

Abstract.—The age and growth of dolphin, *Coryphaena hippurus*, has been determined in wild specimens between 14.4 and 124 cm fork length (FL) caught off Majorca (Balearic Islands, western Mediterranean). Also, several methods have been applied to validate the results obtained and to assess the aging techniques presently used. In accordance with the sexual dimorphism of this species, the length–weight relationship showed negative allometry in females and isometry in males. The high correlation between increment counts and known age in 75 reared larvae from 0 to 38 days old (number of increments = $0.3894 + 0.9846 \cdot \text{days of age}$; $r=0.98$) indicated that the daily deposition of growth increments in sagittal otoliths and regular incremental formation begins on day one. This correlation validated the use of otoliths in the aging of 176 juvenile specimens between 16.5 and 58.5 cm FL, in which the minimum and maximum ages observed were 47 and 176 days, respectively. Nevertheless, the progressive increase in complexity with the ontogenetic development of these structures suggests that this method may underestimate age in adult fish, probably owing to the loss of marginal zones of the otolith during the polishing process. Thus, from 150 specimens between 65 and 124 cm FL, the interpretation of annuli from scales gave ages up to 3 years old, whereas readings of otoliths in 36 specimens of the same size interval gave ages between 0 and 1 year old. Growth parameters were calculated from the age–length relationships of otolith and scale readings in juvenile and adult fish, respectively, and from the analysis of monthly length–frequency distributions, obtained in 1990 and 1991 during the exploitation of juveniles from 18 to 70 cm FL ($n=4084$). The values obtained for L_{∞} ranged from 72.4 cm FL in unsexed juveniles and 110.0 cm FL in females both juvenile and adult, whereas k ranged from 1.6/year in juvenile and adult females and 2.5/year in unsexed juveniles. Although the results obtained were quite different owing to the different length and age range considered, similar results were obtained by comparing the growth performance index (F), and showed the rapid growth of the species.

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Otolith microstructure, age, and growth patterns of dolphin, *Coryphaena hippurus*, in the western Mediterranean

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Dolphin (*Coryphaena hippurus* Linnaeus, 1758) (Pisces: Coryphaenidae) is an epipelagic, top-level predator species widely distributed in the tropical regions of every ocean (Palko et al., 1982). It migrates widely, and in warmer months increases its range to subtropical areas. Thus, it occurs seasonally in the Mediterranean from spring to autumn, when surface waters reach temperatures above 16–18°C (Massuti and Morales-Nin, 1995); mature specimens are occasionally caught in the swordfish (*Xiphias gladius*) fishery with surface longlines at this time, and immature juvenile fish are exploited by small-scale fisheries that deploy surrounding purse nets around fish aggregation devices.

Dolphin age and growth have been determined by means of scale annuli (Beardsley, 1967; Rose and Hassler, 1968), daily growth increments in otoliths (Oxenford and Hunte, 1983; Uchiyama et al., 1986), and modal progression analysis (Wang, 1979; Murray, 1985). In addition, some growth studies have been made of fish of known age reared in captivity (e.g. Hassler and Hogarth, 1977; Ostrowski et al.,

1989; Benetti et al., 1995b). In the Mediterranean, available growth data on this species are related to morphometric relationships (Lozano-Cabo, 1961; Bannister, 1976) and rearing experiments (Reñones et al., 1992; Ayari et al., 1995).

The objective of this paper was to determine, for the first time in the Mediterranean, the age and growth patterns (including juvenile and adult phases) of *C. hippurus*. To support age and growth parameters estimated from readings of scales and otoliths, direct validation by means of rearing experiments and indirect validation based on length–frequency analysis were also applied. Otolith microstructure was analyzed to determine increment patterns and morphological changes during growth and to obtain more precise increment counts.

Material and methods

From May to November 1990 and 1991, fork lengths (FL) of adult specimens ($n=150$) were measured from longline catches. Sex was determined on the basis of the sexual dimorphism of the species (Palko et

al., 1982). Scales were collected above the lateral line, at the level of the pectoral fin, cleaned with 5% KOH, and mounted on slides. Interpretation of scale rings was carried out with a projector at 10× magnification by using the method described by Beardsley (1967). The scarcity of adult fish prevented the use of age validation methods; therefore the annual nature of the rings was established from validated ages from other areas (Beardsley, 1967; Rose and Hassler, 1968). Juvenile fish ($n=4084$) were measured from 65 samplings made between August and December of the same years from small-scale fishery catches. Total weight and sex were recorded for subsamples (adults $n=68$, juveniles $n=282$) selected to cover the size distribution of both sexes. Sagittal otoliths were removed, cleaned, and stored in distilled water. Unbroken otoliths ($n=212$) were embedded in epoxy resin and polished with a graded series of sandpaper and, finally, with 0.3- μm alumina paste. To improve clarity, otoliths were moistened with immersion oil for several hours before reading.

Otoliths have a complex structure, with convex sides, pronounced rostrum and antirostrum, and a demarcated sulcus that terminates in a V-shaped excisural notch (Oxenford and Hunte, 1983). We selected the dorsal side of the otolith to obtain a section with a complete increment sequence. Otoliths were read under a light microscope coupled to a high-resolution video camera and monitor system. Growth increments were counted from the core to the edge of the pararostrum (Oxenford and Hunte, 1983). Incremental counts were made by beginning at the first clearly defined mark that encircled the primordium, which defines the outer edge of the nucleus. Growth increments in juvenile fish otoliths were enumerated along a single axis. In adult fish it was necessary, however, to follow a circuitous path to complete a set of counts, following prominent increments laterally until an area with clear increments was found. Each otolith was read independently by two of the authors; results were accepted only if the readings were coincident or their difference was less than 5%. Growth increments were counted at 500× and verified at 1000×. Microstructural growth increments were studied on fish of 22–43 cm FL ($n=28$) with a scanning electron microscope (SEM). To highlight increment zones, the polished sections were etched for 30 seconds with a 0.1 N HCl solution, or for 60–90 seconds with a 0.2 M EDTA solution.

Von Bertalanffy growth parameters were estimated from age–length relationships obtained from scale and otolith readings by using the FISHPARM program (Prager et al., 1987). These parameters were validated by an independent length-based method by using the ELEFAN I procedure included in the ELEFAN software package (Gayanillo et al.¹). Be-

cause L_{∞} and k are inversely correlated, the growth performance index ($\Phi = 2\log L_{\infty} \log k$) was employed to compare growth rates (Munro and Pauly, 1983).

The temporal relation between ring number and age was determined by using larvae of known age, obtained from eggs spawned in captivity. Larvae hatched on 25 July 1994 and were reared through the juvenile stage up to 38 days, according to the method described by Kraul (1989). Water temperatures during the experiment ranged from 26° to 27°C, within the range of water surface temperature found around the Balearic Islands from June to August, when the species spawns (at 24–27°C; Massutí and Morales-Nin, 1995). The presence of early larval stages has also been reported in the study area during this period (Alemany and Massutí, 1998).

To establish the timing of first ring deposition and early otolith growth, larvae were sampled daily during the first 15 days. Afterwards, three samples were taken at intervals of 7–8 days until the juveniles were 38 days old. Larvae were preserved in buffered alcohol. The standard length (SL) of each larva was measured, and sagittal otoliths ($n=93$) were removed, cleaned, and mounted on slides with epoxy resin. The otoliths were read with an image analysis system connected to a microscope. An iterative semiautomatic system was employed for detection of increments, measurement of otolith radius, and age attribution. Increment clarity was improved by using polarized light, and enhanced digitized images were used for interpretation. Each otolith was read at least twice at 1000× magnification with an oil lens.

Daily periodicity of increments in reared specimens was validated by linear regression analysis of the relation between counts of otolith increments and days. The intercept and the slope were examined with Student's t -test. This method was also used to test the isometry in the allometric indices obtained by applying exponential regression equations to the length–weight relationships.

Results

The parameters of the length–weight relationship for females, males, and the whole population, including unsexed specimens, are shown in Table 1. Isometric growth was found in males (t -test; $P>0.05$), but for females and the population as a whole, a negative allometry was found (t -test; $P<0.01$).

¹ Gayanillo, F. C., M. Soriano, and D. Pauly. 1988. A draft guide to the complete ELEFAN. ICLARM Software Project 2, 70 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

Table 1

Length–weight relationship parameters estimated by exponential regression equations ($y = ax^b$) between fork length (cm) and total weight (g) in *Coryphaena hippurus*. n = number of specimens; SE = standard error of slope; r = correlation coefficient.

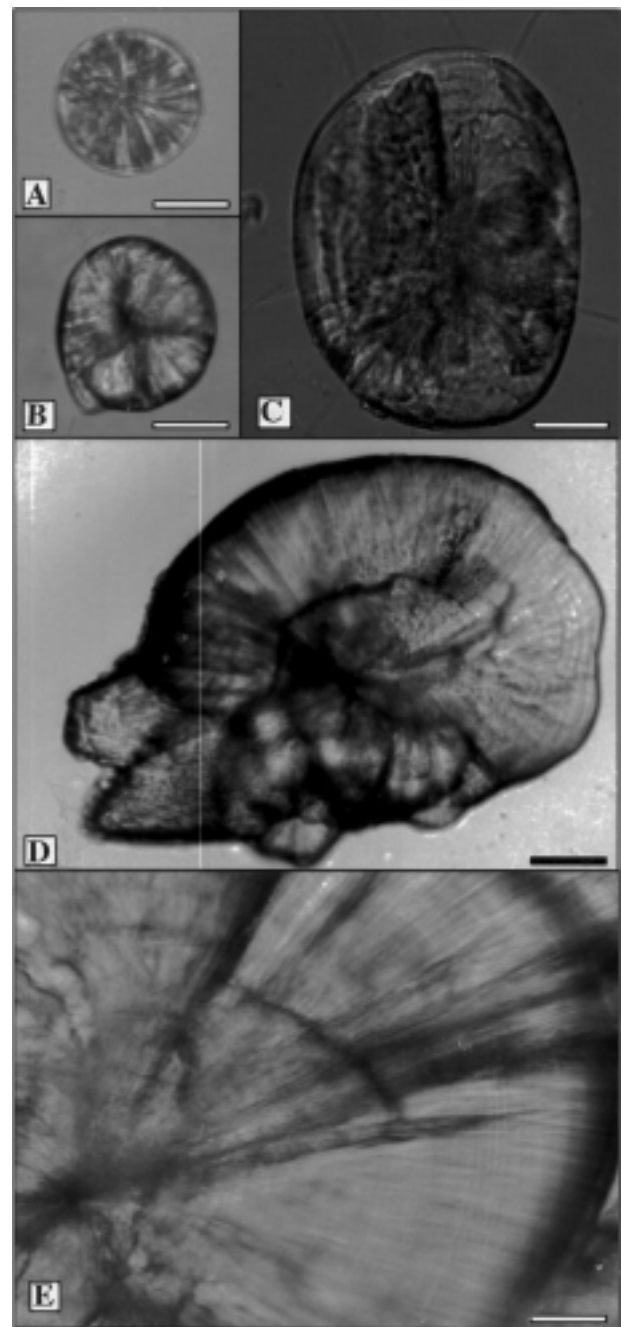
Population	n	a	b	SE	r
Females	192	0.0139	2.8983	0.0011	0.997
Males	154	0.0092	3.0187	0.0018	0.996
Total	350	0.0113	2.9605	0.0007	0.996

The sagittae of *C. hippurus* are small in relation to fish size and generally butterfly-shaped, although they display different structural patterns with ontogenetic development. The larval otoliths are round and the development of the rostrum starts at 8 days (Fig. 1, A and B). The sulcal structure is formed in 12-day-old larvae (Fig. 1C); the rostrum and antirostrum were, on average, separated in 17-day-old larvae (Fig. 1D).

Otoliths prepared for SEM observation showed differences depending on the etching agent. The otoliths etched with EDTA had less clear growth increments than did otoliths etched with HCl. These differences might be due to high protein content in the otoliths, which collapsed when the aragonite crystals were completely removed with EDTA. Whole otoliths showed the presence of concentric laminations or ridges (Fig. 2A) which revealed that the core region grew by the deposition of successive layers on the inner side. Sections of otoliths showed the typical pattern of incremental and discontinuous units, which formed growth increments with variable widths depending on the otolith area (Fig. 2, B and C). Some rhythmic patterns were also evident with 7–14 increment groupings (Fig. 2, B and D).

Under the light microscope, otoliths revealed a pattern of alternating light and dark concentric rings surrounding a core, which was deposited at the earliest stages of development (Fig. 3A). The width of the increments varied from the core to the edge, with narrow increments near the center of the otolith and at the edge, whereas wider ones were laid down from the first to the third month of life (Fig. 3, B and C). These differences in increment width may reflect periods of differential growth. Larger increment patterns, or bands composed of groups of 7–14–28 increments, were also observed (Fig. 3B), suggesting lunar growth rhythms.

From 93 reared larvae of known age, a total of 75 otoliths (81%) could be read under the light micro-

**Figure 1**

Photomicrographs of sagittal otoliths from *Coryphaena hippurus* larvae reared in captivity: (A) 6-day-old larvae of 6.1 mm SL (scale bar=25 μ m); (B) 8-day-old larvae of 8.5 mm SL (scale bar=29 μ m); (C) 12-day-old larvae of 8.8 mm SL (scale bar=34 μ m); (D) 17-day-old larvae of 30 mm SL (scale bar=56 μ m). (E) Poorly defined increments laid down around the core (scale bar=90 μ m).

scope. These larvae measured 3.8–65.0 mm SL, and their otolith radii ranged from 10.7 mm (at day 0,

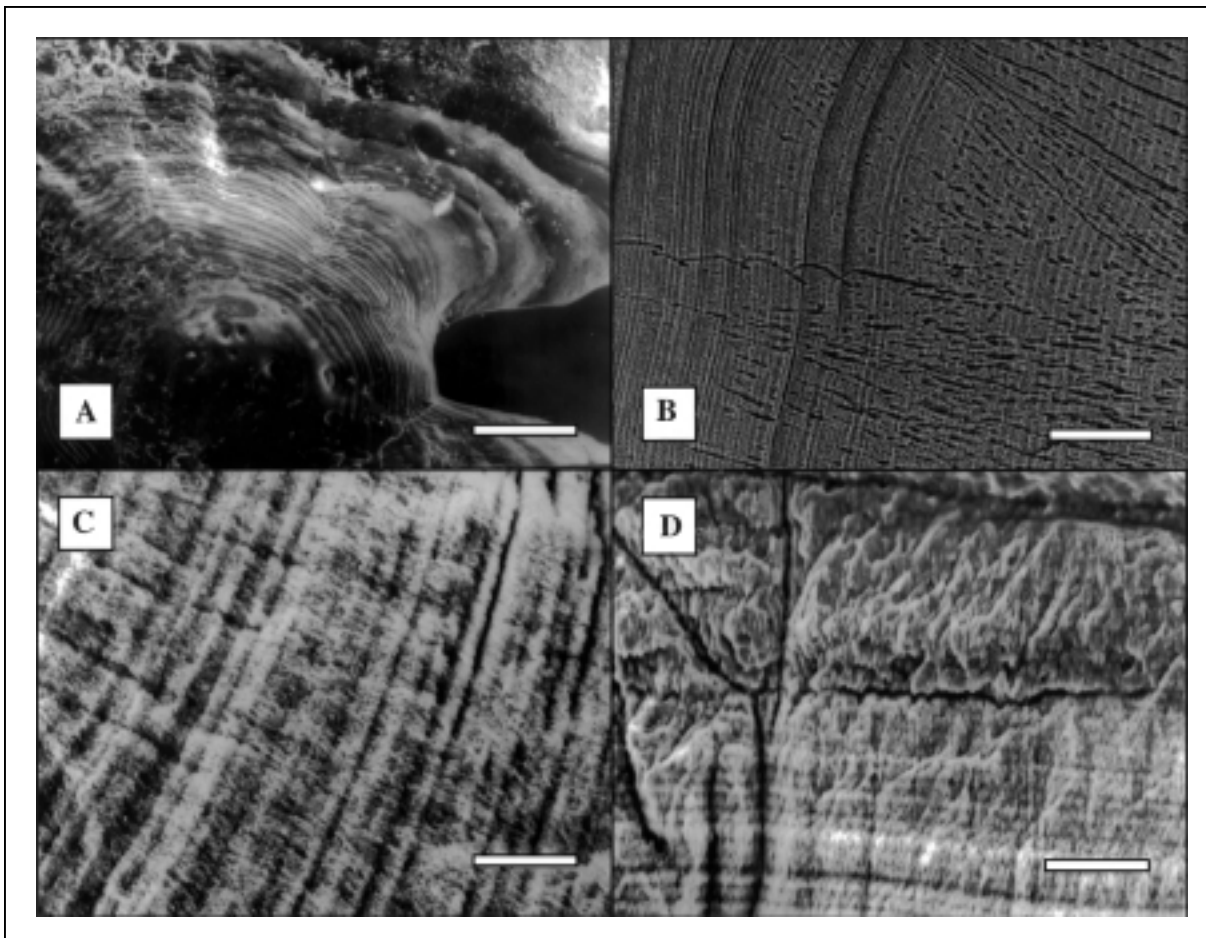


Figure 2

Scanning electron micrographs of *Coryphaena hippurus* sagittal otoliths. (A) Ridges on the surface of the central area of the otolith (scale bar=155 μm); (B) thin increments laid down in the central region of the otolith, showing rhythmic growth patterns of 7- and 14-increment groupings (scale bar=35 μm); (C) wider increments laid down in the outer region of the otolith (scale bar=10 μm); (D) rhythmic growth pattern of 14 daily growth increments (scale bar=15 μm).

$n=1$) to 20.6–23.9 mm (at day 36, $n=3$). In general, poorly defined concentric increments, consisting of an adjacent dark and a light zone, were laid down around the core (Fig. 1E). In relation between age in days and number of increments, neither the x -axis intercept nor the slope were significantly different from 0 and 1, respectively (t -test; $P>0.05$): $y = 0.3894 + 0.9846x$ ($n=75$, $r=0.98$).

From the juvenile fish, 125 otoliths were read (71%), 73 females between 19.5 and 58.5 cm FL and 52 males between 16.5 and 58 cm FL. Observed minimum and maximum ages were 47 and 176 daily growth increments. Of 36 adult fish otoliths studied with the light microscope, only 15 (42%) were able to be interpreted. A high percentage were rejected owing to error in reading precision greater than 5% or to erosion of the marginal zone during the polishing

process. In specimens between 67 and 117 cm FL, the minimum and maximum ages read were 189 and 362 daily growth increments, respectively.

Scales from 139 adult specimens, measuring 65–124 cm FL, could be interpreted (93%). The results showed the presence of three age groups within the population: 67 1-yr-old specimens ranging from 65 to 110 cm FL ($\bar{x}=87.95$, $SD=10.15$), 61 2-yr-olds measuring 73–120 cm FL ($\bar{x}=97.54$, $SD=10.95$) and 11 3-yr-olds measuring 92–124 cm FL ($\bar{x}=108.73$, $SD=10.17$).

The von Bertalanffy growth function was calculated on the basis of the age–length relationships from daily growth rings in juvenile otoliths and annulae in adult scales (Fig. 4). Adult daily ages were not taken into account in these calculations because of observed underestimations in aging adults from

otoliths. Growth parameters for the whole population and by sex are shown in Table 2.

Length-frequency distributions for the 1990 and 1991 fishing seasons, based upon sampling of a fishery on juveniles, are given in Figure 5. Fish caught in this fishery from August to December measured 18–70 cm FL. The monthly length distribution indicated a rapid increase in the mode, mean, and minimum and maximum sizes for the catch. Von Bertalanffy growth parameters for this fraction of the population were estimated for the 1990 and 1991 fishing seasons (Table 2).

Discussion

The length–weight relationships obtained, showing negative allometric growth in females and isometry in males, are in accordance with the sexual dimorphism of *C. hippurus*. In this species there is a characteristic bullhead in males which, in the western Mediterranean, begins its development in individuals around 50 cm FL (Massuti and Morales-Nin, 1997). Similar results are obtained in other areas (Palko et al., 1982; Chatterji and Ansari, 1985), with a negative allometry that is stronger in females than in males.

Our study confirmed the daily nature of otolith growth increments in the first month of life for *C. hippurus* as reared fish. The strong correlation of mean sagittal counts to known fish age validated the use of otolith growth increments in the aging of juveniles up to 40 days old. Because regular incremental formation began on day one, no adjustment was required to estimate age from incremental counts of sagittae from wild fish.

Results suggest that the age of adult specimens is underestimated by the otolith method. This is clear when age–length relationships from daily growth rings in otoliths and from annuli in scales are plotted. For the same size interval, the otolith reading gave ages between 0 and 1 year, whereas interpretation of annuli in scales of adult fish gave ages to 3 years. This might be due to methodological problems in otolith preparation and interpretation. Consequently, the use of scales seems to be the best aging method for adult fish from the Mediterranean, from the point of view both of preparation and of results obtained.

The interpretation of juvenile fish age from daily growth increments seemed accurate, with a low percentage of disagreement between readers. To test the precision of this method, juvenile birthdate distribution was calculated by subtracting age in days from the date of capture. This showed a long period with peaks in the second fortnight of June 1990 and the first fortnight of July 1991 (Fig. 6). This small varia-

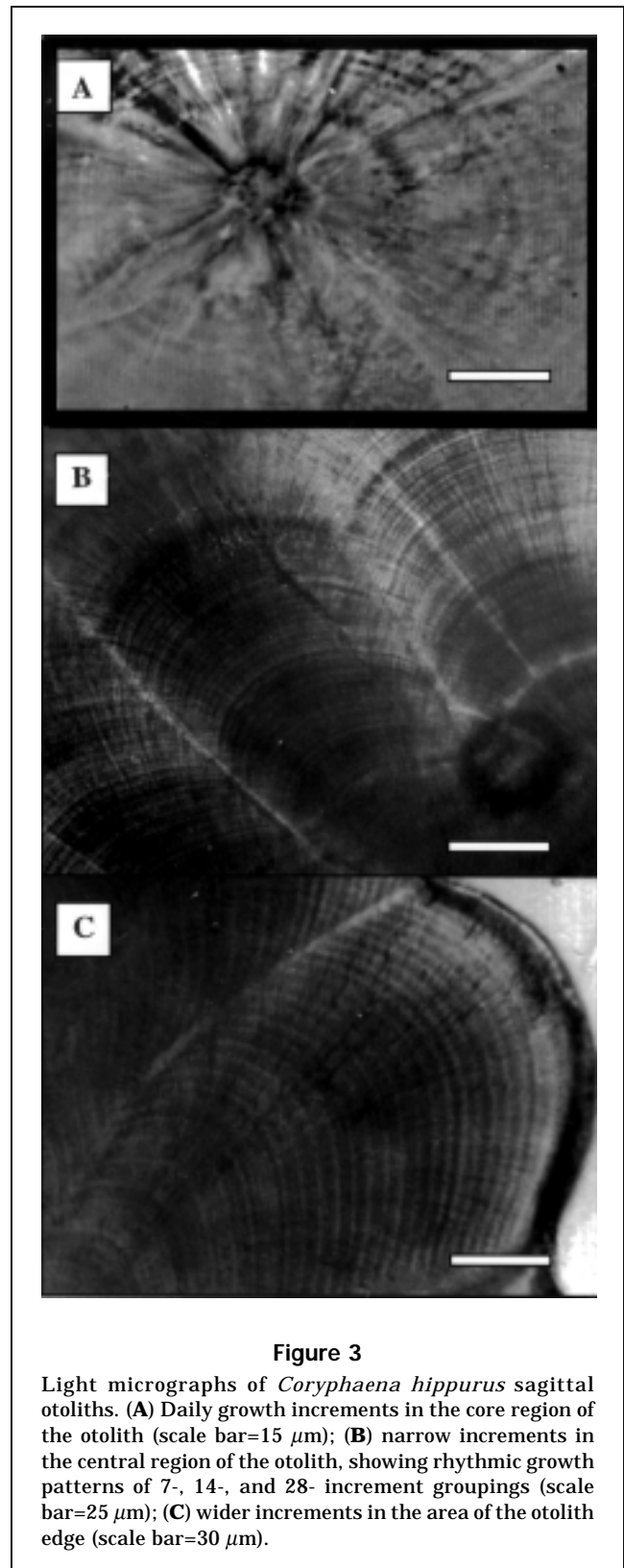


Figure 3

Light micrographs of *Coryphaena hippurus* sagittal otoliths. (A) Daily growth increments in the core region of the otolith (scale bar=15 μm); (B) narrow increments in the central region of the otolith, showing rhythmic growth patterns of 7-, 14-, and 28- increment groupings (scale bar=25 μm); (C) wider increments in the area of the otolith edge (scale bar=30 μm).

tion between years might be due to changes in the spawning peak or to differential mortality (Campana

Table 2

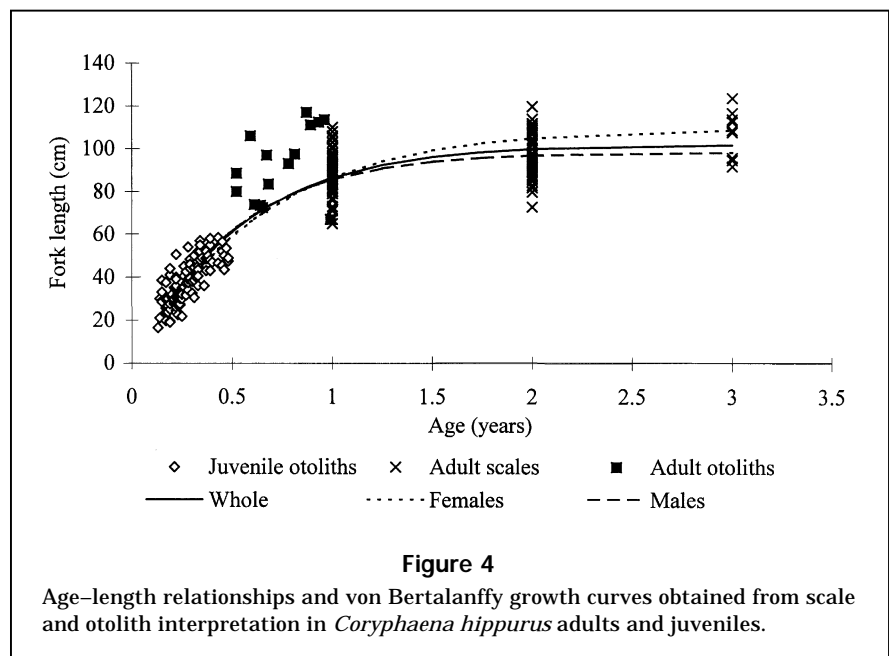
Von Bertalanffy growth parameters for *Coryphaena hippurus* calculated by different methods. The standard errors of each parameter are in parentheses. n = number of specimens; L_{∞} = asymptotic length (cm FL); k = growth coefficient in 1/yr; Rn = goodness-of-fit index; r = correlation coefficient; Φ = growth performance index. LFA is length-frequency analysis; S and O are scale and otolith readings.

Population	Sample	Method	n	L_{∞}	k	t_0	Rn	r	Φ
Juveniles	1990	LFA	2635	72.4	2.5	—	0.447	—	4.118
Juveniles	1991	LFA	1449	74.8	2.5	—	0.304	—	4.146
Females	1990–91	S and O	132	110 (2.62)	1.56 (0.14)	0.008 (0.02)	—	0.92	4.277
Males	1990–91	S and O	132	98.7 (1.59)	2.06 (0.19)	0.024 (0.02)	—	0.91	4.302
Whole	1990–91	S and O	264	102.4 (1.56)	1.90 (0.15)	0.023 (0.02)	—	0.87	4.300

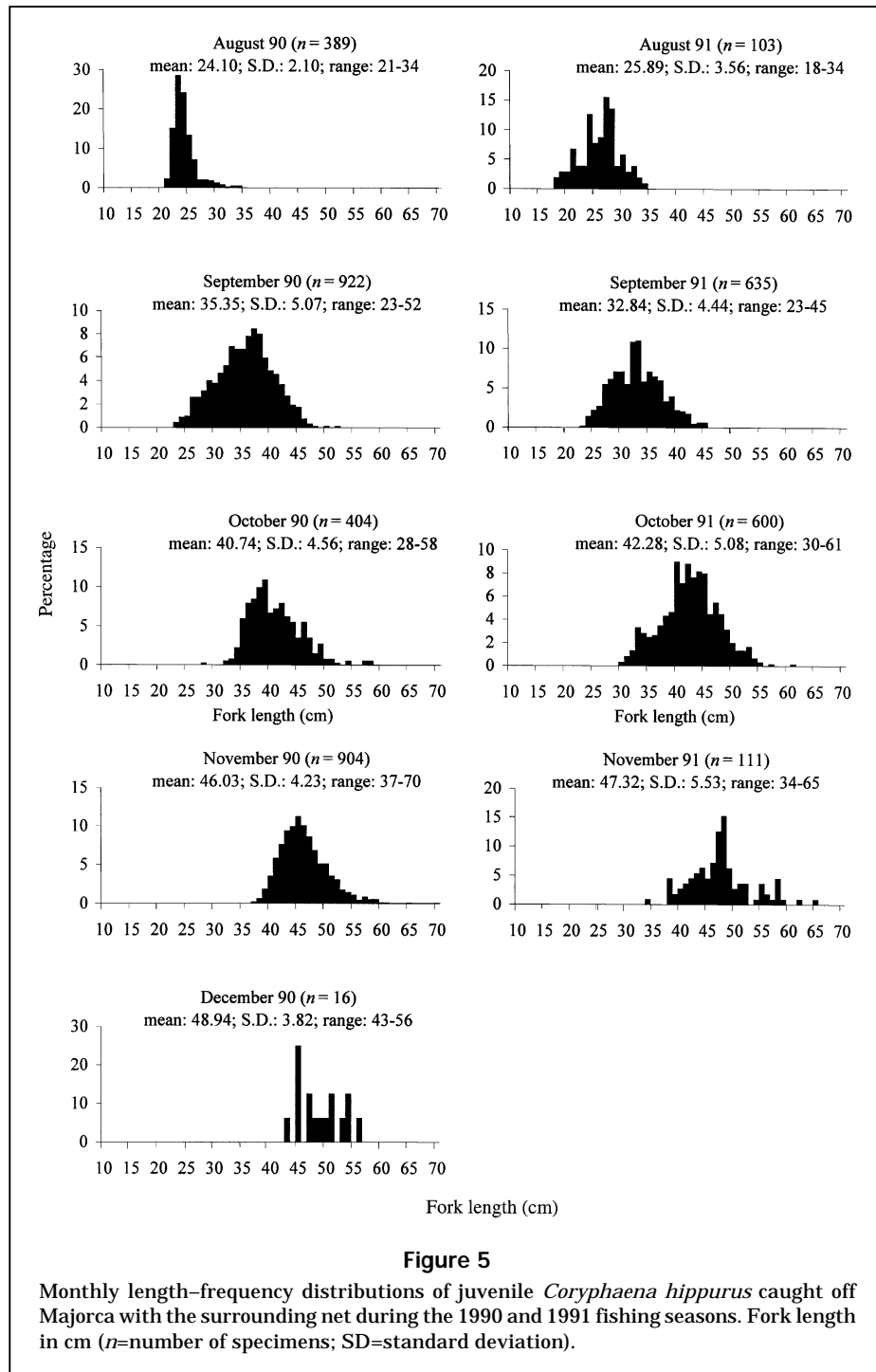
and Jones, 1992). According to our results and those of Uchiyama et al. (1986), the deposition of increments in otoliths begins on the first day of life. In addition, ripe eggs hatch within 50–60 hours after fertilization, depending on temperature (Palko et al., 1982). Thus, hatching distribution can be compared with the spawning period of the species in the area, which is known from adult fish maturity data (Massuti and Morales-Nin, 1995, 1997). The agreement between these hatching dates and the above-mentioned data supports the daily ages determined from otoliths of wild juvenile fish.

Another independent verification method uses link frequency analysis. The modal progression in juvenile catches showed a rapid growth rate, which is reflected by the almost double increase in monthly mean length during the fishing season from late August to early December. This rapid growth is in accordance with results obtained in the Mediterranean and other areas with reared specimens (e.g. Hassler and Hogarth, 1977; Reñones et al., 1992; Ayari et al., 1995; Benetti et al., 1995b), and with the estimates of growth rates between 3 and 10 cm per month, obtained from modal progression analysis on wild specimens in different areas (Wang, 1979; Oxenford and Hunte, 1983; Murray, 1985).

Growth parameters obtained by the two different methods used for the two population groups were quite different owing to the different length ranges



considered. Nevertheless, similar results are obtained with the growth performance index. These values are similar to those calculated from growth parameters reported from scales of annuli by Beardsley (1967) and Rose and Hassler (1968), which were 4.27 and 4.19, respectively. Those calculated from growth parameters obtained by daily growth increments (Uchiyama et al., 1986) were slightly higher (4.52 for females and 4.63 for males), probably owing to the above-mentioned underestimation of age in adult fish with this method, the few adult specimens studied, and the effect of temperature on growth and metabolism. Temperatures can also explain the slower growth rate of *C. hippurus* in the western



North Atlantic Ocean (Beardsley, 1967; Rose and Hassler, 1968), where a decreased feeding rate when water temperature falls below 23°C and a cessation of feeding at 18°C have been reported (Hassler and Hogarth, 1977). By contrast, in Hawaiian waters, where faster growth rates have been reported, this species feeds throughout the year and can be expected to grow continuously (Uchiyama et al., 1986).

The growth-rate values obtained for *C. hippurus* are within the range reported from otolith microstructures by Brothers et al. (1983) for Atlantic bluefin tuna (*Thunnus thynnus*), another top-level predator characteristic of the western Mediterranean epipelagic ecosystem. According to Benetti et al. (1995a), *C. hippurus*, Scombridae species, and *Isurus oxyrinchus*, another Mediterranean pelagic predator, have common factors

in environment and lifestyle which must strongly select for anatomical, biochemical, and physiological adaptations necessary to achieve exceptionally high metabolic rates. Such selection leads to high somatic and gonadal growth rates, rapid digestion, and quick repayment of oxygen debts, all important functions in these active pelagic predators.

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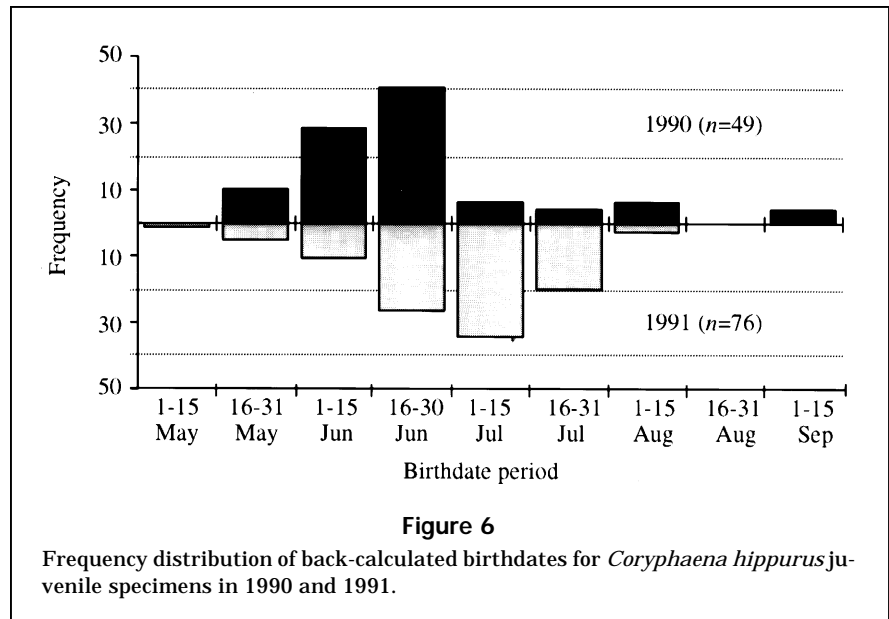


Figure 6

Frequency distribution of back-calculated birthdates for *Coryphaena hippurus* juvenile specimens in 1990 and 1991.

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