A simple generalized model of allometry, with examples of length and weight relationships for 14 species of groundfish

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Allometry is a set of relations between an animal's characteristics and its body size, and is applied in many branches of biological sciences including ecology, physiology, and morphology (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984; Bookstein et al., 1985; Reiss, 1989). Allometry is represented by the power function, $W = AL^{X_2}$, where W is a characteristic of an animal (e.g. body weight), L is its body size, and A and X_2 are its allometric parameters. To determine an allometric relationship for a particular characteristic, the power function is usually, albeit at times inappropriately, double log-transformed into a simple linear equation,

$$Y = X_1 + X_2X_3, \qquad (1)$$

with $Y = \log(W)$, $X_1 = \log(A)$, and $X_3 = \log(L)$, and is then fit to data from different individuals.

Use of allometry in this way assumes constancy of X_1 and X_2 in Equation 1. While both allometric parameters may be treated approximately as constants in certain applications, the assumption may be violated for a wide variety of biological phenomena because of genetic, phenotypic, and/or behavioral variability among individual animals. In fact, Mosimann and James (1979) have concluded that X_2 varies spatially in the Florida red-winged blackbird, *Agelaius phoeniceus*. Variability in X_2 is also implied in Reiss' (1989) hypothesis that X_2 contains phylogenetic information and is less variable intraspecifically than interspecifically. Peters (1983) convincingly demonstrated interspecific variation in X_2 and computed its mean and standard deviation for metabolic rates scaled to body sizes across many animal taxa. Variability in X_1 has not been examined but is certainly implied in the comprehensive appendices of Peters' (1983) book on the ecological implications of body size and in Reiss' (1989) monograph on the allometry of organismic growth and reproduction. X_1 may be strongly negatively correlated with X_2 for length-weight relationships in fish (e.g. Caillouet, 1993).

Variability in X_1 and X_2 may have major implications in the widely used allometric equation because it represents a fundamental concept in biology (Peters, 1983). In this paper, we generalize Equation 1 by explicitly incorporating variability in and correlation between, X_1 and X_2, and study the consequences of such variability and correlation in allometric predictions. The generalized model is demonstrated by using length and weight relationships for 14 species of groundfish of the families Centrolophidae, Haemulidae, Lethrinidae, Lutjanidae, Nemipteridae, and Synodontidae from northern Australian waters.

Model

Suppose that a joint probability distribution of X_1 and X_2 conditional on X_3 could be formed for a group of animals, with each individual having its own pair of allometric parameters which it retains throughout its life, and that values of pairs of allometric parameters are serially independent. The value of Y for the ith individual with allometric parameter pair (X_{1i}, X_{2i}) at X_3 is

$$Y_i = X_{1i} + X_{2i}X_3.$$

For a group of animals selected randomly from the population, the expected value of Y at X_3 is

$$E[Y \mid X_3] = E[X_1 + X_2X_3] \qquad (2)$$

with variance

$$\begin{aligned} V[Y \mid X_3] &= V[X_1 + X_2X_3] \qquad (3) \\ &= E[Y^2 \mid X_3] - E[Y \mid X_3]^2 \\ &= E[(X_1 + X_2X_3)^2] - E[X_1 + X_2X_3]^2. \end{aligned}$$

Given information on how X_1 and X_2 vary, one can develop Equations 2 and 3. X_2 may closely follow a normal distribution for metabolic rate of animals scaled to body size (Peters, 1983), being strongly negatively correlated with X_1 for length-weight relationships in fish (e.g. Caillouet, 1993). We will assume below that X_1 and X_2 follow a joint normal distribution, i.e. $(X_1, X_2) \sim N(\mu_1, \mu_2; \sigma_1^2, \sigma_2^2; \rho)$ with mean μ_i, and variance σ_i^2 of X_i, and correlation coefficient ρ. Under general conditions, the sum (or average) of a number of random variables is approximately normally distributed, and such approximation can be quite good even if that number is relatively small. The above assump-

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tion would be at least approximately valid because both X_1 and X_2 can be regarded as the sum (or average) of numerous (e.g. genetic, phenotypic, and behavioral) random components. Analogous models may be developed for other probability distributions. Under that assumption, Equations 2 and 3 become, respectively,

$$\begin{aligned} E[Y \mid X_3] &= E[X_1 + X_2 X_3] \\ &= \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} \frac{1}{2\pi\sigma_1\sigma_2\sqrt{1-\rho^2}} (x_1 + x_2 X_3) e^{-\frac{1}{2(1-\rho^2)}\left[\frac{(x_1-\mu_1)^2}{\sigma_1^2} - 2\rho\frac{(x_1-\mu_1)(x_2-\mu_2)}{\sigma_1\sigma_2} + \frac{(x_2-\mu_2)^2}{\sigma_2^2}\right]} dx_1 dx_2 \\ &= \mu_1 + \mu_2 X_3, \end{aligned} \tag{4}$$

and

$$\begin{aligned} V[Y \mid X_3] &= V[X_1 + X_2 X_3] \\ &= E[Y^2 \mid X_3] - E[Y \mid X_3]^2 \\ &= E[(X_1 + X_2 X_3)^2] - E[X_1 + X_2 X_3]^2 \\ &= \sigma_1^2 + 2\sigma_1\sigma_2\rho X_3 + \sigma_2^2 X_3^2. \end{aligned} \tag{5}$$

Thus variability in, and correlation between, X_1 and X_2 only affect $V[Y \mid X_3]$. $V[Y \mid X_3]$ increases linearly with ρ from $(\sigma_1 - \sigma_2 X_3)^2$ at $\rho = -1$ through $\sigma_1^2 + \sigma_2^2 X_3^2$ at $\rho = 0$ to $(\sigma_1 + \sigma_2 X_3)^2$ at $\rho = 1$. It quadratically decreases with σ_1, σ_2, and X_3 to a minimum of $\sigma_2^2 X_3^2 (1-\rho^2) \geq 0$ at $\sigma_1 = -\sigma_2 \rho X_3$, $\sigma_1^2(1-\rho^2)$ at $\sigma_2 = -\sigma_1 \rho / X_3$ and $\sigma_1^2(1-\rho^2)$ at $X_3 = -\sigma_1 \rho / \sigma_2$, respectively, and finally increases unboundedly, under the constraint that σ_1, σ_2, and $X_3 \geq 0$. However, if X_1 and X_2 are both deterministic $(\sigma_i^2 = 0, \rho = 0)$, $V[Y \mid X_3] = 0$.

If X_1 is random $(\sigma_1^2 > 0)$ and X_2 is deterministic $(\sigma_2^2 = 0, \rho = 0)$, $V[Y \mid X_3] = \sigma_1^2$. If X_2 is random $(\sigma_2^2 > 0)$ and X_1 is deterministic $(\sigma_1^2 = 0, \rho = 0)$, $V[Y \mid X_3] = \sigma_2^2 X_3^2$. Finally, if X_1 and X_2 are random but independent $(\sigma_1^2 > 0, \sigma_2^2 > 0$ and $\rho = 0)$, $V[Y \mid X_3] = \sigma_1^2 + \sigma_2^2 X_3^2$.

Data and parameter estimation

Data on fish weight at length were collected from Australia's continental shelf in the Timor and Arafura Seas (9–14°S, 127–137°E) from 20 October to 16 December 1990 as part of the Northern Territory Department of Primary Industry and Fisheries' program assessing commercial fish stocks. Of 240 stations allocated randomly within a depth range of 20–200 m, 199 were successfully sampled with a Frank and Bryce trawl net (headline height, 2.9 m; wing spread, 14.4 m; door spread, 60.1 m) at a speed of 1.54–2.06 m·s^{-1}. Nearly 48 tonnes of fish representing about 483 species in 119 families were caught during sampling. A representative subsample of individuals of 14 species, mostly of commercial fish, of the families Centrolophidae, Haemulidae, Lethrinidae, Lutjanidae, Nemipteridae, and Synodontidae were frozen immediately on board, returned to the laboratory, thawed, sexed, measured (fork length) to the nearest 1 mm, and weighed (wet weight) to the nearest 1 g with an electronic balance (Mettler, PC4000). For each of the 14 species, data on individual wet weight at length were pooled across all stations and fit to all cases of Equations 4 and 5 for females, males, and mixed sexes. Parameter estimates indicated by hats (^) were obtained by linear regression for Equation 1 by using SAS regression procedure (SAS Institute Inc., 1985) and by maximizing the general likelihood function,

$$L = \prod_{i=1}^{n} \left[2\pi V[Y \mid X_3] + \sigma_e^2\right]_i^{-\frac{1}{2}} e^{-\frac{[Y_i - E[Y \mid X_3]_i]^2}{2\left[V[Y \mid X_3]_i + \sigma_e^2\right]}},$$

for all other models by using the simplex algorithm of SYSTAT nonlinear regression procedure (Wilkinson, 1989). We included a model error term, σ_e^2, in the likelihood function to show that, in this case, it is compounded with σ_1^2 and is hence equivalent to σ_1^2 and $\sigma_1^2 + \sigma_e^2$ for estimation purposes. For this reason, we treated both error components collectively as 'σ_1^2' during model fitting and result presentation, unless otherwise stated.

Results

Some statistics of fish length and weight data used in this analysis are given in Table 1. We attempted to fit data for mixed sexes (both sexable and unsexable individuals included) and males and females (with unsexable juveniles excluded) of each of 14 species of groundfish to all cases of Equations 4 and 5. However, parameters could be estimated for models with σ_1^2 or σ_2^2 only; those in models simultaneously with σ_1^2 and σ_2^2, or simultaneously with σ_1^2, σ_2^2 and ρ could not be estimated because of overparameterization. Estimates of parameters, derived from linear regression of Equation 1 by using least squares method—equivalent to maximizing the likelihood function

$$L = \prod_{i=1}^{n} \left[2\pi\sigma_1^2\right]^{-\frac{1}{2}} e^{-\frac{[Y_i - E[Y|X_3]_i]^2}{2\sigma_1^2}}$$

and from maximizing the likelihood function

$$L = \prod_{i=1}^{n} \left[2\pi\sigma_2^2 X_3^2\right]^{-\frac{1}{2}} e^{-\frac{[Y_i - E[Y|X_3]_i]^2}{2\sigma_2^2 X_3^2}},$$

are given in Tables 2 and 3 respectively. Estimates in both tables are very similar between sexes for each species and between species, roughly with a species-wide $\hat{\mu}_1 = -10.89$, $\hat{\mu}_2 = 2.99$, $\sigma_1 = -0.006638$ and $\hat{\sigma}_2 = 0.014932$. Thus, while $V[Y|X_3]$ can be treated approximately as a constant, as is usually assumed in previous applications, it does change quadratically with X_3.

Discussion

Peters (1983) observed a large amount of variability in most allometric relationships and recognized a need to identify independent variables of general biological interest other than size. The general model presented in this study takes into account both body size and parameter variability among individual animals in allometric predictions. A major problem in allometry is that allometricians are more apt at providing a statistical description of a new data set than at using their data for hypothesis testing (Peters, 1983). This tendency has led to a plethora of only slightly different allometric equations, none of which can be rejected objectively. Our general model or any of its special cases would form a basis for intrataxal or intertaxal generalizations by treating some of those estimates of allometric parameters as intrataxal or intertaxal variations, hence providing a means for a general "house cleaning" in allometry.

Incorporating more independent variables in allometric modelling may explain more variability in the dependent variable, but it may result in a loss of a basis for comparison between, and manipulation of, allometric equations, such as allometric cancellation (Calder, 1984). The model presented above conforms exactly with conventional allometry and maintains commensuration by its estimated parameter means.

Specification of error structures in allometric models is an essential part of allometric modelling. Errors for Equation 1 are often assumed to be normally distributed with a constant variance, say σ_e^2. Several other interpretations arise from $V[Y|X_3]$ in that, for estimation purposes, σ_e^2 can be interpreted by any combinations of terms on the right-hand side of Equation 5. These and other alternative interpretations may pose problems for some applications. Thus, error structures of an allometric model must be specified cautiously.

There was no gain in precision or accuracy in estimates of allometric parameters in length and weight relationships of some fishes from considering individual variability of allometric parameters. Both Equation 1 and Equations 4 and 5 with σ_1^2 or σ_2^2, alone give an equally adequate description of weight at length data from all 14 species of groundfish concerned. Overparameterization occurred in cases of Equations 4 and 5 simultaneously with σ_1^2 and σ_2^2, or simultaneously with σ_1^2, σ_2^2, and ρ, and, as a result, not all parameters could be estimated from our data. The overparameterization lent further support to this conclusion. Also, although σ_1^2 and σ_2^2 can be estimated separately for each species, they are either equivalent to model error or take such small values (Tables 2 and 3) that $V[Y|X_2]$ can be treated effectively as constant. Finally, when interpreting regression results from various cases of the general model, it should be noted that all other variability will be confounded with, and added to, that of allometric parameters. Our data sets are of moderate sizes (Table 1) and many others of similar size could be expected to behave similarly. Individual variability of allometric parameters probably has a negligible effect on allometric predictions in length and weight relationships of certain fishes. Thus, our work supports the common use of Equation 1 to model intraspecific length and weight relationships in those fishes. However, all parameters in Equations 4 and 5 may be estimable simultaneously for length and weight relationships, as well as for other allometric relationships, if larger data sets or higher taxonomic levels, or both, are used.

A key assumption in our model is that the independent characteristic, L, (e.g. length) has little measurement error relative to the dependent characteristic, W (e.g. weight). Theoretically, this may not be the case. However, we believe that our model will provide good approximations for many allometrically scaled phenomena, such as length and weight relationships in certain fishes. For other allometric phenomena, alternative formulations, such as those of Pienaar and Ricker (1968), Saenger (1989), Seim and Saether (1983), and Shoesmith (1990) may be useful.

$V[Y|X_3]$ is a function of the independent variable whenever there is individual variability in X_2 or in X_1 and X_2. If this is not taken into account in regres-

Table 1

Some statistics of length and weight data for mixed sexes (both sexable and unsexable individuals included), males and females (with unsexable juveniles excluded) of each of 14 species of groundfish caught in northern Australian waters during 20 October to 16 December 1990.

			Fork length (mm)				Body weight (g)			
Sex	Species	n	Mean	SD	Min	Max	Mean	SD	Min	Max
Mixed										
Diagramma pictum	painted sweetlip	413	374.753	135.174	127	610	1,044.94	906.31	27	3,415
Lethrinus fraenatus	blue-lined emperor	48	344.562	63.134	201	450	907.77	469.80	165	1,837
Lethrinus lentjan	red-spot emperor	334	278.521	43.792	190	430	457.04	234.31	143	1,567
Lutjanus erythropterus	scarlet snapper	172	431.105	54.429	255	536	1,269.63	417.65	255	2,373
Lutjanus malabaricus	saddle-tailed snapper	590	377.398	151.595	86	765	1,170.71	1074.90	13	7,251
Lutjanus sebae	red emperor	182	342.346	125.237	94	596	1,144.50	974.22	18	4,736
Lutjanus timorensis	Timor snapper	43	415.256	38.608	211	453	1,339.72	271.27	178	1,663
Lutjanus vittus	one-band snapper	450	188.364	30.864	98	300	114.65	59.41	15	461
Nemipterus furcosus	rosy threadfin-bream	479	164.382	34.187	38	250	95.61	55.97	3	300
Nemipterus hexodon	ornate threadfin-bream	479	149.714	28.517	93	230	73.35	44.00	15	252
Pristipomoides multidens	gold-band snapper	293	314.055	117.079	131	585	818.53	882.70	50	3,800
Pristipomoides typus	sharp-tooth snapper	131	207.130	106.140	87	550	302.01	540.41	12	2,705
Psenopsis humerosa	black-spot butterfish	254	158.106	14.633	105	195	106.74	32.23	25	202
Saurida micropectoralis	short-finned lizardfish	444	261.218	34.039	110	410	194.26	90.32	12	850
Female										
Diagramma pictum	painted sweetlip	185	405.827	118.834	185	610	1,192.71	847.30	88	3,377
Lethrinus fraenatus	blue-lined emperor	32	318.031	48.035	201	445	690.22	313.06	165	1,757
Lethrinus lentjan	red-spot emperor	255	265.435	35.665	194	422	389.43	185.90	146	1,567
Lutjanus erythropterus	scarlet snapper	78	430.731	43.480	345	536	1,285.32	402.82	627	2,373
Lutjanus malabaricus	saddle-tailed snapper	193	472.637	90.217	175	716	1,702.28	811.06	89	5,196
Lutjanus sebae	red emperor	88	386.159	86.001	197	535	1,357.81	791.64	155	3,176
Lutjanus timorensis	Timor snapper	25	414.520	22.417	378	451	1,320.64	207.65	978	1,663
Lutjanus vittus	one-band snapper	212	181.835	24.025	120	262	100.01	41.03	29	289
Nemipterus furcosus	rosy threadfin-bream	240	161.429	25.781	38	230	85.36	40.47	7	239
Nemipterus hexodon	ornate threadfin-bream	270	146.463	23.825	97	208	67.34	33.01	18	176
Pristipomoides multidens	gold-band snapper	98	356.735	117.750	180	585	1,103.23	1,001.25	108	3,800
Pristipomoides typus	sharp-tooth snapper	29	287.034	111.650	135	550	593.48	720.46	42	2,705
Psenopsis humerosa	black-spot butterfish	101	167.050	12.046	138	195	126.50	30.13	61	202
Saurida micropectoralis	short-finned lizardfish	164	284.860	36.753	197	410	256.20	111.99	71	850
Male										
Diagramma pictum	painted sweetlip	119	448.303	111.902	177	594	1,528.94	917.86	77	3415
Lethrinus fraenatus	blue-lined emperor	16	397.625	56.707	216	450	1,342.88	431.39	191	1837
Lethrinus lentjan	red-spot emperor	74	325.743	35.281	220	430	698.30	229.21	202	1469
Lutjanus erythropterus	scarlet snapper	93	433.312	59.850	258	535	1,267.23	421.10	255	2233
Lutjanus malabaricus	saddle-tailed snapper	200	449.215	122.859	183	765	1,622.40	1,121.62	105	7251
Lutjanus sebae	red emperor	45	423.822	94.510	187	596	1,772.42	1,048.84	124	4736
Lutjanus timorensis	Timor snapper	17	428.353	19.193	388	453	1,436.12	183.58	1,021	1613
Lutjanus vittus	one-band snapper	225	197.858	31.901	128	300	132.84	67.83	32	461
Nemipterus furcosus	rosy threadfin-bream	205	178.800	30.351	115	250	120.09	61.04	28	300
Nemipterus hexodon	ornate threadfin-bream	125	165.832	32.361	107	230	99.21	58.00	20	252
Pristipomoides multidens	gold-band snapper	127	333.276	108.795	141	580	897.81	840.95	60	3,475
Pristipomoides typus	sharp-tooth snapper	35	267.314	99.371	114	530	477.31	581.00	27	2,617
Psenopsis humerosa	black-spot butterfish	117	153.821	13.416	105	191	97.19	26.08	25	198
Saurida micropectoralis	short-finned lizardfish	263	249.433	19.805	186	295	161.19	41.16	63	289

sion analysis, too much weight would be given to observations of the dependent variable in the region with high variances, and the analysis will be overly sensitive to chance events or bias affecting observations in this region of the independent variable.

Length and weight relationships in fishes are often required for stock assessment and for intra- and inter-specific comparisons. Although many data are available on weight at length relationships of fishes from New Guinea (Showers, 1993) and New Cale-

Table 2

Estimates of mean and standard error of allometric parameters obtained for mixed sexes, males, and females of each of 14 species of groundfish, caught in northern Australian waters during 20 October to 16 December 1990 by linear regression of Equation 1 by using least squares method. $P \leq 0.0001$ applies to all species for separate sexes.

	Mixed					
Species[1]	$\hat{X}_1$ (SE)	$\hat{X}_2$ (SE)	$n-2$	$F_{1,n-2}$	P	R^2
Diagramma pictum	−11.4249 (0.0650)	3.0427 (0.0111)	411	75,363.608	0.0000	0.9946
Lethrinus fraenatus	−11.1084 (0.2933)	3.0501 (0.0503)	46	3,673.450	0.0001	0.9874
Lethrinus lentjan	−10.8678 (0.1287)	3.0049 (0.0229)	332	17,226.485	0.0001	0.9810
Lutjanus erythropterus	−10.2265 (0.2323)	2.8569 (0.0383)	170	5,550.516	0.0001	0.9701
Lutjanus malabaricus	−10.4713 (0.0478)	2.8926 (0.0082)	588	125,849.921	0.0000	0.9953
Lutjanus sebae	−10.7588 (0.0752)	2.9931 (0.0130)	180	52,732.028	0.0001	0.9966
Lutjanus timorensis	−10.2548 (0.5172)	2.8916 (0.0858)	41	1,134.654	0.0001	0.9643
Lutjanus vittus	−10.5972 (0.0985)	2.9136 (0.0188)	448	23,905.566	0.0000	0.9816
Nemipterus furcosus	−10.6433 (0.1163)	2.9552 (0.0229)	477	16,672.088	0.0000	0.9721
Nemipterus hexodon	−10.8475 (0.1277)	3.0010 (0.0256)	477	13,778.375	0.0000	0.9665
Pristipomoides multidens	−10.4284 (0.0629)	2.9192 (0.0110)	291	69,881.156	0.0000	0.9958
Pristipomoides typus	−10.6474 (0.0672)	2.9462 (0.0128)	129	52,895.132	0.0001	0.9975
Psenopsis humerosa	−11.8119 (0.2644)	3.2487 (0.0523)	252	3,863.670	0.0001	0.9385
Saurida micropectoralis	−12.3581 (0.1948)	3.1560 (0.0351)	442	8,106.551	0.0001	0.9482

	Female				
Species[1]	$\hat{X}_1$ (SE)	$\hat{X}_2$ (SE)	$n-2$	$F_{1,n-2}$	R^2
Diagramma pictum	−11.4854 (0.1323)	3.0526 (0.0222)	183	18,940.693	0.9904
Lethrinus fraenatus	−10.9359 (0.4586)	3.0204 (0.0797)	30	1,435.635	0.9788
Lethrinus lentjan	−11.0141 (0.1823)	3.0314 (0.0327)	253	8,591.353	0.9713
Lutjanus erythropterus	−11.1443 (0.3965)	3.0123 (0.0654)	76	2,120.223	0.9649
Lutjanus malabaricus	−10.6937 (0.1855)	2.9290 (0.0302)	191	9,397.044	0.9800
Lutjanus sebae	−10.9484 (0.2014)	3.0256 (0.0339)	86	7,943.456	0.9892
Lutjanus timorensis	−8.5750 (1.6316)	2.6136 (0.2708)	23	93.182	0.7934
Lutjanus vittus	−10.4418 (0.1823)	2.8824 (0.0351)	210	6,752.525	0.9697
Nemipterus furcosus	−9.0380 (0.2490)	2.6379 (0.0491)	238	2,888.362	0.9236
Nemipterus hexodon	−10.5120 (0.1626)	2.9366 (0.0327)	268	8,081.145	0.9678
Pristipomoides multidens	−10.4544 (0.1318)	2.9235 (0.0226)	96	16,739.747	0.9942
Pristipomoides typus	−10.3553 (0.1890)	2.8933 (0.0337)	27	7,358.630	0.9962
Psenopsis humerosa	−12.0558 (0.5391)	3.2969 (0.1054)	99	978.916	0.9072
Saurida micropectoralis	−12.4764 (0.3404)	3.1777 (0.0603)	162	2,777.965	0.9446

	Male				
Species[1]	$\hat{X}_1$ (SE)	$\hat{X}_2$ (SE)	$n-2$	$F_{1,n-2}$	R^2
Diagramma pictum	−11.8373 (0.1399)	3.1102 (0.0230)	117	18,239.181	0.9936
Lethrinus fraenatus	−11.5601 (0.5382)	3.1252 (0.0901)	14	1,204.055	0.9877
Lethrinus lentjan	−11.1870 (0.3227)	3.0589 (0.0558)	72	3,002.105	0.9763
Lutjanus erythropterus	−9.9051 (0.2875)	2.8006 (0.0474)	91	3,487.397	0.9743
Lutjanus malabaricus	−10.6166 (0.1268)	2.9171 (0.0209)	198	19,525.208	0.9899
Lutjanus sebae	−11.5487 (0.2166)	3.1216 (0.0359)	43	7,544.416	0.9942
Lutjanus timorensis	−9.4597 (1.8694)	2.7597 (0.3085)	15	80.011	0.8316
Lutjanus vittus	−10.5218 (0.1447)	2.9007 (0.0274)	223	11,186.525	0.9804
Nemipterus furcosus	−10.9360 (0.1538)	3.0150 (0.0297)	203	10,282.691	0.9805
Nemipterus hexodon	−10.9499 (0.2803)	3.0188 (0.0550)	123	3,011.431	0.9604
Pristipomoides multidens	−10.3481 (0.1032)	2.9054 (0.0179)	125	26,357.314	0.9952
Pristipomoides typus	−10.3289 (0.1707)	2.8902 (0.0308)	33	8,794.451	0.9961
Psenopsis humerosa	−10.6433 (0.3927)	3.0174 (0.0780)	115	1,495.187	0.9280
Saurida micropectoralis	−11.6679 (0.4003)	3.0307 (0.0726)	261	1,744.792	0.8694

[1] See Table 1 for common names.

Table 3

Estimates of mean and asymptotic standard error (ASE) of allometric parameters obtained for mixed sexes, males, and females of each of 14 species of groundfish, caught in northern Australian waters during 20 October to 16 December 1990 by fitting Equations 4 and 5 with $V[Y|X_3] = \sigma_2^2 X_3^2$ excluding the model error term (σ_e^2).

	Mixed		
Species[1]	$\hat{\mu}_1$ (ASE)	$\hat{\mu}_2$ (ASE)	$\hat{\sigma}_2$ (ASE)
Diagramma pictum	−11.4010 (0.0624)	3.0386 (0.0107)	0.015684 (0.000536)
Lethrinus fraenatus	−11.0788 (0.2791)	3.0450 (0.0480)	0.011364 (0.001120)
Lethrinus lentjan	−10.8528 (0.1295)	3.0022 (0.0231)	0.011431 (0.000427)
Lutjanus erythropterus	−10.2207 (0.2246)	2.8559 (0.0371)	0.011478 (0.000598)
Lutjanus malabaricus	−10.4315 (0.0455)	2.8858 (0.0079)	0.015562 (0.000445)
Lutjanus sebae	−10.7324 (0.0705)	2.9885 (0.0124)	0.013522 (0.000691)
Lutjanus timorensis	−10.3142 (0.4613)	2.9015 (0.0766)	0.010599 (0.001097)
Lutjanus vittus	−10.5948 (0.0968)	2.9132 (0.0186)	0.012502 (0.000405)
Nemipterus furcosus	−10.3566 (0.1275)	2.8986 (0.0252)	0.028576 (0.000918)
Nemipterus hexodon	−10.8451 (0.1281)	3.0006 (0.0257)	0.021340 (0.000683)
Pristipomoides multidens	−10.4311 (0.0626)	2.9196 (0.0111)	0.012057 (0.000483)
Pristipomoides typus	−10.6917 (0.0692)	2.9547 (0.0134)	0.012299 (0.000737)
Psenopsis humerosa	−11.8293 (0.2619)	3.2521 (0.0518)	0.015465 (0.000673)
Saurida micropectoralis	−12.3549 (0.1919)	3.1555 (0.0346)	0.017171 (0.000567)
	Female		
Species[1]	$\hat{\mu}_1$ (ASE)	$\hat{\mu}_2$ (ASE)	$\hat{\sigma}_2$ (ASE)
Diagramma pictum	−11.4694 (0.1271)	3.0499 (0.0214)	0.016512 (0.000844)
Lethrinus fraenatus	−10.8822 (0.4288)	3.0111 (0.0747)	0.011972 (0.001450)
Lethrinus lentjan	−10.9932 (0.1843)	3.0276 (0.0331)	0.011992 (0.000515)
Lutjanus erythropterus	−11.1343 (0.3913)	3.0106 (0.0646)	0.009438 (0.000718)
Lutjanus malabaricus	−10.6957 (0.1742)	2.9293 (0.0284)	0.015106 (0.000754)
Lutjanus sebae	−10.9216 (0.1938)	3.0211 (0.0328)	0.013024 (0.000956)
Lutjanus timorensis	−8.5443 (1.5702)	2.6085 (0.2606)	0.011468 (0.001567)
Lutjanus vittus	−10.4305 (0.1808)	2.8802 (0.0348)	0.012749 (0.000602)
Nemipterus furcosus	−8.0532 (0.2559)	2.4435 (0.0506)	0.030733 (0.001396)
Nemipterus hexodon	−10.4947 (0.1627)	2.9332 (0.0328)	0.017758 (0.000753)
Pristipomoides multidens	−10.4486 (0.1296)	2.9225 (0.0224)	0.012449 (0.000864)
Pristipomoides typus	−10.3916 (0.1853)	2.8998 (0.0333)	0.011512 (0.001461)
Psenopsis humerosa	−12.0680 (0.5276)	3.2992 (0.1032)	0.015033 (0.001037)
Saurida micropectoralis	−12.4710 (0.3370)	3.1768 (0.0598)	0.017557 (0.000955)
	Male		
Species[1]	$\hat{\mu}_1$ (ASE)	$\hat{\mu}_2$ (ASE)	$\hat{\sigma}_2$ (ASE)
Diagramma pictum	−11.7895 (0.1296)	3.1023 (0.0214)	0.012092 (0.000760)
Lethrinus fraenatus	−11.5461 (0.4630)	3.1229 (0.0776)	0.009625 (0.001619)
Lethrinus lentjan	−11.1988 (0.3127)	3.0609 (0.0541)	0.009055 (0.000704)
Lutjanus erythropterus	−9.9036 (0.2774)	2.8003 (0.0458)	0.011754 (0.000834)
Lutjanus malabaricus	−10.5854 (0.1203)	2.9120 (0.0199)	0.014870 (0.000728)
Lutjanus sebae	−11.5462 (0.2006)	3.1212 (0.0334)	0.009834 (0.000989)
Lutjanus timorensis	−9.4896 (1.7559)	2.7646 (0.2898)	0.008735 (0.001411)
Lutjanus vittus	−10.5171 (0.1433)	2.8998 (0.0272)	0.012371 (0.000566)
Nemipterus furcosus	−10.9048 (0.1524)	3.0089 (0.0295)	0.014279 (0.000690)
Nemipterus hexodon	−10.9325 (0.2732)	3.0153 (0.0538)	0.023605 (0.001481)
Pristipomoides multidens	−10.3460 (0.1004)	2.9051 (0.0175)	0.011230 (0.000680)
Pristipomoides typus	−10.3560 (0.1709)	2.8951 (0.0311)	0.010902 (0.001254)
Psenopsis humerosa	−10.6920 (0.3878)	3.0271 (0.0771)	0.014853 (0.000951)
Saurida micropectoralis	−11.6947 (0.3976)	3.0356 (0.0721)	0.016898 (0.000725)

[1] See Table 1 for common names.

donia (Kulbicki et al., 1993), systematic data are lacking from northern Australian waters. Because our data covered relatively large size ranges of each of the 14 species of fish concerned, our estimates of allometric parameters and associated relationships will improve stock assessments of major groundfish in northern Australian waters.

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