ovaries of ripe fish, the appearance of semi-ripe, ripe and spent fish year-round (see Table 2), and the observation that the average sizes of semi-ripe and ripe fish do not differ significantly (Student's t-test; mean size (mm SL) of semi-ripe fish = 903.89, of ripe fish = 939.79, t = 1.253, P>0.05).

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Table 1. Genetic distances and similarities (Rogers, 1972) among populations of the queen conch. Based on 10 polymorphic enzymes.

Below diagonal: genetic distances. Above diagonal, genetic similarity.

Population	N	1	2	3	4	5	6	7	8
1. Bermuda		****	.908	.893	.824	.894	.897	.895	.897
2. Belize Samba		.092	****	.964	.865	.919	.966	.973	.970
3. Belize, Large		.107	.036	****	.853	.902	.942	.964	.954
4. Belize Cay		.176	.135	.147	****	.918	.847	.871	.864
5. Petit St. Vincent		.106	.081	.098	.082	***	.092	.926	.905
6. Pine Cay		.103	.034	.058	.153	.098	****	.952	.967
7. French Cay		.105	.027	.036	.129	.074	.048	****	.963
8. PLandon Cay		.103	.030	.046	.136	.095	.033	.037	****

TABLE 2. The monthly percentage of ripe and spent dolphin (_Coryphaena_ _hippurus_) caught at Barbados, and Florida (Beardsley 1967).

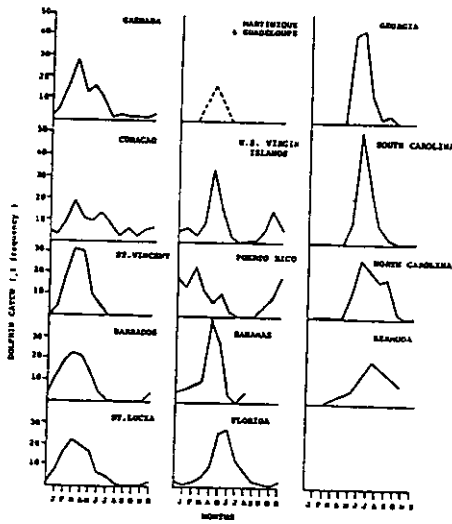| Location		J	F	M	A	M	J	J	A	S	O	N	D
	Females												
BARBADOS	No.fish	6	22	40	11	45	4	2	–	–	–	5	3
	% ripe or spent	83.3	50.0	95.0	81.8	100.0	100.0	50.0	–	–	–	40.0	66.7
	Males												
	No.fish	–	20	14	7	21	12	5	–	–	–	–	–
	% ripe or spent	–	10.0	28.6	57.1	76.2	75.0	40.0	–	–	–	–	–
FLORIDA	**Females**												
	No.fish	56	19	44	55	75	61	133	179	23	68	33	22
	% ripe or spent	21.4	26.3	38.6	3.6	1.3	0	13.5	42.5	17.4	8.8	15.15	4.5

Figure 1. Seasonality of the dolphin fisheries in the Western Central Atlantic, shown in geographical order from south to north. Note that raw catch data were not available for Martinique and Guadeloupe, but duration of season and peak month were known.
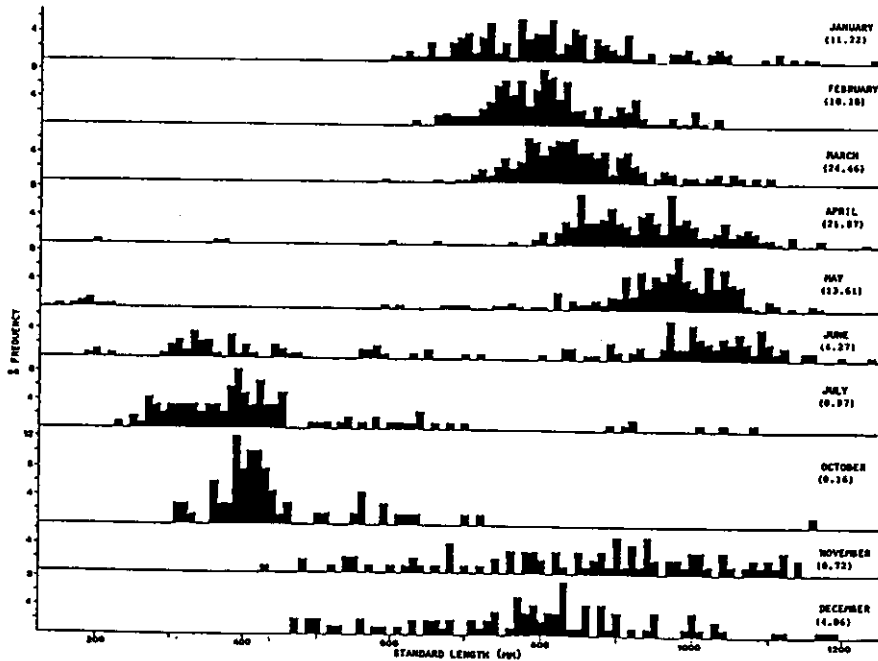

Figure 2. The size-structure of the dolphin Coryphaena hippurus landed by the Barbados commercial fishery over 10 months. The values in parentheses are the percentage of total annual catch by weight landed each month.

Size, age and growth.--The average size of fish caught during peak fishing season in five territories differs in each (Figure 3). Using scale annuli for aging, Beardsley (1967) and Rose and Hassler (1968) showed that most fish taken in Florida (74%) and North Carolina (80%) belonged to the 0=group age class and 98% and 96% respectively were less than 2 years old. At Barbados, the dolphin fishery exploits fish less than 1 year old; no scale annuli were found in a sample of 558 fish, and otolith rings indicated that fish up to 1100 mm SL were less than 250 days old.

Length-weight relationships for dolphin from three territories are shown in Figure 4. Raw data were not available from North Carolina or Miami and therefore a statistical comparison was not possible, however, a visual comparison shows no differences between them.

Average first year growth rates of dolphin are presented in Table 3. In the region to the northwest of the Virgin Islands, dolphin grow more slowly than in the southeast Caribbean. Size at earliest sexual maturity of dolphin from Florida was reported as 324 mm SL for females and 393 mm SL for males (Beardsley, 1967). Earliest sexual maturity in Barbados dolphin was observed at 610 mm SL for females and 735 mm SL for males, ie. at approximately 4 months old. Given the differences in growth rates at the two localities (Table 3), the Barbados fish are younger at sexual maturity than the Florida fish, whilst being considerably larger.

Table 3. Average first year growth rates for wild populations of the dolphin Coryphaena hippurus from 3 locations in the Western Central Atlantic.

Location	Aging techniques	Number fish	Mean first year growth rate (mm SL/day)	Data source
N. Carolina	Scale annuli	593	1.64	Rose and Hassler (1968)
Florida	Scale annuli	121	1.82	Beardsley (1967)
Barbados	Otolith rings	50	4.71	Oxenford and Hunte (1983)

Fecundity and egg size.--Fecundity increases significantly with fish size for Florida dolphin (Beardsley, 1967) and Barbados dolphin (Figure 5). Dolphin from Florida have higher fecundity at size than those from Barbados. This is interesting, given the slower growth rate of the former.
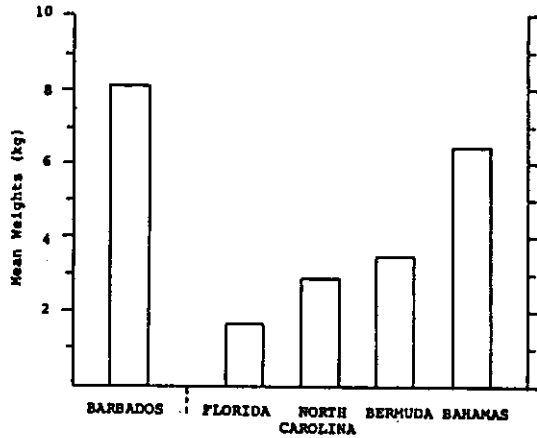
Figure 3. Mean weights of individuals of Coryphaena hippurus landed during peak fishing seasons at five locations in the Western Central Atlantic.
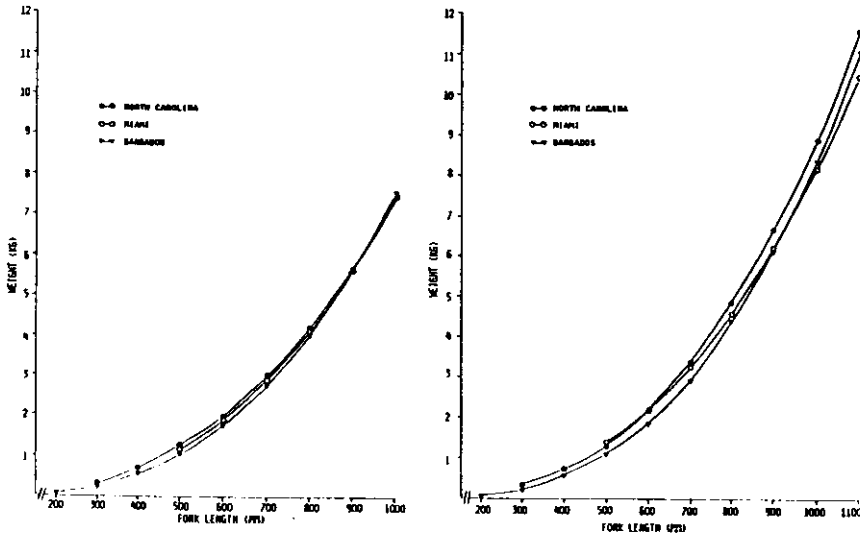

Figure 4. Length-weight relationships for females (a) and males (b) of the dolphin Coryphaena hippurus from three locations in the Western Central Atlantic. The equations for males and females respectively, are: for North Carolina, Wt(kg) = 0.05×10^{-8} FL$^{2.75}$ (mm) and Wt(kg) = 1.27×10^{-7} FL$^{2.59}$ (mm) (Rose and Hassler 1968); for Florida, Wt(kg) = 1.45×10^{-7} FL$^{2.58}$ (mm) and Wt(kg) = 5.75×10^{-8} FL$^{2.77}$ (mm) (Beardsley, 1967); for Barbados Wt(kg) = 1.24×10^{-8} FL$^{2.94}$ (mm) and Wt(kg) = 2.22×10^{-8} FL$^{2.84}$ (mm).

The diameters of mature dolphin eggs in the ovaries and ducts of fish from Florida range between 1.00 and 1.70 mm (from Beardsley, 1967), and those collected off Hatteras, North Carolina by Hassler and Rainville (1975) were approximately 1.3 mm in diameter. Barbados dolphin eggs from the ovaries and ducts of the most mature fish were between 0.86 and 1.25 mm in diameter. Since the average size of mature eggs is not a function of fish length in the Barbados dolphin (linear regression, r=0.353, b=0.0001), the data suggest that mature eggs from fish in the north (Florida) are larger than those from fish in the south (Barbados).

Electrophoresis.--The electrophoretic survey of the 55 presumptive loci which could be consistently scored and were therefore considered useful for routine population surveys showed that 39 were fixed for the same alleles in both samples. Moreover, of the 16 loci possessing alternate alleles, 12 were close to fixation. Only 2 isocitric dehydrogenase (IDH-2,3) and two esterase (EST-1,2) loci had alternate alleles at a frequency >0.05, and could therefore be used for comparative purposes. These 2 enzymes are highly polymorphic in both samples of $\underline{C}$. $\underline{hippurus}$ and the allelic frequencies at IDH-2 in dolphin at Miami were significantly different from those at Barbados (chi-squared 2 x 4 contingency test, X^2 = 12.652, P <.05; Table 4). Note that the variation oberved at IDH-2 did not differ significnatly from that expected under Hardy-Weinberg equilibrium for either population (chi-squared goodness of fit; for Barbados X^2 = 6.337, P >0.05; for Miami X^2 = 14.435, P >0.05).

The loci in both enzyme systems have overlapping allelic mobilities. IDH-2 and IDH-3 share alleles with relative mobilities to 100, 123 and 86. IDH-2 has a fourth allele at 68 and IDH-3 has a 'null' allele. EST-1 and EST-2 share all or some of four alleles with relative mobilities to 100, 96, 84 and 74. Except for IDH-2, this made it impossible to assign genotypes to the oberved phenotypes, given the absence of inheritance data. It was possible to determine which alleles belongs to which locus in IDH, and to assign genotypes, because in heart tissue extracts only IDH-2 was expressed. The presence of the 'null' allele ensured that it remained impossible to assign genotypes at the IDH-3 locus. Seventeen phenotypes were observed at IDH-2,3 loci in liver extracts (see Figure 6), and a comparison of their frequencies in Miami and Barbados fish showed a significant difference between the two samples (chi-squared 2 x 17 contingency test, X^2 = 84.73, P <0.05; Table 5). This implies a considerable difference in allelic frequencies at the IDH-2,3 loci between Miami and Barbados dolphin. Eleven phenotypes were observed at EST-1,2 loci in heart extracts (see Figure 7), and a comparison of their frequencies showed no significant difference between the two samples (chi-squared 2x11 contingency test, X^2 = 16.397, P >0.05; Table 6).
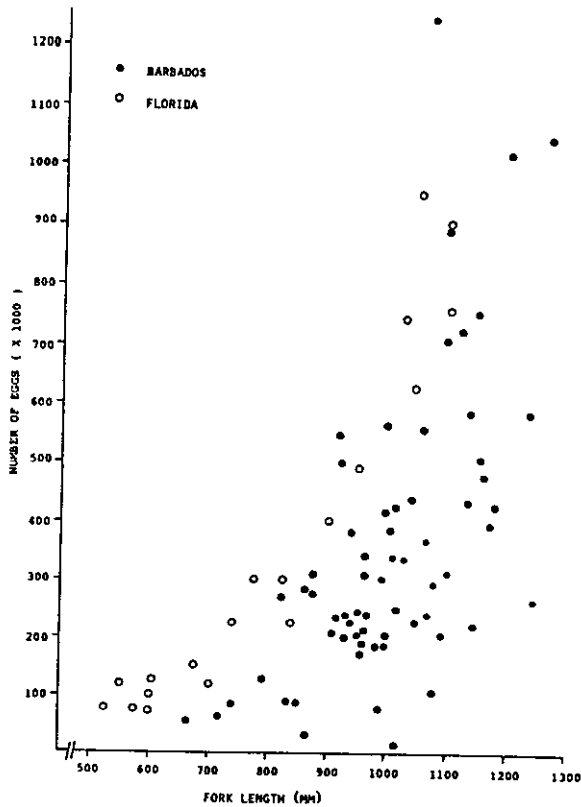
Figure 5. Fecundity-length relationships for females of
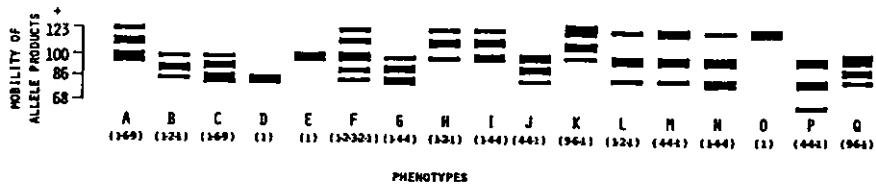_Coryphaena hippurus_ from Florida (Beardsley 1967), and Barbados.

Figure 6. A starch-gel zymogram of the dimeric enzyme isocitric
dehydrogenase, showing the phenotypes observed at IDH-2,3 loci
in liver extracts of the dolphin _Coryphaena hippurus_ from the
Western Central Atlantic. Values in parentheses show banding
intensities.

Table 4. Allelic frequencies observed at IDH-2 locus in heart extracts of the dolphin _Coryphaena hippurus_ from Miami and Barbados. Values in parentheses are those expected if the allelic frequencies do not differ.

Location	Number fish	Allele frequencies			
		68	86	100	123
Miami	509	1 (0.46)	319 (285.33)	683 (712.88)	15 (19.33)
Barbados	597	0 (0.54)	301 (334.67)	866 (836.12)	27 (22.67)

SYNTHESIS AND DISCUSSION

Dolphin is a highly prized game and food fish, and consequently seasonality in catch data is likely to reflect seasonality in local abundance of dolphin in the various territories. This view was supported by interviews with commercial and sport fishermen throughout the region. Antagonistic fishing seasons for dolphin in the northwestern and southeastern extremes of the region superficially suggest a common stock; with the dolphin being near Florida in summer, and in the Eastern Caribbean in late winter and spring. However, the catch data from the Virgin Islands and Puerto Rico are inconsistent with a single-stock hypothesis. This hypothesis predicts that Puerto Rico would catch most dolphin between April and May, the time when their catches are lowest. It is therefore suggested that there are at least two stocks of dolphin in the Western Central Atlantic, with migration circuits as shown in Figure 8. Give the seasonality of catch in other territories, the bimodal fishing season in the Virgin Island is better explained by an overlappng of ranges of two separate stocks than by a bi-annual visit of a single stock. It is proposed that the southern stock makes an annual migration northwards through the Eastern Caribbean from early spring through the early summer. It passes near Grenada in February/March, near St. Vincent, Barbados and St. Lucia in March/April, near Martinique and Guadeloupe in April, and near the Virgin Islands in April/May. The latter event produces one of the two catch peaks experienced in the Virgin Islands. At this point the continuity of the pattern northwards is disrupted, since the stock does not pass Puerto Rico. It seems likely that the dolphin move eastward from the Virgin Islands into the Atlantic to begin a return migration southwards.

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The northern stock of dolphin occurs at Puerto Rico during the winter season, being most abundant in February. A sequence of peak months may be followed northwards from there; through the Bahamas in April/May, Florida and Georgia in May/June, North Carolina in June/July, eastwards to Bermuda in July/August, southwards to the Virgin Islands in November, giving that territory its second annual peak, and then finally back to Puerto Rico by December.

The mean size of individuals caught in the different territories supports the proposed circuit for the northern stock (see Figure 3). Small fish are predominant during the summer moths when the stock is near Florida, North Carolina and Bermuda. These are presumably the young-of-the-year fish spawned during winter and spring. The mean size taken by the sport fishery in Florida is 1.69 kg and in Bermuda, where they occur one month later, it is 3.85 kg. The size difference presumably reflects growth within the cohort. The largest fish are taken by Puerto Rico, where Erdman (1956) reports that dolphin up to 23 kg in weight occur during the peak winter fishing season, and by the Bahamans where they mean weight during the peak fishing month is 6.4 kg. This suggests continued growth of the cohort as it leaves Bermuda and returns southwards into the northern Caribbean for the winter. Note that since dolphin are serial spawners, and since fecundity is proportional to size, most spawning by a cohort will occur when the individuals in the cohort are large. For northern dolphin, this would be when the stock in near Puerto Rico ie. at the southern, or up-current limit of the range. Peak spawning near Puerto Rico is reported to occur in early spring (February), when large dolphin are abundant (Erdman, 1956). The apparent bi-modal spawning season near Florida (see Table 2) suggests that some mature fish approach Florida in spring, are replaced by an immature cohort during the peak fishing season in summer (mean fish weight 1.69 kg, see Figure 3), and that some members of the latter cohort are beginning to spawn by July.

In Barbados, the stock is composed of fish approximately 5 1/2 months old in February, with a mean standard length of 812.2 mm (Figure 2). Growth within the cohort occurs throughout the fishing season to June, when the average fish size is 1007.8 mm SL. After this, abundance drops sharply (Figure 1) as the cohort leaves Barbadian waters migrating northwards. During early summer (June/July) and early autumn (October) some very small dolphin (less than 2% of the annual catch by weight), are landed as bycatch of the flying fish fishery (see Figure 2). They presumably represent the first of the young-of-the-year cohort, most of which do not appear in Barbadian waters until winter, travelling in from the south. The catch from November to January is primarily this young-of-the-year group, with a few very large mature adults from the previous year. Many of these young-of-the-year are already mature when arriving at Barbados in November, and all are ripe by the time the cohort leaves Barbados in June (see Table 2). Note too, that the cohort is estimated to have been spawned primarily between September and January, at which time the parent stock
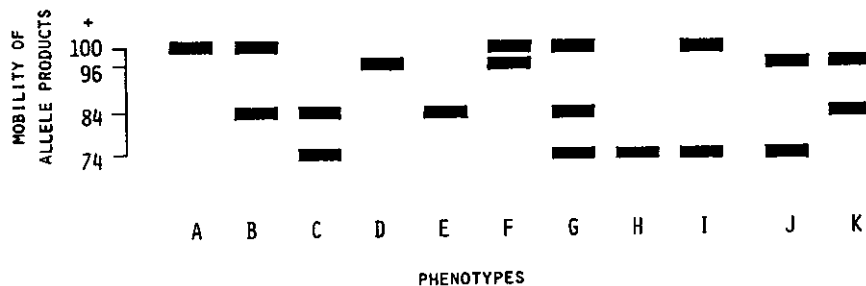
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Figure 7. A starch-gel zymogram of the monomeric enzyme esterase, showing the phenotypes observed at EST-1,2 loci in heart extracts of the dolphin _Coryphaena hippurus_ from the Western Central Atlantic.
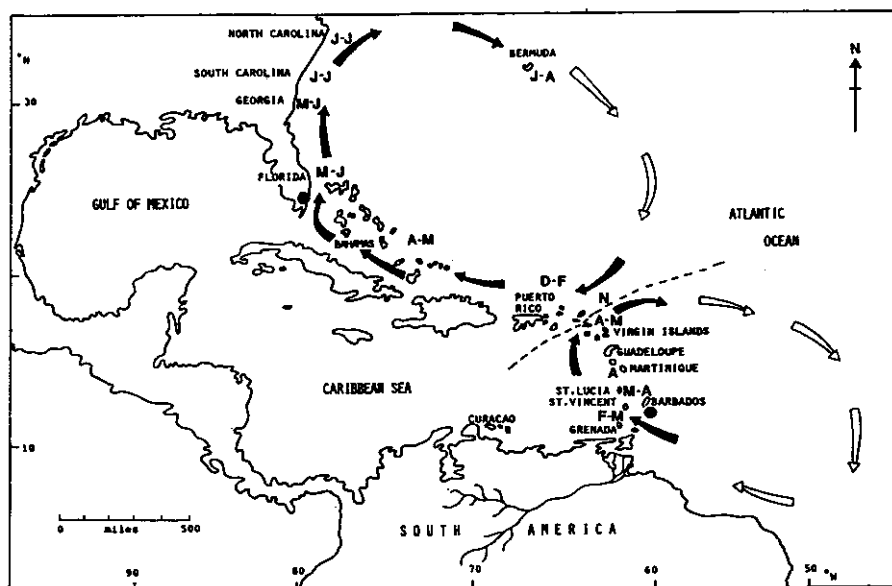

Figure 8. Proposed migration circuits for northern and southern stocks of the dolphin _Coryphaena hippurus_ in the Western Central Atlantic. Letter symbols (e.g., A-M) indicate months of peak catch.

⟹ Proposed migration where catch data not available.

● Indicates sample locations.

would be towards the southeastern (up-current) extreme of its proposed migration circuit.

The northern and southern groups of dolphin differ in most life history traits investigated. Fecundity at a given size is higher, growth rate slower, size at sexual maturity smaller and age at maturity greater for northen dolphin than for southern. No scale annuli were found in southern dolphin. Beardsley (1967) suggested that the formation of annuli in Florida was correlated with the 5°C temperature reduction occurring in the Florida Current during winter. Hence, their absence in southern dolphin suports the assertion that the groups may be distinct.

Ripe eggs in Barbados dolphin are smaller than those in dolphin from Florida and North Carolina. Intra-specific variation in egg size is common in fish, but the variation is not known to be environmental and is typically a funciton of fish age (Bagenal, 1971). Mature egg size does not increase with fish size/age for Barbados dolphin. The differences observed in maximum egg size of southern and northern dolphin are therefore suggestive of separate stocks. Note that intra-specific, presumably genetic, differences in egg size are known for different spawning groups of herring (Cushing, 1967) and sockeye salmon (Bagenal, 1971).

Differences in life history traits of northern and southern dolphin could theoretically be environmental. However, a single-stock hypotheis is not suported by the results of the electrophoretic survey of dolphin from Miami and Barbados. Genetic similarities between populations may be coincidental, but differences strongly suggest population segregation. Statistically significant differences in allele frequencies between two groups do not require an absence of gene flow, but the amount must be minimal for the genetic difference to persist (Aspinwall, 1974; Allendorf and Phelps, 1981). Conse-quently, the significant difference in the allele frequencies of the two populations, at the IDH-2 locus in heart extracts, and in the phenotypic frequencies at the IDH-2,3 loci in liver extracts, is inconsistent with the assertion that there is a single dolphin stock.

There are three major implications of the proposed migration circuits for regional fisheries. Firstly, territories apparently exploiting a common stock have been identified and can be encouraged to develop joint management programs. Secondly, territories not exploiting dolphin but lying in the path of migrating stocks, can be encouraged to develop dolphin fisheries. Thirdly, territories presently replacing their traditional fishing boats with oceanic vessels may be able to increase the duration of their fishing season through more accurate knowledge of the location of stocks throughout the year. Further work is now required to more rigorously 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.

TABLE 5. Phenotypic frequencies observed at IDH-2,3 loci in liver extracts of dolphin _Coryphaena hippurus_ from Miami and Barbados. Values in parentheses are those expected if the phenotypic frequencies do not differ.

Location	Phenotypes																	No. fish
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	
Miami	5	137	13	41	199	0	5	14	1	35	0	1	0	1	1	1	0	454
	(17.88)	(145.19)	(15.17)	(23.84)	(189.08)	(5.42)	(2.71)	(18.96)	(0.54)	(28.17)	(1.08)	(1.63)	(0.54)	(0.54)	(0.54)	(0.54)	(2.17)	
Barbados	28	131	15	3	150	10	0	21	0	17	2	2	1	0	0	0	4	384
	(15.12)	(122.81)	(12.63)	(20.16)	(159.92)	(4.58)	(2.29)	(16.04)	(0.46)	(23.83)	(0.92)	(1.37)	(0.46)	(0.46)	(0.46)	(0.46)	(1.83)	

TABLE 6. Phenotypic frequencies observed at EST-1,2 loci in heart extracts of the dolphin _Coryphaena hippurus_ from Miami and Barbados. Values in parentheses are those expected if the frequencies do not differ.

Location	Phenotypes											No. fish
	A	B	C	D	E	F	G	H	I	J	K	
Miami	107	60	10	76	86	6	14	39	43	26	12	479
	(103.08)	(62.34)	(9.88)	(68.52)	(82.10)	(12.35)	(11.11)	(40.12)	(45.06)	(29.63)	(14.81)	
Barbados	60	41	6	35	47	14	4	26	30	22	12	297
	(63.92)	(38.66)	(6.12)	(42.48)	(50.90)	(7.65)	(6.89)	(24.88)	(27.94)	(18.37)	(9.19)	

ACKNOWLEDGMENTS

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