

Abstract.—The shapes and volumes of swimbladders of yellowfin tuna, *Thunnus albacares*, were measured from freshly caught fish from the eastern Pacific Ocean. Direct measurements of swimbladder volumes were obtained from a geometric reconstruction with 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 were not significantly different from those obtained with the corresponding volumetric displacements. There is a nonlinear relationship between yellowfin swimbladder volumes and fish lengths. The mean swimbladder volume was 1.33% of body volume 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 tuna, we speculate on the potential distance at which dolphins could be detected by yellowfin tuna.

Shape, volume, and resonance frequency of the swimbladder of yellowfin tuna, *Thunnus albacares*

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The shape and volume of the swimbladder of yellowfin tuna, *Thunnus albacares*, is obviously important because it functions as a hydrostatic organ, which lowers the energy costs of locomotion (Magnuson, 1973; Alexander, 1993). The yellowfin swimbladder may also function in acoustic detection, providing increased sensitivity in hearing, thus enhancing the ability of fishes to detect other organisms, such as dolphins and prey (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% (Harden Jones and Pearce, 1958) to as much as 95% (Foote, 1980) of the acoustic target strength for some fish.

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 tuna independent of dolphins. Studies suggest that yellowfin tuna schools could be detected at much greater ranges

(20 to 40 km) than are currently feasible (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 assessing yellowfin tuna or other large pelagic fish.

Nero¹ 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 swimbladders were modeled as gas-filled spheres (Feuillade et al., 1996). Nero's models (1996) included swimbladder volume estimates of approximately 5% of fish volume for yellowfin tuna 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 our study were 1) to obtain direct measurements

¹ Nero, R. W. 1996. Model estimates of acoustic scattering from schools of large yellowfin tuna. Report NRL/MR/774-95-7708. Naval Research Laboratory, Ocean Acoustics Branch, Acoustics Division, Stennis Space Center, MS 39529-5004, 21 p.

of swimbladder shapes and volumes from freshly caught yellowfin tuna 50 to 150 cm in length, 2) to compare the swimbladder displacement volumes with volumes estimated from geometric reconstruction, 3) to compare the swimbladder volumes estimated from geometric reconstruction for freshly caught and frozen-and-thawed specimens, and 4) to calculate swimbladder resonance frequencies as functions of fish length and depth.

All four objectives are directly related to designing a low-frequency, long-range acoustic detection system to locate large yellowfin tuna. The first objective provides direct measurements of the relation between swimbladder volume and fish length, upon which are based acoustic target strength estimates. The previously modeled relationship was based upon smaller yellowfin tuna (Magnuson, 1973; Nero, 1996). The second and third objectives were to ascertain the practicality of obtaining swimbladder volumes by means other than volumetric displacement of the swimbladder from freshly caught fish, thus providing both a simpler method and wider sampling opportunities. The last objective allows incorporation of fishery information (fish size and swimming depth) to select a particular frequency, or frequency range, in order to optimize an acoustic detection system.

Materials and methods

Yellowfin tuna specimens were caught by rod and reel. Seventeen 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°56'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 was measured 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, with 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, including the attached extraneous tissues. The volume of the swimbladder wall was not determined and should be considered insignificant, being extremely thin, with respect to volumetric displacement.

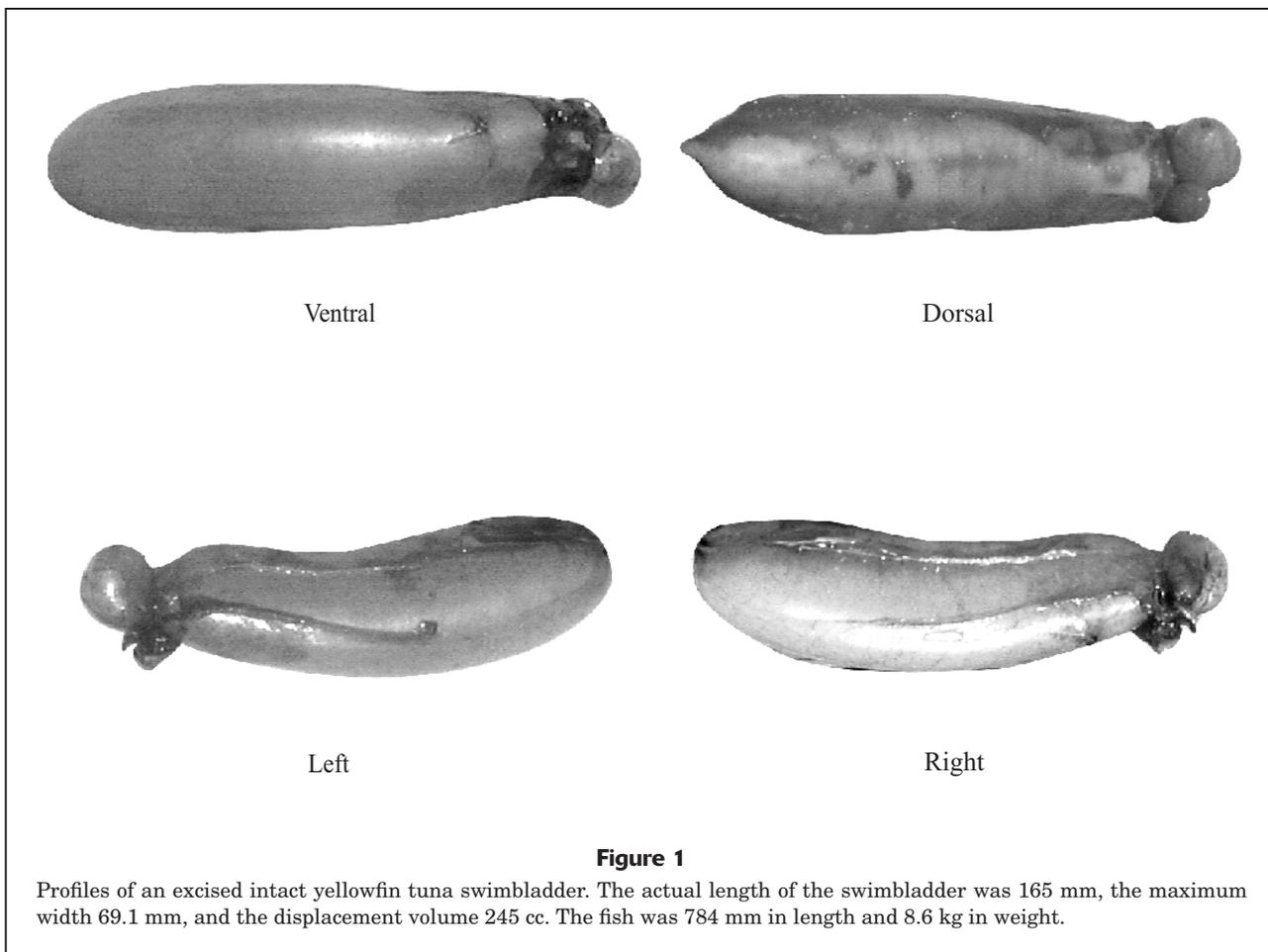
Estimates of swimbladder volumes were also computed by a geometric reconstruction from the bladder's length and width measurements. Based on the above four measurements of each bladder, an algorithm was employed to estimate the volumes between several cross sections. Cross sections of the swimbladder 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 by a geometric reconstruction for 62 frozen and thawed yellowfin tuna, ranging in length from 35 to 149 cm (Schaefer, 1999), 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 provided definitive views of the overall shape (Fig. 1). The swimbladder is cylindrically shaped and has medial bulging and hemispheric ends. There are paired protuberances on the rostral-dorsal surface. The protuberances are commonly of unequal size (the left is larger than the right) and they fit into sockets located on each side of the vertebral column. As size increased in the yellowfin specimens we examined (Table 1), the ratio of the swimbladder length to the width remained fairly constant, around a mean of 3.1 (range: 2.2–4.8). The swimbladder shape, however, changed noticeably, particularly at the caudal end (Fig. 2).

The swimbladder has thin elastic walls except for the thicker walls of the protuberances. The dorsal surface of the swimbladder is attached to a sheet of thick connective tissue, situated along the dorsal wall of the abdominal cavity adjacent to the vertebral column. In larger specimens, there is a prominent cord of connective tissue originating from the posterior area of this tissue and extending anteriorly to the area of the sockets at the rostral end of the swimbladder. This distinct cord of connective tissue



is situated directly adjacent to the dorsal wall of the swimbladder.

The relationship of swimbladder volume obtained from volumetric displacement, to fish length for the freshly caught yellowfin tuna is shown in Figure 3. The relationship is described by a power function:

$$Y_x = 0.000000005 x^{3.5715}, \quad (r^2=0.87, n=46) \quad (1)$$

where Y_x = swimbladder volume at fish length x .

The relationship of swimbladder volume, obtained from volumetric displacement and expressed as a percentage of the body volume (estimated from body weight) to weight for freshly caught yellowfin tuna 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. The relation between the swimbladder volume, expressed as the percentage of body volume to body weight is described by the following linear function:

$$Y_x = 1.0822 + 0.0146x, \quad (r^2=0.17, n=46) \quad (2)$$

where Y_x = swimbladder volume, expressed as a percentage of body volume, at weight x .

The relationship of swimbladder volume (estimated from geometric reconstruction) to volume obtained from volumetric displacement for freshly caught yellowfin tuna is shown in Figure 5. The relationship was described and analyzed by the following linear function, with the intercept set to zero:

$$Y_x = 1.0735x, \quad r^2=0.96, n=46 \quad (3)$$

where Y_x = swimbladder volume estimated from geometric reconstruction for the corresponding volumetric displacement x .

The regression coefficient is significantly different from 1 ($t_{0.05(2),44}=2.41$; $P<0.05$). However, it is apparent from Figure 5 that the two techniques produce similar estimates, providing credence to the estimation of volume from geometric reconstruction.

Analysis of covariance applied to the log-transformed swimbladder volumes by geometric recon-

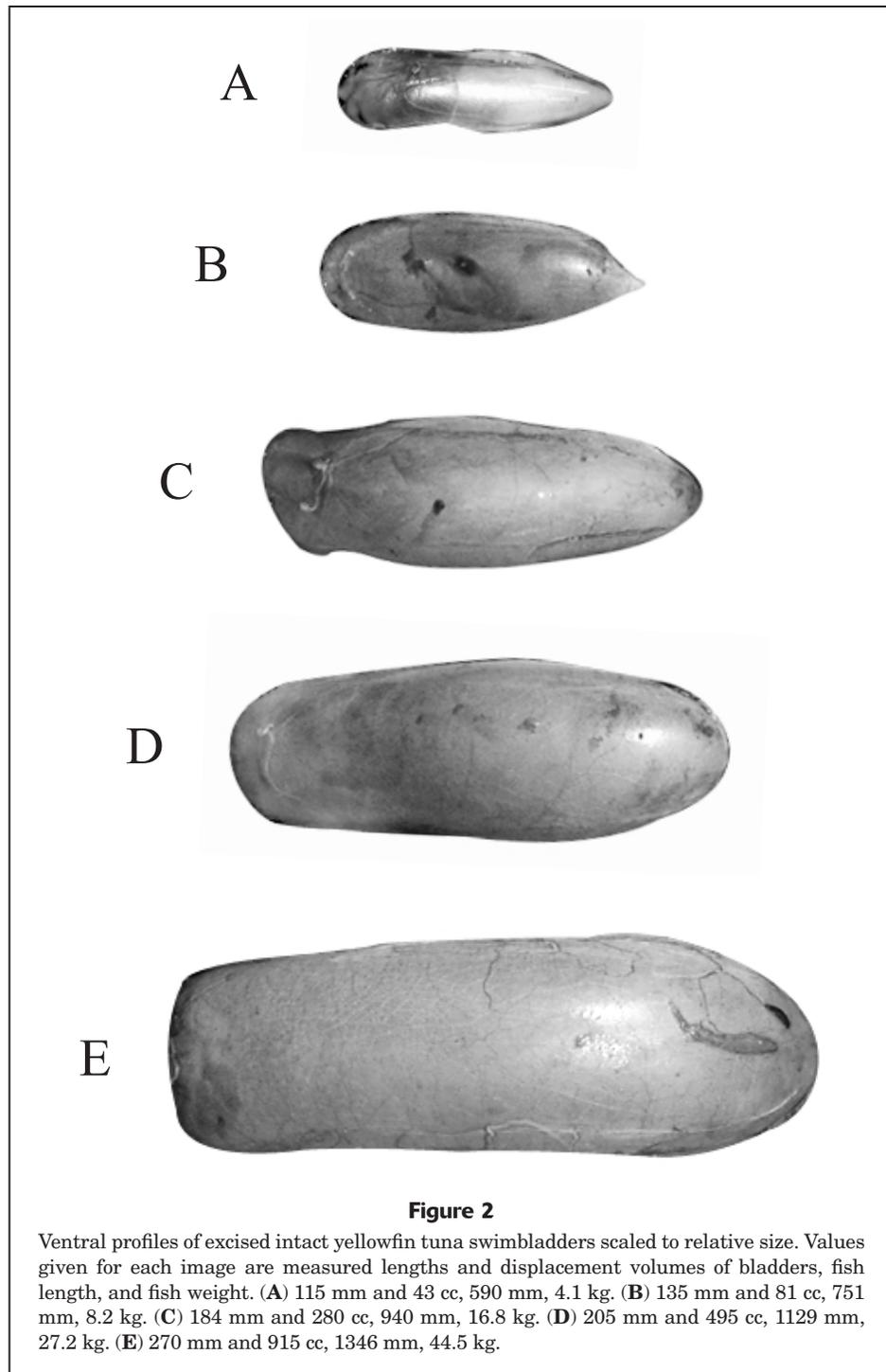
Table 1

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

struction and fish-length data truncated to a length range of 60 to 119 cm from the present study ($n=36$) and from Schaefer (1999) ($n=24$) indicated

no significant difference in the test for equality of slopes ($F=2.50$, $P=0.12$) or equality of adjusted means ($F=2.38$, $P=0.13$). In addition, an approxi-



mate F -ratio statistic (Zar, 1974) indicated that the sample power functions fitted to the data of percentage of swimbladder volume (obtained from geometric reconstruction) to fish length (57 to 157 cm, $n=46$) from our study and (35 to 149 cm, $n=62$) from Schaefer's study (1999) are estimating the same population regression function ($F=2.65$, $P>0.10$). It thus

appears appropriate to pool the two sets of data for yellowfin tuna swimbladder volumes obtained from geometric reconstruction, in order to provide the most comprehensive model possible.

The relation of swimbladder volume (estimated by geometric reconstruction) and length of the yellowfin tuna from our study, combined with that from Schae-

fer's (1999) is shown in Figure 6. The relationship is well described by a power function fitted to the nontransformed data by means of a weighted regression procedure:

$$Y_x = 0.00000002 x^{3.0601}, \quad (r^2=0.83, n=108) \quad (4)$$

([fish length range:
353 to 1569 mm])

where Y_x = a swimbladder volume at fish length x .

The weighting employed consisted of the reciprocal of the variance about the volumes within each 200-mm length interval.

Swimbladder resonance frequency

The monopole-dominant resonance frequency of a swimbladder (Andreeva, 1964) is approximated by using a spherical volume of gas (Love, 1978) as follows:

$$\text{Resonance frequency} = \sqrt{\frac{3\Gamma P}{4\pi^2 r^2 D}} \quad (5)$$

where $\Gamma = 1.4$;

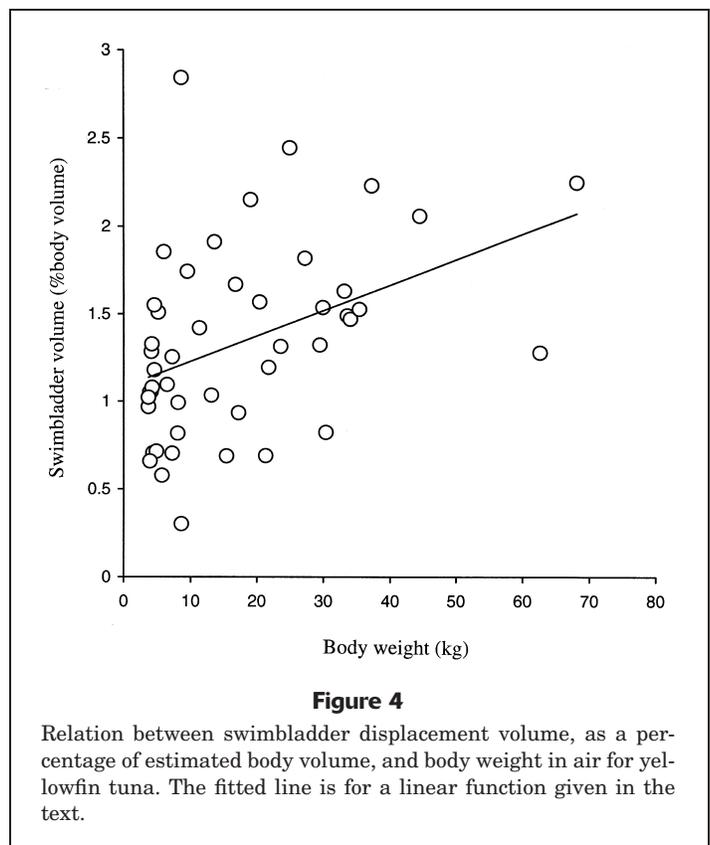
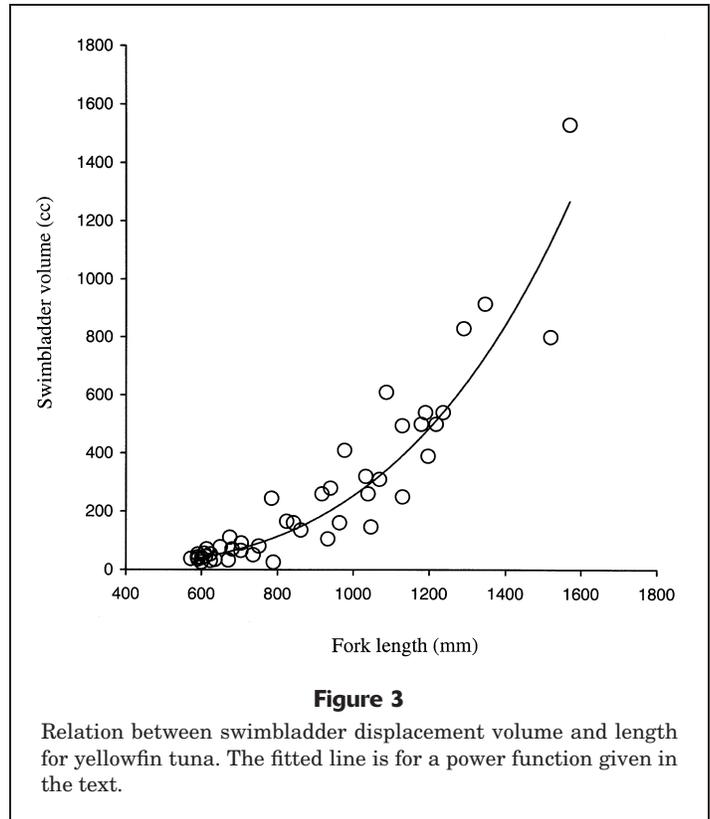
r = radii of equivalent sphere in meters;

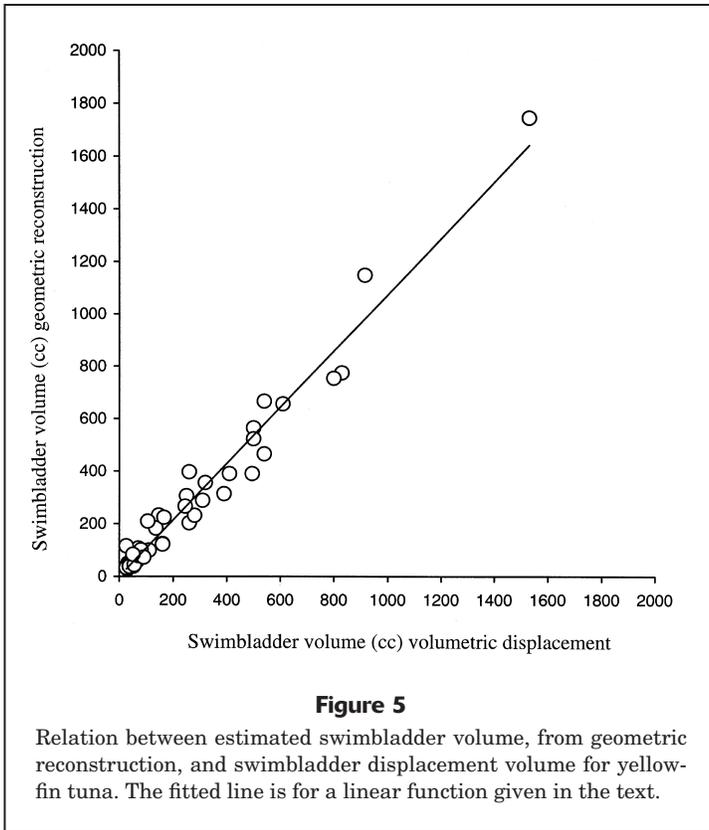
D = density of fish flesh (1050 kg/m³);
and

P = sound speed parameter at depth Z defined as

$$P = \left[1 + \left[\frac{Z_{\text{meters}}}{10_{\text{meters}}} \right] \right] \times 10100 \text{ Pascals} . \quad (6)$$

Because yellowfin tuna swimbladders are not spherical, the predicted resonance frequency must be adjusted to account for the approximate prolate spheroid shape of the swimbladder (Figs. 1 and 2). Weston (1967) has provided a formula and figure (Chap. 5, p 59, Fig. 5.2) for this adjustment using the ratio of the swimbladder's maximum (a) and minimum (b) radii (e.g. 1/2 length and 1/2 width). From the figure, we interpolated the magnitude of the upward adjustment at various depths, incorporating Boyle's Law to account for changes in volume with depth. The swimbladder's maximum radius (a) was held constant at all depths because it is firmly attached to the connective tissue sheet adjacent 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 (Fig. 6), and determined the percent increase in the expected resonance frequency. The regression coefficient ($b=1.053$) for the linear relationship of swimbladder volume estimated by geometric reconstruction to the volume estimated from the equation for a prolate spheroid is not significantly different from 1 ($t_{0.05(2),106}=1.84$; $P>0.05$). Solving for b yields:

$$b_{\text{depth}} = \sqrt{\frac{V_{\text{depth}}}{\frac{4}{3}\pi a}} \quad (7)$$

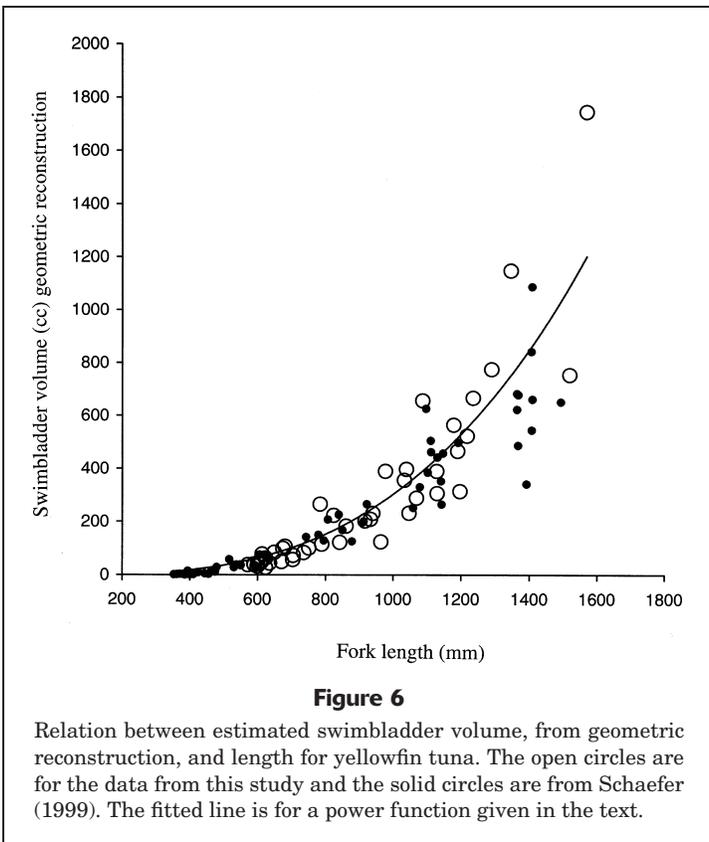
Resonance frequencies for swimbladders of yellowfin tuna of various lengths and at various depths were estimated (Fig. 7), using the above equations and the predictive regression function for swimbladder volumes for fish lengths (Fig. 6). Applying this correction increased resonance frequencies between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

Discussion

Swimbladder shape and volume

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

The swimbladder volume estimates derived by geometric reconstruction in this study and in Schaefer (1999) appear to provide realistic representations for swimbladders of live yellowfin tuna swimming at the surface of the ocean. All of the intact swimbladders within the abdominal cavities for those specimens were sufficiently inflated so that the bladders were taut, rather than flaccid. Many of the yellowfin tuna 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 similar to those described for cod (Ona, 1990). In addition, yellowfin tuna are physoclistous, and the



inflation and deflation of the swimbladder is controlled through special glands that function in the secretion or resorption of gases from, or to, the blood (Alexander, 1993). Virtually nothing is known about inflation and deflation rates in swimbladders of tunas, but it would appear from studies of other fishes (Alexander, 1993) that swimbladder volume adjustments would be extremely slow in relation to the rapid swimming speeds during vertical forays by these species (Holland et al., 1990).

Geometric reconstruction of swimbladders in yellowfin tuna was previously derived from radiographs to estimate volumes, which were validated by volumetric displacement (Chang and Magnuson, 1968). It is apparent from the results of that study and our study that the geometric reconstruction method is sufficiently accurate for deriving estimates of volumes of swimbladders of yellowfin tuna, and possibly other tunas as well. Obtaining swimbladder volumetric data by geometric reconstruction is more practical than by volumetric displacement because of the additional time required and potential of puncturing the swimbladder when excising for determination of volumetric displacement. 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 an x-ray unit for obtaining these estimates.

Magnuson (1973) reported that swimbladder volumes for 11 yellowfin tuna specimens, 44 to 82 cm in length, ranged from around 0.25% to 4.0% of body volume (estimated from Fig. 4a of Magnuson, 1973). The swimbladder volumes in our study, derived from volumetric displacements, expressed as a percentage of the estimated body volumes (Fig. 4) had a mean of about 1.3%, with a range of about 0.3% to 2.84%, and almost no relation with increasing mass. Swimbladder volumes, from the present study, for yellowfin tuna in the length range presented in Magnuson (1973) appear to be significantly lower (Fig. 4). The data of Magnuson (1973) were based upon measured volumetric displacements of the fish, whereas in the present study body volume was estimated, without adjusting for fish density because 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, expressed as a percentage of body weight, would be increased by only 0.07% on average. This small increase in volume does not account for the apparent differences in swimbladder volumes between the present study and those in Magnuson (1973). In addition,

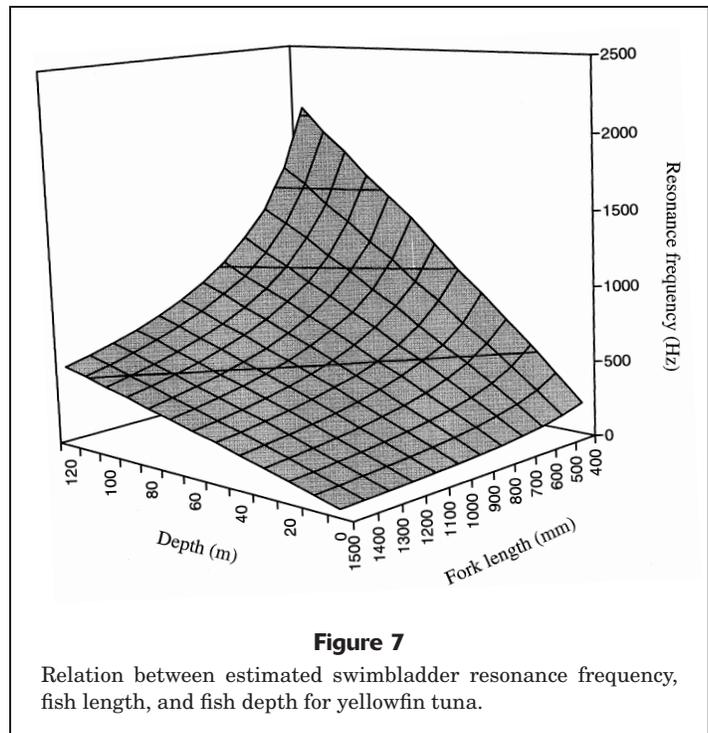


Figure 7
Relation between estimated swimbladder resonance frequency, fish length, and fish depth for yellowfin tuna.

although Magnuson (1973) reported that specimens of 2 kg or less have no gas in the bladder, Schaefer (1999) reported yellowfin swimbladders are inflated with measurable quantities of gas in specimens as small as 0.85 kg (353 mm) (Fig. 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 (Bayliff, 1998), the thermocline depth ranges from about 40 to 120 meters (Fiedler, 1992). Resonance frequency will change with depth because volume is the primary determinant of the resonance frequency of a swimbladder. 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 frequencies (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 re 1 μ Pa for yellowfin

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 decrease in Nero's reported school target strengths could result from the smaller swimbladder volumes that we measured for fish of similar lengths, depending upon the swimbladder's contribution to target strength at high frequencies (Harden Jones and Pearce, 1958; Foote, 1980).

Nero (1996) estimated low-frequency target strengths for schools of yellowfin tuna at various depths, fish lengths, and packing densities but noted school target strength was complicated 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 as a result of the smaller swimbladder volumes we report. 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 the 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. Although vision (Guthrie and Muntz, 1993) and chemoreception (Hara, 1993) are presumably important to yellowfin tuna in foraging, sex, and social communication, acoustic sensory capacities probably provide greater detection potential because of the light attenuation 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 a greater distance than that by either visual or chemoreceptive senses (Hawkins, 1993). Although the swimbladder of yellowfin tuna may enhance their acoustic detection and their ability to detect sounds, the size and shape of their swimbladder does not appear to provide for any directional information. Directionality in hearing, however, may exist in yellowfin tuna based on the anatomy and organization of the inner ears (Hawkins, 1993).

The physiological behavior of yellowfin tuna and the affect that it potentially has on the acoustic characteristics of the swimbladder should be considered. For instance, the swimming behavior of yellowfin tuna, exemplified by vertical excursions, may enable individuals to actively control the resonance frequen-

cies of their swimbladders (Fig. 7) and to potentially enhance their ability to sense their environment, as previously proposed by Feuillade and Nero (1998) for other fish with swimbladders. By varying the resonance frequency of the swimbladder, yellowfin tuna may be able not only to amplify acoustic signals but also filter auditory signals and thus improve acoustic detection in the presence of high levels of ambient noise (Hawkins, 1993).

Because estimates of yellowfin tuna swimbladder resonance frequencies presented in our study were within the range of frequencies audible to yellowfin tuna (Iverson, 1967) and because swimbladders may enhance yellowfin tuna hearing (Blaxter and Tytler, 1978; Blaxter, 1980), it is tempting to speculate about the potential distance at which yellowfin tuna could become aware of dolphins (*Stenella* spp. and *Delphinus delphis*) or prey, predators, or conspecifics through sound reception. Identification of a mechanism that facilitates the yellowfin tuna and porpoise bond in the eastern Pacific (National Research Council, 1992) may provide a means of breaking the bond prior to setting nets that encircle dolphins, thus enabling the capture of yellowfin tuna without catching dolphins. If the mechanism is an attractant (i.e. yellowfin tuna move towards the sounds of dolphins or other oceanic sounds, or towards the sounds of both), then the possibility exists to attract larger yellowfin tuna artificially with acoustical devices. Active sounds produced by dolphins include clicks, bangs, and whistles (Schevill, 1964; Tivolga, 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 re 1 μ Pa (Au, 1993). Passive sounds resulting from tail-slaps, breaches, and other behaviors have also been described as loud (Hult, 1982; Smolker and Richards, 1988). The energy at frequencies between 50 and 1100 Hz is of particular interest because yellowfin tuna have been shown to respond to sounds in this range—the most sensitive responses occurring between 300 and 500 Hz (Iverson, 1967).

Sound intensity decreases with range as a sound propagates through the water, primarily because of transmission loss associated with spherical spreading of the wavefront and absorption (Richardson et al., 1995). At 500 Hz, absorption loss is approximately 0.013 dB/km (Urlick, 1983) and total transmission loss can be approximated from spreading loss alone over relatively short distances. We used the best hearing sensitivity at 500 Hz reported by Iversen (1967) for small yellowfin tuna (83 dB re 1 μ Pa) as the minimum received source level (SL) a tuna can hear. In the absence of published data on SL at 500 Hz associated with low-frequency sounds

produced by *Stenella* and *Delphinus*, we use the maximum SL measured for jaw pops of *Tursiops truncatus*, 163 dB re 1 μ Pa (Finneran et al., 2000). Maximum detection range under spherical spreading conditions is calculated as:

$$\text{Range} = 10 (SL_{\text{initial}} - SL_{\text{received}}) / 20. \quad (8)$$

In the absence of other sounds (e.g. ambient noise), we estimated that yellowfin tuna in the eastern Pacific Ocean may be able to detect a 500-Hz sound of 163 dB re 1 μ Pa out to a distance of approximately 10 km.

Ambient noise in offshore waters results primarily from wind and waves (Richardson et al., 1995) and can mask reception of other sounds. In the region of the eastern Pacific Ocean, where a yellowfin tuna fishery exists, the sea surface is characterized by frequent periods of light winds with wind speed less than 5 m/s (sea state 2) more than 60% of the time (Webb, 1998). At 500 Hz and with sea state 2, broadband ambient noise is approximately 85 dB re 1 μ Pa (Richardson et al., 1995), and would probably mask the ability of tuna to detect our hypothetical 83-dB dolphin sound at the maximum distance we calculated. We are unaware of any data on critical ratios or critical band widths associated with tuna hearing, from which we could estimate the effective received level required for a tuna to detect our sound in the presence of this ambient noise. However, the source level received by a yellowfin tuna would have to be higher than ambient noise level, thus reducing detection distance.

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 Pacific Ocean. Whether larger yellowfin tuna actively search for dolphins to increase their probability of remaining within food-rich habitat (Fiedler et al., 1998) or whether the dolphin's sonar echolocation ability detects yellowfin tuna (Au, 1993), the swimbladder may play an important role in both sound reception and detectability as an acoustical target. Further research should be conducted on yellowfin tuna bioacoustics, including hearing sensitivity in larger yellowfin tuna, determination of the role of the swimbladder in hearing sensitivity, and measurements of source level sounds produced by dolphins and other marine organisms at frequencies below 1 kHz, referenced to a source.

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