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BIOLOGY AND FISHERY OF DOLPHINFISH AND RELATED SPECIES. *E. MASSUTÍ and B. MORALES-NIN (eds.)*

Biology of the dolphinfish (*Coryphaena hippurus*) in the western central Atlantic: a review*

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SUMMARY: The dolphinfish, *Coryphaena hippurus*, is a circum-tropical oceanic epipelagic species which is of significant importance to both commercial and sport fisheries in the western central Atlantic. Despite this, little attention has been paid to conducting biological stock assessments and developing management strategies for this species, and it remains unmanaged across most of the region. This paper summarizes aspects of the biology of dolphinfish that are relevant to assessment and management from studies of this species in the southeastern United States, Gulf of Mexico and the Caribbean. Throughout their range in the western central Atlantic, dolphinfish are seasonally abundant and presumed to be highly migratory. They exhibit high growth rates, early maturity, batch spawning over an extended season, a short life span and a varied diet. Marked differences in some biological characteristics and in the frequency of IDH-2 alleles between dolphinfish from the southeastern USA and the Caribbean suggest a relatively complex stock structure for this species, which needs further investigation to improve the information base for development of management strategies for dolphinfish across this region.

Key words: Dolphinfish, *Coryphaena hippurus*, biology, western central Atlantic, review

INTRODUCTION

The dolphinfish (*Coryphaena hippurus*) is one of relatively few circum-tropical oceanic pelagic species. Dolphinfish are found in tropical and subtropical surface ocean water apparently restricted to waters warmer than 20ºC (Gibbs and Collette, 1959). They are of significant economic importance throughout their global distribution. In the western central Atlantic they have had a long tradition of seasonal importance to the sports and commercial fisheries of many countries (e.g. Collette, 1978; Palko *et al.,* 1982; FAO, 1994; NMFS, 1996; see also Table 1). Despite their wide distribution and economic importance, they have been the subject of relatively few biological studies in the western central Atlantic (Mahon, 1996) and species-specific management is virtually non-existent in most of the region. Management is currently restricted to minimum size and bag limits in the state waters of Florida and North Carolina, and is now being considered for federal waters (R. Nelson pers. comm., see also SAFMC, 1997).

A comprehensive review of biological data available on dolphinfishes (Coryphaenidae) was undertaken by Palko *et al*. (1982). Here, that review is partially updated by examining the biological data currently available for *Coryphaena hippurus* (subsequently referred to simply as dolphinfish) in the western central Atlantic, which is considered to be of direct relevance to fisheries management.

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TABLE 1. – Summary of locations and approximate seasonality of commercial and/or sport fisheries for dolphinfish (*Coryphaena hippurus*) within the western central Atlantic.

Area	Location	Approximate seasonality	Selected References
Southeastern USA	North Carolina South Carolina Georgia East Florida	April-Sept	Ellis (1957) Iversen (1962) Beardsley (1967) Rose and Hassler (1969) Hassler and Hogarth (1977) Gentle (1977) Manooch and Laws (1979) Palko *et al*. (1982) Brusher and Palko (1985) Oxenford and Hunte (1986a)
Southern USA (Gulf of Mexico)	West Florida Alabama Mississippi Louisiana Texas	May-Oct	Baughman (1941) Springer and Pirson (1958) Fable (1981) Palko *et al*. (1982) Bentivoglio (1988)
Central America (Caribbean coast)	Mexico	?	FAO (1996)
Northern Caribbean	Bahamas Hispaniola Puerto Rico US Virgin Islands	Jan-June	Erdman (1956) Olsen and Wood (1982) Appeldoorn and Meyers (1993) Perez and Sadovy (1991) Perez *et al*. (1992) Rivera Betancourt (1994)
Eastern Caribbean	Guadeloupe Martinique Dominica St. Lucia Barbados St. Vincent Grenada Tobago	Dec-June	Mahon *et al*. (1981) Sacchi *et al*. (1981) Murray (1985) Oxenford and Hunte (1986a) Hunte (1987) Mahon *et al*. (1990) Mahon (1993) FAO (1996) Mohammed (1996)
Southern Caribbean	Curacao	Dec-July	Zaneveld (1961)
South America	Northeast Brazil	?	Monteiro *et al*. (1996)
Atlantic	Bermuda	March-Dec	Oxenford and Hunte (1986a)

DISTRIBUTION AND ABUNDANCE

Adults

In the western central Atlantic, dolphinfish have been recorded as far north as George's Bank, Nova Scotia (Vladykov and McKenzie, 1935; Tibbo, 1962) and as far south as Rio de Janeiro, Brazil (Ribeiro, 1918; Shcherbachev, 1973). However, it is generally considered to be common only from North Carolina, throughout the Gulf of Mexico and Caribbean to the northeast coast of Brazil, and is only seasonally abundant at these locations (see Table 1).

Even though landings of dolphinfish reported to the Food and Agricultural Organisation (FAO) within the western central Atlantic significantly under-represent actual landings of this species (Oxenford, in press; Mahon, 1999), they still indicate that dolphinfish are among the top seven oceanic pelagic species landed in this region, giving an indication that they are indeed abundant. There have been no attempts to estimate actual abundance, but time-series of catch per unit effort data for dolphinfish are available for several locations in the Caribbean (see Oxenford, 1985; Hunte, 1987; Oxenford and Hunte, 1987; Mahon *et al.,* 1990; Mahon and Oxenford, 1999) and these generally show no indication of stock declines.

Young

There have been few systematic surveys for young dolphinfish over the western central Atlantic. In the Gulf Stream, juvenile dolphinfish (100-400

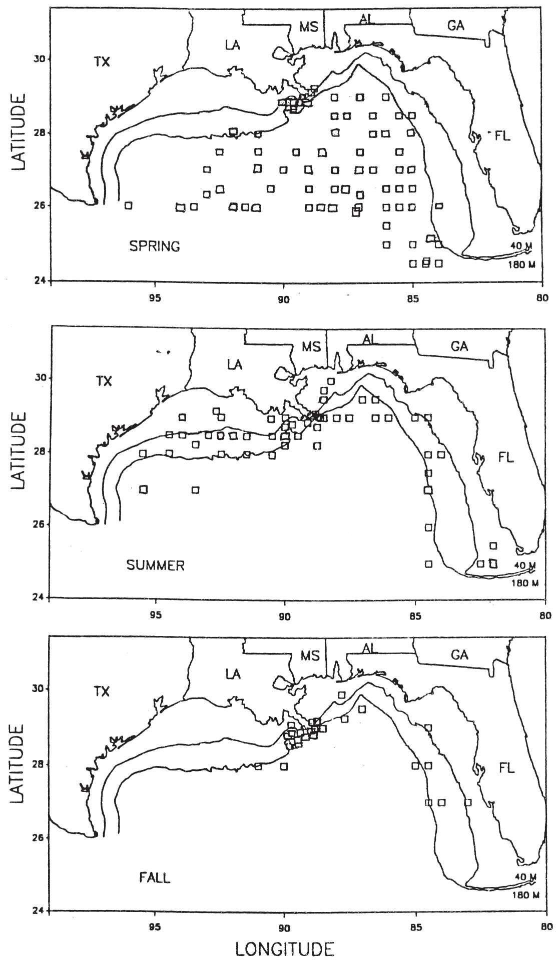


FIG. 1. – Distribution of dolphinfish (*Coryphaena hippurus*) larvae in the northern Gulf of Mexico by season, as determined by catches in bongo and neuston net tows. Seasons (spring: March-May; summer: June-August; fall: September-November) are combined across years (1982-1984). Adapted from Ditty *et al.* (1994).

mm SL) have been reported during spring, summer and fall (Gibbs and Collette, 1959). Off North Carolina, young dolphinfish have been reported in March and May (Anderson *et al.,* 1956a,b), in late summer (La Monte, 1952; Beardsley, 1967) and in October (Anderson and Gehringer, 1957).

Juvenile dolphinfish (100-400 mm SL) have been reported in the Florida Current in all seasons, but appear particularly abundant in early summer (e.g. Gibbs and Collette, 1959; Beardsley, 1967).

In the Gulf of Mexico, distribution of larval dolphinfish has been described by several authors (e.g. Powles, 1981; Richards *et al.,* 1984; Kelley *et al.,* 1986; Ditty *et al.,* 1994) (Fig. 1). They are apparently present in the Gulf from at least April through to November, and are found in shelf and oceanic waters, although more commonly in the latter (Ditty *et al.,* 1994). Most occurred in water temperatures at or greater than 24°C (range: 21.4 - 32°C) and in salinities at or greater than 33‰ (range: 18.7 - 37.8‰). Furthermore, particularly high abundance was reported near the Mississippi River delta (Ditty *et al.*, 1994). Off Texas, young dolphinfish have been reported in the summer (Pew, 1957; Springer and Pirson, 1958), and Gibbs and Collette (1959) report juveniles in the Gulf of Mexico in spring and summer.

Larval dolphinfish have been reported off Barbados year-round (Lao, 1989), and both larval and juvenile dolphinfish have been sampled in the southeastern Caribbean waters during April/May (Oxenford *et al.*, 1995; Hunte *et al.,* 1995).

REPRODUCTIVE CHARACTERISTICS

Population sex ratio

There are several references to sex ratio of dolphinfish catches from different locations in the western central Atlantic, and these are summarised in Table 2. Generally, females outnumber males in the catch, but sex ratios do appear to differ with size of fish (Rose and Hassler, 1974; Oxenford,1985) and with season (Oxenford, 1985) (Table 3).

TABLE 2. – Overall sex ratios reported for dolphinfish (*Coryphaena hippurus*) landings in the western central Atlantic.

Location	Frequency		Size range (mm)	Sex ratio (m:f)	Reference
	males	females			
North Carolina	428	821	450-1275 FL	1:1.9	Rose and Hassler (1974)
Gulf Stream	30	27	313-1165 SL	1:0.9	Gibbs and Collette (1959)
Florida Current	222	392	-	1:1.8	Oxenford (1985)
Puerto Rico	150	450	-	1:3	Erdman (1976)
	266	622	358-1479 FL	1:2.3	Perez *et al.* (1992)
	55	115	430-1480 FL	1:2.1	Rivera-Betancourt (1994)
Virgin Islands	25	47	-	1:1.9	Mather (1954)
Gulf of Mexico	36	43	250-1210 SL	1:1.2	Bentivoglio (1988)
Barbados	773	2353	400-1200 SL	1:3	Oxenford (1985)

TABLE 3. – Sex ratios by size and season for dolphinfish (*Coryphaena hippurus*) landings in the western central Atlantic.

Location	Month	Fish size (mm)*	Frequency males	Frequency females	Sex ratio (m:f)		Reference
North Carolina	-	450-600	281	685	1:2.4		Rose and Hassler (1974)
	-	601-800	85	97	1:1.1	1:1.9	
	-	801-1275	62	39	1:0.6		
Barbados	Nov	844	17	29	1:1.7		Oxenford (1985)
	Dec	794	23	56	1:2.1		
	Jan	821	94	256	1:2.7		
	Feb	812	59	240	1:4	1:3	
	Mar	846	150	600	1:4		
	Apr	925	256	750	1:2.9		
	May	921	126	330	1:2.6		
	Jun	778	28	56	1:2		Oxenford (1985)
	Jul	433	9	24	1:2.7		
	Aug	656	2	2	1:1	1:2	
	Sept	587	1	5	1:5		
	Oct	446	5	5	1:1		

* sizes are given as range in mm FL for North Carolina and as means in mm SL for Barbados

The tendency to female biased sex ratios is believed to result from inadvertent selection for females by fishers as a result of intersexual differences in behaviour of dolphinfish, rather than a real difference in sex ratio at conception or in larval and juvenile mortality rates of males and females (Nakamura, 1971; Rose and Hassler, 1974; Oxenford, 1985). Oxenford (1985) suggested that small-sized males and all sizes of females spend more time associated with floating objects than large-sized males, which tend to spend more time in open water, possibly travelling between female dominated schools below rafts. Hence catches of small-sized fish are likely to have a sex ratio approximating 1:1, whilst catches of large-sized fish will be female biased if taken in association with floating objects or male biased if taken in open water. Observations reported by Perez *et al*. (1992) support this suggestion. Likewise, the slight male bias in the sex ratio reported by Gibbs and Collette (1959) could have resulted from the fact that the majority of their samples were taken by subsurface long-line gear and not from around floating objects.

Description of maturity stages

Maturity stages of male and female dolphinfish in the western central Atlantic have been described by several authors (e.g. Beardsley, 1967; Oxenford, 1985; Perez *et al*., 1992; Table 4). It is clear from the similarity of these descriptions that dolphinfish are relatively easy to classify into well defined maturity stages based on a combination of visual observation of the gonads and egg size distributions in females.

For dolphinfish from the Florida Current, Beardsley (1967) described 5 maturity stages (I-immature, II-early maturing, III-late maturing, IV-ripe, V-spent) for females; and 2 stages (I-immature or resting, II-mature) for males, based on visual appearance, and also provided examples of egg size distributions (Table 4a). It was noted that no running ripe fish were observed.

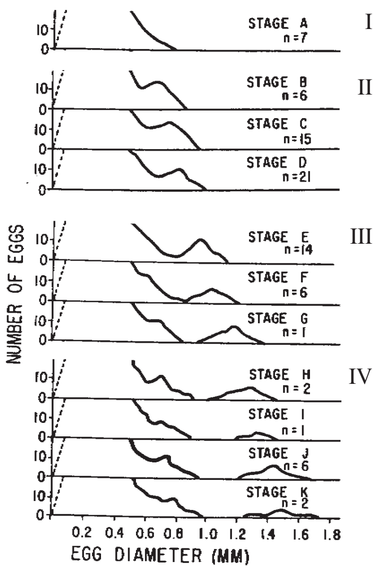
For dolphinfish from Puerto Rico, Perez *et al*. (1992) described 4 maturity stages (I-immature, II-mature (inactive), III-mature (active), IV-post spawned) for females and 3 stages (I-mature (inactive), I-mature (ripe), III-spent) for males and provided both a visual and a microscopic description for each (Table 4b).

For dolphinfish from the Gulf of Mexico, Bentivoglio (1988) used the 5 maturity stages for females and two maturity stages for males as described by Beardsley (1967) (Table 4a).

For dolphinfish from Barbados, Oxenford (1985) also described 4 maturity stages (I-immature, II-maturing, III-mature, IV-spent) for females, and 2 stages (I-immature, II-mature) for males, noting that fish in running ripe condition were not observed, presumably because this state occurs rapidly and only during the pairing and spawning process. It was also noted that spent males could not be differentiated from mature males. A description of each maturity stage based on visual appearance and an example of the typical egg size distribution for each stage is given in Table 4c.

Table 4. – Description of the gonads at each maturity stage for male and female dolphinfish (*Coryphaena hippurus*) from (a) Florida Current (after Beardsley, 1967), (b) Puerto Rico (after Perez *et al*., 1992), and (c) Barbados (after Oxenford, 1985).

(a) Florida Current Dolphinfish

SEX	MATURITY STAGE		DESCRIPTION	APPROXIMATE EGG SIZE DISTRIBUTION
Females	I	Immature	Ovaries long, thin, hollow tubes, diameter 3-4 mm; eggs microscopic; ovary wine-red to pink.	
	II	Early maturing	Ovary slightly enlarged; diameter 10-15 mm; eggs visible to the naked eye through the ovary wall, but no distinct size groups distinguishable; pale yellow.	
	III	Late maturing	Ovary much enlarged; at least two distinct size groups of eggs easily visible to the naked eye; bright yellow to orange.	
	IV	Ripe	Ovary distended, half filling the body cavity; lumen full of large, clear eggs which give the ovary a speckled appearance.	
	V	Spent	Ovaries flaccid, hollow tubes; a few remnants of ripe ova may remain in the lumen or folds of the ovary, usually visible by microscopic examination; dull red and discoloured, particularly at the posterior end; numerous blood clots.	
Males	I	Immature or resting	Testes small, firm to the touch; no milt extruded after cutting and squeezing.	
	II	Mature	Testes enlarged; milt extruded after cutting and squeezing.	

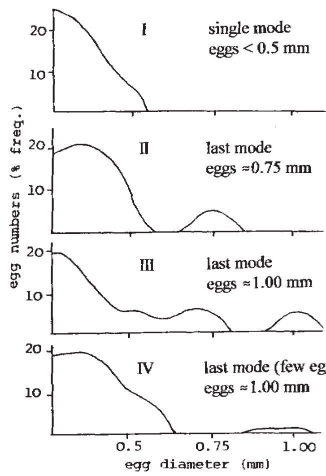
(b) Puerto Rico Dolphinfish

SEX	MATURITY STAGE		DESCRIPTION
Females	I	Immature	Small diameter gonad lobules are bright orange, neither eggs nor blood vessels visible macroscopically. *Microscopic description*: Oocytes stages 1 and 2 (previtellogenic) and perhaps, a few oocytes early stage 3. Lamellae looks compact within a thin muscular tunica (i.e. ovary wall). Small blood vessels surround ovary walls and there is no evidence of prior spawning (i.e. disorganized and loose appearance of ovary, muscle bundles, oocytes stage 4 or atretic bodies).
	II	Mature (inactive)	Turgid gonad lobules are round and orange colour, eggs and small veins visible macroscopically. *Microscopic description*: First time spawners have compact ovaries with oocytes in stages 2, 3 maybe a few early stage 4 and a thin muscular tunica. Oocyte stage 3 (i.e. early vitellogenic) begin to predominate the field of view (i.e. 400x). If previous spawning occurred, ovary shows a slightly disorganized appearance, oocytes stage 3 predominate and few atretic oocytes may be present. Also muscular tunica seems slightly thicker than in immature gonads.
	III	Mature (active)	Gonad lobules could be completely turgid or slightly flaccid with pale orange or yellow colour. Large translucent eggs visible through ovary wall with large blood vessels surrounding the ovaries. *Microscopic description*: Oocytes stages 1, 2, 3 and 4 present. Ripe gonads are completely turgid and mid to late stage 4 dominates the field of view by more that 50% (i.e. 400x). Some hydrated oocytes and postovulatory follicles may be observed. Oocytes stage 4 have distinctive thick zona radiata. Muscular tunica is thin. When female is between spawns, gonad lobules are slightly flaccid and healthy oocytes in late stages 4 and mid 4 may be equally abundant. The muscular tunica gets thick and scattered degenerated oocytes could be observed in a disorganized ovary.
	IV	Post-spawned	Gonad lobules completely flaccid and reduced in diameter. Blood vessels present. *Microscopic description*: In early postspawners, many healthy oocytes stage 3 with atretic oocytes stage 4 are observed. In late postspawners, oocytes stage 3 and 4 may be present. Many atretic oocytes are present in several degeneration stages. Stretched muscular tunica, looks slightly thin like immature ovary but large compressed blood vessels surround the ovary walls. Disorganized and muscle bundles across ovary are present.

TABLE 4. (Cont.) – Description of the gonads at each maturity stage for male and female dolphinfish (*Coryphaena hippurus*) from (a) Florida Current (after Beardsley, 1967), (b) Puerto Rico (after Perez *et al.*, 1992), and (c) Barbados (after Oxenford, 1985).

SEX	MATURITY STAGE		DESCRIPTION
Males	I	Mature (inactive)	Testes lobules are laterally compressed (narrow), firm and show some convolutions. Colour may vary with freshness of sample. Most samples collected to date have a dark pink/brown appearance. No milt extrudes when cut or squeezed. *Microscopic description*: Crypts of spermatogonia and early spermatogenesis develop together around each seminiferous tubule. Gonad small and compact. Few or no sperms are present.
	II	Mature (or ripe)	Testes lobules are narrow. They could be small and compact like immature testes or have convolutions. Tissue feels soft. Milt may extrude when cut or slightly squeezed. Colour varies from pale pink to white. *Microscopic description*: The seminiferous tubules are cysts in several stages of spermatogenesis. Throughout the testes, the cysts have the sinuses partially or totally full of spermatides and/or sperm. Seminiferous tubules closer to the central or efferent ducts are connected and elongated, partially or totally full of spermatozoa.
	III	Spent	Testes are flaccid with dark pink/brown colour. They may be confused with immature testes. *Microscopic description*: Disorganized appearance and elongated cysts. Crypts of spermatocytes and spermatides are present, but most seminiferous tubules and sinuses are empty and some have remnants of sperms. Some spermatogonia may be observed.

(c) Barbados Dolphinfish

SEX	MATURITY STAGE		DESCRIPTION	APPROXIMATE EGG SIZE DISTRIBUTION
Females	I	Immature	Bright/dark orange, firm, narrow ovaries. No eggs visible through ovary wall.	
	II	Maturing	Medium orange, firm, enlarged ovaries. Eggs visible through ovary wall and small blood vessels over surface of ovary.	
	III	Mature	Pale orange/yellow, soft swollen ovaries. Eggs and large blood vessels visible.	
	IV	Spent	Pale orange, large flaccid ovaries. Few eggs visible and large blood vessels.	
Males	I	Immature	Narrow, slightly lobed, firm testes. Colour varies from pale flesh to dark brown/pink. No milt exudes when cut.	
	II	Mature	Large, highly lobed, soft, fragile testes. Colour varies from pale flesh to dark brown/pink. Milt exudes when cut and squeezed.	

Age and size at maturity

Several authors have provided size and/or age at maturity data for dolphinfish from the western central Atlantic (Beardsley, 1967; Schekter, 1982; Oxenford, 1985; Bentivoglio, 1988; Perez *et al.,* 1992; Table 5). Whilst there are differences in both the age and size of dolphinfish at first maturity from different locations, there is general agreement that all dolphinfish in the western central Atlantic reach sexual maturity in the first year of life, and that females reach maturity at a smaller size but similar age to males (Table 5).

In the Florida Current, Beardsley (1967) reported that female dolphinfish begin to mature (reach stage II) at about 350 mm FL (about 6-7 months old), at 450 mm FL 50% are mature, and at 550 mm FL 100% are mature, whilst males mature at a slightly larger size (427 mm FL) than females. Schekter (1982) reported first spawning in laboratory reared dolphinfish from the Florida Current at 6 1/2 months old and at an average weight of 2.5 kg (~ 565 mm FL).

In Puerto Rico, Perez and Sadovy (1991) and Perez *et al.* (1992) reported that the smallest mature female observed was 400 mm FL (384 mm

TABLE 5. – Summary of reproductive characteristics reported for dolphinfish (*Coryphaena hippurus*) from the western central Atlantic.

Reproductive parameter	Sex	Florida Current			US Virgin Islands	Puerto Rico	Gulf of Mexico	Barbados	
		Beardsley (1967)	Schekter (1982)*[1]	Perez *et al.* (1992)	Perez *et al.* (1992)	Perez and Sadovy (1991), Perez *et al.* (1992)	Bentivoglio (1988)	Oxenford (1985)	Perez *et al.* (1992)
Size at first maturity (mm FL)	M	427	565	-	-	-	528	805	-
	F	350	-	-	-	400	490-520	667	-
ize class at 100% maturity (mm FL)	M	-	-	-	-	-	-	1178	-
	F	550	-	-	-	600	-	931	-
Approx. age at first maturity (mo.)	M	6-7	6.5	-	-	-	4	4	-
	F	6-7	-	-	-	-	3-4	4	-
Mature egg size range (mm diam.)	F	1-1.7	-	-	-	0.85-1.56	-	0.86-1.25	-
Mean mature egg size (mm diam.) and sample size (n=no. fish)	F	-	-	1.03 n=3	1.08 n=2	1.10 n=25	-	0.97 n=69	1.07 n=2
Batch fecundity range and sample size (n=no. fish)	F	85,000-938,000 n=19	-	-	-	219,670-1,548,457 n=25	-	58,000-1,243,770 n=69	-
Batch fecundity-fork length relationship ($Y=aX^b$) Y is no. mature eggs X is mm FL	F	$Y \sim 2.52 \cdot 10^{-4} X^{3.12}$*[2]	-	-	-	$Y=6.03 \cdot 10^{-7} X^{3.98}$	-	$Y=2.7 \cdot 10^{-6} X^{3.67}$	-

*[1] Data are for laboratory reared F_1 generation of Florida broodstock
*[2] Relationship calculated by extrapolation of data from fecundity at size graph

SL), but cautioned that more smaller fish need to be examined to more accurately determine the minimum size at maturity. All fish larger than 600 mm FL were found to be mature, i.e. at stage II or more(Fig. 2a).

In the Gulf of Mexico, Bentivoglio (1988) reported early maturing (Stage II) females as small as 275 mm FL (2 months old). However, not until Stage III (late maturing) were at least two distinct size classes of eggs apparent. He therefore concluded that females reach first maturity between 490 and 520 mm FL (3-4 months old).The smallest mature (Stage II) male was 528 mm FL (4 months old).

In Barbados, Oxenford (1985) provided length frequency distributions for male and female dolphinfish at each maturity stage (Fig. 3). Females were considered to have reached first maturity when a group of large translucent eggs could be clearly distinguished with the naked eye from the mass of smaller pale orange undeveloped eggs in the ovaries (i.e. Stage II gonads), and males were also considered to have reached first maturity when the testes appeared swollen and soft (Stage II gonads). Females were reported to mature at a smaller mini-

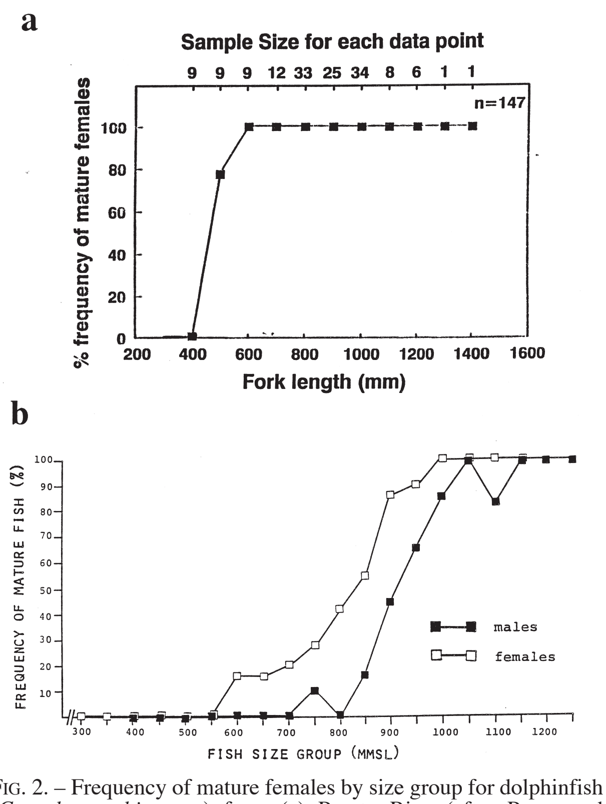


FIG. 2. – Frequency of mature females by size group for dolphinfish (*Coryphaena hippurus*) from (a) Puerto Rico (after Perez and Sadovy, 1991), and (b) Barbados (after Oxenford, 1985).

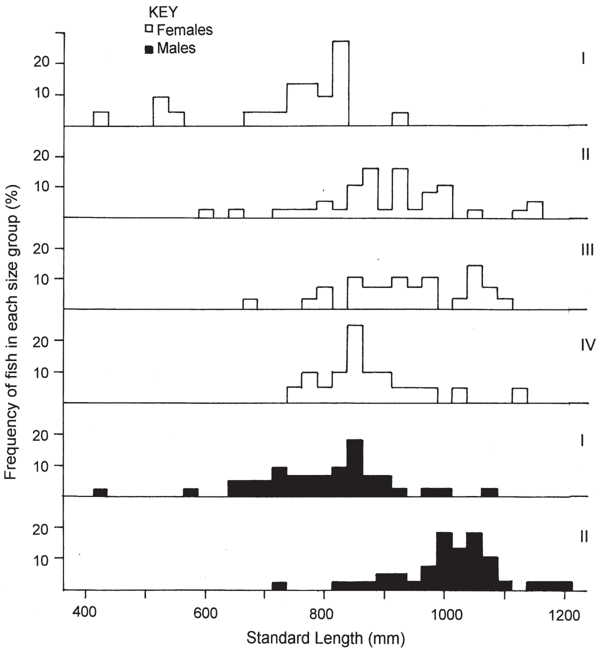


FIG. 3. – Size frequency distributions at each maturity stage for male and female dolphinfish (*Coryphaena hippurus*) from Barbados (after Oxenford, 1985).

mum size (610 mm SL or 667 mm FL) than males (735 mm SL or 805 mm FL), but at approximately the same age (112 days for females, 108 days for males). By 5 1/2 months (850 mm SL or 931 mm FL for females and 1074 mm SL or 1178 mm FL for males) 99% of fish were reported to be fully mature (Fig. 2b).

Gonasomatic indices

Limited gonasomatic index (GSI) data are available for dolphinfish from the western central

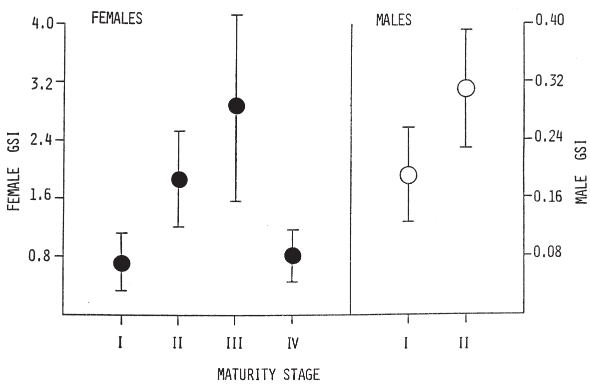


FIG. 4. – Mean gonasomatic index (GSI) at each maturity stage for male and female dolphinfish (*Coryphaena hippurus*) from Barbados (after Oxenford, 1985).

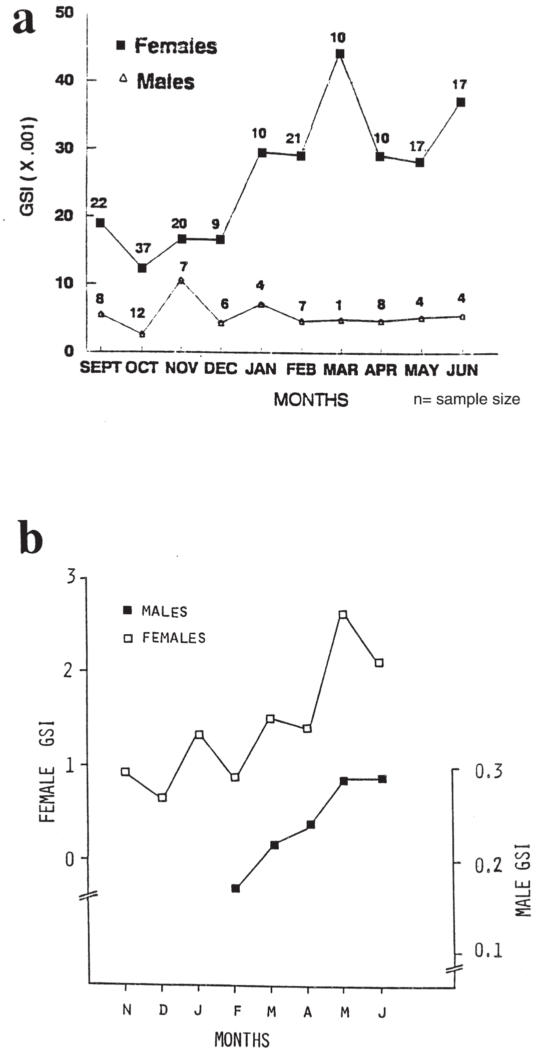


FIG. 5. – Monthly mean gonasomatic indices (GSI) for male and female dolphinfish (*Coryphaena hippurus*) from (a) Puerto Rico (after Perez *et al.*, 1992), and (b) Barbados (after Oxenford, 1985).

Atlantic. GSI values for mature individuals have only been reported from Barbados, and range from 1.02 to 7.90% for mature (Stage II and III) females. For mature (Stage II) males they are considerably lower, ranging from 0.19 to 0.48% (Oxenford, 1985). Mean GSI values at each maturity stage for both sexes are also given by Oxenford (1985) for dolphinfish from Barbados (Fig. 4).

Population monthly mean GSI values for both sexes are available for dolphinfish from Puerto Rico (Perez *et al.*, 1992) and from Barbados (Oxenford, 1985) (Fig. 5). Puerto Rico dolphinfish appear to have higher GSI values than Barbados dolphinfish, and show a different seasonal pattern.

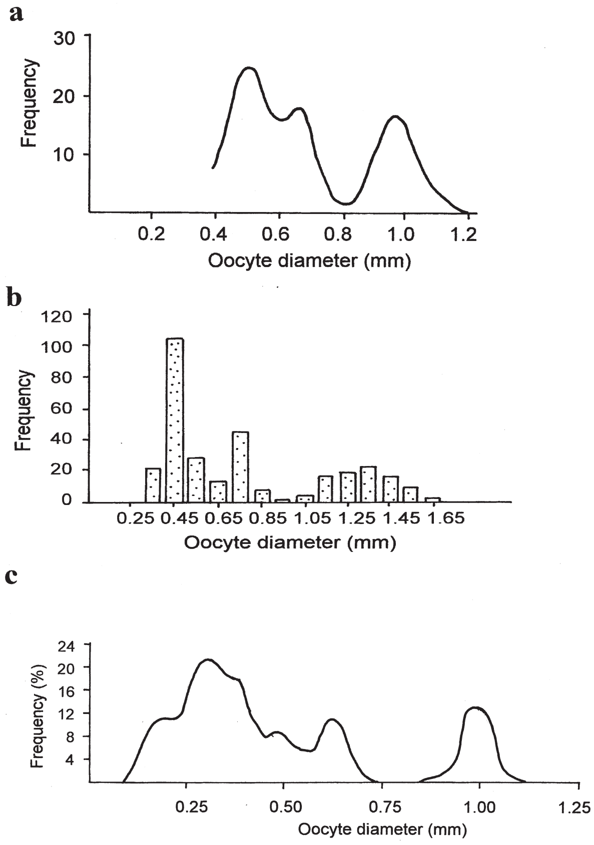


FIG. 6. – Egg size distributions in the ovaries of female dolphinfish (*Coryphaena hippurus*) from (a) Florida Current (after Beardsley, 1967), (b) Puerto Rico (after Perez *et al.*, 1992), and (c) Barbados (after Oxenford, 1985).

Fecundity and egg size

Dolphinfish from the western central Atlantic typically have two or three size classes (batches) of eggs in the ovaries: one heterogeneous size class of small eggs, and one or two more homogeneous size classes of larger maturing or mature eggs (Beardsley, 1967; Oxenford, 1985; Perez *et al.,* 1992; Fig. 6). Mean mature egg size appears to vary slightly with location and/or with author, ranging from 0.97 to 1.10 mm diameter (Table 5). Hassler and Rainville (1975) estimated dolphinfish eggs from North Carolina to be approximately 1.3 mm diameter, and Ditty *et al.* (1994) reported a mean size of 1.4 mm diameter from the Gulf of Mexico. However, it should be noted that these apparently larger eggs were collected from the plankton rather than from the ovaries of ripe fish.

Batch fecundity estimates for dolphinfish in the western central Atlantic range from 58,000 to 1.5 million (Table 5) and are strongly influenced by fish size. Batch fecundity - length relationships are available for dolphinfish from Florida, Puerto Rico and Barbados and all show an exponential increase in egg number with fish size, the exponent being between 3 and 4 (Table 5, Fig. 7). Dolphinfish from the Florida Current and Puerto Rico appear to have very similar fecundity-size relationships, whilst Barbados dolphinfish appear to be less fecund at size.

Spawning season and location

There are numerous references to time of spawning for dolphinfish in the western central Atlantic (e.g. Palko *et al.*, 1982) which clearly show protracted multiple spawning behaviour. The presence of several size classes of eggs in the ovaries indicates that they are batch spawners and probably spawn at least two or three times in each spawning period (Beardsley, 1967; Oxenford, 1985; Perez and Sadovy, 1991). Schekter (1982) reported almost continous spawning from dolphinfish brood stock captured from the Florida Current and held in captivity for several months.

Off North Carolina, spawning dolphinfish have been reported in May and June (Schuck, 1951), dolphinfish eggs have been collected in July and August (Hassler and Rainville, 1975), and peak spawning is reported to occur during June and July (Rose, 1966).

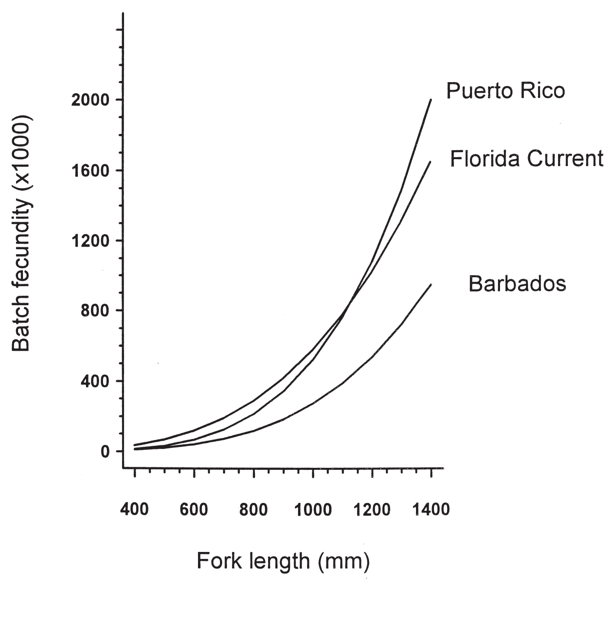


FIG. 7. – Comparison of fecundity-length relationships reported for dolphinfish (*Coryphaena hippurus*) in the western central Atlantic. Relationship for Florida Current was obtained by extrapolation of graphical data given by Beardsley (1967). Relationships for Puerto Rico and Barbados dolphinfish were given by Perez *et al.* (1992) and Oxenford (1985) repectively.

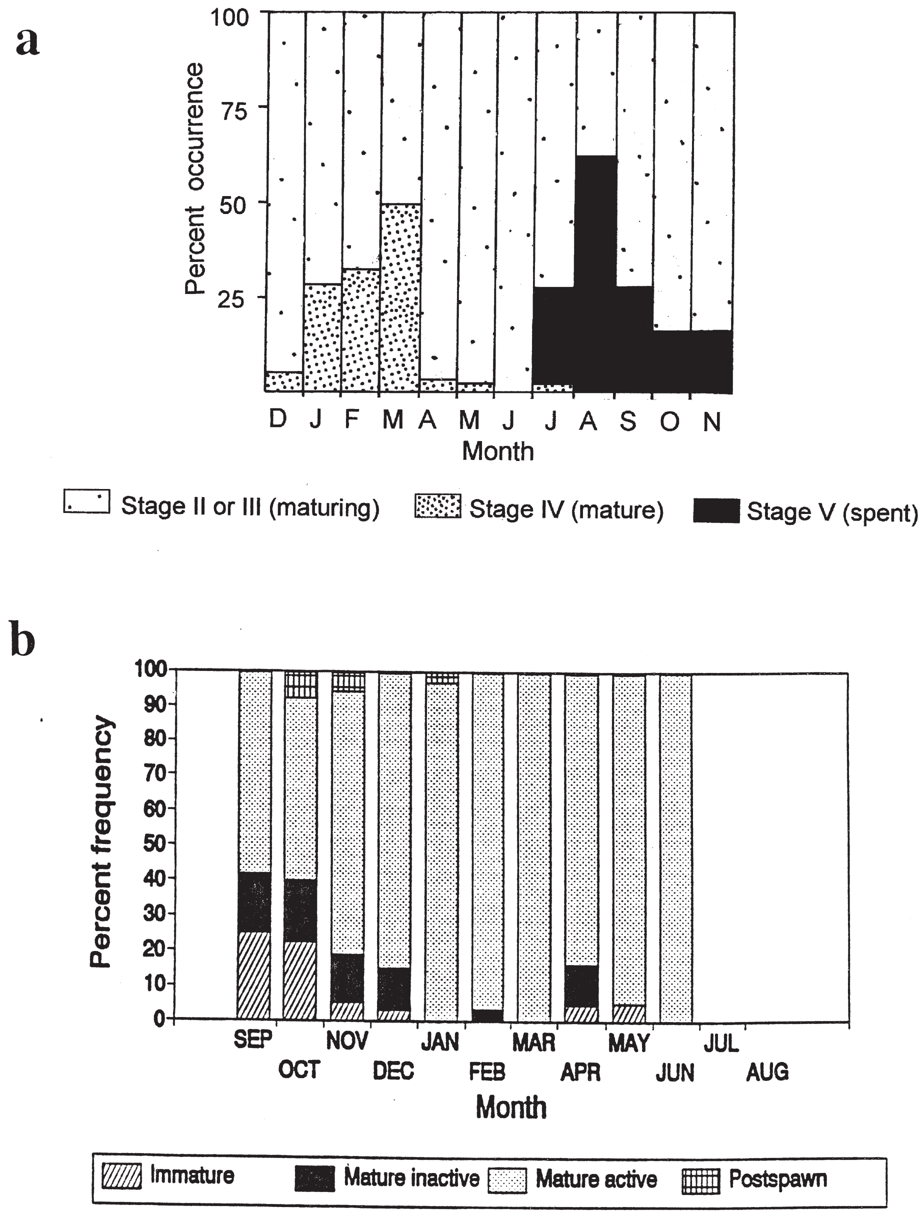


FIG. 8. – Relative frequency of each maturity stage for female dolphinfish (*Coryphaena hippurus*) from (a) Florida Current (after Beardsley, 1967), and (b) Puerto Rico (after Perez *et al.*, 1992).

In the Florida Current, the presence of very young dolphinfish throughout most of the year suggests that dolphinfish spawn there almost year-round (Gibbs and Collette, 1959; Beardsley, 1967; Shcherbachev, 1973; Fahay, 1975; Powles and Stender, 1976). Beardsley (1967) reports a spawning season from November to July with a peak in spawning activity from January to March (Fig. 8a).

In Puerto Rico, ripe females occur throughout much of the year (September-June; Perez and Sadovy, 1991; Perez *et al.,* 1992; Fig. 8b), although peak spawning events appear, from mean GSI data, to occur in March and in June (Fig. 5a).

In the Gulf of Mexico, the presence of small dolphinfish larvae year-round suggests that dolphinfish are spawning all year in the south and at least from April to December in the northern Gulf, with possible peaks in the spring and early fall (Ditty *et al.,* 1994).

In Barbados ripe and spent fish are reported to occur in all months that the dolphinfish fishery is active (November-June) and peak spawning appears, from mean GSI data, to be from May through June or possibly longer (Oxenford, 1985) (Table 6, Fig. 5b). Larval dolphinfish occur off Barbados in all months and are most common from February to May (Lao, 1989).

TABLE 6. – Percentage of mature male (Stage II) and female (Stage II, III and III) dolphinfish (*Coryphaena hippurus*) and mean sizes of both sexes observed in the pelagic fishery catch each month in Barbados (after Oxenford,1985).

Months	Nov.	Dec.	Jan.	Feb.	March	April	May	June
Females (n)	5	3	6	22	40	11	15	4
% mature	40.0	66.7	83.3	50.0	95.0	81.8	100	100
Mean size (mm SL)	683	867	848	802	897	886	937	835
Males (n)	-	-	-	20	14	7	21	12
% mature	-	-	-	10.0	28.6	57.1	76.2	75.0
Mean size (mm SL)	-	-	-	775	896	934	996	987

Location of dolphinfish spawning in the western central Atlantic is poorly documented, but presumably widely spread, based on reports of the location of ripe fish and small larvae from the southeastern USA, Gulf of Mexico, Puerto Rico and Barbados (see above). Ditty *et al*. (1994) infer from the distribution of very small (less than 7 mm) larvae in the Gulf of Mexico that spawning occurs in the oceanic waters of the Gulf rather than on the shelf there. Oxenford and Hunte (1986a) contend that maximum spawning by the proposed northeastern and southeastern Caribbean dolphinfish populations will occur when the dolphinfish are large. For the northeastern stock this will be in the vicinity of Puerto Rico at the most up-current limit of their proposed range. For the southeastern stock maximum spawning is also proposed to occur at the most up-current limit of the migration circuit, off the north coast of Brazil (Oxenford and Hunte, 1986a).

LENGTH-WEIGHT RELATIONSHIPS, GROWTH RATES AND LONGEVITY

Length-weight relationships, estimated size-at-age, growth rate and longevity data are available for dolphinfish from several locations in the western central Atlantic, and there is general agreement that dolphinfish is a short-lived (most live < 2 yr), fast-growing species (e.g. Rose and Hassler, 1968; Beardsley, 1967; Schekter, 1982; Oxenford, 1985; Oxenford and Hunte, 1983, 1986a; Bentivoglio, 1988; Rivera Betancourt, 1994).

TABLE 7. – Summary of length-weight relationships for dolphinfish (*Coryphaena hippurus*) from the western central Atlantic given in the form: $Wt = aL^b$, where Wt is weight in kg and L is fork length in mm.

Location	Sex	Range in length (mm FL)	Sample size (no. fish)	a	b	kg at 1000 mm FL	Data source
North Carolina	All	672-966	18	$2.00 \cdot 10^{-9}$	3.22	9.21	Schuck (1951)*[1]
North Carolina	Males	275-1350	176	$0.50 \cdot 10^{-7}$	2.75	8.89	Rose and Hassler (1968)
	Females	310-1275	325	$1.27 \cdot 10^{-7}$	2.59	7.76	
Florida	Males	550-1300	19	$1.45 \cdot 10^{-7}$	2.58	7.97	Beardsley (1967)*[2]
	Females	500-1225	40	$5.75 \cdot 10^{-8}$	2.71	7.60	
Puerto Rico	All	381-1479	852	$3.02 \cdot 10^{-8}$	3.49	891?	Perez *et al*.(1992)*[3]
	Males	490-1479	261	$1.78 \cdot 10^{-8}$	3.62	1289?	
	Females	445-1310	591	$5.75 \cdot 10^{-8}$	3.36	691?	
Puerto Rico	All	358-1323	332	$1.41 \cdot 10^{-8}$	2.92	8.11	Perez and Sadovy (1991)
Puerto Rico	All	381-1479	170	$3.80 \cdot 10^{-8}$	2.78	8.31	Rivera Betancourt (1994)
Cuba	All	500-1200	56	$3.21 \cdot 10^{-5}$	2.67	7.02	Garcia-Arteaga *et al*. (1997)*[4]
Barbados	All	160-1365	365	$1.45 \cdot 10^{-8}$	2.91	7.85	Oxenford (1985)
	Males	239-1365	123	$1.24 \cdot 10^{-8}$	2.94	8.31	
	Females	160-1240	207	$2.22 \cdot 10^{-8}$	2.84	7.58	

*[1] Relationship given in original text appears to be in error. Relationship given here was recalculated with data extrapolated from length-weight graph
*[2] Relationships given in original text were wrong (confirmed by pers. comm. with author on 11.5.84.). Relationships given here are recalculated from extrapolation of data shown in the length-weight graph
*[3] Relationships given in original text appear to be in error
*[4] Relationship is for length in cm

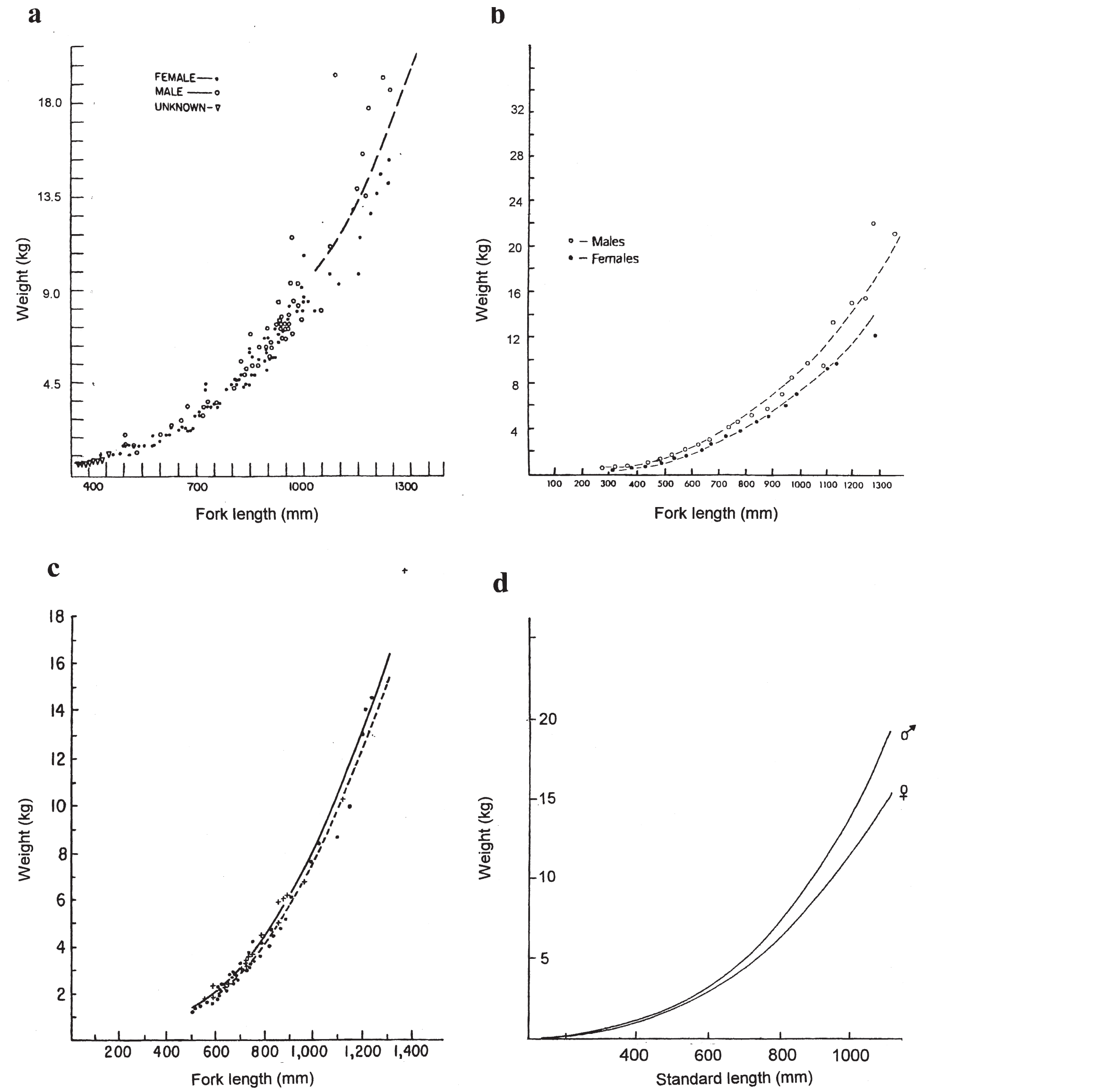


FIG. 9. – Length-weight relationships for male and female dolphinfish (*Coryphaena hippurus*) from (a) Gulf Stream (after Gibbs and Collette, 1959), (b) North Carolina (after Rose and Hassler, 1968), (c) Florida Current (after Beardsley, 1967), and (d) Barbados (after Oxenford, 1985).

Length-weight relationships

Length-weight relationships have been reported for dolphinfish from North Carolina (Schuck, 1951; Rose and Hassler, 1968), from the Gulf Stream (Gibbs and Collette, 1959), from the Florida Current (Beardsley, 1967), from Puerto Rico (Perez and Sadovy, 1991; Perez *et al.,* 1992; Rivera Bertancourt, 1994), from Cuba (Garcia-Arteaga *et al.,* 1997), and from Barbados (Oxenford, 1985), and are summarised in Figure 9 and/or Table 7. Most report larger mean size and greater weight-at-size for males than females, but there appears to be little difference in the length-weight relationships between locations (Oxenford and Hunte, 1986b) (Fig. 10).

Size-at-age and growth rates

Age and growth rates have been reported for dolphinfish from a number of locations in the western central Atlantic using scale annuli (Beardsley, 1967; Rose and Hassler, 1968), daily growth checks in otoliths (Oxenford and Hunte, 1983; Bentivoglio, 1988; Rivera Bertancourt, 1994), monthly progression of length frequency data (Oxenford and Hunte, 1983; Murray, 1985), and length or weight measurements of captive or known-age laboratory reared fish (Herald, 1961; Beardsley, 1967; Hassler and Rainville, 1975; Hagood *et al.,* 1981; Schekter, 1982; Prescod and Hunte, 1997). Although marked differences in first year growth rates occur between

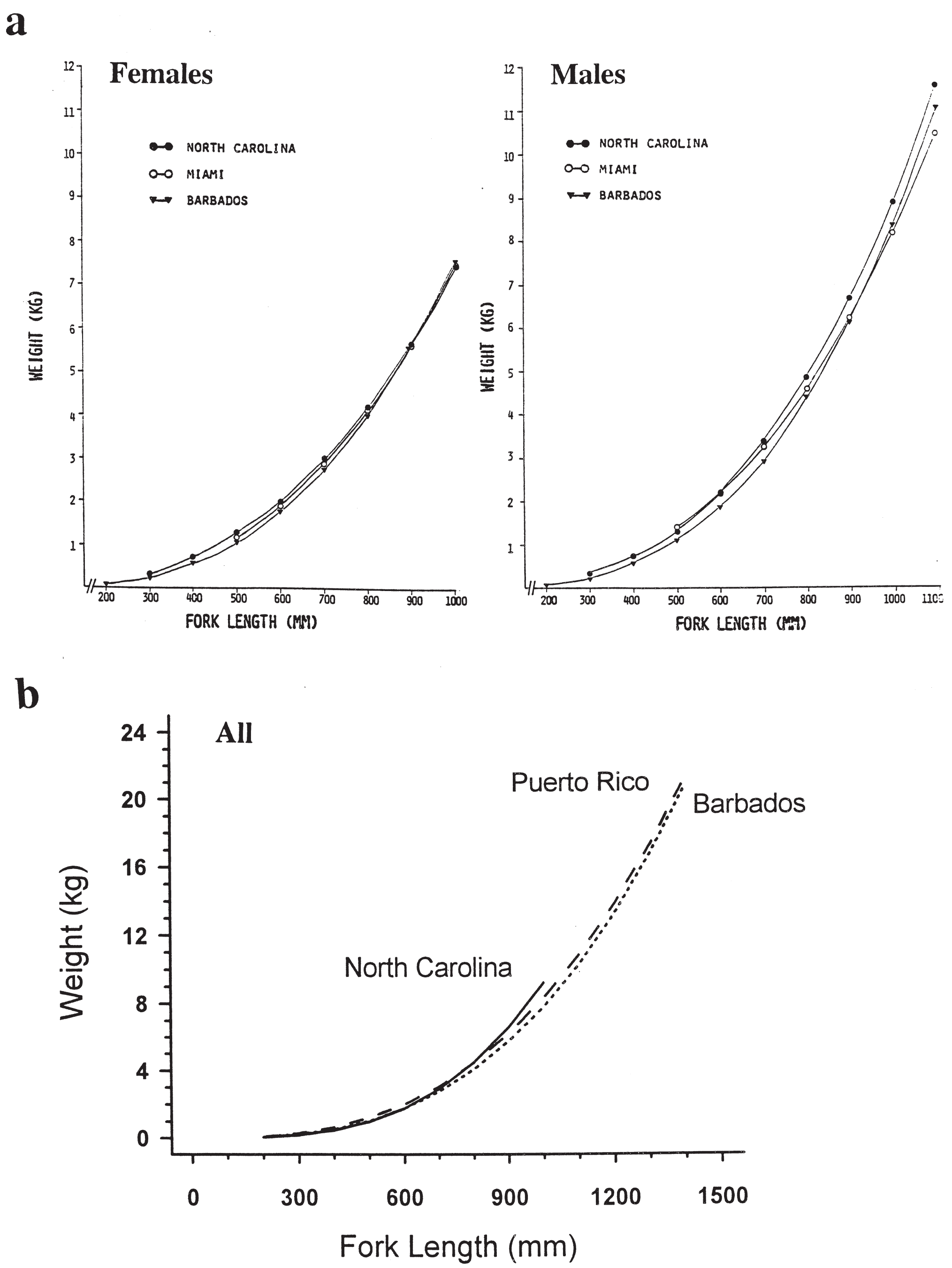


FIG. 10. – Comparison of length-weight relationships reported for dolphinfish (*Coryphaena hippurus*) in the western central Atlantic. (a) shown separately by sex (after Oxenford and Hunte, 1986b), and (b) overall (calculated from data presented by Schuck, 1951 for North Carolina, by Rivera Betancourt, 1994 for Puerto Rico, and by Oxenford, 1985 for Barbados).

locations (Table 8), there is general agreement that dolphinfish in the western central Atlantic grow extremely fast (first year growth estimates for wild fish range from 1.43 to 4.71 mm d^{-1}) and have an average longevity of less than 2 years.

In North Carolina, Rose and Hassler (1968) examined scales for annuli in 738 dolphinfish. They found 593 0-group fish (size range: 400-725 mm FL, mean: 572 mm FL), 117 I-group fish (size range: 650-1100 mm FL, mean: 868 mm FL), 20 II-group fish (size range: 900-1300 mm FL, mean: 1108 mm FL), and 8 III-group fish (size range: 1100-1430 mm FL, mean 1269 mm FL). A mean first year growth rate of 1.56 mm FL d^{-1} is inferred from these data. Rose and Hassler (1968) suggested a maximum life span of 4 yr for North Carolina dol-

TABLE 8. – Summary of first year growth rate estimates for dolphinfish *Coryphaena hippurus* from the western central Atlantic. For captive or laboratory reared fish the source of the fish is given in parentheses.

Location	No. of fish	Aging method	1st year growth rate ($mm\ d^{-1}$)	Size range examined	Data source
Gulf of Mexico	19	daily otolith checks	0.49 SL	850-1210mm SL	Bentivoglio (1988)
Laboratory reared (North Carolina)	28	days known	1.07 TL	15-101 mm TL	Hassler and Rainville (1975)
Barbados	25	daily otolith checks	1.43 SL	700-1100 mm SL	Oxenford and Hunte (1983)
Barbados	1084	progression of size frequency	1.53 SL	600-1200 mm SL	Oxenford and Hunte (1983)
North Carolina	593	scale annuli	1.56 FL	300-653 mm FL	Rose and Hassler (1968)
St. Lucia	2953	progression of size frequency	1.78 FL	693-1674 mm FL	Murray (1985)
Florida Current	121	scale annuli	1.99 FL	475-1175 mm FL	Beardsley (1967)
Puerto Rico	121	daily otolith checks	2.52 FL	550-1325 mm FL	Rivera Betancourt (1994)
Captive (Florida)	1	days known	~2.65 FL	400-1060 mm FL	Beardsley (1967)
Laboratory reared (Florida)	?	days known	~2.73 SL	0-2.5 kg	Schekter (1982)
Gulf of Mexico	81	daily otolith checks	3.88 SL	250-1210 mm SL	Bentivoglio (1988)
Captive (Florida)	2	days known	~3.91 FL	0.7-16.8 kg	Herald (1961, cited by Beardsley, 1967)
Barbados	50	daily otolith checks	4.71 SL	174-1100 mm SL	Oxenford and Hunte (1983)
Laboratory reared (North Carolina)	30	days known	~5.88 SL	0.5-5.6 kg	Hassler and Hogarth (1977)
Captive (Florida)	4	days known	~9.66 SL	0.7-5 kg	Schekter (1982)
Laboratory reared (Florida)	?	days known	2.67-3.98*	fingerlings - juv.	Prescod and Hunte (1997)

* measurement in $g\ d^{-1}$ over a maximum of 150 days

TABLE 9. – Von Bertalanffy growth curve parameters and growth performance factor (P; from Pauly, 1979) for dolphinfish (*Coryphaena hippurus*) from the western central Atlantic.

Location	Group	Growth parameters					Reference
		L_{oo} (mm)	W_{oo} (kg)	k (annual)	t_o (years)	P	
North Carolina	All	1733 FL	-	0.31	-	-	Rivera Betancourt (1994; data from Rose and Hassler, 1968)
Florida	All	1650 FL	-	0.68	-	-	Rivera Betancourt (1994; data from Beardsley, 1967)
	Males	1670 FL	-	0.53	-	-	Pauly (1978; data from Beardsley, 1967)
	Females	1350 FL	-	0.62	-	-	
Puerto Rico	All	1457 FL	-	2.19	-0.046	-	Rivera Betancourt (1994)
	Males	1381 FL	-	2.55	0.023	-	
	Females	1506 FL	-	1.82	-0.087	-	
Gulf of Mexico	All	1940 FL	-	1.12	0.033	-	Bentivoglio (1988)
	All	1427 FL	-	3.13	-	-	Rivera Bertancourt (1994; using reworked data from Bentivoglio, 1988)
Barbados	All	1208 SL	16.2	3.49	0.055	4.75	Oxenford (1985)
	Males	1260 SL	21.8	5.24	0.089	5.06	
	Females	1221 SL	16.2	3.43	0.063	4.74	
St. Lucia	All	2361 FL	-	0.53	-0.173	-	Murray (1985)

phinfish, but noted that 96% die before they are 2 years old. There are also growth rate data for dolphinfish reared in captivity from North Carolina brood stock indicating early juvenile growth of 1.07 mm TL d^{-1} (Hassler and Rainville 1975) and approximately 5.88 mm SL d^{-1} (Hassler and Hogarth 1977). Von Bertalanffy growth curve parameters were estimated by Rivera Betancourt (1994) for North Carolina dolphinfish using data from Rose and Hassler (1968) and are given in Table 9.

In Florida, Beardsley (1967) examined scales for annuli in 511 dolphinfish. He found 121 I-group fish (size range: 400-1175 mm FL, mean: 725 mm FL), 9 II-group fish (size range: 1025-1325 mm FL, mean: 1175 mm FL), 1 III-group fish (1425), and 1 IV-group fish (1525 mm FL). A mean first year growth rate of 1.99 mm FL d^{-1} is inferred from these data (Table 8). Beardsley (1967) noted that males grow faster and appear to reach larger maximum size than females. He suggested that the maximum life span for Florida dolphinfish was 4 yr, although most (98%) die before they are 2 years old. There are also growth rate data for small numbers of dolphinfish held or reared in captivity from wild caught Florida fish or Florida brood stock indicating daily growth rates of approximately 2.65 mm FL for a single fish held in the Miami Seaquarium (Beardsley, 1967); 2.73 mm SL for F_1 generation fish (Schekter, 1982); 3.91 mm FL for 2 fish held at the Florida Marineland Marine Studios (Herald, 1961; cited by Beardsley, 1967); 9.66 mm SL for 4 wild females held as brood stock (Schekter, 1982); and between 2.67 and 3.98 g (over

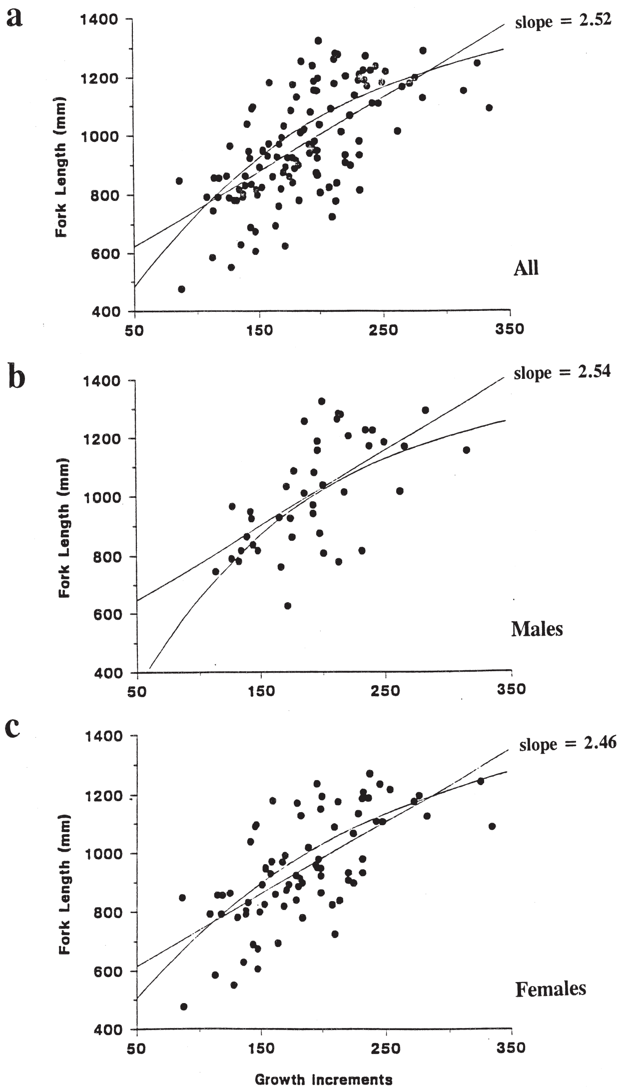


FIG. 11. – Relationship between daily growth increments in sagittal otoliths and fork length for dolphinfish (*Coryphaena hippurus*) from Puerto Rico. Slope of regression line indicates mean first year growth rate and curve indicates the von Bertalanffy growth curve for (a) all fish, (b) males, and (c) females (after Rivera Betancourt, 1994).

80 and 150 days respectively) for Florida reared fingerlings held in sea pens off the northwest coast of Barbados (Prescod and Hunte 1997) (Table 8). Von Bertalanffy growth curve parameters were estimated by Pauly (1978) and Rivera-Betancourt (1994)for Florida fish using data provided in Beardsley (1967) and are given in Table 9.

In Puerto Rico, Rivera Betancourt (1994) used daily growth checks in the sagittal otoliths of dolphinfish from 550 to 1325 mm FL, and reported an average first year growth rate of 2.52 mm FL d^{-1} (Fig. 11, Table 8). Differential growth rates between the sexes was also reported by Rivera Betancourt (1994) for Puerto Rico dolphinfish, with males growing faster (2.54 mm FL d^{-1}) than females (2.46 mm FL d^{-1}) during their first year (Fig. 11). Von Bertalanffy growth curve parameters were also provided by Rivera Betancourt (1994) for all Puerto Rico dolphinfish and for males and females separately (Table 9).

In the Gulf of Mexico, Bentivoglio (1988) used presumed daily growth checks in sagittal otoliths of dolphinfish and reported an average first year growth rate of 3.88 mm SL d^{-1} (4.15 mm FL d^{-1}) for fish of size range 250-1200 mm SL (Fig. 12), and 0.49 mm SL d^{-1} (0.61 mm FL d^{-1}) for large-sized fish (850-1200 mm SL). Bentivoglio (1988) reported a longevity of less than 1 yr. Von Bertalanffy growth curve parameters were also provided for dolphinfish from the Gulf of Mexico by Bentivoglio (1988) and by Rivera Betancourt (1994) using Bentivoglio's data (Table 9).

In the eastern Caribbean, Oxenford and Hunte (1983) did not detect any scale annuli in 558 dolphinfish from Barbados, but were able to read presumed daily growth checks in the sagittal otoliths of dolphinfish from 174-1100 mm SL, inferring an overall average first year growth rate of 4.71 mm SL d^{-1}, and an average growth rate in large fish (600-

TABLE 10. – Mortality estimates for dolphinfish (*Coryphaena hippurus*) from the western central Atlantic.

Location	Mortality parameter	Mortality model	Fish group	Instantaneous mortality (annual)	Percentage actual mortality (annual)	Reference
Gulf of Mexico	Total (Z)	Robson and Chapman (1961)	All	8.18	99.97	Bentivoglio (1988)
				8.23	99.97	
				8.67	99.98	
Barbados	Total (Z)	Ricker (1975)	All	3.93	98.03	Oxenford (1985)
		Beverton and Holt (1956)		5.84	99.71	
		Hoenig (1983)		4.22	98.53	
	Natural (M)	Pauly (1980)	All	2.56	92.23	Oxenford (1985)
			Males	3.30	96.29	
			Females	2.52	91.94	
St. Lucia	Total (Z)	Ziegler (1979)	All	3.53	97.07	Murray (1985)
	Natural (M)	Pauly (1983)	All	0.66	48.28	Murray (1985)

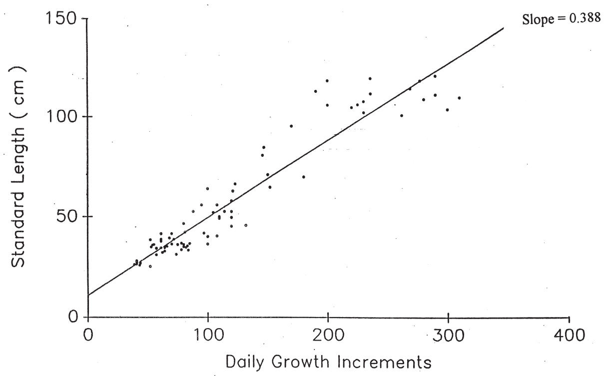


FIG. 12. – Relationship between daily growth increments in sagittal otoliths and standard length for dolphinfish (*Coryphaena hippurus*) from Gulf of Mexico. Slope of regression line indicates mean first year growth rate for both sexes (after Bentivoglio, 1988).

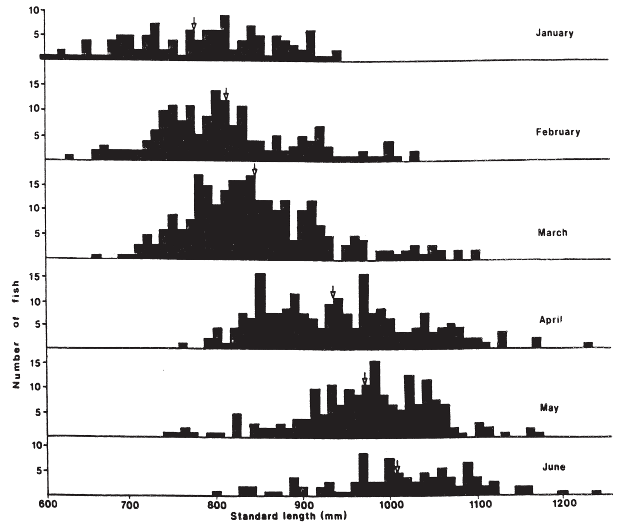


FIG. 14. – Monthly progression of length frequency distributions for adult cohort of dolphinfish (*Coryphaena hippurus*) landed by the pelagic fishery in Barbados. Arrows indicate monthly mean size (after Oxenford and Hunte, 1983).

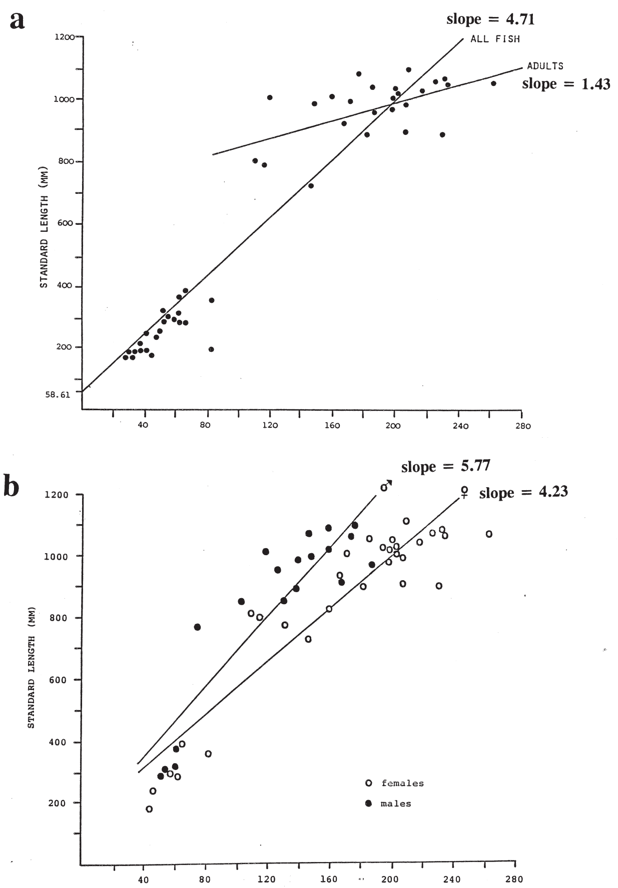


FIG. 13. – Relationship between daily growth increments in sagittal otoliths and standard length for dolphinfish (*Coryphaena hippurus*) from Barbados. Slope of regression lines indicates mean first year growth rates for (a) all fish and separately for adults (after Oxenford and Hunte, 1983), and (b) males and females separately (after Oxenford, 1985).

1200 mm SL) of 1.43 mm SL d^{-1} (Table 8, Fig. 13a). Monthly progression of the mean size of dolphinfish landed by the commercial fishery in Barbados indicated a similar growth rate (1.53 mm SL d^{-1}) for large fish (600-1200 mm SL) (Fig. 14). Differential growth rates between the sexes was also reported by Oxenford (1985) for Barbados dolphinfish, with males growing faster (5.77 mm SL d^{-1}) than females (4.23 mm SL d^{-1}) during their first year (Fig. 13b). Oxenford (1985) found no fish older than one year and concluded that Barbados dolphinfish are essentially annual, living to a maximum of around 14 months. Von Bertalanffy growth curve parameters and growth performance factor (P; from Pauly, 1979) were also provided by Oxenford (1985) for all Barbados dolphinfish and for males and females separately (Table 9, Fig. 15). Murray (1985) used the probability paper method of Cassie (1954) to examine monthly progression of size frequency data for dolphinfish landed by the commercial fishery in St. Lucia, and concluded that it was possible to follow five growth trajectories showing growth rates of between 32 and 81 mm per month. These data infer a mean growth rate for adult dolphinfish (693-1674 mm FL) from St. Lucia of 1.78 mm FL d^{-1} (Table 8). Murray (1985) also provided von Bertalanffy growth curve parameters from these data (Table 9).

Mortality rates and longevity

Athough longevity estimates have been made by several authors (see above), there are only three studies which report mortality estimates for dolphinfish from the western central Atlantic (Oxenford, 1985; Murray, 1985; Bentivoglio, 1988; Table 10).

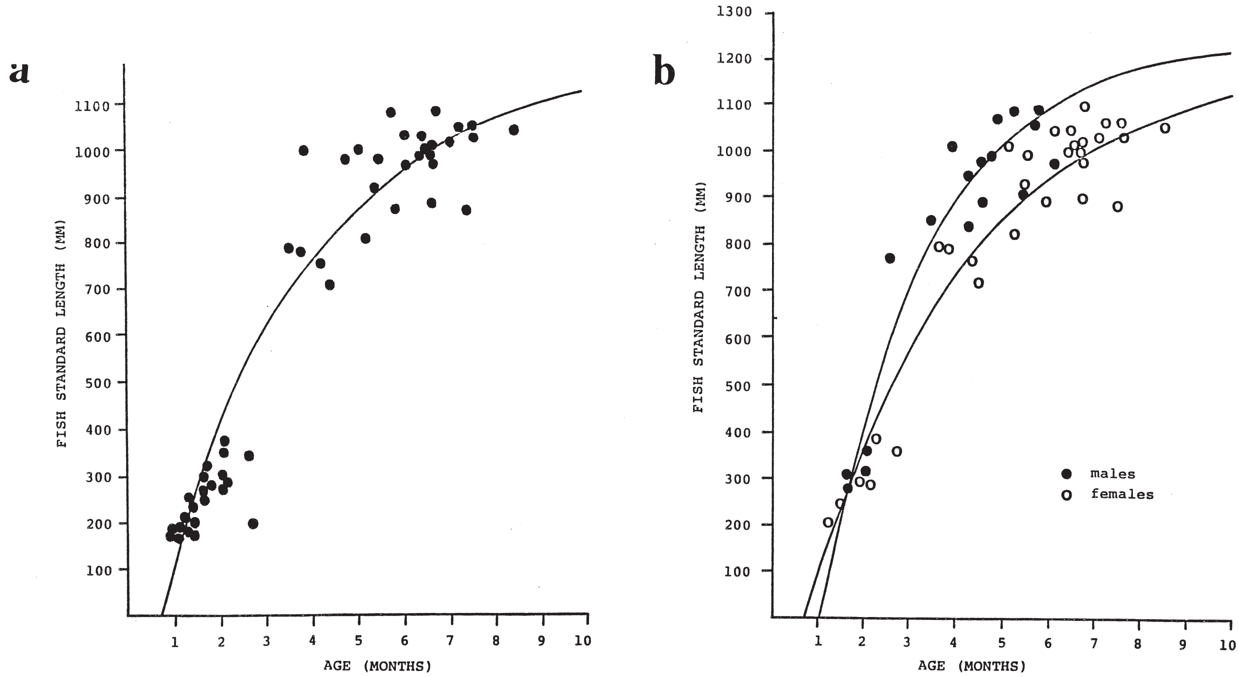


FIG. 15. – Von Bertalanffy growth curves for dolphinfish (*Coryphaena hippurus*) from Barbados showing (a) all fish, and (b) males and females separately (after Oxenford, 1985).

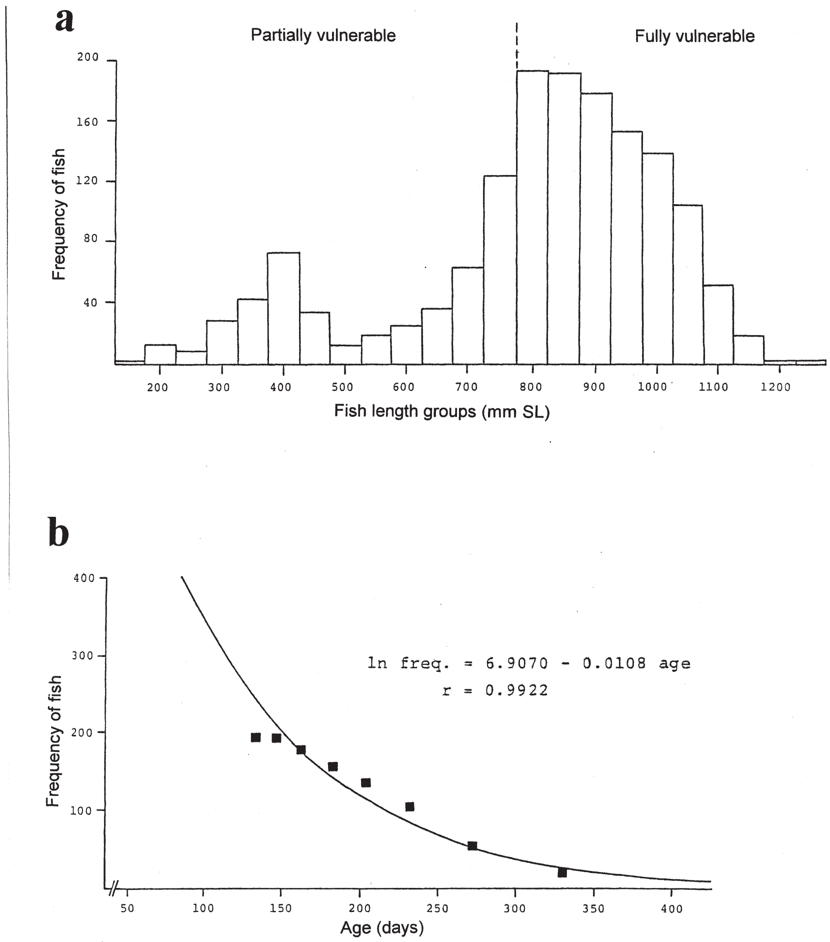


FIG. 16. – Catch data used in estimation of total mortality of dolphinfish (*Coryphaena hippurus*) from Barbados, showing (a) length frequency distribution of the dolphinfish catch taken by the pelagic fishery, and (b) catch curve derived from age-converted size frequency of fully vulnerable individuals (after Oxenford, 1985).

TABLE 11. – Dietary importance (by rank) of the five main prey categories of dolphinfish (*Coryphaena hippurus*) from the western central Atlantic, assessed by (a) numerical abundance, (b) frequency of occurrence in the stomachs, and (c) total bulk (weights, volumes or lengths).

(a). Numerical abundance

Location		Southeastern and Gulf states of USA	Gulf Stream	North Carolina	Barbados	Barbados
Data source		Manooch *et al*. (1984)	Gibbs and Collette (1959)	Rose and Hassler (1974)	Lewis and Axelsen (1967)	Oxenford and Hunte (1999)
No. dolphinfish		2219	46	396	70	397
Fish	Ammodytidae	.	3	.	.	.
	Balistidae	1	5	3	4	4
	Carangidae	5	.	2	.	.
	Coryphaenidae	.	.	4	.	.
	Dactylopteridae	.	.	.	1	1
	Exocoetidae	.	.	.	3	3
	Gempylidae	.	1	.	.	.
	Monacanthidae	.	.	.	2	.
	Nomeidae	.	.	.	5	.
	Ostraciidae	.	.	5	.	.
	Scombridae	.	2	.	.	.
	Syngnathidae	3	.	.	.	.
	Tetraodontidae	.	4	.	.	.
Invertebrates	Cephalopoda	.	.	.	.	5
	Decapoda	4	.	1	.	.
	Mysidacea	.	.	.	.	2
	Stomatopoda	2	.	.	.	.

(b). Frequency of occurrence

Location		Southeastern and Gulf states of USA	Gulf Stream	North Carolina	Barbados	Barbados
Data source		Manooch *et al*. (1984)	Gibbs and Collette (1959)	Rose and Hassler (1974)	Lewis and Axelsen (1967)	Oxenford and Hunte (1999)
No. dolphinfish		2219	46	396	70	397
Fish	Balistidae	1	3	2	4	3
	Carangidae	4	5	1	.	.
	Dactylopteridae	.	.	.	2	1
	Exocoetidae	5	.	4	1	2
	Monacanthidae	.	4	.	3	.
	Tetraodontidae	.	.	.	.	5
Invertebrates	Cephalopoda	3	1	5	5	4
	Decapoda	2	2	3	.	.

(c). Total bulk (weights, volumes or lengths)

Location		Southeastern and Gulf states of USA	North Carolina	Barbados
Data source		Manooch *et al*. (1984)	Rose and Hassler (1974)	Oxenford and Hunte (1999)
No. dolphinfish		2219	396	397
Fish	Balistidae	3	4	4
	Carangidae	4	3	.
	Coryphaenidae	1	5	.
	Dactylopteridae	.	.	1
	Diodontidae	5	.	.
	Exocoetidae	2	1	2
	Scombridae		2	.
	Trichiuridae	.	.	5
Invertebrates	Mysidacea	.	.	3

For Gulf of Mexico dolphinfish, Bentivoglio (1988) used the Robson and Chapman (1961) least squares method to estimate mortality rates from otolith-aged specimens using various time intervals to obtain a range of total instantaneous mortality values (Z) between 8.18 and 8.67, which suggest actual annual mortality rates of between 99.97 and 99.98% (Table 10).

For eastern Caribbean dolphinfish, Oxenford (1985) used the size structure of dolphinfish taken by the commercial pelagic fishery in Barbados (Fig. 16a) and size-at-age data (Fig. 15a) to determine the size/age at which dolphinfish become fully vulnerable to the fishery (775 mm SL, 4 mo), and to construct a catch curve (Fig. 16b) and estimate an annual instantaneous total mortality (Z = 3.9). Oxenford (1985) also provided alternative estimates of Z using: the relationship of Beverton and Holt (1956) and an average size of 937 mm SL for fully vulnerable fish; and the relationship of Hoenig (1983) and an estimated t_{max} of one year (Table 10). All estimates predict an actual total annual mortality (A) of between 98.0 and 99.7% (Table 10). Oxenford (1985) also provided estimates of natural mortality for dolphinfish from Barbados, using the empirical formula of Pauly (1980), a mean water temperature of 28°C and von Bertalanffy parameters for all fish (L_{oo} = 155.9 cm TL, annual k = 3.49) (Table 10).

Murray (1985) used the catch curve method of Ziegler (1979) to estimate an annual instantaneous total mortality (Z = 3.53) for dolphinfish from St. Lucia, predicting an actual total annual mortality (A) of 97.1% (Table 10). Murray (1985) also provided an estimate of natural mortality for dolphinfish from St. Lucia, using the empirical formula of Pauly (1983), a mean water temperature of 27.5°C and von Bertalanffy parameters for all fish (L_{oo} = 236.1 mm TL, annual k = 0.532) (Table 10).

The estimates of total mortality for eastern Caribbean dolphinfish are very similar. However, the natural mortality estimates differ markedly, as a result of using an empirical formula dependent on very different estimates of growth curve parameters for Barbados and St. Lucia dolphinfish. Given that the growth curve for Barbados dolphinfish was estimated from size-at-age using otolith increments over a wide size range of fish (174-1100 mm SL), and the St. Lucia growth curve was estimated from monthly progression of size frequencies of adult fish only (693-1674 mm FL), the former is likely to be more representative.

PREY AND PREDATORS

Diet

Several authors have commented on the diet of dolphinfish from the western central Atlantic (e.g. from the Atlantic: Shcherbachev, 1973; southeast and Gulf coast of the USA: Manooch *et al.,* 1984; North Carolina: Schuck, 1951; Rose and Hassler, 1974; Gulf Stream: Gibbs and Collette, 1959; Barbados: Lewis and Axelsen, 1967; Oxenford, 1985; Oxenford and Hunte, 1999). The relative importance of prey items to dolphinfish reported by these studies is summarised by ranking the top 5 prey items according to frequency of occurrence; numerical abundance; and bulk in Table 11. Larval dolphinfish feeding habits have also been reported by Schekter (1972) who examined 11 specimens (size range 5.8 - 37.3 mm) from the Florida Current, and found 146 prey items in their stomachs (85 copepods, 49 invertebrate eggs, 2 fish and 10 unidentified objects). All studies agree that dolphinfish feed on a wide variety of fish and invertebrates, including: juveniles of large oceanic epipelagic species; juveniles and adults of small oceanic epipelagic species; juveniles and adults of mesopelagic species that demonstrate diurnal migrations to the surface; and pelagic larvae and juveniles of neritic benthic species. This suggests that dolphinfish probably forage opportunistically rather than selectively, a feeding strategy that appears to be common among tropical pelagic species.

A comparison of diets by frequency of occurrence of prey items in dolphinfish stomachs is also given in Fig. 17 for dolphinfish from the southeastern and Gulf states, North Carolina, Gulf Stream and Barbados. It is apparent that there are geographical differences in the diet, which probably reflect differences in availability of prey items, rather than differential selection by dolphinfish from different locations. It is interesting that there is a fairly strong similarity in the diets of dolphinfish from Barbados reported by different studies conducted 18 yr apart.

Two studies (Manooch *et al.,* 1984; Oxenford and Hunte, 1999) calculated indices of relative importance (IRI) for prey items of dolphinfish, to give a less biased assessment of the diet, and these are given in Table 12 for dolphinfish from the southeastern and Gulf coasts of the USA, and for Barbados.

Variations in the diet of dolphinfish have been associated with predator size (Shcherbachev, 1973; Rose and Hassler, 1974; Manooch *et al.,* 1984; Oxenford and Hunte, 1999), with predator sex (Oxenford and Hunte, 1999), and with season (Manooch *et al.,* 1984; Oxenford and Hunte, 1999).

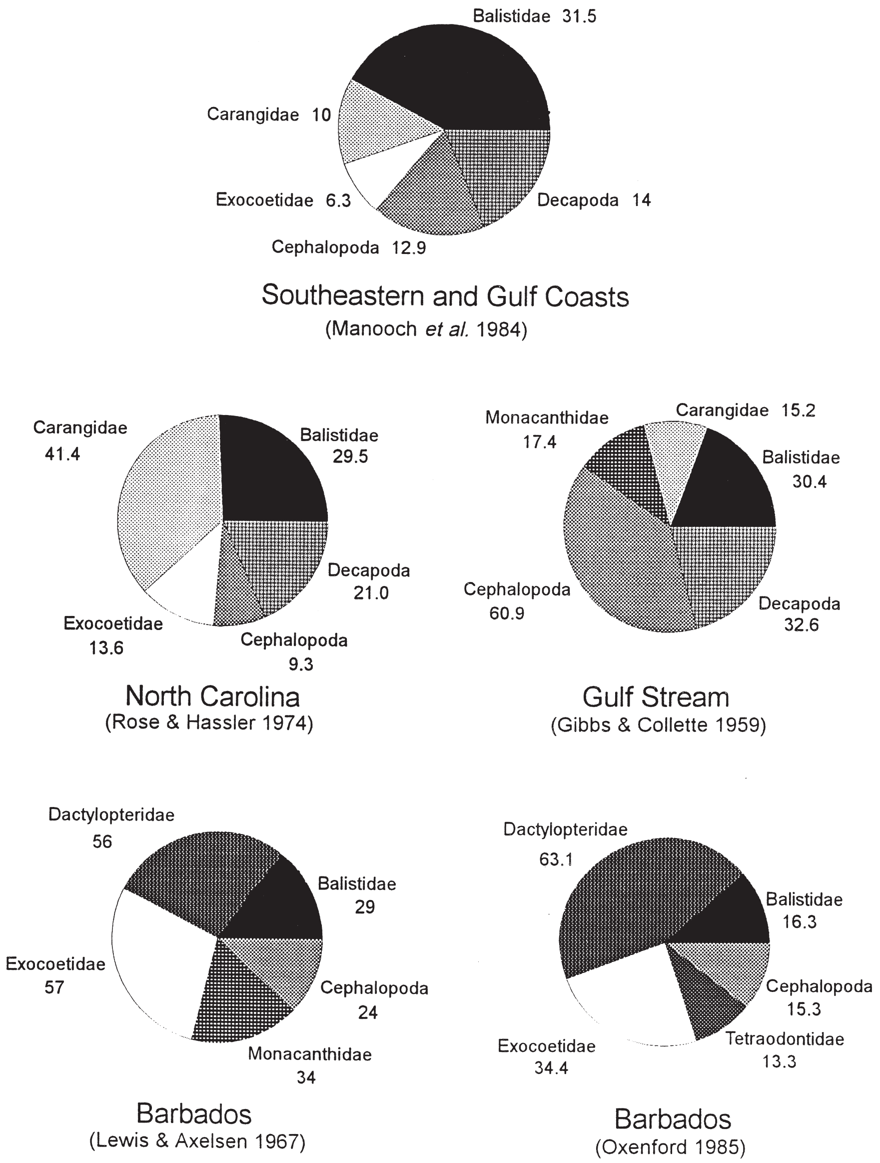


FIG. 17. – Comparisons of dolphinfish (*Coryphaena hippurus*) diets from the western central Atlantic based on percent frequency of occurrence of the major prey items in stomachs. Data sources are shown in parentheses.

Predators

The diets of other oceanic pelagic species indicate that dolphinfish, particularly juveniles, serve as prey for many oceanic fish. Their predators include large tuna (Parin, 1968; *Thunnus alalunga*: Murphy, 1914; *T. albacares*: Penrith, 1963; Dragovich and Potthoff, 1972; Takahashi and Mori, 1973; Matthews *et al.*, 1977), sharks (Parin, 1968; *Hexanchus griseus*: Bigelow and Schroeder, 1948), marlin (Sund and Girigorie, 1966; Parin, 1968; *Makaira nigircans*: Farrington, 1949; Takahashi and Mori, 1972; *Tetrapturus albidus*: Wallace and Wallace, 1942; Nakamura, 1971; Nakamura and Rivas, 1972; *T. audax*: Abitia-Cardenas *et al.*, 1997), sailfish (*Istiophorus platypturus*: Beardsley *et al.*, 1972; Takahashi and Mori, 1973) and swordfish (*Xiphias gladius*: Gorbunova, 1969).

MOVEMENTS, MIGRATION AND STOCK STRUCTURE

Dolphinfish are considered to be highly migratory, being only seasonally abundant over most of their range in the western central Atlantic (Table 1). However, for an oceanic pelagic species, it is relatively small (maximum size 200 cm TL and 25 kg),

TABLE 12. – Relative dietary importance of the main prey categories of the dolphinfish (*Coryphaena hippurus*) from the southeastern and Gulf states of the USA (after Manooch *et al*., 1984), and Barbados (after Oxenford and Hunte, 1999). IRI - index of relative importance.

Prey category	IRI rank Southeastern and Gulf States of USA	IRI rank Barbados
Dactylopteridae	.	1
Exocoetidae	4	2
Mysidacea	.	3
Balistidae	1	4
Cephalopoda	5	5
Tetraodontidae	11.5	6
Trichiuridae	.	7
Coryphaenidae	7	8
Carangidae	2	9
Monacanthidae	.	10
Diodontidae	9	11
Scombridae	10	12
Decapoda	3	.
Stomatopoda	8	.
Syngnathidae	6	.
Stomateidae	11.5	.

short-lived (essentially an annual species) and tends to approach coastal waters. It is therefore likely to have a more complex stock structure (i.e. a larger number of smaller stocks with more localised migration circuits) than has been proposed for many of the larger highly migratory truely oceanic species such as the marlins, swordfish and large tunas (e.g. yellowfin, bigeye, albacore) which grow to sizes in excess of 100 kg, are long-lived (> 6 yr) and are considered to have between one and three Atlantic-wide stocks (Oxenford, in press).

Movements and migration patterns

Palko *et al*. (1982) report that migrations and movements of dolphinfish are likely to be affected by the movement of drifting objects on the high seas, with which they are often closely associated. Direct evidence of dolphinfish movements within the western central Atlantic are very limited. Although tagging programmes have included dolphinfish in the western central Atlantic (e.g. Rose and Hassler, 1968; NMFS, 1996; CFRAMP, pers. comm.), sample sizes have either been very small or results of dolphinfish tag recaptures have not been published in the primary literature. However, several authors have proposed migration hypotheses for dolphinfish.

Oxenford and Hunte (1986a) proposed two migration circuits in the northeast and southeast Caribbean, based largely on seasonality of the dolphinfish fisheries by location and mean size at capture. They suggest a northeastern migration circuit incorporating the northern Caribbean islands, the southeastern United States and Bermuda, and a southeastern circuit incorporating the southeastern Caribbean islands and the north coast of Brazil (Fig. 18). Dolphinfish following the northeastern circuit are believed to travel northwestwards from around Puerto Rico in February through the Bahamas in April/May, to Florida and Georgia by May/June, South and North Carolina by June/July, and then onwards in a southeasterly direction into the Atlantic, passing Bermuda in July/August and

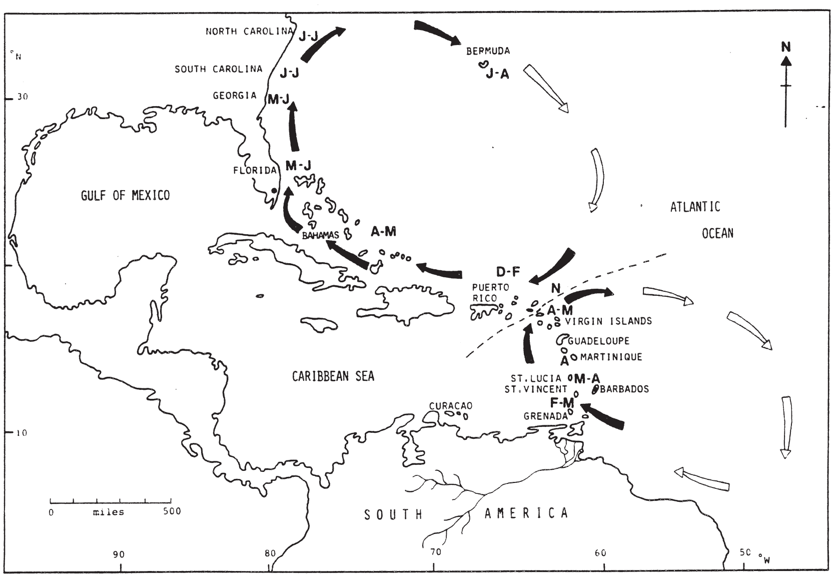


FIG. 18. – Proposed migration circuits and locations of putative northeastern and southeastern Caribbean dolphinfish (*Coryphaena hippurus*) stocks in the western central Atlantic (after Oxenford and Hunte, 1986a). Dark arrows indicate segments of the circuits for which seasonality and size data are available; clear arrows indicate areas where no data are available.

reaching the Virgin Islands and Puerto Rico again by November/December. Dolphinfish following the southeastern circuit are believed to travel northwards, passing Grenada in February/March, St. Vincent, Barbados, St. Lucia and Martinique in March/April, Dominica and the Virgin Islands in April/May and then onwards in a southeasterly direction into the Atlantic and back down to the northeast coast of South America.

Part of the proposed northeastern circuit is supported by Mather (pers. comm., cited by Rose and Hassler, 1968), who reported 2 tag recaptures showing displacement from the Florida coast 97 km and 260 km northwards. Additional support for this hypothesis is also found in Beardsley (1967), who reported that dolphinfish probably move northward from Florida during spring and summer, and in Gibbs and Collette (1959), who suggested that the spring abundance of dolphinfish in northern Caribbean islands (Virgin Islands and Puerto Rico) may be a prespawning migration, mainly by females. The proposed south to north migration of dolphinfish along the Atlantic coast of the USA is strongly supported in some years by observed patterns of peak occurrence in the sport fisheries (Palko *et al.,* 1982). However, in other years their CPUE data for the sport fishery support a synchronised offshore to onshore movement of dolphinfish, possibly reflecting the differences in the distance of blue water from the shore (Palko *et al.,* 1982). Perez *et al.* (1992) suggest an alternative westerly migration route for the southeastern dolphinfish population, based on the observation of a second peak in abundance of dolphinfish in Puerto Rico. They suggest that the southeastern population would pass the Virgin Islands and southern Puerto Rico during April/May and migrate either southwest into the Caribbean Sea or westward into the Gulf of Mexico. In the Gulf of Mexico, CPUE data from the sport fishery indicates an offshore-onshore movement of dolphinfish (Palko *et al.,* 1982).

Stock structure

There has been one preliminary investigation of dolphinfish stock structure within the western central Atlantic, which suggests that there are at least two separate unit stocks in the Caribbean Sea, located in the northeast and southeast (Oxenford and Hunte, 1986a). The hypothesis was based on: observed seasonality (months of peak abundance) and mean size of dolphinfish from commercial and sport fisheries (which suggested two different migration circuits; Fig. 18); a comparison of life history characteristics of dolphinfish from North Carolina, Florida and Barbados (which showed marked differences in average first year growth rates, fecundity-length relationships, size and age at first maturity, and mean mature egg size); and observed differences in allelic frequencies at the IDH-2 locus determined through electrophoresis.

Possible alternative hypotheses of (1) a generalised north-south movement of a broadly distributed population, and (2) a seasonal onshore-offshore movement, have been suggested by Mahon and Mahon (1987). However, no alternative stock structure hypothesis has yet been tested. The proposed location of the boundary between the putative contiguous stocks remains unclear. For example, Perez and Sadovy (1991) noted two abundance peaks and differences in the mean size of dolphinfish landed on the north and south coasts of Puerto Rico and suggested that two populations may be present seasonally in Puerto Rico. However, a comparison of reproductive traits between dolphinfish landed on the north and south coasts of Puerto Rico failed to detect differences between them (Perez *et al.,* 1992). Furthermore, a comparison of growth rates of dolphin occurring on the north and south coasts of Puerto Rico failed to find expected differences, and were similar to growth rates of the southeastern stock (Rivera-Betancourt, 1994). Three explanations were proposed by Rivera Bertancourt (1994): (i) that Puerto Rico dolphinfish represent the northern extreme of the southeastern stock, (ii) that Puerto Rico dolphinfish belong to a smaller intermediate stock, or (iii) that age and growth studies for the northern study were flawed and that there is only a single stock.

The existence of additional stocks particularly within the Gulf of Mexico and central/western Caribbean is very likely, but has not been investigated. This remains a high priority issue for resolution, if appropriate stock assessments are to be conducted and management strategies are to be developed for dolphinfish in the western central Atlantic.

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