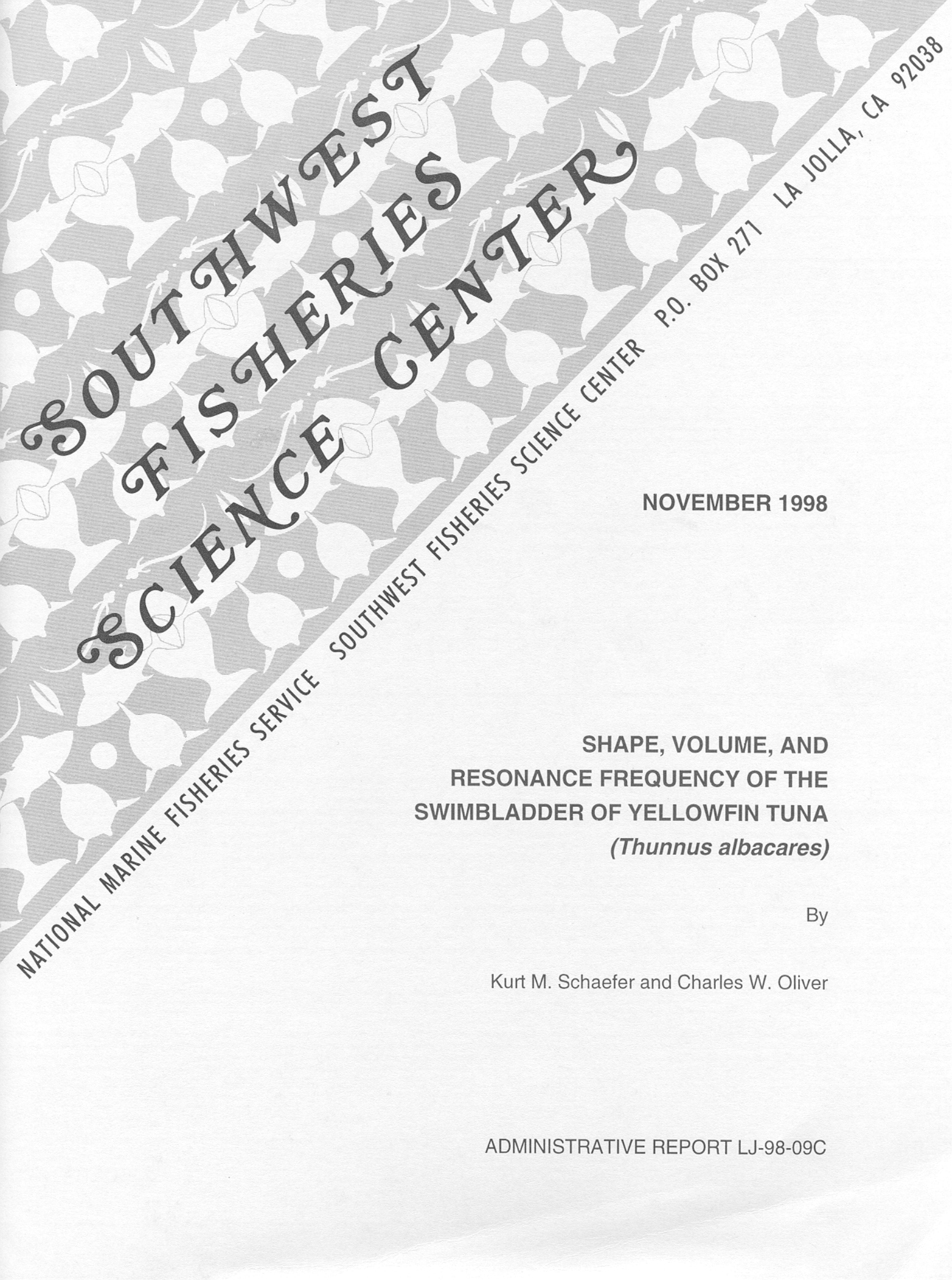




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SHAPE, VOLUME, AND
RESONANCE FREQUENCY OF THE
SWIMBLADDER OF YELLOWFIN TUNA
(*Thunnus albacares*)

By

Kurt M. Schaefer and Charles W. Oliver

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**SHAPE, VOLUME, AND RESONANCE FREQUENCY OF
THE SWIMBLADDER OF YELLOWFIN TUNA (*THUNNUS
ALBACARES*)**

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Explanatory Note

This report is one in a series on the potential for technology applications to enhance efficiency in commercial fisheries, reduce the catch of non-targeted species, and provide new tools for fishery assessments in support of the NMFS strategic goals to build sustainable fisheries and recover protected species. We hope the distribution of this report will facilitate further discussion and research into the application's potential usefulness, but should not be construed as an endorsement of the application by NMFS.

Pursuant to changes in the Marine Mammal Protection Act in 1988, the NMFS' SWFSC began another series of ETP-related studies in 1990, focused on developing and evaluating methods of capturing yellowfin tuna, which do not involve dolphins. This series of studies has been conducted within the SWFSC's Dolphin-Safe Research Program. Studies on the potential use of airborne lidar (LIght Detection And Ranging) systems began in 1991, and studies on low-frequency acoustic systems to detect fish schools at ranges much greater than currently possible were initiated during 1995. In addition to their use as an alternative to fishing on dolphins, these systems have potential to increase the efficiency of the fishing operations by locating fish schools not detectable by customary visual means, and as a fishery-independent tool to conduct population assessments on pelagic fish. They also have potential to adversely impact marine animals.

The Dolphin-Safe Research Program is investigating, through a series of contracts and grants, five airborne lidars: 1) the NMFS-developed "Osprey" lidar (Oliver et al. 1994), 2) the Kaman Aerospace Corporation's FISHEYE imaging lidar (Oliver and Edwards 1996), 3) the NOAA Environmental Technology Laboratory's Experimental Oceanographic Fisheries Lidar (Churnside et al. 1998), 4) the Arete Associates 3D Streak-Tube Imaging Lidar, and 5) the Detection Limited's lidar. An initial study on the potential effects of airborne lidars on marine mammals will be completed during 1998 (Zorn et al. 1998).

The Dolphin-Safe Research Program has completed, through a series of contracts and grants, acoustic system studies on 1) the acoustic target strength of large yellowfin tuna schools (Nero 1996), 2) acoustic detection parameters and potential in the eastern tropical Pacific Ocean (Rees 1996), 3) the design of two towed acoustic systems (Rees 1998, Denny et al. 1998), 4) **measurements of swimbladder volumes from large yellowfin tuna (Schaefer and Oliver 1998)** and, 5) the potential effects of low-frequency sound on marine mammals (Ketten 1998).

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ABSTRACT

The shapes and volumes of swimbladders of yellowfin tuna were determined from freshly-caught fish from the eastern Pacific Ocean. Direct measurements of swimbladder volumes were obtained from a geometric reconstruction using morphometric measurements of intact bladders, and by volumetric displacements of the same intact bladders excised from 46 fish (57 to 157 cm in length). The estimates of the swimbladder volumes obtained from geometric reconstruction are not significantly different from the corresponding volumetric displacements. There is a significant nonlinear relationship between yellowfin swimbladder volumes and fish lengths. The mean swimbladder volume, expressed as a percentage of body volume, was 1.33%, with a minimum of 0.30% and a maximum of 2.84%. A comprehensive model, based on the data from this study and those from a previous investigation, is presented for the relationship of yellowfin swimbladder volumes, estimated from geometric reconstruction, and fish lengths for 108 specimens (35 to 157 cm). This predictive model was then used with other formulae to estimate yellowfin tuna swimbladder resonance frequencies for fish lengths and fish depths. Because these resonance frequencies are within the range of frequencies audible to yellowfin, we speculate on the potential distance dolphins could be detected by yellowfin tuna.

INTRODUCTION

Shapes and volumes of swimbladders of yellowfin tuna are obviously important with respect to the function of the swimbladder as a hydrostatic organ, which lowers the energy costs of locomotion (Magnuson, 1973; Alexander, 1993). The swimbladder of yellowfin may also function in acoustical detection by tuna, providing increased sensitivity in hearing which enhances the fishes' ability to acoustically detect other organisms, such as dolphins and prey, in their environment (Iverson, 1967; Hawkins, 1993). In addition, the swimbladder may also function in acoustical detection of tuna by other species. At low frequencies (< 2 kHz), the maximum acoustic target strength occurs at a resonance frequency determined by the volume of the swimbladder (Love, 1978). At high-frequencies (2-200 kHz), the swimbladder has been reported to account for 50% (Jones and Pearce, 1958) to as much as 95% (Foote, 1980) of the acoustic target strength for some fish. Volberg (1963) reported a reduction in target strength at high frequencies for bass and perch with deflated swimbladders, but no appreciable change in measured target strengths for yellowfin tuna with normal swimbladders and deflated and flooded swimbladders.

Low-frequency acoustic detection and tracking of yellowfin tuna schools is being investigated by the U.S. National Marine Fisheries Service as an alternative method of locating yellowfin independent of dolphins. Studies suggest that yellowfin schools can be detected at much greater ranges (20 to 40 km) than are currently feasible (Rees, 1996; Rees, 1998). Development of an acoustic detection system could greatly increase the efficiency of commercial fishing, and might also provide a fishery-independent method for assessment of yellowfin or other large pelagic fish.

Nero (1996) used two acoustic-scattering models to estimate the target strengths of yellowfin tuna schools: a model for very low frequencies (50–1000 Hz) assumed to be near swimbladder resonance (Feuillade *et al.*, 1996; Feuillade and Nero, 1998), and a high-frequency (2–200 kHz) model for frequencies well above swimbladder resonance (Love, 1977; Love, 1981). Yellowfin tuna swimbladders were modeled as gas-filled spheres (Feuillade *et al.*, 1996). The models of Nero (1996) included swimbladder volume estimates of approximately 5% of fish volume for yellowfin in excess of 80 cm in length, extrapolated from Magnuson's (1973) relationship of swimbladder volume to fish length for yellowfin tuna 44 to 82 cm in length.

The objectives of the present study were: 1) obtain direct measurements of swimbladder shapes and volumes from freshly-caught yellowfin tuna 50 to 150 cm in length, 2) compare the swimbladder displacement volumes with volumes estimated from geometric reconstruction, 3) compare the swimbladder volumes estimated from geometric reconstruction for freshly-caught and frozen-and-thawed specimens, and 4) calculate swimbladder resonance using existing acoustic models.

MATERIALS AND METHODS

Yellowfin tuna specimens were caught by rod and reel. 17 specimens, 57 to 70 cm in length, were collected from a skiff during October 1997, in the vicinity of the Frailes Islands (lat. 7°20' N, long. 80°08' W). An additional 29 specimens, 71 to 157 cm in length, were collected aboard the MV *Royal Polaris*, a San Diego-based long-range sportfishing boat, during January and February 1998, primarily in the vicinities of Alijos Bank (lat. 24°49' N, long. 115°W) and Hurricane Bank (lat. 16°52'N, long. 117°30'W).

Freshly caught specimens were assigned an identification number. Fish length was measured with a caliper to the nearest millimeter and fish weight with an electronic balance to the nearest pound. Cutting the abdominal cavity open from the anus to the isthmus and removing most of the viscera exposed the swimbladder. A photograph of the intact swimbladder was then taken with a digital camera. Morphometric measurements of length and three widths (rostral, medial, and caudal), were taken for each intact swimbladder using a dial caliper, to the nearest tenth of a millimeter. The inflated swimbladder and some extraneous tissue were excised from the abdominal cavity, and the volumetric displacement was measured in a graduated cylinder to the nearest 5 ml. The swimbladder was then punctured and the volumetric displacement of the tissue measured. The estimated volume of gas in the swimbladder was calculated as the difference between displacement volumes of the inflated and deflated swimbladder.

Estimates of swimbladder volumes were also computed from a geometric reconstruction of the bladder's length and width measurements. Based on the above four morphometric measurements of each bladder, a geometric algorithm was employed to estimate the volumes between several cross sections. Cross sections of the swimbladder were assumed to be elliptical.

The rostral and caudal ends of the bladders were assumed to be hemispheres. The total estimate of the volume of gas within the swimbladder was the sum of all the geometrical units.

Estimates of swimbladder volumes from a geometric reconstruction of the bladders, for 62 frozen and thawed yellowfin tuna ranging in length from 35 to 149 cm (Schaefer, 1998), were included in this study for both comparative and comprehensive analyses.

RESULTS

Swimbladder Shape and Volume

Photographic images of the ventral, dorsal, left, and right profiles of an excised intact swimbladder of yellowfin tuna provide definitive views of the overall shape (Figure 1). The swimbladder has elastic walls, and is shaped like a cylindrical chamber with bulbous ends and paired horns on the rostral-dorsal surface. The interior and exterior walls of these horns are thicker than the rest of the bladder wall, and fit into pits adjacent to either side of the vertebral column. As size increases in the yellowfin specimens we examined (Table 1), the ratio of the swimbladder length to the width remains fairly constant, around a mean of 3.1 (range: 2.2-4.8). The swimbladder shape however, changes noticeably particularly at the caudal end (Figure 2).

The relationship of swimbladder volumes obtained from volumetric displacement, to fish lengths for the freshly caught yellowfin is shown in Figure 3. The relationship is well described by a power function fitted to the non-transformed data:

$$Y_x = 0.000000005 x^{3.5715}$$

where Y_x = a swimbladder volume at fish length x ; $r^2 = 0.87$; and $n = 46$.

The relationship of swimbladder volumes, obtained from volumetric displacement and expressed as a percentage of the body volume estimated from body weight, to the weights for freshly-caught yellowfin, is shown in Figure 4. The mean volume was 1.33% (95% CI = 0.16) with minimum and maximum values of 0.30% and 2.84%, respectively. There is a significant ($P = 0.01$), but very loose relationship between the swimbladder volume expressed as percentage of

body volume and body weights for the following polynomial function fitted to the non-transformed data:

$$Y_x = 1.0048 + 0.0243x + -0.0002x^2$$

where Y_x = a swimbladder volume, expressed as a percentage of body volume, at weight x ; $r^2 = 0.18$; and $n = 46$.

The relationship of swimbladder volumes estimated from geometric reconstruction, to the volumes from volumetric displacement for freshly caught yellowfin, is shown in Figure 5. The relationship was described and analyzed by the following linear function fitted to the non-transformed data:

$$Y_x = -1.6872 + 1.0763x$$

where Y_x = a swimbladder volume estimated from geometric reconstruction for the corresponding volumetric displacement x ; $r^2 = 0.96$; and $n = 46$. Although it is apparent from Figure 5 that the two techniques produce similar estimates, the regression coefficient for the complete data set is significantly different than 1 ($t_{0.05(2),44} = 2.41$; $P < 0.05$). However, four data points from specimens ranging in length from 129 to 157 cm largely influence the regression coefficient. A refitting of the linear function to the non-transformed data, excluding these four data points, indicates the regression coefficient ($b = 0.985$) is not significantly different from 1 ($t_{0.05(2),40} = -0.33$; $P > 0.05$), providing credence to the estimates of the volumes obtained from geometric reconstruction.

Analysis of covariance applied to the log-transformed swimbladder volumes obtained from geometric reconstruction, fish length data from the present study truncated to a length range of 600 to 1197 mm ($n = 36$), and log-transformed data from Schaefer (1998) truncated to a length range of 607 to 1192 mm ($n = 24$), indicated no significant difference in the test for equality of slopes ($F = 2.50$, $P = 0.12$) or equality of adjusted means ($F = 2.38$, $P = 0.13$). It thus appears appropriate to pool the two sets of data for yellowfin swimbladder volumes obtained from geometric reconstruction, in order to provide the most comprehensive model possible.

The relationship of swimbladder volumes estimated from geometric reconstruction and lengths of the yellowfin from the present study combined with those from Schaefer (1998) is shown in Figure 6. The relationship is well described by a power function fitted to the non-transformed data, using a weighted regression procedure:

$$Y_x = 0.00000002 x^{3.0601}$$

where Y_x = a swimbladder volume at fish length x ; $r^2 = 0.83$; and $n = 108$ (fish length range: 353 to 1569 mm). The weighting employed consisted of the reciprocal of the variance about the volumes within each 200-mm length interval.

Swimbladder Resonance Frequency

Using the swimbladder volumes we measured at the surface (1 Atmosphere), expected volumes at depths can be calculated using Boyle's Law:

$$\text{Volume}_{\text{depth}} = \frac{\text{Pressure}_{\text{surface}} \times \text{Volume}_{\text{surface}}}{\text{Pressure}_{\text{depth}}}$$

The monopole-dominant resonance frequency of a swimbladder (Andreeva, 1964) is approximated using a spherical volume of gas (Love, 1978) as shown below.

$$\text{Resonance Frequency} = \sqrt{\frac{3\Gamma P}{4\rho^2 r^2 D}}$$

$$P = \left[1 + \left[\frac{Z_{\text{meters}}}{10_{\text{meters}}} \right] \right] \times 101000 \text{ Pascals}$$

where

$$\Gamma = 1.4$$

r = radii of equivalent sphere (meters)

D = density of fish flesh (1050 kg/m³)

P = sound speed parameter at depth Z

Because yellowfin swimbladders are not spherical, the expected resonance frequency must be adjusted to account for the swimbladder's approximate prolate spheroid shape (Figures 1 and 2). Weston (1967) provides a formula using the ratio of the swimbladder's maximum (**a**) and minimum (**b**) radii (*e.g.*, ½ length and ½ width), and a figure (Chap. 5, p59, Fig. 5.2) from which we interpolated the magnitude of the upwards adjustment at various depths. We assumed the swimbladder's maximum radii (**a**) to remain constant at all depths because it is firmly attached to the dorsal wall of the abdominal cavity. We calculated the expected minimum radii (**b**) at various depths using the predictive regression function for swimbladder volumes at the surface for fish lengths (Figure 6), and determined the percent increase in the expected resonance frequency. Solving for **b** yields:

$$b_{\text{depth}} = \sqrt{\frac{V_{\text{depth}}}{\frac{4}{3}P a_{\text{depth}}}}$$

Resonance frequencies for swimbladders of yellowfin tuna of various fish lengths and at various depths were estimated (Figure 7), using the above equations and the predictive regression function for swimbladder volumes for fish lengths (Figure 6). Applying Weston's (1967) correction increased resonance frequencies between 5% and 26% for yellowfin tuna from 40 to 150 cm and depths from 0 to 120 m.

DISCUSSION

Swimbladder Shape and Volume

Godsil and Byers (1944) previously described the shape of the swimbladder of yellowfin tuna. Additional information from the present study regarding yellowfin tuna swimbladder shape is provided through the digital images of the various views of the swimbladder (Figures 1 and 2) and the morphometric information presented in Table 1.

The swimbladder volume estimates derived from geometric reconstruction in this study, and that of Schaefer (1998), appear to provide realistic representations for swimbladders of live yellowfin swimming at the surface of the ocean. All of the intact swimbladders within the abdominal cavities for those specimens were sufficiently inflated so the bladders were taut, rather than flaccid. Many of the yellowfin stomachs were relatively full, and there was a broad range in the stage of gonadal development. There was no extrusion of the bladder or other organs from the initial incision into the abdominal cavity for any specimen. Thus, it does not appear there were any deformations or reduction in swimbladder volumes within the body cavity as described for cod (Ona, 1990).

Geometric reconstruction of swimbladders in yellowfin tuna were previously derived from radiographs for estimating volumes and validated by volumetric displacements (Chang and Magnuson, 1968). It is apparent from the results of that study and the present study that geometric reconstruction methodology is sufficiently accurate for deriving estimates of volumes of swimbladders of yellowfin tuna, and possibly other tunas as well. Furthermore, unless there are instances where it is not feasible to cut open the abdominal cavity of specimens, it does not appear to be necessary to employ a x-ray unit for obtaining these estimates.

Magnuson (1973) reported swimbladder volumes for 11 yellowfin specimens, 44 to 82 cm in length, ranged from around 0.25% to 4.0% of body volume (obtained by eye from Figure 4a of Magnuson, 1973). He concluded that volumes increased allometrically with increasing fish mass. The data presented in this study do not support this allometric growth. The swimbladder volumes in the present study, derived from volumetric displacements, expressed as a percentage of the estimated body volumes (Figure 4) had a mean of about 1.3% with a range of about 0.3% to 2.84%, and almost no relationship with increasing mass. Swimbladder volumes, from the present

study, for yellowfin in the length range presented in Magnuson (1973) appear to be significantly lower (Figure 4). The data in Magnuson (1973) is based upon measured volumetric displacements of the fish, whereas in the present study body volume was estimated, without correcting for fish density since those values were not available for these specimens. However, we calculated the body volumes from weights for specimens from the present study using an adjustment factor for density of 1.05 g/ml (Magnuson, 1973), and found swimbladder volumes would be increased by only 0.07 % on average. This small increase in body volume does not account for the apparent differences in swimbladder volumes between the present study and those in Magnuson (1973). In addition, although Magnuson (1973) reported that specimens of 2 kg or less have no gas in the bladder, Schaefer (1998) reported yellowfin swimbladders become inflated with measurable quantities of gas in specimens as small as 0.85 kg (353 mm) (Figure 6).

Swimbladder Resonance Frequency

Acoustic tracking studies have shown that yellowfin tuna occupy the lower mixed layer during daylight and waters closer to the surface at night (Carey and Olson; 1982; Holland *et al.*, 1990; Block *et al.*, 1997). Although they appear to make frequent, short excursions toward the surface, they spend very little time at the surface. In the area of the eastern Pacific surface fishery (Anonymous, 1998), the thermocline depth ranges from about 40 to 120 meters (Fiedler, 1992). Because its volume primarily determines the resonance frequency of a swimbladder, the frequency will also change with depth. Thus, the acoustic target strength of a tuna, or school of tunas, will vary as the swimbladder volumes vary at depth for low-frequency acoustic detection systems.

Nero (1996) modeled target strengths for schools of larger yellowfin tuna for both high frequency (2-200 kHz), and low frequencies (below 2 kHz), using an assumed swimbladder volume equal to 5% of fish volume for calculating resonance frequencies. Nero's (1996) high-frequency model predicted target strengths of 2.5, 1.6, and 0.9 dB for tuna schools of 80, 100, and 130-cm fish respectively. The decreasing trend in school target strength as fish length and bladder volume increases as shown in Nero (1996), results primarily from the reduced number of fish in a modeled 15-kg school. Some additional decrease in Nero's reported school target strengths could result from the smaller swimbladder volumes we measured for fish of similar lengths, depending

upon the swimbladder's contribution to target strength at high frequencies (Jones and Pearce, 1958; Volberg, 1963; Foote, 1980).

Nero (1996) provides low-frequency target strengths for schools of yellowfin tuna at various depths, fish lengths, and packing densities, but noted the effect on school target strength is unclear because of interference and coupled resonance effects dependent on the fish size, numbers, aspect, and packing density. We expect Nero's reported school target strengths, for low frequencies, to decrease with both fish length and depth as a result of the smaller swimbladder volumes we measured. Because resonance frequency varies inversely with swimbladder volume, overestimating volume results in predicted lower resonance frequencies. Direct measurement of resonance frequency and target strength of *in situ* swimbladders would eliminate need to model these parameters and provide better information to optimize an acoustic detection system for large yellowfin tuna.

Yellowfin tuna monitor their environment through the use of sensory organs for visual, chemoreceptive, and acoustic information accompanied by their swimming activity patterns. Although vision (Guthrie and Muntz, 1993) and chemoreception (Hara, 1993) are presumably important to yellowfin in foraging, sex, and social communication, acoustic sensory capacities are probably adaptive in detection because of the light-filtering and chemical dilution effects in the ocean (Hawkins, 1993). Sounds can travel great distances in the sea, depending upon the sound propagation characteristics of the water and the sound frequency and source level. Reception and processing of sounds by fish presents the potential for detection at greater distance than by either visual or chemoreceptive senses (Hawkins, 1993). The swimming behavior of yellowfin, exemplified by vertical excursions, enables individuals to actively control the resonance frequencies of their swimbladders (Figure 7) and to potentially enhance their ability to sense their environment, as previously proposed by Feuilleade and Nero (1998) for other fish with swimbladders.

Because estimates of yellowfin swimbladder resonant frequencies presented in this study are within the range of frequencies audible to yellowfin (Iverson, 1967), and because their swimbladders may enhance their hearing (Blaxter, 1980), it is tempting to speculate about the potential distance that yellowfin could become aware of dolphins (*Stenella* spp.) or prey, predators, or conspecifics through sound reception. Identification of a mechanism that facilitates the tuna/porpoise bond in the eastern Pacific (National Research Council, 1992) may provide a

means of breaking the bond prior to encircling dolphins, thus enabling the capture of tuna without catching dolphin. If the mechanism is an attractant (*i.e.*, tuna move to the sounds of dolphins and/or other oceanic sounds), then the possibility exists to artificially attract larger yellowfin tuna using acoustical devices. Active sounds produced by dolphins include clicks, bangs, and whistles (Schevill, 1964; Tavorga, 1965; Norris and Mohl, 1983; Watkins and Wartzok, 1985; Marten *et al.*, 1988) at peak frequencies as high as 160 kHz and peak source levels up to 228 dB (Au, 1993). Passive sounds resulting from tail-slaps, breaches, and other behaviors have also been described as loud (Hult, 1982; Smolker and Richards, 1988). Of particular interest, is the energy at frequencies between 50 and 1100 Hz, because yellowfin tuna have been shown to respond to sounds in this range, with the most sensitive responses occurring between 300 and 500 Hz (Iverson, 1967). Measurements of the source level spectra of active and passive sounds produced by *Stenella* spp., referenced to a source, are needed.

In the absence of published data on source levels associated with the low-frequency component of various dolphin sounds, we estimate the potential range at which yellowfin tuna could detect 300-500 Hz sounds (Table 2) using maximum source levels for higher frequencies (Au, 1993). As sound propagates through the water, sound intensity decreases with range, primarily due to spreading of the wavefront. This transmission loss can be expressed as $TL = t \log R$ (Au, 1993), where t is a coefficient describing the type of spreading; spherical: $t = 20$, cylindrical: $t = 10$ (Au, 1993). Using the best hearing sensitivity reported for small yellowfin tuna (Iversen, 1967), we calculated maximum detection range as:

$$R = 10^{(SL-83)/t}$$

where

- SL = source level of sound in dB (re: 1μPa)
- 83 = best hearing threshold of yellowfin tuna in dB (re: 1μPa) (Iversen 1967)
- t = coefficient of transmission loss incorporating spreading and absorption loss

At a source level of 160 dB (re: 1μPa), we estimate yellowfin tuna in the eastern Pacific could potentially detect a 500 Hz sound at a distance of 3.2-19.0 km (Table 2). These estimates are based on the hearing sensitivity of small yellowfin tuna (Iverson, 1967), which are below the size which commonly associate with dolphins in the EPO. It may be that detection distances for yellowfin tuna greater than about 80 cm in length are far greater because of improved hearing sensitivity and lower resonance associated with their larger swimbladders (Figure 7).

The swimbladder of yellowfin tuna may function as a key mechanism in the formation of the bond between yellowfin tuna and dolphins in the eastern tropical Pacific Ocean. Whether it is larger yellowfin tuna actively searching for dolphins to increase their probability of remaining within food-rich habitat (Fiedler *et al.*, 1998), or because of the dolphin's sonar echolocation ability to detect yellowfin tuna (Au, 1993), the swimbladder may play an important role in both sound reception and as an acoustical target. Further research should be conducted on yellowfin tuna bioacoustics with particular emphasis on the potential function of the swimbladder.

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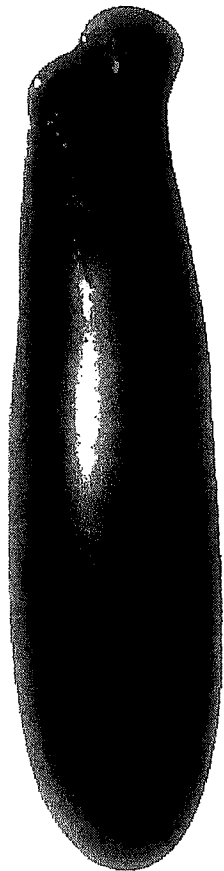
Table 1. Measurements of fresh yellowfin tuna and their swimbladders. The volumes are volumetric displacements in seawater.

Fish		Swimbladder		
Length (mm)	Weight (kg)	Length (mm)	Maximum Width (mm)	Volume (cc)
572	3.7	102.0	31.3	38
590	4.1	114.9	32.3	43
591	4.1	109.9	36.9	53
591	3.7	107.0	25.9	36
600	3.9	100.8	26.7	26
601	3.9	103.6	36.1	41
608	4.2	112.6	31.0	56
611	4.3	110.2	35.0	46
614	4.6	119.2	34.6	71
624	4.6	115.6	30.2	54
624	4.4	123.3	25.8	31
636	4.9	101.4	34.4	35
650	5.2	111.3	38.3	78
671	5.7	118.1	39.7	33
675	6.0	136.7	42.4	111
681	6.5	128.7	45.0	71
704	8.1	109.3	41.9	66
705	7.3	132.0	54.1	91
736	7.3	143.0	48.2	51
751	8.2	135.0	47.3	81
784	8.6	165.0	69.1	245
789	8.6	114.0	51.3	26
824	9.5	163.0	58.4	166
842	11.3	164.0	50.6	161
861	13.2	158.0	44.9	136
917	13.6	178.0	64.9	260
933	15.4	168.0	64.9	106
940	16.8	184.0	51.6	280
964	17.2	174.0	52.3	161
977	19.1	205.0	61.6	410
1033	20.4	195.0	61.9	320
1039	21.8	228.0	61.7	260
1047	21.3	196.0	48.5	147
1069	23.6	193.0	61.7	310
1087	24.9	240.0	79.1	610
1129	27.2	205.0	66.3	495
1130	30.4	195.0	66.9	250
1179	33.6	205.0	75.9	500
1190	33.1	235.0	69.8	540
1197	29.5	207.0	71.1	390
1218	34.0	213.0	76.8	500

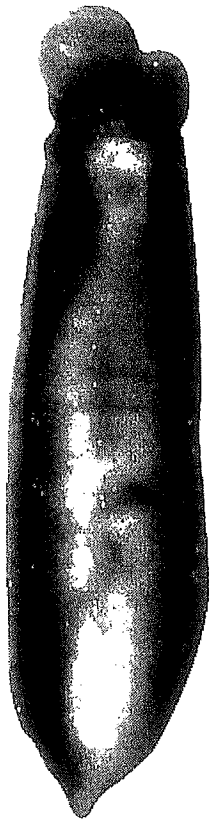
1236	35.4	215.0	75.6	540
1290	37.2	260.0	74.5	830
1346	44.5	270.0	79.5	915
1519	62.6	230.0	104.6	800
1569	68.0	295.0	114.2	1530

Table 2. Estimated detection ranges at which yellowfin tuna, *Thunnus albacares*, in the eastern tropical Pacific could hear 300-500 Hz sounds, assuming projected source levels and three propagation loss model coefficients.

Source Level (dB re: 1μPa)	Range (kilometers)		
	Transmission loss coefficient (t)		
	22	20	18
100	0.006	0.007	0.009
110	0.017	0.022	0.032
120	0.048	0.071	0.114
130	0.137	0.224	0.408
140	0.390	0.708	1.468
150	1.110	2.239	5.275
160	3.162	7.079	18.957
170	9.006	22.387	68.129
180	25.650	70.795	244.844
190	73.053	223.872	879.923
200	208.057	707.946	3162.278
210	592.553	2238.721	11364.637
220	1687.612	7079.458	40842.387



Ventral



Dorsal



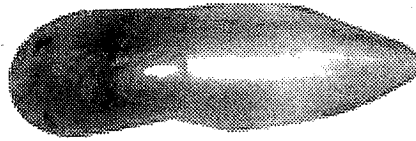
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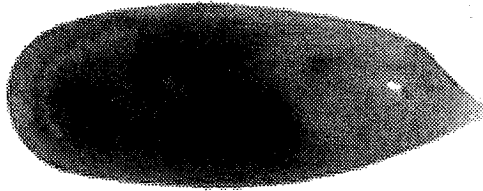
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FIGURE 1. Profiles of an excised intact yellowfin tuna swimbladder. The actual length of the swimbladder was 165 mm, the maximum width 69.1 mm, and the displacement volume 245 cc. The fish was 784 mm in length and 8.6 kg in weight.

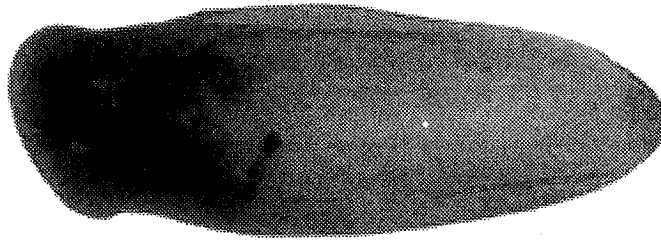
a.



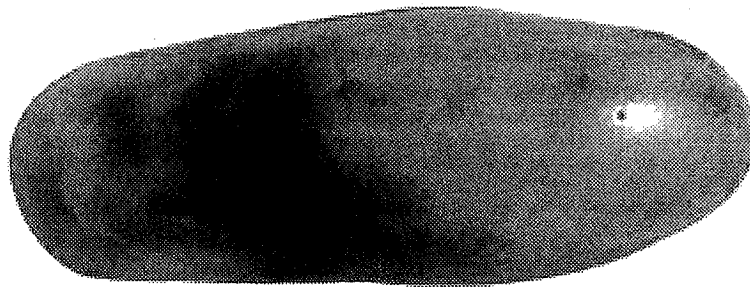
b.



c.



d.



e.

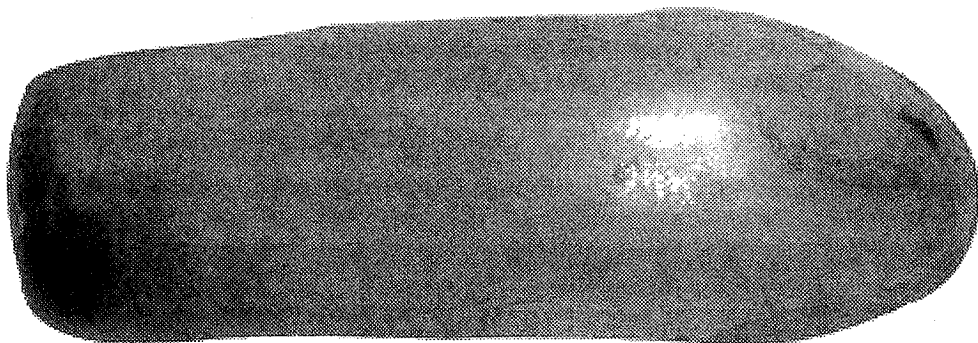


FIGURE 2. Ventral profiles of excised intact yellowfin tuna swimbladders scaled to relative size. Values given for each image are measured lengths and displacement volumes of bladders, fish length, and fish weight. a) 115 mm and 43 cc, 590 mm, 4.1 kg. b) 135 mm and 81 cc, 751 mm, 8.2 kg. c) 184 mm and 280 cc, 940 mm, 16.8 kg. d) 205 mm and 495 cc, 1129 mm, 27.2 kg. e) 270 mm and 915 cc, 1346 mm, 44.5 kg.

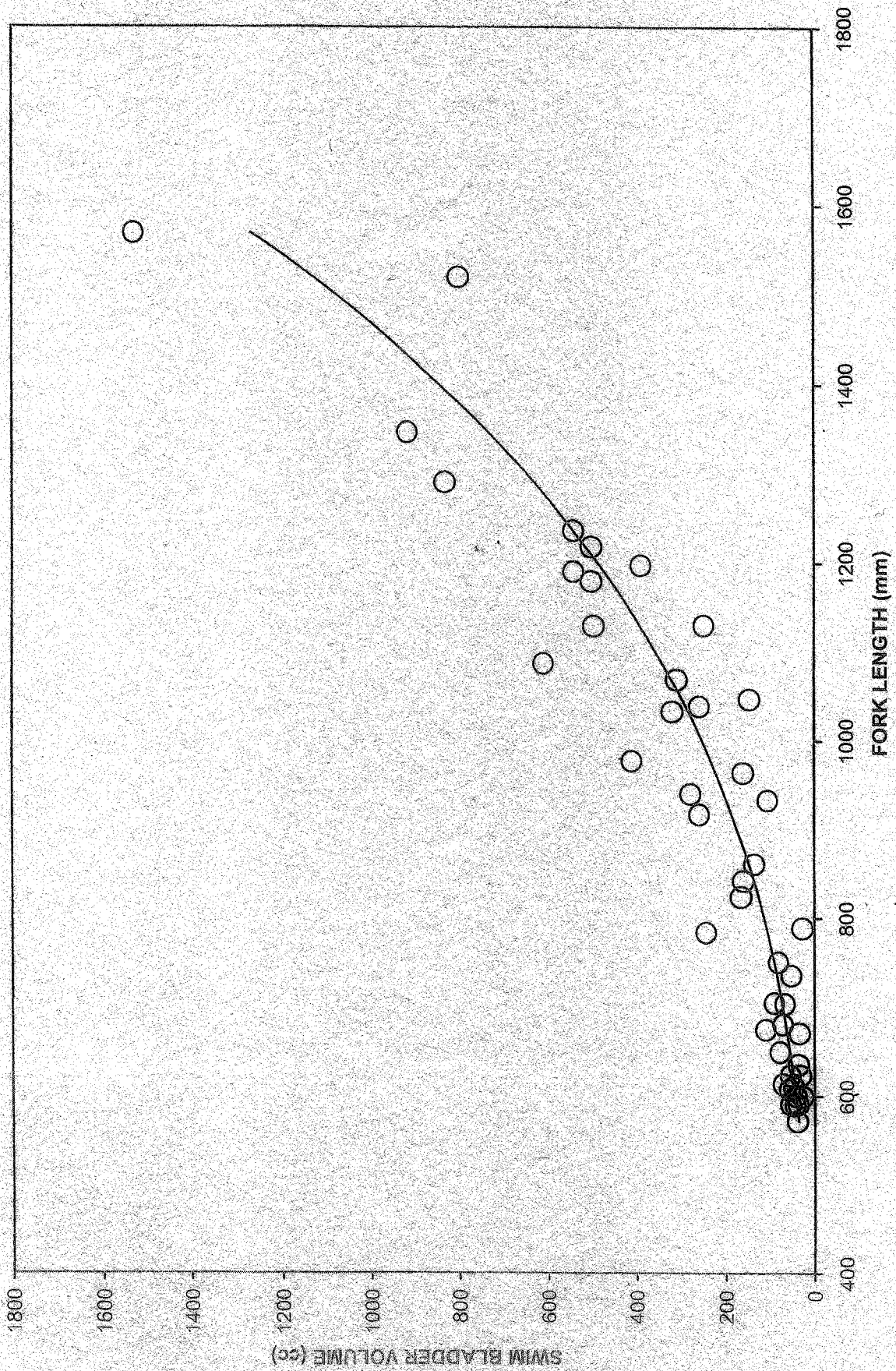


FIGURE 3. Relationship between swimbladder displacement volume and length for yellowfin tuna. The fitted line is for the power function given in the text.

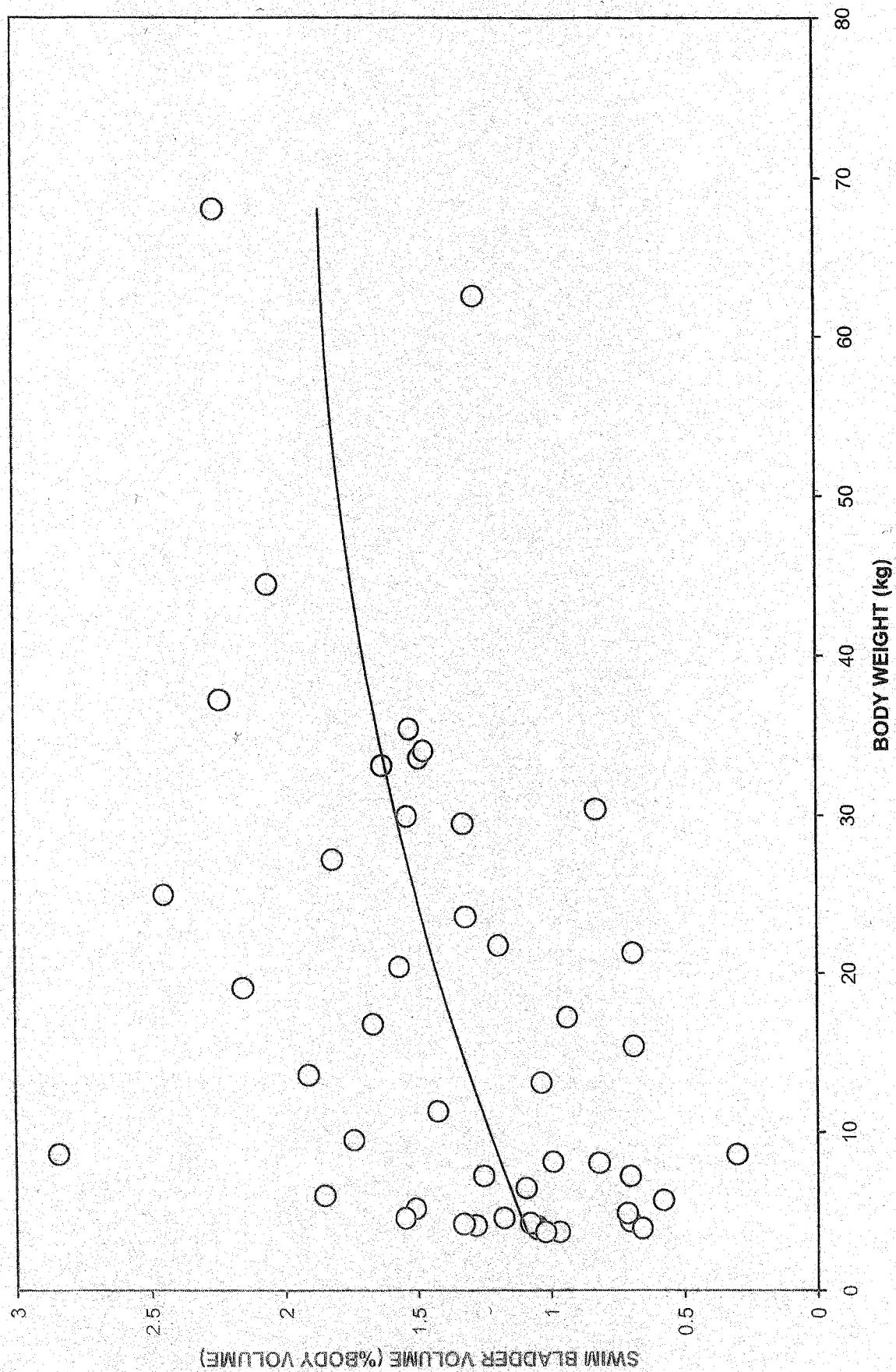


FIGURE 4. Relationship between swimbladder displacement volume, as a percentage of estimated body volume, and body weight for yellowfin tuna. The fitted line is for a polynomial function given in the text.

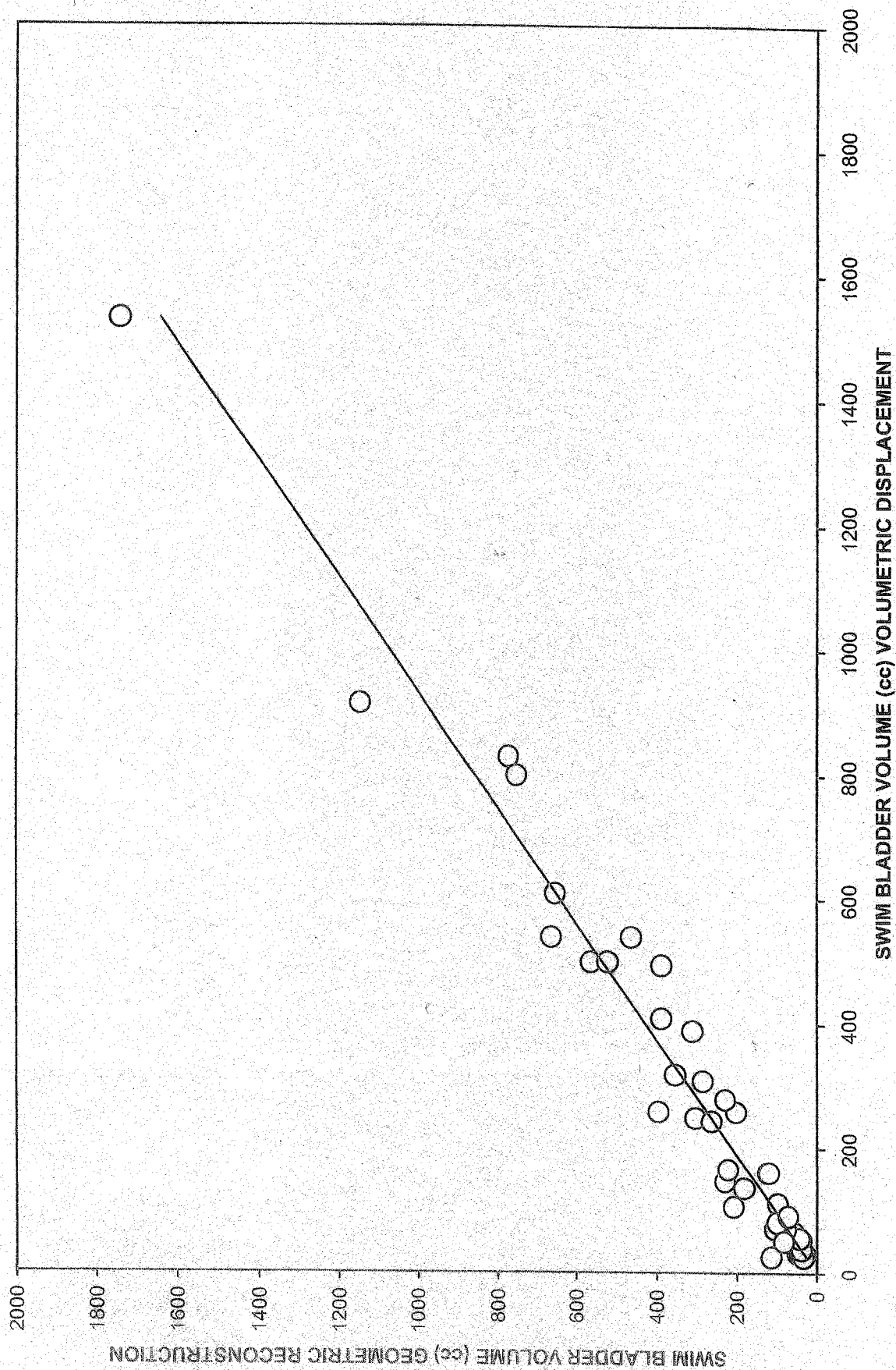


FIGURE 5. Relationship between estimated swimbladder volume, from geometric reconstruction, and swimbladder displacement volume for yellowfin tuna. The fitted line is for a linear function given in the text.

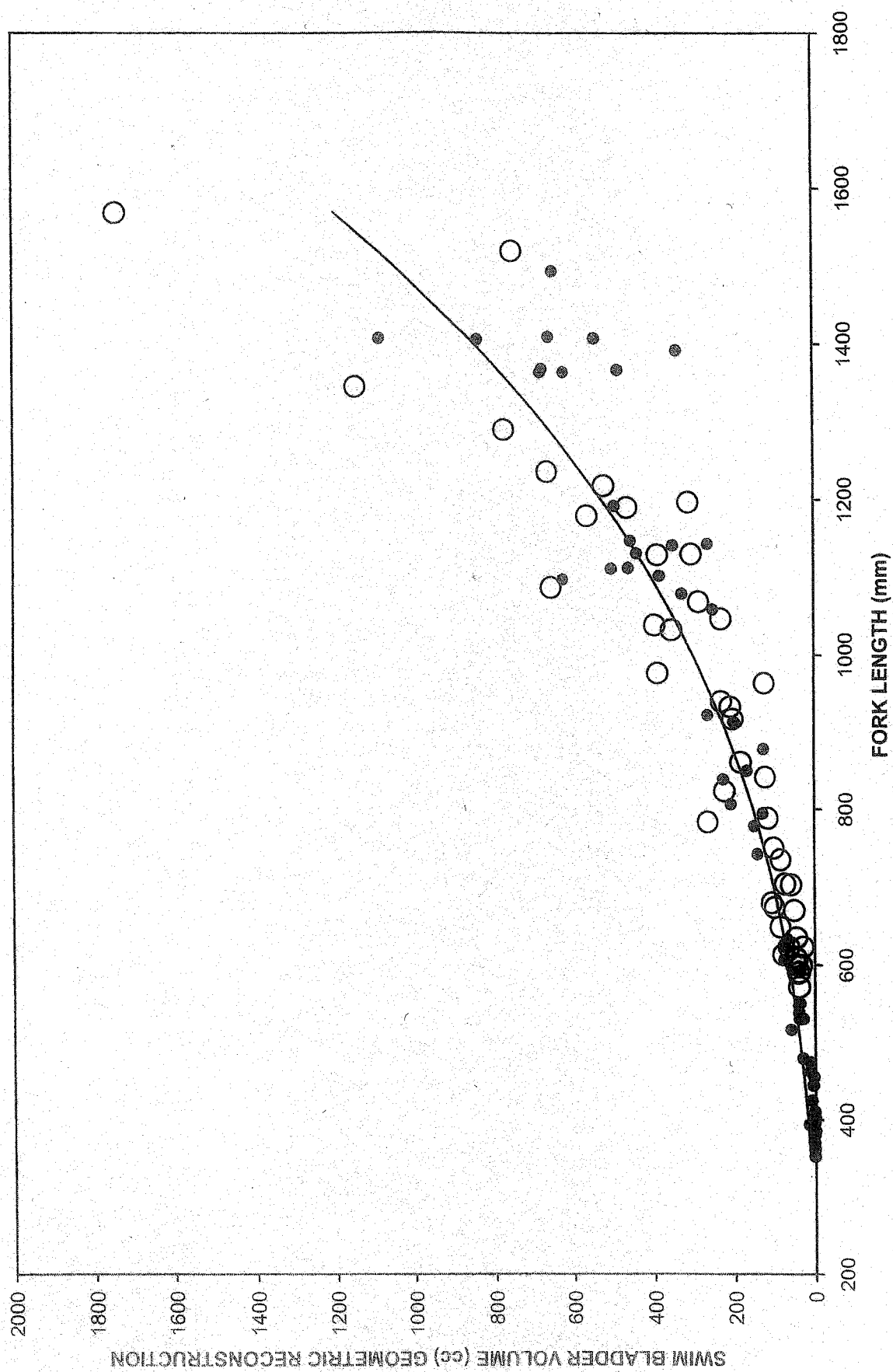


FIGURE 6. Relationship between estimated swimbladder volume, from geometric reconstruction, and length for yellowfin tuna. The open circles are for the data from this study and the solid circles are from Schaefer (1998). The fitted line is for a power function given in the text.

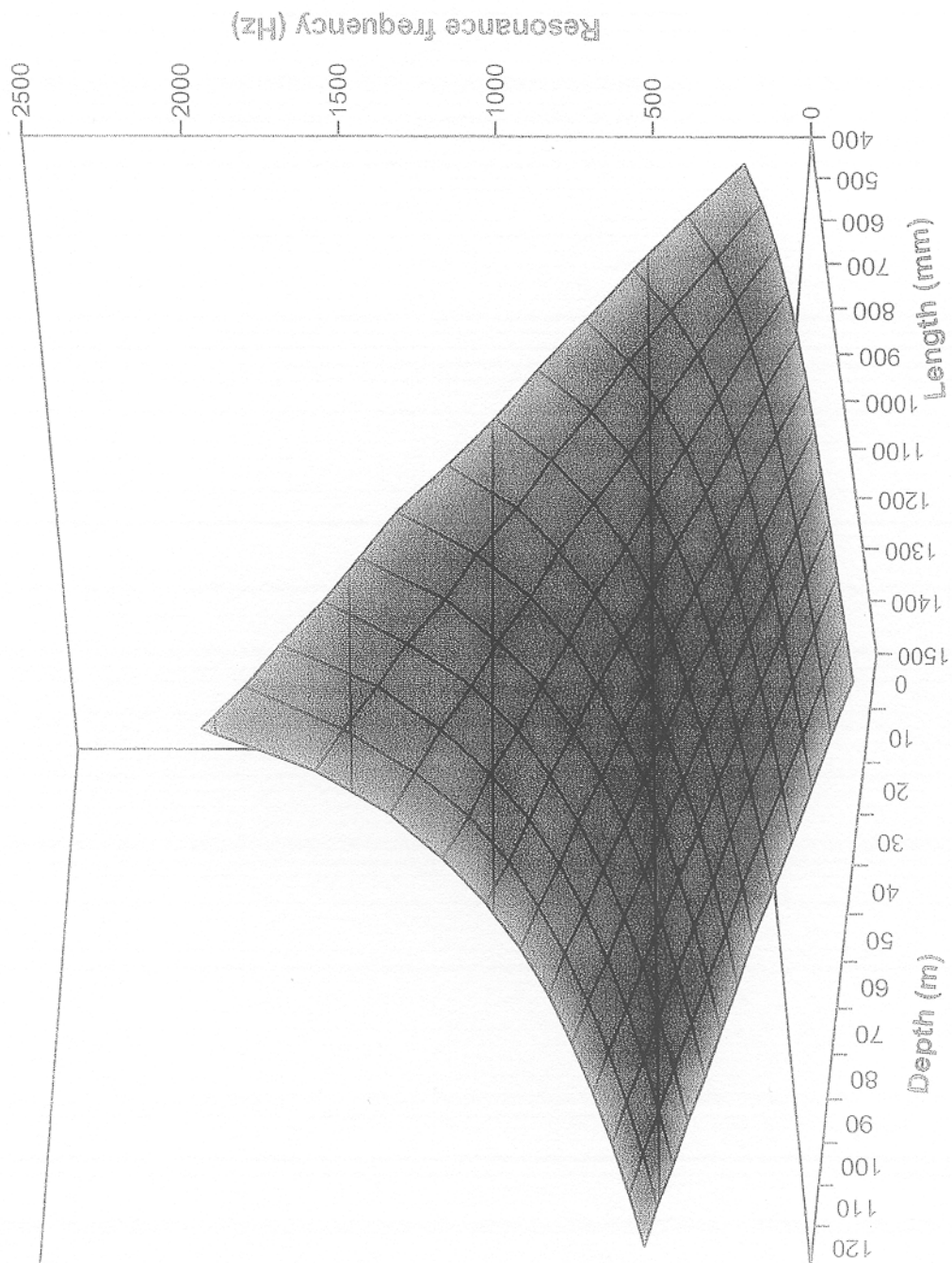


FIGURE 7. Relationship between estimated swimbladder resonance frequency, fish length, and fish depth.