Age and growth of dolphinfish, *Coryphaena hippurus*, off Puerto Rico

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Abstract.–Dolphinfish, *Coryphaena hippurus*, off Puerto Rico were sampled over an 8-month period to study age and growth from daily increments recorded in the sagittae. A total of 121 otoliths were analyzed. Growth was rapid and nonlinear. No significant differences in growth rate were observed based on sex or on location of capture (north or south coast). The von Bertalanffy growth parameters were L_∞ = 1457 mm *FL*, K = 2.19/yr, and t_0 = –0.046 yr. With these values, extrapolated growth over the first year averaged 3.6 mm FL/day. An existing hypothesis of two separate stocks (north and south) in the vicinity of Puerto Rico predicts that fish from the north coast caught primarily in the winter would show a much slower growth rate than fish from the south coast caught primarily in the spring. The absence of growth differences between coasts does not match this prediction; however previous growth estimates for the northern stock may have been underestimated. On the basis of these results, the stock structure and migration pattern of dolphinfish are likely to be more complicated than originally postulated.

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The dolphinfish, *Coryphaena hippurus* L., is a pelagic and migratory fish, distributed worldwide throughout tropical and subtropical waters (Gibbs and Collette, 1959; Shcherbachev, 1973). Migrating stocks support important sport and commercial fisheries. In the northwestern Atlantic they are fished off North Carolina (Rose and Hassler, 1968), Florida (Beardsley, 1967), in the Gulf of Mexico (Gibbs and Collette, 1959), off Puerto Rico (Erdman, 1956; Pérez and Sadovy, 1996), off the U.S. Virgin Islands and the Windward Islands (Mahon et al., 1981), and off Barbados (Oxenford and Hunte, 1986).

Age and growth for dolphinfish have been studied in detail by Beardsley (1967), Rose and Hassler (1968), Wang (1979), Oxenford and Hunte (1983), Uchiyama et al. (1986), and Bentivoglio (1988). No such studies have been conducted for fish off Puerto Rico. For the Caribbean region, the most relevant studies are those of Beardsley (1967), off Miami, and Oxenford and Hunte (1983) in Barbados. Beardsley (1967), using annuli on scales, found dolphinfish distributed among five age groups: 379 in group 0, 121 in group I, 9 in group II, 1 in group III, and 1 in group IV. In that study, the mean growth rate in the first year was 1.82 mm SL/day. Oxenford and Hunte (1983) assumed daily increment formation in the otolith and obtained a linear growth rate of 4.71 mm SL/day for all fish. The rate for adult fish (±700 mm SL) was 1.43 mm SL/day. Oxenford and Hunte's assumption of daily increment formation was validated indirectly by comparing their estimated growth rates to modal progression in length frequency distributions; their study was subsequently validated directly by Uchiyama et al. (1986) in a study of Hawaiian dolphinfish. Determination of age from annuli has not been validated and remains subjective.

Dolphinfish have sexually dimorphic growth; older male fish show an enlargement of the forehead (Schuck, 1951; Lozano-Cabo, 1961). Oxenford (1985) and Uchiyama et al. (1986) reported differences in the growth rate in length between sexes, but other studies have reported growth as a combination of both sexes; specifically, Rose and Hassler (1968) found no differences in length at age between males and females.

Oxenford and Hunte (1986) proposed a migration circuit in the western Central Atlantic for two separate northern and southern stocks (Fig. 1). One stock is located southeast, and the other northwest, of Puerto Rico and the Virgin Islands. Abundance of dolphinfish in Puerto Rico peaks from November to January and again (albeit to a lesser degree) from April to June (Pérez and Sadovy, 1996). The U.S. Virgin Islands also has a bimodal distribution in abundance, with a large peak in April–May and small

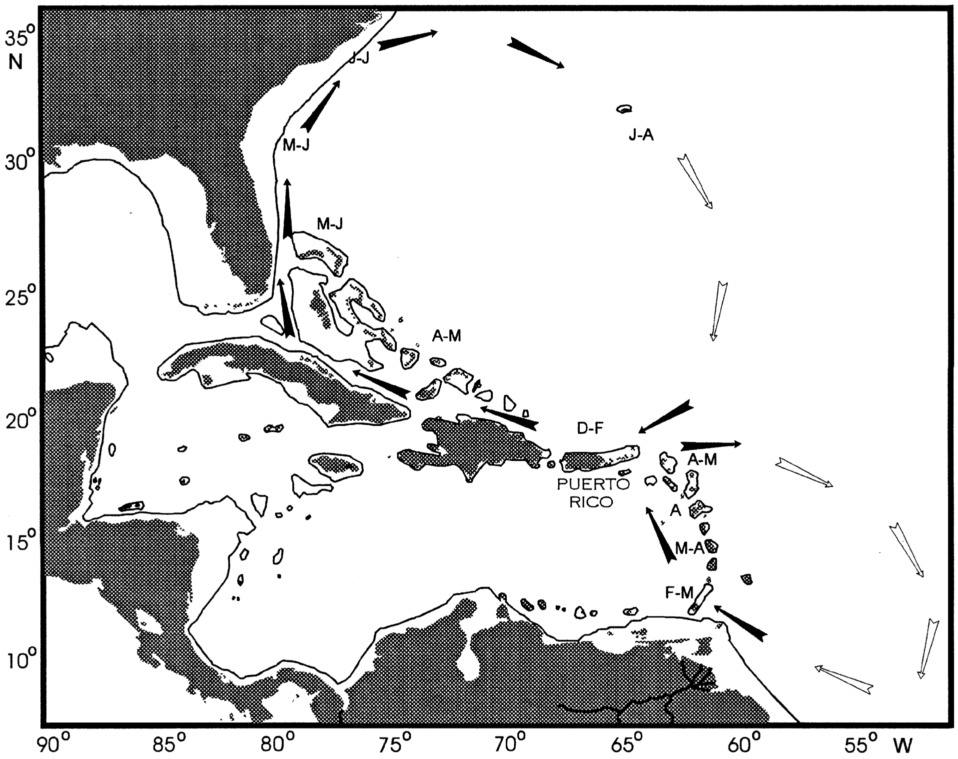

Figure 1

Proposed migration circuits for northern and southern stocks of dolphinfish, *Coryphaena hippurus*. Solid arrows indicate proposed migration route, open arrows indicate proposed migration route where catch data are not available. Letter symbols indicate months of peak catch. Redrawn from Oxenford and Hunte (1986).

peak in November. Assuming the migration circuit of the two-stock hypothesis (Oxenford and Hunte, 1986), we interpret the major peak in Puerto Rico as coinciding with the presence of the northern stock, whereas the minor peak coincides with the appearance of the southern stock in the Virgin Islands. The two-stock hypothesis is based on three main observations. First, there are differences in life-history parameters between dolphinfish from the southeast United States (North Carolina and Florida) and those from Barbados. Southern dolphinfish grow faster, attain sexual maturity at a larger size, have lower fecundity for size, and have smaller eggs than northern dolphinfish (Oxenford and Hunte, 1986). Second, the gene flow between both groups is slight. The difference in allele frequencies of the IDH-2 locus in heart extracts and in phenotypic frequencies at the IDH-2,3 loci in liver extracts indicates infrequent breeding between the stocks (Oxenford and Hunte, 1986). Third, the seasonality of catch between regions is different (Oxenford and Hunte, 1986). Because Puerto Rico lies along the boundary for the two proposed stocks, it is an ideal location to test the two-stock hypothesis.

The purpose of our study was to determine age and growth of dolphinfish in Puerto Rico. Comparison of growth rates between Puerto Rico and other areas (Florida, Barbados) was used to test the two-stock hypothesis. Of specific interest was the comparison of growth between fish from the north and fish from the south coasts. All fish from the north coast were caught during the period when abundance first peaked, whereas 92% of the fish from the south coast were caught during the period of the second peak in abundance.

Materials and methods

Dolphinfish were collected from sportfishing tournaments and commercial fishing villages from September 1991 to April 1992. Twelve dolphin tournaments were held in Puerto Rico, five on the north coast and seven on the south coast. Fifteen billfish tournaments were visited for additional samples. Purchased fish or fish heads supplemented samples when necessary. Fish were caught by trolling lines. Data on date and site of collection, standard, fork, and total lengths, weight, and sex were recorded. All fish were measured to the nearest millimeter and weighed to the nearest 50 grams. Heads were separated from the body at the site of collection and kept frozen.

The removal and preservation of otoliths followed the methods of Panella (1980) and Brothers (1987). A sagittal (longitudinal) cut through the midline of the frozen head was made with an electric band saw. Under a dissection microscope, sagittae were removed from the sacculi and extraneous tissue was removed. Sagittae were used owing to their relatively larger size in comparison with the lapillus and asteriscus. Each pair of sagittae was stored in glycerin for clearing in labeled vials.

Examination of external otolith microstructure was used to determine age (Panella, 1971). Sagittae were placed on glass slides in glycerin. Otolith structure was examined and the radius measured under a compound light microscope with transmitted light at 200×. Translucent and opaque lines were counted following the procedure of Oxenford and Hunte (1983). Otolith rings were assumed to be daily lines (Uchiyama et al., 1986) and were counted from the focus to the edge of the posterior rostrum.

All otoliths were read twice at random. If there was any difference in reading (10% or more), the otolith was discarded. A subsample of ten otoliths was sent to Hazel Oxenford (Bellairs Research Institute of McGill University, in Barbados) for additional reading and verification of counts. Otoliths were sent in coded vials with no information about length, weight, or sex. Fish length, from which otoliths were sent, ranged from 630 mm FL to 1325 mm FL.

The relation between fish fork length and daily increment of the sagittae was determined with a predictive linear regression of length on number of rings (Ricker, 1975, Francis, 1990). Following Oxenford and Hunte (1983) and Bentivoglio (1988), growth rates were calculated from the linear regressions and reported as mm/day. Analyses were done by coast (north and south) and by sex (male and female). Differences between growth-rate estimates were compared by using a homogeneity of slopes test (ANOVA) (Sokal and Rohlf, 1981).

For a more realistic representation of growth, age-length data were also modeled by using the von Bertalanffy growth function,

$$l_t = L_\infty\left(1-e^{-k(t-t_0)}\right),$$

where l_t = length (mm) at time t (years);
L_∞ = asymptotic length;
k = the growth coefficient; and
t_0 = the hypothetical age at which length equals zero.

Parameters were estimated by a nonlinear regression with SYSTAT (Wilkinson, 1987).

Results

A total of 170 dolphinfish were collected during the eight-month sampling period. From this total, 80 were captured off the north coast and 90 were captured off the south coast. The size range from the south coast was broader than that from the north: north = 475 mm FL (1.25 kg) to 1283 mm FL (18.50 kg); south = 381 mm FL (0.70 kg) to 1479 mm FL (25.00 kg); in addition, the largest fish were found on the south coast. From the total sample, 55 were male and 115 were female. Males were slightly larger than females: males = 630 mm FL (2.50 kg) to 1479 mm FL (25.00 kg); females = 381 mm FL (0.07 kg) to 1283 mm FL (19.75 kg).

The relation between standard length (SL) and fork length (FL) was linear and expressed by the equation

$$SL = -1.37 + 0.92\,FL \qquad (r=0.99).$$

The relation between the logarithms of fish weight (W) and fork length was linear and expressed by the equation

$$\log W = -4.42 + 2.78 \log FL \qquad (r=0.98).$$

Otoliths were collected from 22 males and 38 females from the north coast, and from 21 males and 40 females from the south coast. Otoliths were not collected from all fish owing to difficulties in making the longitudinal cut through the head, to breakage during dissection, or to loss during extraction from the cranial tissue. Thus, for the age and growth determinations, fork lengths ranged on the north coast from 746 mm FL to 1283 mm FL for males and from 475 mm FL to 1222 mm FL for females. Males on the south coast ranged from 625 mm FL to 1325 mm FL, and females ranged from 550 mm FL to 1275 mm FL.

Examination of the external structure of the otolith showed clear growth increments. On large otoliths, increments tended to be tightly spaced on the edge of the rostrum. Reading daily increments in this area was difficult owing to poor resolution even after clearing in glycerin; however, independent readings by Oxenford were within 10%. The oldest individual had 336 increments.

Figure 2 shows the length and number of otolith increments for all fish. Linear growth rate was 2.52 mm FL/day for all fish (Table 1, Fig. 2). Differences in linear growth rates by sex or coast (Table 1) were not significant. For the comparison by sex, however, the test approached significance, with P=0.138. Given the variability in data, the power of this test was probably low. Furthermore, growth was clearly nonlinear and decreased over time. To reach a size of 600 mm FL in 100 days, cumulative growth would have to be 6 mm FL/day. The maximum observed cumulative growth rate was 9.5 mm FL/day for a fish of 1303 mm FL and 137 increments. On average, fish of 110–150 days grew 3.3 mm FL/day, those 170–220 days old grew 2.9 mm FL/day and those 230–270 days of age grew 2.1 mm FL/day. Parameter values for the von Bertalanffy model (Fig. 2) are shown in Table 2. It was not possible to fit the model to the data sorted by both coast and sex, owing to reduced sample size in relation to large amount of variance. Differences between sexes were the greatest, and the confidence limits on k indicated statistical significance would occur at a P-value of approximately 0.06. Extrapolation of the von Bertalanffy equation for all individuals predicted a cumulative growth rate of 3.59 mm FL/day over the first year.

Table 1

Summary of results for linear regressions of sagittal rings on fork length. All = all aged fish, M = male, F = female, N = north coast, S = south coast, n = number of fish. r = coefficient of correlation.

Group	Slope	(SE)	Intercept	(SE)	r	n
All	2.52	(0.26)	497	(141)	0.66	121
MN	2.14	(0.67)	535	(134)	0.58	22
FN	2.35	(0.46)	493	(130)	0.65	38
MS	2.23	(0.72)	641	(144)	0.58	21
FS	2.34	(0.45)	535	(142)	0.64	40
N	2.28	(0.37)	506	(129)	0.63	60
S	2.37	(0.39)	558	(146)	0.62	61
M	2.54	(0.50)	518	(148)	0.62	43
F	2.46	(0.31)	493	(136)	0.67	78

Discussion

All linear growth rates for dolphinfish (Table 1) were greater than those reported by Beardsley (1967) and Rose and Hassler (1968) (Table 3). However, use of linear growth estimates is justified largely by the high variability observed in fork lengths for a given age; high variability masks any underlying growth pattern, thus making a linear model the simplest and most parsimonious, but not necessarily the most realistic model. A better approach is to use a biologically realistic model, in this case the von Bertalanffy model. The resulting parameters of the von Bertalanffy model for the Puerto Rico data are consistent with the known biology of dolphinfish. Asymptotic lengths were in accord with known maximum lengths, values of t_0 were very close to zero, even though they represented extrapolations of three months (=25% of maximum age observed), and growth coefficients were high. Growth rates predicted for dolphinfish from these equations give a different picture from those provided by the linear model. For all fish, growth averaged over 1 year was 3.59 mm FL/day (3.31 mm SL/day); growth averaged over the first 6 months was 5.57 mm FL/day (5.13 mm SL/day). These rates are comparable to the higher values reported in Table 3.

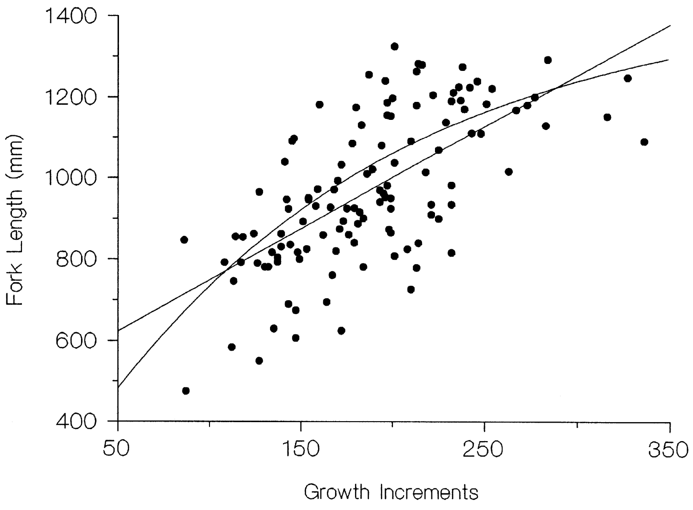

Figure 2

Relation between fork length and number of sagittal rings for dolphinfish from Puerto Rico. Straight line indicates linear growth over all fish. Curved line indicates growth according to the von Bertalanffy model (see text).

Growth rates for dolphinfish reported from previous studies (Table 3) are of questionable value when they lack uniformity in length units and in the time over which growth is evaluated, when growth is not portrayed accurately, and when the size for which growth is reported is unclear. The use of the von Bertalanffy growth function allows standardization for comparison of growth. Parameters for the von Bertalanffy model were calculated for four previous studies in which length-at-age data were reported (Table 4). Comparisons using Φ' (=log$K$ + 2logL_∞), the growth performance index of Pauly and Munro (1984), suggests

Table 2

Von Bertalanffy growth parameters (L_∞ = asymptotic length, K = growth coefficient, t_0 = length at age = 0) and standard errors (in parentheses) calculated from captured dolphinfish. n = number of fish.

Group	n	L_∞ (mm FL)	K (per yr)	t_0 (yr)
All fish	121	1457 (59)	2.19 (<0.365)	–0.046 (0.037)
North coast	60	1289 (66)	2.19 (<0.365)	–0.090 (0.054)
South coast	61	1493 (69)	2.19 (<0.365)	–0.006 (0.046)
Male	43	1380 (92)	2.55 (0.365)	0.023 (0.064)
Female	78	1506 (79)	1.82 (<0.365)	–0.087 (0.048)

Table 3

Estimated growth rates (mm/day) for *Coryphaena hippurus* at various locations. n = number of fish, P = period of sampling in months (adapted from Oxenford and Hunte, 1983; and Bentivoglio, 1988).

Location	n	P	Aging method	Growth rate	Reference
Gulf of Mexico	19	5	otolith count	0.49 SL	Bentivoglio, 1988 for fish >900 mm FL
North Carolina	26	3	days known	1.07 TL	Hassler and Rainville, 1975
Barbados	25	18	otolith count	1.43 SL	Oxenford and Hunte, 1983 for fish 700–1100 mm SL
North Carolina	593	3	scale annuli	1.64 SL	Rose and Hassler, 1968
Straits of Florida	121	12	scale annuli	1.82 SL	Beardsley, 1967
Taiwan	?	19	modal progression	2.96 SL	Wang 1979
Hawaii	7	6	days known	2.82 SL♀	Uchiyama et al., 1986
	11	14	otolith count	3.19 SL♂	
Florida	?	?	days known	3.03 SL	Schekter, personal commun. in Oxenford and Hunte, 1983
Puerto Rico	121	8	otolith count	3.31 SL	Our study
Hawaii	94	2–3	days known	3.56 SL	Hagood et al., 1981
Gulf of Mexico	81	5	otolith count	3.88 SL	Bentivoglio, 1988
Barbados	50	18	otolith count	4.71 SL	Oxenford and Hunte, 1983
Florida Marineland	2	?	days known	4.80 SL	Herald, 1961
Miami Seaquarium	1	?	days known	5.28 SL	Beardsley, 1971
North Carolina	30	1–2	days known	5.88 SL	Hassler and Hogarth, 1977

Table 4

Von Bertalanffy growth parameters calculated for dolphinfish from previous studies. $\Phi' = \mathrm{Log}(K)+2\mathrm{Log}(L_\infty)$.

Location	L_∞ (mm FL)	K (per yr)	Φ'	Reference
North Carolina	1733	0.31	5.59	Rose and Hassler, 1968
Straits of Florida	1650	0.68	6.27	Beardsley, 1967
Gulf of Mexico	1427	3.13	6.80	Bentivoglio, 1988
Puerto Rico	1457	2.19	6.67	Our study
Barbados	1436	2.87	6.77	Oxenford and Hunte, 1983

that dolphinfish in North Carolina and Florida grow more slowly than in the Gulf of Mexico, Puerto Rico (Φ'=6.67), and Barbados, or that values of K in the northern areas are underestimated (Table 4). These slower growth rates are derived from unvalidated studies of scales. Furthermore, the age at the time of first annulus formation may be significantly less than one year, depending on the difference between the period of annulus formation (presumably in winter) and the spawning season. It is distinctly possible that otolith studies in these areas might show significantly faster growth and younger fish. This possibility is also raised by the rapid growth rates of dolphinfish from these areas when maintained in aquaria (Herald, 1961; Beardsley, 1971; Hassler and Hogarth, 1977), which are among the highest reported (Table 3).

The two-stock hypothesis of Oxenford and Hunte (1986) predicts that fish sampled off Puerto Rico from November to March (north coast fish) should show distinctly different growth rates from fish sampled from March to May (south coast fish). However, no such differences were found, and in general growth rates were similar to those reported for the proposed southern stock (Oxenford and Hunte, 1983). Figure 3 shows that most fish sampled may have belonged to a single cohort whose distribution shifted over time. The size differences between fish from the north coast (primarily January–February) and those from the south coast (March–April) can be explained by growth over the 8-month sampling period. There is an influx of small fish in April off the south coast; the growth rates of these fish are equal to those of the rest of the sample. Although these fish may represent the appearance of a different (e.g. southern) stock, an equally likely explanation is that they represent the entry of a new cohort. Dolphinfish are known to spawn several cohorts over the year (Beardsley, 1967; Oxenford, 1985; Pérez and Sadovy, 1996), and a similar appearance of small fish occurs off Barbados in June, where only one stock is hypothesized. Annual length-frequency data from the south coast of Puerto Rico (Fig. 4 in Pérez and Sadovy, 1996) show considerable variation in the most abundant size class landed (from 800–1100 mm FL), which may reflect variations in the relative strengths of the two cohorts.

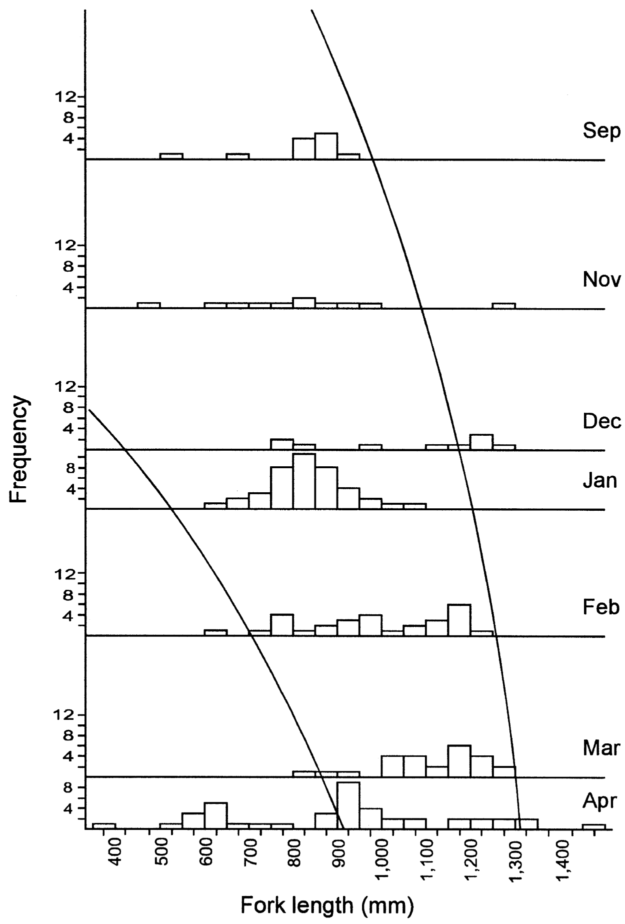

Figure 3

Length-frequency distributions of dolphinfish from Puerto Rico by month. Vertical position of the horizontal axes represents the mean sampling date for each month. Curves indicate the von Bertalanffy growth rate estimated from otoliths and are positioned to indicate the main cohort of fish sampled.

These observations do not necessarily negate the two-stock hypothesis if, as postulated above, growth rates for northern dolphinfish are much greater than previously reported. In addition to growth rate, the hypothesis is also based on differences in other life-history parameters, but more recent studies cast doubt on the significance of most of these. Data in Pérez et al.[1] show trends in several parameters related to reproduction. Both the range and mean size of mature oocytes show a gradual increase in fish from Florida, Puerto Rico, and Barbados, although sizes were identical for the north and south coasts of Puerto Rico. A trend of increasing slope among length-fecundity relationships was also evident.[1] Length of minimum maturity in females also increased along the same gradient, from 324 SL mm for Florida (Beardsley, 1967), 400 mm FL (369 mm SL) for Puerto Rico,[1] to 610 mm SL for Barbados (Oxenford and Hunte, 1986). These results, however, could equally be interpreted as representing a cline, as opposed to data for distinct stocks (Mahon and Mahon, 1987). Genetic data showing differences is based on the extremes of the distribution (Florida, Barbados) and thus cannot be used to interpret what occurs at a mid location such as Puerto Rico.

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[1] Pérez, R. N., A. Román, and G. A. Rivera. 1992. Investigation of the reproductive dynamics and preliminary evaluation of landings data of the dolphinfish *Coryphaena hippurus*, L. Puerto Rico Department of Natural Resources, Puerto Rico Fisheries Research Laboratory, P.O. Box 3665, Mayaguez, Puerto Rico 00680. Final Report D-J F26-1, 95 p.

Furthermore, the perceived movements of dolphinfish in the vicinity of Puerto Rico is complex. In Puerto Rico, fish generally are caught in abundance first on the north coast and then on the south coast. Fish are caught in the Mona Passage on the west side of Puerto Rico but not off the east coast over the Puerto Rican–Virgin Islands shelf.[1] Off the U.S. Virgin Islands there is a bimodal distribution of catch over time similar to that for Puerto Rico. For recreational boats operating out of St. Croix, increases in catch rates, particularly in the spring are first observed to the southeast, then move progressively closer to St. Croix and then St. Thomas-St. John.[2] The implied direction of movement is from southeast to northwest, opposite to that predicted by the two-stock hypothesis. The temporal distribution of dolphinfish along the southeast coast of the Dominican Republic is similar to that off the south coast of Puerto Rico,[3] but in contrast, off the southwest coast, dolphinfish catch rates show a single sharp peak in the month of November.[4] In agreement with Mahon and Mahon (1987), the real stock structure and migration pattern of dolphinfish are likely to be more complicated than originally proposed, a point well appreciated by Oxenford and Hunte (1986).

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