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Structure and volume of the hoki, *Macruronus novaezelandiae* (Merlucciidae), swimbladder

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The structure of the hoki, *Macruronus novaezelandiae*, swimbladder is similar to well-developed swimbladders in other deep water fish that undergo extensive diel vertical migrations. The preponderance of a globular mass of submucosal tissue in the posterio-ventral floor of the swimbladder in large individuals is an unusual feature of unknown function, but has characteristics similar to regressed swimbladders that occur in some species of the Myctophidae. Two out of three different estimates of swimbladder volume were significantly lower than ' neutral buoyancy volume ' estimates, probably because the swimbladders were inflated artificially without accounting for their natural compliancy and internal pressure. Volume estimates from such swimbladders may reduce substantially the accuracy of target strength estimates from morphometry-based models of the swimbladder. However, this may be a trivial consideration in acoustic surveys compared to the probable occurrence of diel and seasonal variation in swimbladder shape and volume.

Key words: hoki; swimbladder; volume.

I. INTRODUCTION

Adult hoki, *Macruronus novaezelandiae* Hector, occur within the mesopelagic zone around New Zealand and southern Australia (Ayling & Cox, 1982). They contribute substantially to the trawl fishery in New Zealand, with annual landings exceeding 150 000 t. Hydroacoustic surveys have been used in New Zealand to monitor the abundance of hoki since 1985 (Do & Surti, 1990). Such surveys require knowledge of the reflectivity or target strength of representative individuals in the fish population. Because hoki inhabit deep water, it is difficult to obtain target strength estimates from the insonification of live fish. Since the swimbladder can account for over 90% of the target strength in gadiformes (Foote, 1980), such as hoki, a mathematical model of the reflectivity of the hoki's swimbladder has been used to estimate its target strength (Do & Surti, 1990).

Despite the significance of the hoki swimbladder, its anatomy has never been studied. First details of its shape and volume were studied by Do & Surti (1990). In addition to target strength, the volume of the teleost swimbladder has been used to estimate fish buoyancy and swimbladder gaseous exchange rates. Numerous techniques have been used to estimate swimbladder volume (see Table I), although their merits are seldom discussed. In this study, the anatomy of the hoki swimbladder is examined and three methods are used to estimate its volume. Differences in volume estimates between methods are discussed.

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TABLE I. Method categories of techniques used in other studies to estimate swimbladder volume

Method	Reference
1. Measure the weight and volume of the fish, then calculate the volume of the swimbladder that would be necessary to make the fish neutrally buoyant in its environment of a known density.	Sand & Hawkins, 1974; Gee, 1988; (Tester, 1940; Black, 1948; Harden Jones, 1951; Butler & Pearcy, 1972; Bone, 1973; Neighbors & Nafpaktitis, 1982)*.
2. Immerse the swimbladder (either naturally or artificially inflated) in a fluid and measure the volume of fluid it displaces.	Harden Jones, 1951; Chang & Magnuson, 1968; Horn, 1975; Hesthagen & Koefoed, 1979; Do & Surti, 1990; Ona, 1990.
3. Measure the dimensions of the swimbladder and calculate its volume from the volume formula for a chosen geometric shape.	Marshall, 1960; Haslett, 1962; Chang & Magnuson, 1968; Butler & Pearcy, 1972; Kleckner & Gibbs, 1972; Horn, 1975; Robinson, 1981.
4. Digitize sections of the swimbladder (or cast of the swimbladder) and calculate its volume from mathematical integrations of the sections.	Foote, 1985; Foote & Ona, 1985; Do & Surti, 1990; Ona, 1990.
5. Apply external pressure to an intact swimbladder and determine its volume from the inverse proportionality of the pressure applied.	Kanwisher & Ebeling, 1957; Alexander, 1959; Brawn, 1965; Sand & Hawkins, 1974.
6. Extract the gas from an intact swimbladder and measure its volume.	Black, 1948; Robinson, 1981; Harden Jones, 1951; Bone, 1973; Harden Jones & Scholes, 1985; Ona, 1990.

*These authors did not actually calculate the volume of the swimbladder, but could have done from their specific gravity and volume measurements of the fish.

II. MATERIALS AND METHODS

Hoki were sampled from a single midwater trawl haul from a spawning aggregation in Cook Strait Canyon, Cook Strait, New Zealand in August 1989 at a depth of 300 m.

The vascular network, attachment, and position of the swimbladder were studied from dissections of numerous thawed fish. Tissue types and microstructures were determined from swimbladder sections stained, separately, with haematoxylin and eosin, Sudan black, and Van Gieson trichrome. Estimates of the surface area of the elliptical gas gland and resorptive area, the length of the retia, and the volume of the swimbladder, were compared with Marshall's (1960) data from other teleosts.

In many of the 27 hoki examined, a globular mass of submucosal tissue which occluded the posterior swimbladder lumen, was removed and measured to the nearest ml by displacement in water in a 10 ml graduated cylinder.

Only three of the existing techniques for estimating swimbladder volume (Table I) were used, because hoki swimbladders usually rupture from their rapid ascent in a trawl. For each of these methods, fish were selected over a wide range of sizes, but within a given size class the selection was arbitrary.

Method 1 (Table I) estimated the volume of each of 15 swimbladders from freshly caught fish (40–100 cm long; nine males, six females; all with empty stomachs and mature or maturing gonads) by measuring the weight and volume of each fish and calculating the volume of gas necessary to make the fish neutrally buoyant in an environment of known density. To determine the volume of a fish, it was weighed to the nearest 0·1 g with a triple beam balance while suspended in air (W_a), and again while suspended, with its

swimbladder deflated, in a large bucket of sea water (W_w) of a determined density. No more than five fish were weighed in the same sea water. Each exchange of sea water was sampled, its temperature recorded, its salinity measured with a salinometer and its density (D_w) determined from its salinity and temperature.

The fish's volume (V_f) was calculated from the equation $V_f=(W_a - W_w)/D_w$. The volume of gas in the swimbladder necessary for neutral buoyancy (V_s) is: $V_s=(W_a/D_e) - V_f$. The density of the fish's environment (D_e) was assumed to be 1·026 g ml^{-1} based on density measurements at about the same time of year, 2 years prior to this study (New Zealand Division of Scientific and Industrial Research, unpublished data).

Method 2 (Table I) estimated the volume of each of 10 swimbladders from thawed fish (53–83 cm long; all males). The excised swimbladder was filled with sawdust through the rupture in its wall until it was fully distended and then the rupture was sutured closed with cotton thread. The volume was measured to the nearest ml by displacement in water in a 100 ml graduated cylinder.

Method 3 (Table I) estimated the volume of each of 42 swimbladders, of which 15 were preserved and the remaining 27 were from thawed fish (53–86 cm long; all males). The preserved swimbladders came from the same fish that were used in the method 1 estimations. They were fixed in 10% buffered formalin and stored in 70% ethyl alcohol. Each swimbladder's major (a) and minor (b) semi-axes were measured to the nearest mm and the volume of a prolate spheroid ($4/3\ \pi ab^2$) was calculated.

III. RESULTS

Hoki are euphysoclists (physoclists whose areas of gas secretion and resorption are distinctly separate). The approximately ellipsoidal swimbladder is located retroperitoneally and adjacent to the kidney, lying along vertebrae 4–18. About one-third of its anterio-dorsal length is attached firmly to the body wall by the tunica externa, while the remainder is attached by only loose connective tissue (Fig. 1). Each anterio-lateral side of the swimbladder forms a small projection directed anteriorly. The swimbladder ends in a small cone, often folded underneath. Tissue within the anterior projections, the cone, the gas gland, and the submucosa, determines the swimbladder's internal shape. The well-developed gas gland lies along the first third of the anterio-ventral floor of the swimbladder (Fig. 1) and increases in area (gg) with fish length (l): $\log(gg) = -2{\cdot}71 + 1{\cdot}77 \log(l)$ (least squares regression, $r^2=0{\cdot}86$; $n=15$ preserved swimbladders). The gas gland epithelium is single layered with cells of 18 μm maximal length (measured from three fish 66–93 cm long), similar to the small-sized cells described by Marshall (1960). The rete mirabile is unipolar.

The large darkened and highly vascularized ellipsoidal resorptive area of the dorsal mucosa (the ' oval ') increases in area (ra) with fish length (l): $\log(ra) = -2{\cdot}16 + 1{\cdot}71 \log(l)$ (least squares regression, $r^2=0{\cdot}81$; $n=15$ preserved swimbladders). The mucosal fold (' oval edge ') is evident within the dorsal wall of the swimbladder.

The blood circulation of the gas gland and resorptive area is typical of most physoclistous swimbladders (Lagler *et al.*, 1977; Fänge, 1983). Blood is supplied to the gas gland by the retial artery, from the coeliacomesenteric artery, and is carried away by the retinal vein into the hepatic portal vein (Fig. 1). Blood is supplied to the capillary network of the resorptive area by the dorsal aorta and is carried away by the posterior cardinal vein.

The tissue layers of the hoki swimbladder are similar to those of most physoclists (Fänge, 1953); however, it was not possible to identify the hoki's

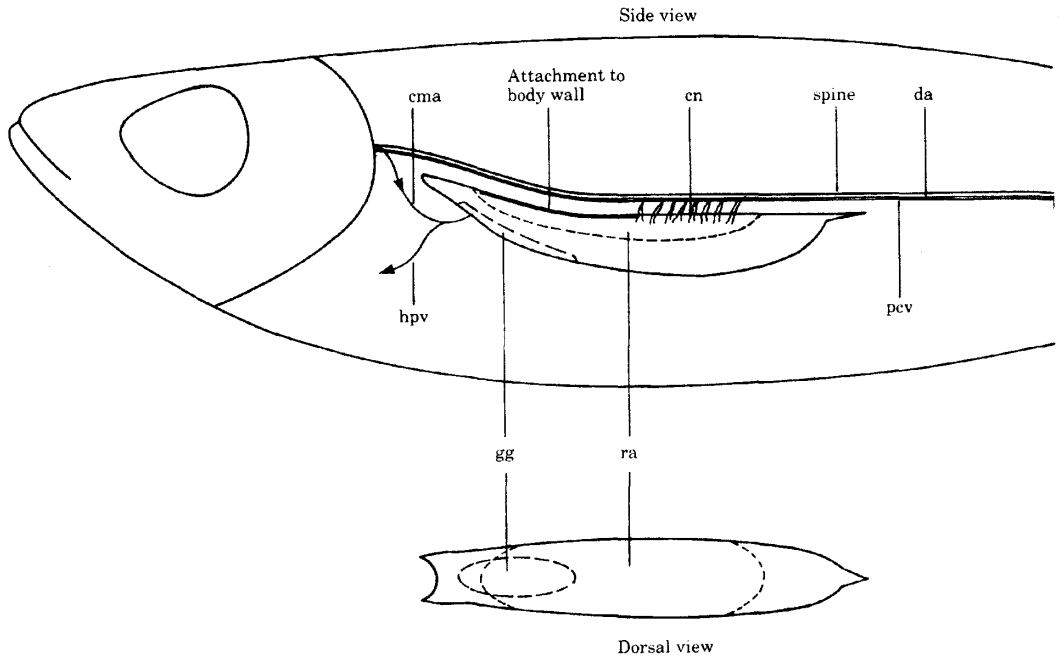

FIG. 1. Position and shape of the swimbladder within the body cavity of an adult hoki (*Macruronus novaezelandiae*) (cma, coeliacomesenteric artery; cn, capillary network; da, dorsal aorta; gg, gas gland; hpv, hepatic portal vein; pcv, posterior cardinal vein; ra, resorptive area).

muscularis mucosae. The tunica externa is composed of an outside layer of dense collagen, and in hoki, a well-developed inner layer of smooth muscle. Its dorsal region is thinner than its ventral region only within the area of its attachment to the body wall.

Like most physoclistous swimbladders, the submucosa in the ventral region is relatively thick. In some fish, the submucosa in the posterio-ventral region formed an unusual globular mass with a variable volume that increased with fish length to a maximum of 2·4 ml (Fig. 2). The submucosa does not contain lipids.

Least squares regression analysis was used to test for differences in swimbladder volume between methods of estimation. The allometric relationship between the volume (v) and linear dimension (l) of an animal is expressed by the power function: $v=al^b$. Its linearized form, $\log(v)=\log(a)+b\log(l)$, is decribed by the simple linear regression model:

$$Y=\beta_0+\beta_1 X+\varepsilon,$$

where Y and X denote $\log(v)$ and $\log(l)$, respectively. Linear regression analysis is suitable to test for differences between such relationships. Rather than fitting a separate simple regression model to the data from each method, a single multiple regression model was fitted to the data from all methods simultaneously, using standard statistical procedures (e.g. Neter *et al.*, 1989). The model included interaction terms and qualitative variables indicating the method of volume estimation. Such a model yields the same response functions as those produced from fitting separate regression models and differences between response functions can be tested efficiently using the coefficients from the single multiple regression model.

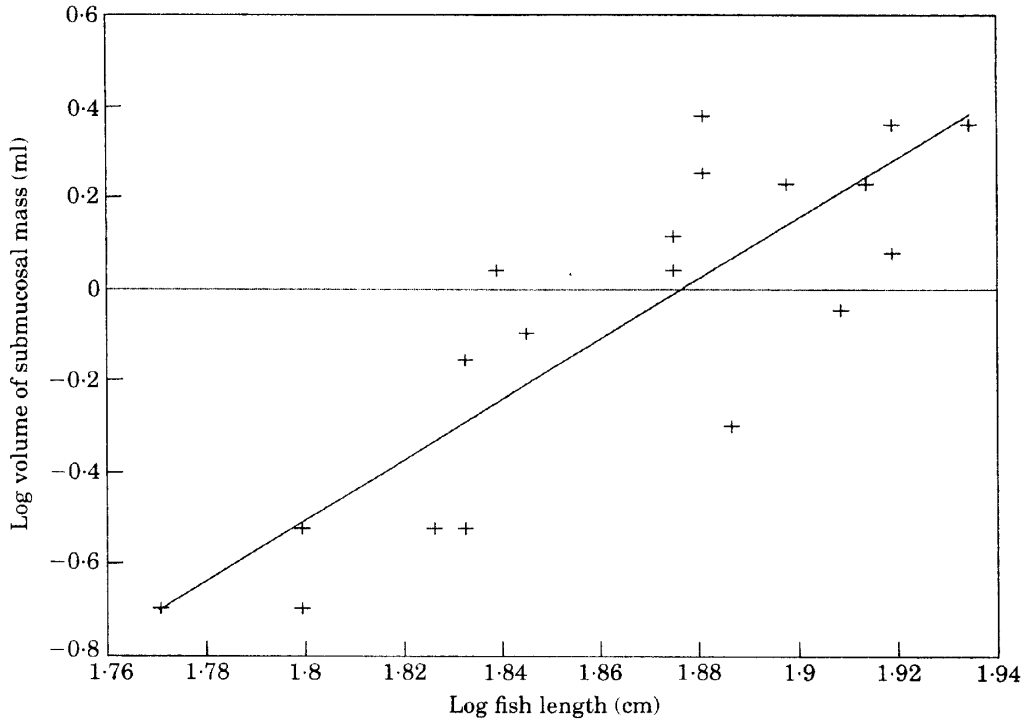

FIG. 2. Volume of the submucosal mass (m) in the posterio-ventral floor of the hoki (*Macruronus novaezelandiae*) swimbladder regressed on fish length (l) [$\log(m) = -12{\cdot}40 + 6{\cdot}61 \log(l)$, $r^2 = 0{\cdot}71$; measured from male fish; eight fish ranging from 53 to 69 cm long had swimbladders without a measurable amount of the mass, and therefore, were not included in the regression analysis].

Hence the full model,

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_4 + \beta_5 X_1 X_2 + \beta_6 X_1 X_3 + \beta_7 X_1 X_4 + \varepsilon,$$

was fitted to the data, where Y denotes the response variable log(swimbladder volume), X_1 denotes the predictor variable log(fish length), and X_2 to X_4 denote qualitative variables where $X_2 = 1$ if indicating method 2 and 0 otherwise, $X_3 = 1$ if indicating method 3 using preserved swimbladders and 0 otherwise, and $X_4 = 1$ if indicating method 3 using non-preserved swimbladders and 0 otherwise. Note that method 1 is indicated when X_2, X_3, and X_4 are equal to 0 simultaneously. After fitting the full model, the interaction term $\beta_6 X_1 X_3$ was deleted from the model at $P = 0{\cdot}66$, leading to a reduced model with all predictor variables significant at $P < 0{\cdot}015$.

Differences in volume estimates between methods were tested using the regression coefficients from the reduced model. Method 1 volume estimates (Fig. 3) were significantly different from estimates from the preserved swimbladders in method 3 (slope difference: $P = 0{\cdot}66$; assuming a common slope, intercept difference: $P < 0{\cdot}001$), and volume estimates from both of these methods were significantly different from estimates from method 2 and the non-preserved swimbladders in method 3 (slope difference: $P < 0{\cdot}014$). Method 2 volume estimates were significantly different from estimates from the non-preserved swimbladders in method 3 (slope difference: $P = 0{\cdot}54$; assuming a common slope, intercept difference: $P < 0{\cdot}001$).

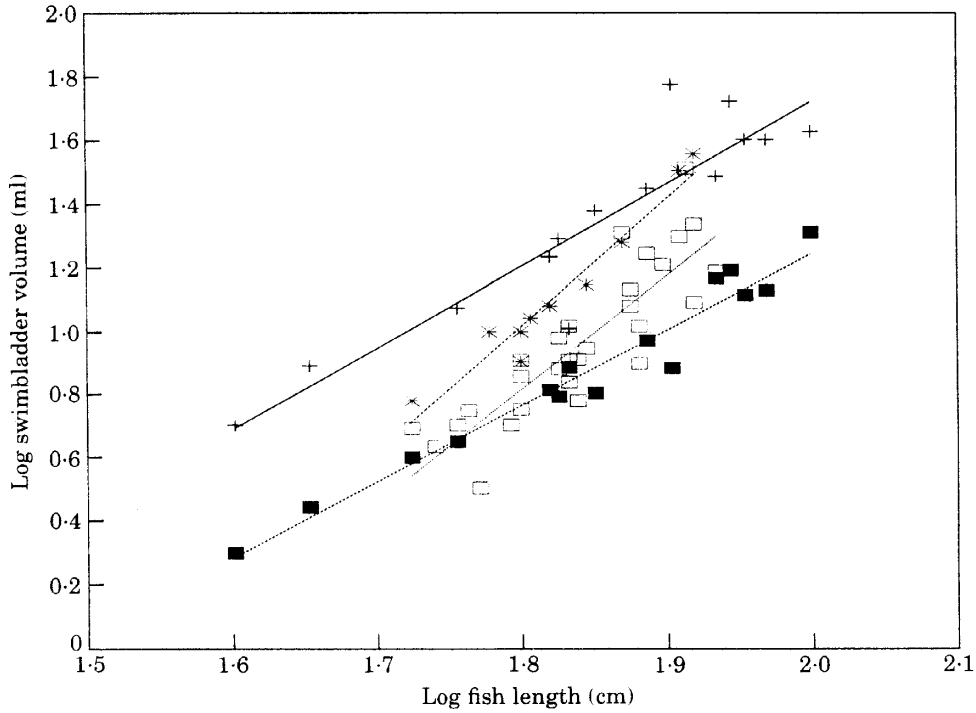

FIG. 3. Estimates of the volume of the hoki (*Macruronus novaezelandiae*) swimbladder regressed on fish length (l) for each of the three volume estimation methods, method 1 (v_1) [—+—], method 2 (v_2) [· · · * · · ·] and method 3 using non-preserved (v_3) [· · · □ · · ·] and preserved (v_{3p}) [· · · ■ · · ·] swimbladders [$\log(v_1) = -3{\cdot}42 + 2{\cdot}57 \log(l)$, $r^2 = 0{\cdot}85$; $\log(v_2) = -6{\cdot}31 + 4{\cdot}07 \log(l)$, $r^2 = 0{\cdot}94$; $\log(v_3) = -5{\cdot}72 + 3{\cdot}63 \log(l)$, $r^2 = 0{\cdot}75$; $\log(v_{3p}) = -3{\cdot}58 + 2{\cdot}41 \log(l)$, $r^2 0{\cdot}96$].

IV. DISCUSSION

Fish that prey actively in the productive, upper 1000 m of the ocean, require well developed muscle and skeletal tissue, making the individual more dense than its surrounding environment. These species have compensated for their negative buoyancy by evolving a well developed swimbladder (Marshall, 1960). Hoki make extensive diel vertical migrations to feed (Clark, 1985; Bulman & Blaber, 1986). Some adult individuals migrate from depths of more than 400 m to within 50 m of the surface and back down again within a 24-h period (Fig. 2 in Bulman & Blaber, 1986), so it is not surprising that hoki have a well-developed euphysoclistous swimbladder.

Such swimbladders have a thickened submucosa (particularly in the region of the gas gland) whose function is unclear. Fänge (1953) suggested that the ' jelly-like ' consistency of the submucosa serves to allow independent movement of the mucosa from the remainder of the swimbladder during contractions of the muscularis mucosa. Marshall (1960) suggested that the reticular spaces of the submucosa may be filled with serous fluid and that a voluminous, semi-fluid submucosa might prevent the formation of ' kinks ' in the swimbladder from compression during vertical descents. Failure of the submucosal spaces in hoki to accept histological stains is consistent with Marshall's suggestion that such spaces are filled with serous fluid. However, the function of the thickened submucosa remains speculative.

The still greater thickening of the submucosa into the formation of a globular mass in the posterio-ventral floor of the swimbladder is an unusual feature, but has characteristics similiar to regressed swimbladders that occur in some species of the Myctophidae. Regressed swimbladders become proportionately smaller with growth and often accumulate fat in the submucosa. They occur in at least seven bathypelagic families within three orders, and presumably extend the fish's vertical range, because the proportional change in swimbladder volume for a given change in pressure decreases with decreasing volume (Marshall, 1960). In myctophids, the occurrence of regressed swimbladders varies among and within species, and regression can result in a thickened submucosa which lacks fat (Butler & Pearcy, 1972; Kleckner & Gibbs, 1972). Similarly, the posterio-ventral mass of submucosa in the hoki swimbladder is variable among individuals, increases with growth (Fig. 2) and lacks fat, but is more localized and is not associated with a proportionate decrease in swimbladder size.

In addition to swimbladder morphology, myctophids vary in body lipid and water content, such that some individuals do not maintain neutral buoyancy (Butler & Pearcy, 1972; Bone, 1973; Neighbors & Nafpaktitis, 1982). Apparently, other fish besides myctophids do not maintain neutral buoyancy. Hesthagen & Koefoed (1979) found seasonal differences in the volume of the swimbladder, and hence buoyancy, in the sand goby (*Pomatoschistus minutus* L.). Harden Jones & Scholes (1985) suggested that the Atlantic cod (*Gadus morhua* L.) may be neutrally buoyant only at the top of their vertical range. Blaxter & Tytler (1978) felt that it is unlikely that any species with a gas-filled swimbladder can maintain neutral buoyancy over its entire vertical range. Given the extensive diel vertical migrations hoki undertake, perhaps they too do not maintain neutral buoyancy at all times.

Even if neutral buoyancy is achieved, Ona (1990) showed that a fish's swimbladder can vary in shape and volume due to changes in stomach content, gonadal development, fat content, and external pressure. Concerning hydroacoustic surveys, he concluded that a ' standard ', fixed target strength had no biological basis and suggested that for acoustic biomass estimates, *in situ* target strength of the fish should be monitored continually. Given these considerations, and that the use of *ex situ* ' morphometry-based ' (Foote, 1991) estimates of target strength cannot be avoided, method 1 should estimate most accurately the neutral buoyancy volume of the swimbladder, because it is based on the fish's specific gravity and hence, reflects its physiological state (see Ona, 1990).

Methods 2 and 3 implicitly estimate the maximum capacity of the swimbladder. However, estimates from these methods are suspect if swimbladders are inflated artificially without accounting for their natural compliancy and internal pressure. In the Atlantic cod, a 100% increase in swimbladder volume is possible through an internal excess pressure of only 6 cm H_2O (Sand & Hawkins, 1974). An under-distended swimbladder would result in an underestimate of its maximum capacity. This may explain why methods 2 and 3 yielded lower estimates than method 1. Concomitantly, Do & Surti's (1990) volume estimates of artificially inflated hoki swimbladders, using method 4 (Table I), were significantly lower (Fig. 4) than present method 1 estimates (least squares

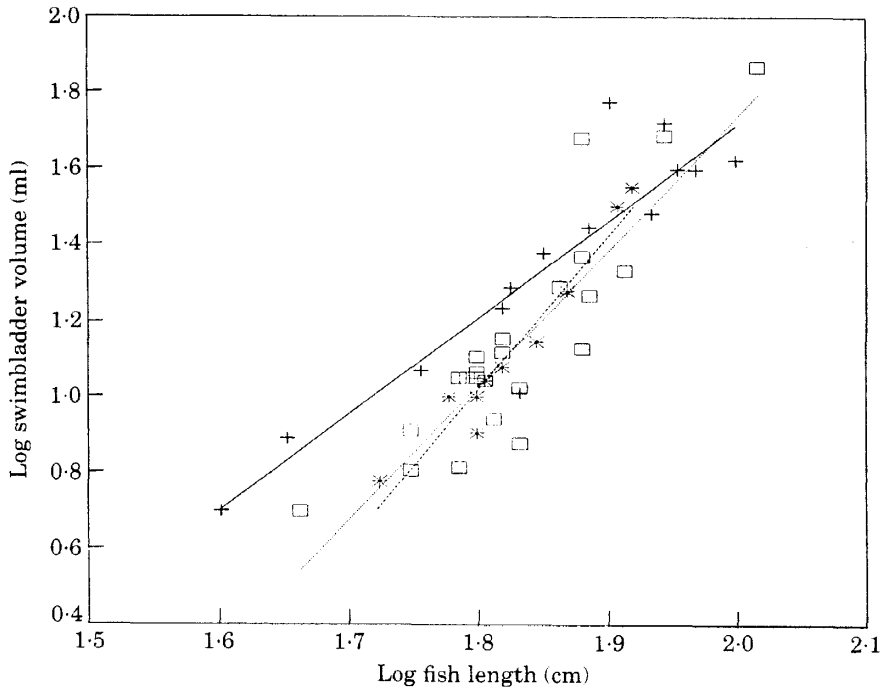

FIG. 4. Estimates of the volume of the hoki (*Macruronus novaezelandiae*) swimbladder regressed on fish length (l). Estimates derived from methods 1 [—+—] and 2 [· · · * · · ·] from the present study are compared to estimates derived by Do & Surti (1990) [· · · □ · · ·] (v_{ds}) [$\log(v_{ds}) = -5{\cdot}36 + 3{\cdot}55 \log(l)$, $r^2 = 0{\cdot}79$; regression equations for methods 1 and 2 from the present study are given in Fig. 3].

mutliple regression analysis; slope difference: $P = 0{\cdot}04$), and similar to estimates from method 2 (slope difference: $P = 0{\cdot}52$; assuming a common slope, intercept difference: $P > 0{\cdot}99$).

Estimates from method 3 may suffer further biases from oversimplifying the geometric shape of the swimbladder. Preserving the swimbladder before measuring its dimensions yield still lower estimates from shrinkage of the tissues (Robinson, 1981; present study: Fig. 3).

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