A BEAK KEY FOR EIGHT EASTERN TROPICAL PACIFIC CEPHALOPOD SPECIES WITH RELATIONSHIPS BETWEEN THEIR BEAK DIMENSIONS AND SIZE

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ABSTRACT

A method of identifying the beaks and estimating body weight and mantle length of eight common species of eastern tropical Pacific cephalopods is presented. Twenty specimens were selected from each of the following species: *Symplectoteuthis oualaniensis, Dosidicus gigas, Ommastrephes bartramii, Onychoteuthis banksii, Abraliopsis affinis, Pterygioteuthis giardi, Liocranchia reinhardti,* and *Loligo opalescens.* Seven dimensions measured on the upper beak and five dimensions measured on the lower beak are converted to ratios and compared individually among the species using an analysis of variance procedure and Tukey's ω. Significant differences ($\alpha \leq 0.05$) observed among the species' beak ratios means, in addition to structural characteristics, are used to construct artificial keys for the upper and lower beaks of the eight species. Upper and lower beak dimensions are used as independent variables in a linear regression model with mantle length and body weight (log transformed). Two equations are given for estimating the length and weight for each species from the upper or lower beak. One uses the rostral length dimension because of its durability and the second uses a dimension derived from a stepwise regression procedure.

The importance of cephalopods as prey is well documented for whales (Gaskin and Cawthorn 1967; Clarke et al. 1976; Clarke 1977), seals (Austin and Wilki 1950; Laws 1960), seabirds (Ashmole and Ashmole 1967; Imber 1978), tunas (Pinkas et al. 1971; Matthews et al. 1977), tunas and porpoise (Perrin et al. 1973), and sharks (Clarke and Stevens 1974; Tricas 1979). Due to the rapid digestion of the softer body parts, however, the cephalopod's beak is often the only identifiable structure remaining in these predator's stomachs as evidence of feeding on cephalopods. Consequently, the accuracy of specific identifications and estimates of cephalopod biomass consumed by these predators often suffers.

Two methods have generally been used to approach the problem of characterizing cephalopod beaks. A descriptive method was used most notably by Clarke (1962, 1980), Mangold and Fioroni (1966), and Pinkas et al. (1971). Families, genera, and occasionally species were identified from structural characteristics of the beak. A biometric method was used by Wolff (1977) and Wolff and Wormuth (1979) to separate two species of ommastrephid squid with beak dimensions. It was suggested that the method could be expanded to include other species of cephalopods.

This study presents a key based on structural and biometric differences among the beaks of eight species of cephalopods. The species of cephalopods examined were: *Symplectoteuthis oualaniensis* (Lesson), *Dosidicus gigas* (d'Orbigny), *Ommastrephes bartramii* (Lesueur), *Onychoteuthis banksii* (Leach), *Abraliopsis affinis* (Pfeffer), *Pterygioteuthis giardi* Fischer, *Liocranchia reinhardti* (Steenstrup), and *Loligo opalescens* Berry. Regression equations of body weight and mantle length from beak dimensions are also presented.

MATERIALS AND METHODS

The cephalopods for this study were obtained from Southwest Fisheries Center, National Marine Fisheries Service, and Invertebrate Collection, Scripps Institution of Oceanography, La Jolla, Calif. Twenty specimens of each species were selected in the maximum mantle length range available. Table 1 shows the ranges for mantle length and body weight and collection locations for the cephalopods. The buccal masses were removed, after the specimens were measured and weighed, and placed in a solution saturated with sodium borate and trypsin (8 g trypsin/l sodium borate solution) for 6 to 10 d.

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TABLE 1.—Mantle length (ML) ranges, body weight ranges, and collection locations for the species (nla = specimens collected in the Pacific but specific location not available).

Species	ML range (mm)	Weight range (g)	Number of specimens	Lat.	Long.
Symplectoteuthis oualaniensis	130-290	79-927	1	00°33′ S	111°14′ W
			2	03°25′ S	110°31′ W
			2	06°49′ S	86°14′ W
			1	05°12′ S	91°49′ W
			1	08°09′ S	100°31′ W
			1	05°46′ S	102°31′ W
			1	00°26′ S	109°28′ W
			1	01°15′ S	112°51′ W
			2	02°40′ S	116°11′ W
			1	00°01′ S	118°03′ W
			2	00°46′ S	105°35′ W
			1	02°52′ S	97°21′ W
			3	07°19′ S	94°24′ W
			1	05°14′ S	83°32′ W
Dosidicus gigas	196-321	191-842	2	00°33′ S	111°14′ W
			3	02°52′ S	97°21′ W
			3	07°49′ S	81°38′ W
			3	05°14′ S	83°32′ W
			1	01°46′ S	108°58′ W
			2	00°26′ S	109°28′ W
			1	06°49′ S	86°14′ W
			1	11°38′ S	87°13′ W
			1	06°00′ S	96°16′ W
			1	04°30′ S	89°16′ W
			1	11°30′ S	93°18′ W
			1	05°02′ S	91°49′ W
			1	02°52′ S	97°21′ W
			1	11°44′ S	83°56′ W
Ommastrephes bartramii	85-165	11-118	4	30°03′ N	156°11′ W
			2	30°08′ N	135°02′ W
			5	24°18′ N	155°00′ W
			9	28°11′ N	155°17′ W
Onychoteuthis banksii	40-130	3-67	2	13°00′ N	132°00′ W
			1	nla	
			1	25°10′ N	121°22′ W
			10	13°49′ N	118°59′ W
			3	18°00′ N	113°00′ W
			3	00°28′ N	105°53′ W
Abraliopsis affinis	19-26	0.5-4.3	5	24°06′ N	109°37′ W
			6	nla	
			7	11°31′ N	131°08′ W
			2	05°42′ N	86°53′ W
Pterygioteuthis giardi	16-30	0.3-1.4	1	05°02′ S	91°49′ W
			2	11°44′ S	83°56′ W
			2	10°24′ N	107°46′ W
			2	06°30′ N	139°00′ W
			2	00°04′ N	127°47′ W
			2	00°20′ N	120°21′ W
			9	01°21′ N	130°47′ W
Liocranchia reinhardti	23-125	1-24	1	00°30′ N	96°50′ W
			3	18°32′ N	119°51′ E
			1	32°34′ N	117°29′ W
			1	12°40′ N	112°46′ W
			14	13°49′ N	118°59′ W
Loligo opalescens	80-153	12-49	7	34°00′ N	120°10′ W
			6	26°30′ N	114°50′ W
			7	33°29′ N	117°47′ W

The beaks were then removed from the buccal masses and placed in 40% isopropyl alcohol.

Beak dimensions were measured with vernier calipers or an occular micrometer. Seven dimensions were measured on the upper beak of each specimen: length of the rostrum (RL), rostral tip to inner margin of wing (RW), length of hood (HL), width of the wing (WW), wing to crest length (WCL), jaw angle width (JW) and length of the crest (CL). Five dimensions were measured on the lower beak of each specimen: rostral tip to inner posterior corner of lateral wall (RC), rostral tip to inner margin of wing (RW), length of the rostrum (RL), length of the wing (WL), and jaw angle width (JW) (Fig. 1). These dimensions were transformed to ratios to remove the dimensionality. Comparisons among species' beak ratios were made with a one-way classification analysis of variance procedure (ANOVA). The ratios were normally distributed and the ratio

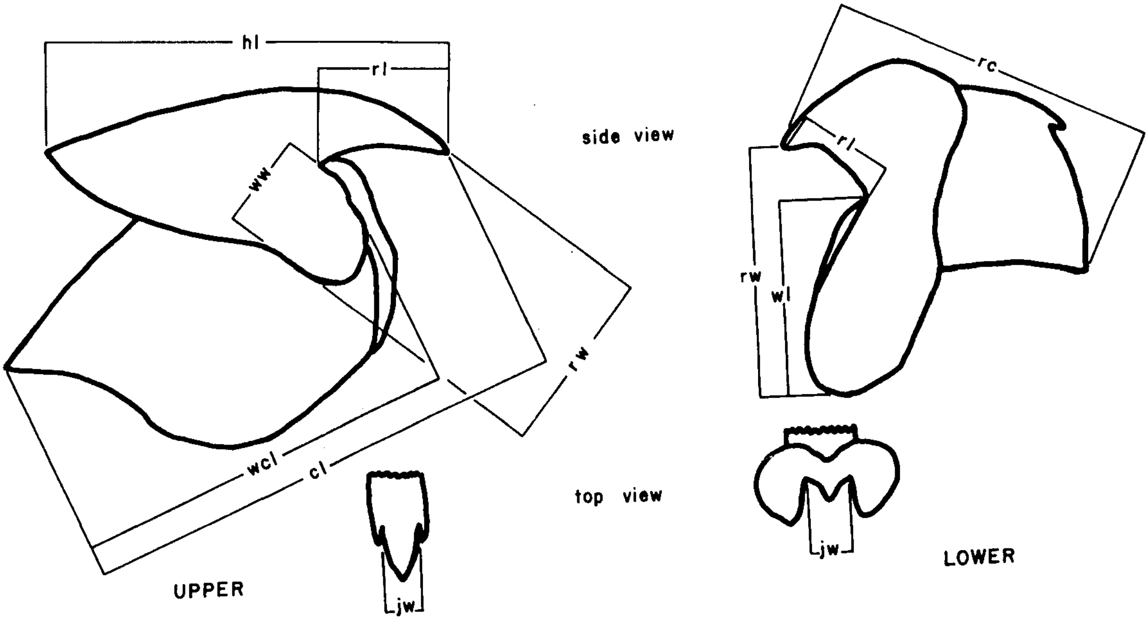


FIGURE 1.—Dimensions measured on the upper and lower beak.

transformation met the criteria for validity as described by Anderson and Lydic (1977). Tukey's ω procedure was used to test for significant differences ($\alpha \leq 0.05$) among 21 ratio means from the upper beak and 10 ratio means from the lower beak for each species. This procedure involves the computation of a confidence interval from the formula: $\omega = q_\alpha\ (p,\ n_2)\ s_{\bar{x}}$, where ω is a range for the treatment means with a given probability level ($\alpha \leq 0.05$), q is the studentized range, p is the number of treatments, n_2 is the error degrees of freedom and $s_{\bar{x}}$ is the standard error of the treatment means (Steel and Torrie 1960). Simple linear regressions were calculated to express the relationship between a beak dimension and the mantle length and log transformed body weight. An AMDAHL 470 V/6 computer[2] performed the majority of computations.

RESULTS

The results of the ANOVA procedure are summarized in Tables 2 and 3. The species' means are ranked and the standard error of the treatment mean for each ratio is given. These tables form the basis for the construction of the biometric portion of the beak key. Combinations of descriptive characteristics and significant beak ratios are used to identify the eight species of cephalopods. Separate keys are provided for the upper and lower beak.

The ratio values presented in the key are midpoints between species' means and often greatly exceed the stated significance level ($\alpha \leq 0.05$) as indicated by the confidence interval for the species' means which follows in parentheses. Additional descriptive characteristics and alternate beak ratios are given to corroborate the initial identification. Figures 3-10 show upper and lower beaks for each of the species. A few of the alternate ratios in the upper and lower beak key have species' means which are not significantly different. These ratios can be considered reliable since Hartley (1955) suggested that the experimentwise error rate could be relaxed considerably below the standard $\alpha \leq 0.05$ level due to the conservative nature of Tukey's ω procedure. Additional alternate ratio values can be determined from Table 2 to distinguish species if the ratios in the key are not satisfactory (e.g., damaged beak). The descriptive characteristics follow a slightly modified version of Clarke's terminology (1962, 1980) with several additions as shown in Figure 2. This key should be used with caution on specimens which are greatly outside the size range of this study.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Upper beak ratio means ($\bar{x}$) and standard error of the treatment means ($s_{\bar{x}}$) ($\omega = 4.3_{0.5}$ (8, 152) $s_{\bar{x}}$), So = *Symplectoteuthis oualaniensis*, Dg = *Dosidicus gigas*, Ob = *Ommastrephes bartramii*, Obnk = *Onychoteuthis banksii*, Aa = *Abraliopsis affinis*, Pg = *Pterygioteuthis giardi*, Lr = *Liocranchis reinhardti*, Lo = *Loligo opalescens*.

$s_{\bar{x}}$	Ratio	Species							
0.0130	RL/RW	So	Dg	Ob	Obnk	Aa	Pg	Lr	Lo
	$\bar{x}$	0.766	0.682	0.606	0.599	0.592	0.580	0.523	0.485
0.0051	RL/HL	So	Aa	Dg	Obnk	Pg	Ob	Lr	Lo
	$\bar{x}$	0.354	0.345	0.335	0.316	0.313	0.309	0.290	0.246
0.0351	RL/WH	So	Aa	Dg	Obnk	Pg	Ob	Lr	Lo
	$\bar{x}$	1.507	1.341	1.282	1.190	1.151	1.111	0.941	0.863
0.0058	RL/WCL	So	Dg	Ob	Aa	Pg	Obnk	Lr	Lo
	$\bar{x}$	0.358	0.354	0.319	0.306	0.287	0.287	0.261	0.211
0.0148	RL/JW	Obnk	So	Dg	Aa	Ob	Pg	Lr	Lo
	$\bar{x}$	1.349	1.215	1.161	1.128	1.061	1.042	0.963	0.936
0.0038	RL/CL	So	Dg	Ob	Aa	Pg	Obnk	Lr	Lo
	$\bar{x}$	0.288	0.280	0.252	0.234	0.226	0.218	0.211	0.177
0.0136	RW/HL	Aa	Lr	Pg	Obnk	Ob	Lo	Dg	So
	$\bar{x}$	0.585	0.557	0.542	0.528	0.510	0.509	0.491	0.463
0.0571	RW/WW	Aa	Obnk	Pg	So	Dg	Ob	Lr	Lo
	$\bar{x}$	2.254	1.980	1.979	1.968	1.878	1.831	1.799	1.757
0.0141	RW/WCL	Ob	Dg	Aa	Lr	Pg	So	Obnk	Lo
	$\bar{x}$	0.526	0.519	0.518	0.502	0.496	0.467	0.452	0.435
0.0532	RW/JW	Obnk	Lo	Aa	Lr	Pg	Ob	Dg	So
	$\bar{x}$	2.257	1.955	1.916	1.851	1.806	1.758	1.705	1.586
0.0190	RW/CL	Ob	Dg	Lr	Aa	Pg	So	Lo	Obnk
	$\bar{x}$	0.416	0.411	0.405	0.396	0.391	0.376	0.365	0.364
0.0751	HL/WW	So	Aa	Dg	Obnk	Pg	Ob	Lo	Lr
	$\bar{x}$	4.253	3.870	3.827	3.756	3.660	3.594	3.460	3.244
0.0095	HL/WCL	Dg	Ob	So	Pg	Lr	Aa	Obnk	Lo
	$\bar{x}$	1.058	1.033	1.010	0.917	0.901	0.884	0.856	0.855
0.0593	HL/JW	Obnk	Lo	Dg	Ob	So	Pg	Lr	Aa
	$\bar{x}$	4.277	3.846	3.474	3.453	3.431	3.332	3.324	3.279
0.0061	HL/CL	Dg	Ob	So	Lr	Pg	Lo	Obnk	Aa
	$\bar{x}$	0.837	0.817	0.813	0.728	0.722	0.718	0.689	0.677
0.0055	WW/WCL	Ob	Lr	Dg	Pg	Lo	So	Aa	Obnk
	$\bar{x}$	0.288	0.280	0.277	0.253	0.249	0.238	0.232	0.230
0.0309	WW/JW	Obnk	Lo	Lr	Ob	Pg	Dg	Aa	So
	$\bar{x}$	1.148	1.135	1.036	0.966	0.922	0.910	0.861	0.811
0.0045	WW/CL	Ob	Lr	Dg	Lo	Pg	So	Obnk	Aa
	$\bar{x}$	0.228	0.226	0.219	0.210	0.199	0.192	0.185	0.178
0.0785	WCL/JW	Obnk	Lo	Aa	Lr	Pg	So	Ob	Dg
	$\bar{x}$	5.014	4.516	3.719	3.693	3.642	3.399	3.342	3.284
0.0038	WCL/CL	Lo	Lr	So	Obnk	Dg	Ob	Pg	Aa
	$\bar{x}$	0.841	0.808	0.806	0.805	0.791	0.791	0.788	0.767
0.0033	JW/CL	Dg	Ob	So	Lr	Pg	Aa	Lo	Obnk
	$\bar{x}$	0.241	0.238	0.238	0.219	0.218	0.207	0.188	0.162

TABLE 3.—Lower beak ratio means ($\bar{x}$) and standard error of the treatment means ($s_{\bar{x}}$).

$s_{\bar{x}}$	Ratio	Species							
0.0138	RC/RW	Lo	Dg	Pg	Aa	Ob	So	Obnk	Lr
	$\bar{x}$	1.235	1.232	1.213	1.209	1.200	1.199	1.186	1.142
0.0509	RC/RL	Lo	Lr	Pg	Obnk	Ob	Aa	Dg	So
	$\bar{x}$	4.058	3.580	3.424	3.222	2.967	2.960	2.807	2.783
0.0221	RC/WL	Dg	So	Ob	Aa	Obnk	Pg	Lo	Lr
	$\bar{x}$	1.829	1.756	1.700	1.689	1.644	1.552	1.526	1.513
0.879	RC/JW	Lr	Lo	Aa	Ob	Pg	Dg	Obnk	So
	$\bar{x}$	4.402	4.025	3.852	3.673	3.525	3.357	3.341	2.996
0.0504	RW/RL	Lo	Lr	Pg	Obnk	Ob	Aa	So	Dg
	$\bar{x}$	3.289	3.139	2.828	2.722	2.475	2.459	2.323	2.280
0.0148	RW/WL	Dg	So	Ob	Aa	Obnk	Lr	Pg	Lo
	$\bar{x}$	1.485	1.465	1.418	1.398	1.387	1.327	1.280	1.236
0.0729	RW/JW	Lr	Lo	Aa	Ob	Pg	Obnk	Dg	So
	$\bar{x}$	3.867	3.258	3.179	3.066	2.918	2.822	2.727	2.500
0.0115	RL/WL	Dg	So	Ob	Aa	Obnk	Pg	Lr	Lo
	$\bar{x}$	0.653	0.632	0.577	0.575	0.512	0.457	0.425	0.380
0.0274	RL/JW	Aa	Ob	Lr	Dg	So	Obnk	Pg	Lo
	$\bar{x}$	1.308	1.243	1.235	1.197	1.077	1.037	1.032	0.996
0.0597	WL/JW	Lr	Lo	Pg	Aa	Ob	Obnk	Dg	So
	$\bar{x}$	2.911	2.641	2.296	2.284	2.168	2.039	1.838	1.709

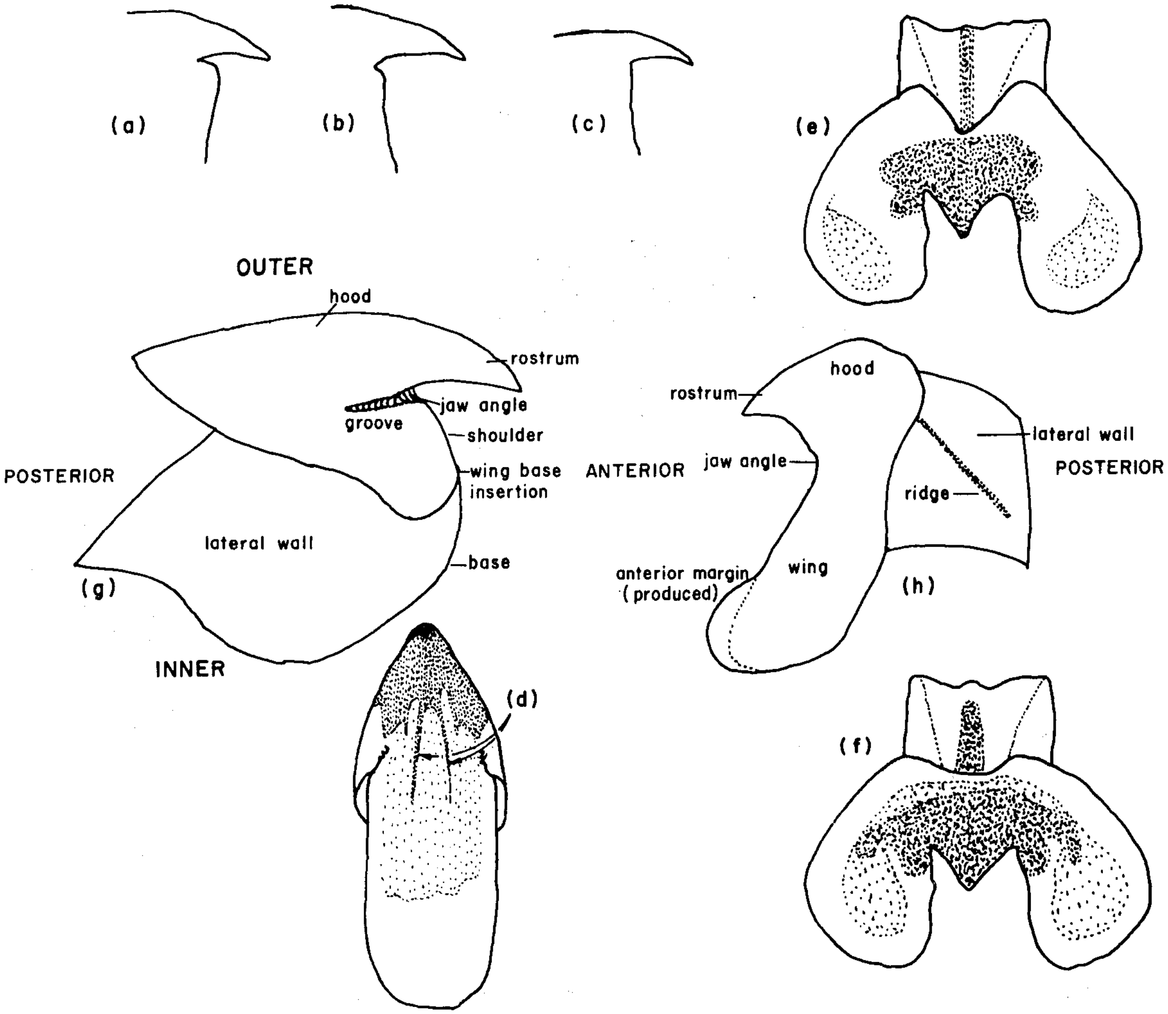


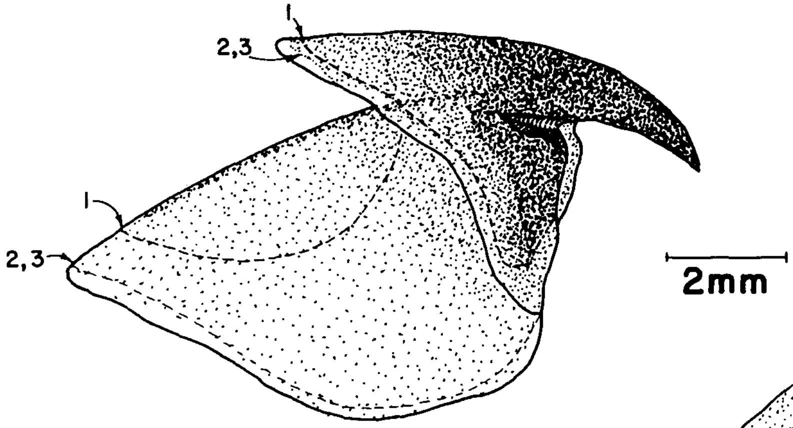
FIGURE 2.—Descriptive characteristics of the upper and lower beak; (a) deeply recessed jaw angle, (b) moderately recessed jaw angle, (c) jaw angle not recessed, (d) pigment stripes on inner surface of rostrum and crest, (e) hood deeply notched at crest, (f) hood slightly notched at crest, (g) upper beak characteristics, (h) lower beak characteristics.

KEY TO THE UPPER BEAK

*Alternate beak ratio
**Alternate beak ratio CI greater than the difference between the species means.

1a.	Jaw angle deeply recessed	6
1b.	Jaw angle not deeply recessed	2
2a.	Prominent groove at jaw angle	3
2b.	Groove absent at jaw angle	4

3a. RL/JW >1.24 (CI_{05} = 1.349±0.032); *HL/JW >3.78 (CI_{05} = 4.277±0.127); *RL/HL <0.33 (CI_{05} = 0.316±0.011) .... *Onychoteuthis banksii*
Jaw angle slightly recessed; anterior-posterior groove at jaw angle ⅓ of RL (Fig. 2); wing base inserted ¾ down anterior margin of lateral wall; pigment changes with growth shown in Figure 3.



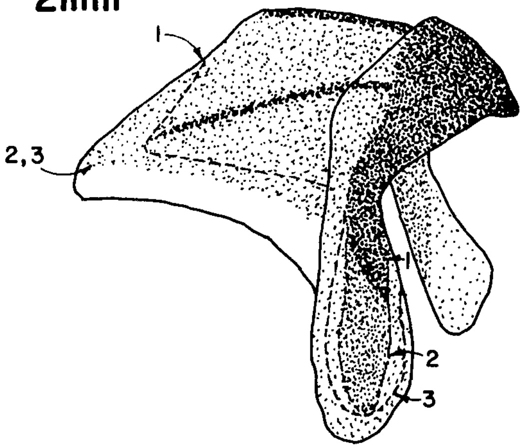
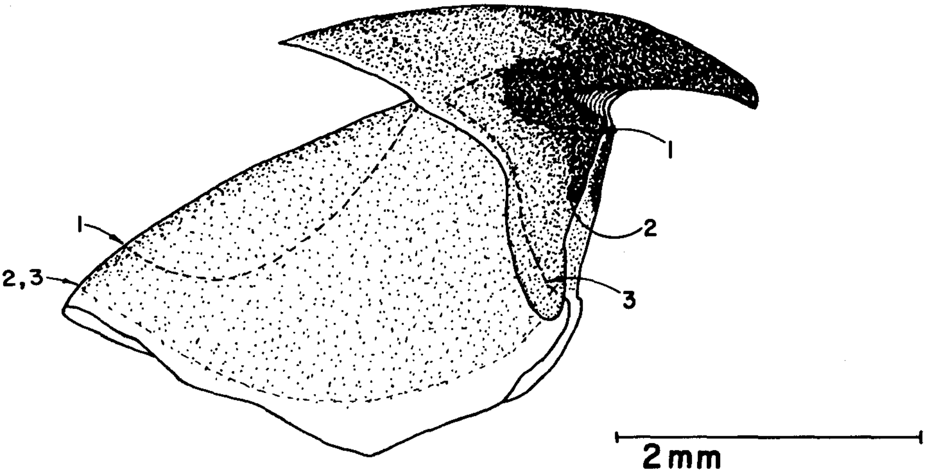


FIGURE 3.—The upper (U) and lower (L) beak of *Onychoteuthis banksii* (1 - ML = 40 mm, URL = 0.11 cm, LRL = 0.12 cm; 2 - ML = 84 mm, URL = 0.195 cm, LRL = 0.191 cm; 3 - ML = 130 mm, URL = 0.24 cm, LRL = 0.24 cm).

3b. RL/JW <1.24 (CI_{05} = 1.128±0.032); *HL/JW <3.78 (CI_{05} = 3.279±0.127); *RL/HL >0.33 (CI_{05} = 0.345±0.011) .... *Abraliopsis affinis*
Jaw angle slightly recessed; anterior-posterior groove at jaw angle <¼ of RL (Fig. 2); wing base inserted just above base of anterior margin of lateral wall; pigment changes with growth shown in Figure 4.



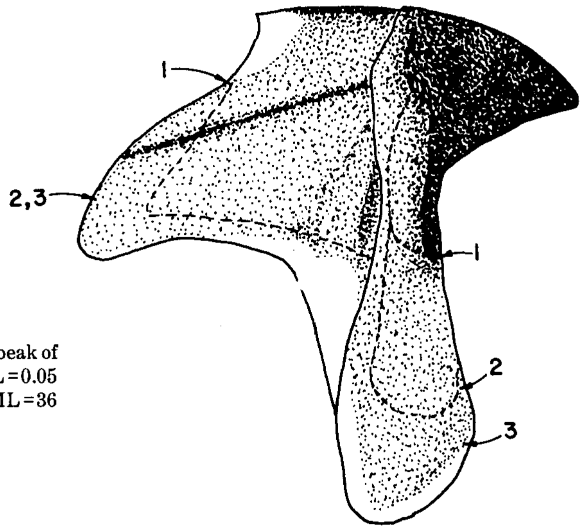


FIGURE 4.—The upper (see bottom of p. 362) and lower beak of *Abraliopsis affinis* (1 - ML = 19 mm, URL = 0.05 cm, LRL = 0.05 cm; 2 - ML = 32 mm, URL = 0.10 cm, LRL = 0.10 cm; 3 - ML = 36 mm, URL = 0.12 cm, LRL = 0.14 cm).

4a. RL/JW <1.003 (CI_{05} = 0.963±0.032).. 5

4b. RL/JW >1.003 (CI_{05} = 1.043±0.032); *RL/HL >0.301 (CI_{05} = 0.313±0.011); *RL/CL >0.218 (CI_{05} = 0.226±0.008) .... *Pterygioteuthis giardi*

Jaw angle not recessed; wing base inserted just above base of anterior margin of lateral wall; pigment changes with growth shown in Figure 5.

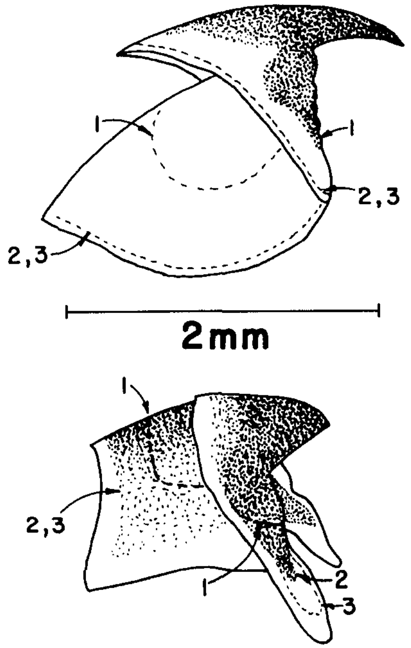


FIGURE 5.—The upper and lower beak of *Pterygioteuthis giardi* (1 - ML = 16 mm, URL = 0.03 cm, LRL = 0.03 cm; 2 - ML = 22 mm, URL = 0.05 cm, LRL = 0.05 cm; 3 - ML = 30 mm, URL = 0.06 cm, LRL = 0.05 cm).

5a. RL/HL >0.268 (CI_{05} = 0.290±0.011); *RL/CL >0.194 (CI_{05} = 0.211±0.008); *JW/CL >0.204 (CI_{05} = 0.219±0.007) .... *Liocranchia reinhardti*
Jaw angle not recessed; wing base inserted ⅔ down anterior margin of lateral wall; pigment changes with growth shown in Figure 6.

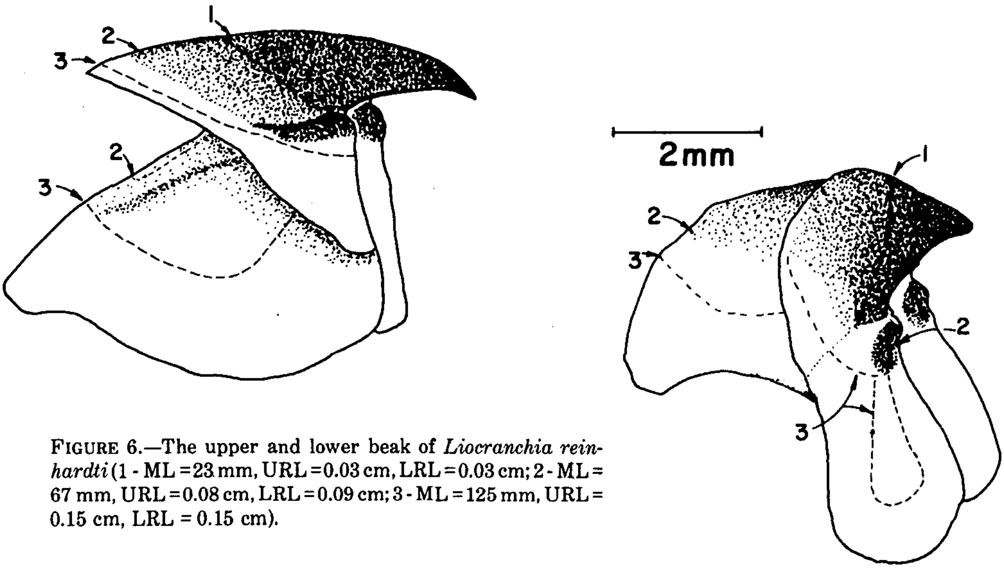


FIGURE 6.—The upper and lower beak of *Liocranchia reinhardti* (1 - ML = 23 mm, URL = 0.03 cm, LRL = 0.03 cm; 2 - ML = 67 mm, URL = 0.08 cm, LRL = 0.09 cm; 3 - ML = 125 mm, URL = 0.15 cm, LRL = 0.15 cm).

5b. RL/HL <0.268 (CI_{05} = 0.246±0.011); *RL/CL <0.194 (CI_{05} = 0.177±0.008); *JW/CL <0.204 (CI_{05} = 0.188±0.007) .... *Loligo opalescens*
Jaw angle not recessed; wing base inserted just above base of anterior margin of lateral wall; pigment changes with growth shown in Figure 7.

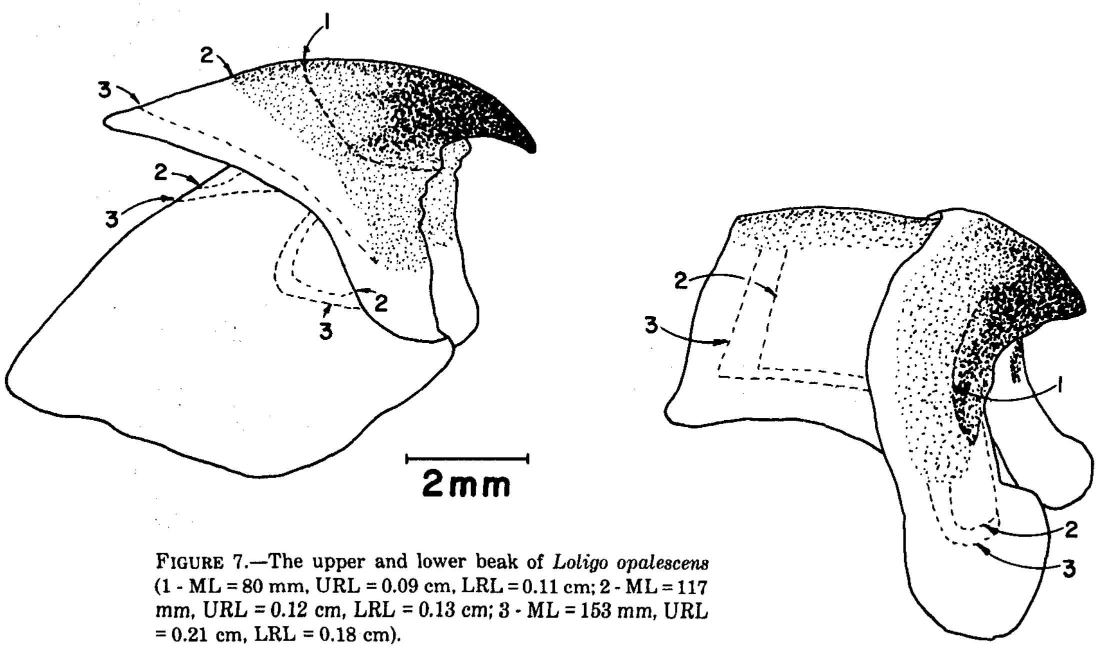


FIGURE 7.—The upper and lower beak of *Loligo opalescens* (1 - ML = 80 mm, URL = 0.09 cm, LRL = 0.11 cm; 2 - ML = 117 mm, URL = 0.12 cm, LRL = 0.13 cm; 3 - ML = 153 mm, URL = 0.21 cm, LRL = 0.18 cm).

6a. RL/JW >1.111 (CI_{05} = 1.161±0.032) 7

6b. RL/JW <1.111 (CI_{05} = 1.061±0.032); *RL/HL <0.322 (CI_{05} = 0.309±0.011); *RL/CL <0.266 (CI_{05} = 0.252±0.008) .... *Ommastrephes bartramii*

Jaw angle deeply recessed; wing base inserted ⅔ down anterior margin of lateral wall; two pigment stripes present as in *Dosidicus gigas* (Fig. 2), remain in beaks with URL >0.60 cm; pigmentation in lateral wall is absent in beaks with URL <0.60 cm; other pigment changes with growth shown in Figure 8.

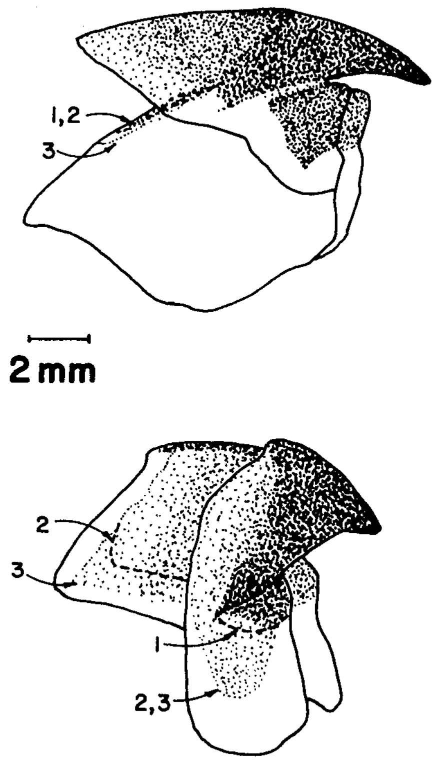


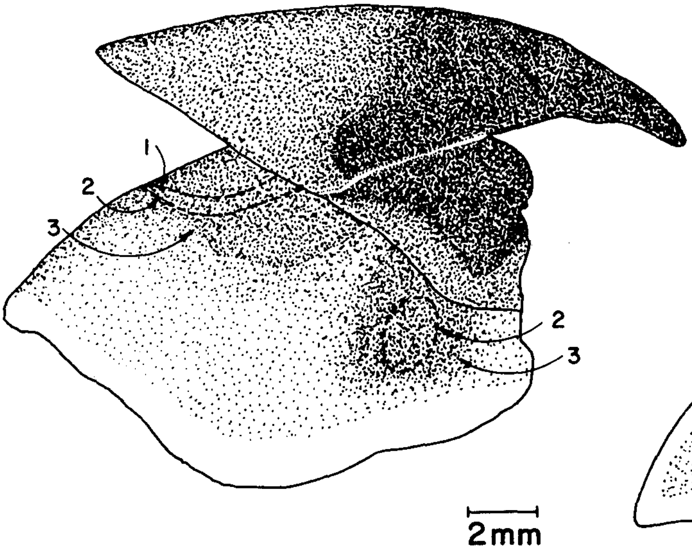
FIGURE 8.—The upper and lower beak of *Ommastrephes bartramii* (1 - ML = 85 mm, URL = 0.15 cm, LRL = 0.15 cm; 2 - ML = 140 mm, URL = 0.28 cm, LRL = 0.31 cm; 3 - ML = 165 mm, URL = 0.40 cm, LRL = 0.41 cm).

7a. HL/CL >0.825 (CI_{05} = 0.838±0.013); *RL/HL <0.344 (CI_{05} = 0.334±0.011); **RL/JW<1.188 (CI_{05} = 1.161±0.032) .... *Dosidicus gigas*

Jaw angle deeply recessed; wing base inserted ½ way down anterior margin of lateral wall; two pigment stripes extend from the inner surface of the rostrum posteriorly onto the inner surface of the crest (Fig. 2)[3]; ridges and grooves more prominent than

[3]Rancurel, P. 1980. Note pour servir a la connaissance de *Symplectoteuthis oualaniensis* (Lesson 1830) (Cephalopoda, Oegopsida) : Variations ontogeniques du bec superieur. Cahiers de L'Indo-Pacifique 2(2):217-232.

pigment stripe in beaks with URL >0.60 cm; pigment changes with growth shown in Figure 9.



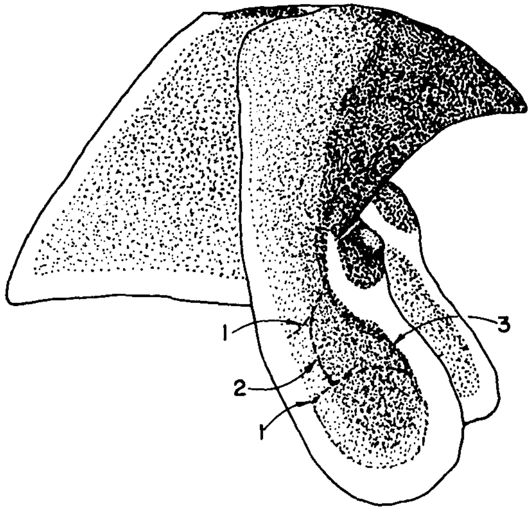
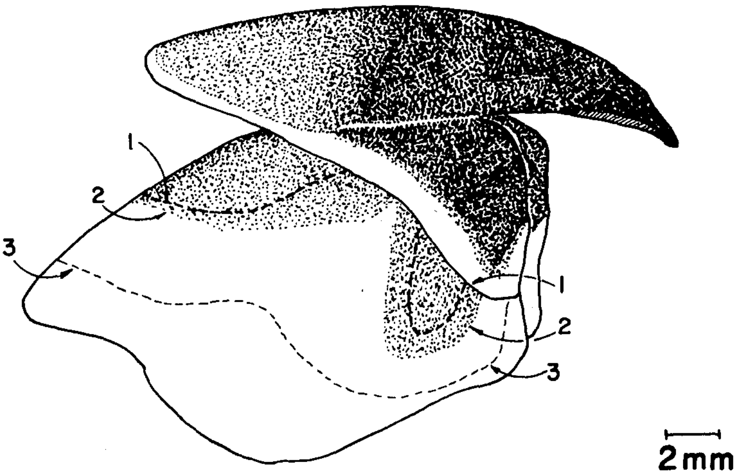


FIGURE 9.—The upper and lower beak of *Dosidicus gigas* (1 - ML = 196 mm, URL = 0.46 cm, LRL = 0.41 cm; 2 - ML = 237 mm, URL = 0.57 cm, LRL = 0.55 cm; 3 - ML = 321 mm, URL = 0.79 cm, LRL = 0.75 cm).

7b. HL/CL <0.825 ($CI_{05} = 0.813 \pm 0.013$); *RL/HL >0.344 ($CI_{05} = 0.354 \pm 0.011$); *RL/JW >1.188 ($CI_{05} = 1.215 \pm 0.032$) .... *Symplectoteuthis oualaniensis*
Jaw angle deeply recessed; wing base inserted ½ down anterior margin of lateral wall; two pigment stripes present as in *D. gigas* (Fig. 2); ridges and grooves more prominent in beaks with URL >0.50 cm; pigment changes with growth shown in Figure 10.



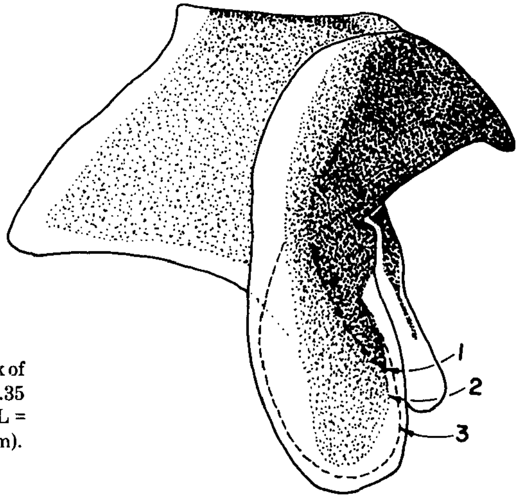


FIGURE 10.—The upper (see bottom of p. 366) and lower beak of *Symplectoteuthis oualaniensis* (1 - ML = 130 mm, URL = 0.35 cm, LRL = 0.33 cm; 2 - ML = 188 mm, URL = 0.55 cm, LRL = 0.50 cm; 3 - ML = 290 mm, URL = 0.76 cm, LRL = 0.70 cm).

KEY TO THE LOWER BEAK

1a. Ridge or fold on lateral wall 2
1b. Ridge or fold absent on lateral wall.. 3

2a. RL/JW >1.173 (CI_{05} = 1.308±0.059); *RC/RL <3.091 (CI_{05} = 2.96±0.122).......... .... *Abraliopsis affinis*
Jaw angle not recessed; no hood notch at crest; anterior-posterior ridge or fold on lateral wall[4] (Fig. 2); pigment changes with growth shown in Figure 4.
2b. RL/JW <1.173 (CI_{05} = 1.037±0.059); *RC/RL >3.091 (CI_{05} = 3.222±0.122)......... .... *Onychoteuthis banksii*
Jaw angle not recessed; no hood notch at crest; prominent anterior-posterior ridge on lateral wall (Fig. 2); pigment changes with growth shown in Figure 3.

3a. Jaw angle strongly recessed.. 6
3b. Jaw angle slightly or not recessed 4

4a. RL/JW >1.134 (CI_{05} = 1.235±0.059); *RW/JW >3.565 (CI_{05} = 3.87±0.157)......... .... *Liocranchia reinhardti*
Jaw angle slightly recessed; no hood notch at crest; pigment changes with growth shown in Figure 6.
4b. RL/JW <1.134 (CI_{05} = 1.032±0.059) 5

5a. RC/RL >3.741 (CI_{05} = 4.058±0.122); *RL/WL <0.418 (CI_{05} = 0.380±0.033) .... *Loligo opalescens*
Jaw angle not recessed; no hood notch at crest; anterior margin of lower wing often produced; pigment changes with growth shown in Figure 7.
5b. RC/RL <3.741 (CI_{05} = 3.424±0.122); *RL/WL >0.418 (CI_{05} = 0.457±0.033) .... *Pterygioteuthis giardi*
Jaw angle not recessed; no hood notch at crest; pigment changes with growth shown in Figure 5.

[4]A ridge or fold on the lateral wall of the lower beak is characteristic in many cephalopod species (e.g., *Histioteuthis* spp.).

6a. RL/JW >0.604 ($CI_{05} = 0.632 \pm 0.033$) 7

6b. RL/WL <0.604 ($CI_{05} = 0.577 \pm 0.033$); **RC/RL >2.890 ($CI_{05} = 2.97 \pm 0.122$) .... *Ommastrephes bartramii*

Jaw angle recessed; no hood notch at crest (Fig. 2); pigment changes with growth shown in Figure 8.

7a. RL/JW >1.137 ($CI_{05} = 1.197 \pm 0.059$); **RC/JW >3.175 ($CI_{05} = 3.360 \pm 0.189$) .... *Dosidicus gigas*

Jaw angle recessed; the hood is deeply notched at the crest (Fig. 2); pigment changes with growth shown in Figure 9.

7b. RL/JW <1.137 ($CI_{05} = 1.077 \pm 0.059$); **RC/JW <3.175 ($CI_{05} = 2.990 \pm 0.189$) .... *Symplectoteuthis oualaniensis*

Jaw angle recessed; the hood is moderately notched at the crest (Fig. 2); pigment changes with growth shown in Figure 10.

The wet body weight and mantle length values for each species were used in linear regression equations to establish a relationship with a beak dimension. The regression equation has the form: $y = a + bx$, where y = weight or mantle length, a = y intercept, b = slope of the regression line, and x = beak dimension. Initially a stepwise procedure, based on r^2 values, was used to determine if combinations of beak dimensions would improve the estimate. Adding more than one independent variable to the regression equations did not substantially increase the r^2 values of the body weight and mantle length equations.

The upper and lower beak of each species is represented by a pair of equations for mantle length and a pair of equations for body weight (Tables 4, 5). The first set of equations represents the best single independent variable equation derived from the stepwise regression procedure. The second set of equations retains the durable RL dimension of the upper and lower beak as the independent variable for all eight species. For the body weight equations all values were transformed to natural logarithms before regression.

DISCUSSION

The research on cephalopod beak ratios was initiated to determine whether species could be separated and identified by comparing different beak dimensions. Once this had been established, the primary use of such a technique was considered to be stomach content analysis. The condition of beaks removed from preserved, identified specimens is ordinarily much better than that of specimens removed from a predator's stomach. Therefore, other beak characteristics, in addition to maximum separation between species' means, were considered when the beak ratios for the key were selected. The selection was based on a dimension's durability under mechanical and chemical action, the effect such action would have on the accuracy of the beak dimension's measurement, and the ability to separate the ratio means at a given confidence level ($\alpha = 0.05$). Consequently, small dimensions with easily

TABLE 4.—Regression equations and r^2 values for mantle length and body weight, upper beak regression equations in centimeters, asterisk indicates best regression based on r^2.

Species	Mantle length (mm)	r^2	Body weight (g)	r^2
Symplectoteuthis	**ML* = −2.17 + *CL* 105.2	0.95	*ln *W* = 3.7 + ln *CL* 3.1	0.98
oualaniensis	*ML* = −10.9 + *RL* 382.2	0.81	ln *W* = 7.6 + ln *RL* 3.2	0.95
Dosidicus	**ML* = 65.8 + *CL* 86.2	0.95	*ln *W* = 4.3 + ln *CL* 2.23	0.97
gigas	*ML* = 41.1 + *RL* 346.8	0.87	ln *W* = 7.3 + ln *RL* 2.54	0.91
Liocranchia	**ML* = −5.4 + *JW* 804.7	0.96	*ln *W* = 7.2 + ln *JW* 2.34	0.88
reinhardti	*ML* = −3.2 + *RL* 806.9	0.94	ln *W* = 7.0 + ln *RL* 2.22	0.87
Abraliopsis	**ML* = 4.1 + *CL* 63.7	0.93	*ln *W* = 3.3 + ln *CL* 2.86	0.90
affinis	*ML* = 9.1 + *RL* 216.1	0.87	ln *W* = 6.0 + ln *RL* 2.2	0.85
Onychoteuthis	**ML* = −22.1 + *CL* 127.6	0.92	*ln *W* = 9.4 + ln *RL* 3.8	0.93
banksii	*ML* = −31.0 + *RL* 641.0	0.87	ln *W* = 9.4 + ln *RL* 3.8	0.93
Pterygioteuthis	**ML* = 2.1 + *RW* 230.9	0.76	*ln *W* = 3.8 + ln *CL* 2.75	0.87
giardi	*ML* = 7.3 + *RL* 289.8	0.62	ln *W* = 5.8 + ln *RL* 2.04	0.83
Ommastrephes	**ML* = 42.4 + *HL* 95.8	0.99	*ln *W* = 3.7 + ln *CL* 2.4	0.98
bartramii	*ML* = 51.4 + *RL* 282.4	0.94	ln *W* = 6.7 + ln *RL* 2.15	0.96
Loligo	**ML* = −5.7 + *CL* 153.5	0.94	*ln *W* = 6.0 + ln *RW* 2.25	0.80
opalescens	*ML* = 42.2 + *RL* 542.7	0.79	ln *W* = 5.7 + ln *RL* 1.21	0.65

TABLE 5.—Regression equations and r^2 values for mantle length and body weight, lower beak regression equations in centimeters, asterisk indicates best regression based on r^2.

Species	Mantle length (mm)	r^2	Body weight (g)	r^2
Symplectoteuthis	**ML* = −11.93 + *RC* 115.4	0.96	*ln *W* = 4.7 + ln *RC* 3.2	0.98
oualaniensis	*ML* = 6.98 + *RL* 392.5	0.93	ln *W* = 7.8 + ln *RL* 3.0	0.96
Dosidicus	**ML* = 68.0 + *WL* 207.7	0.95	*ln *W* = 4.97 + ln *RC* 2.3	0.95
gigas	*ML* = 44.2 + *RL* 357.9	0.84	ln *W* = 7.4 + ln *RL* 2.48	0.91
Liocranchia	**ML* = 0.85 + *JW* 956.8	0.94	*ln *W* = 7.76 + ln *JW* 2.3	0.88
reinhardti	*ML* = −1.09 + *RL* 802.2	0.89	ln *W* = 6.7 + ln *RL* 2.1	0.80
Abraliopsis	**ML* = 6.3 + *RC* 77.7	0.95	*ln *W* = 3.8 + ln *RC* 2.5	0.91
affinis	*ML* = 9.8 + *RL* 192.8	0.88	ln *W* = 5.5 + ln *RL* 2.1	0.81
Onychoteuthis	**ML* = −22.5 + *RC* 177.7	0.93	*ln *W* = 4.7 + ln *RC* 3.5	0.94
banksii	*ML* = −28.9 + *RL* 610.0	0.95	ln *W* = 9.1 + ln *RL* 3.7	0.89
Pterygioteuthis	**ML* = 2.3 + *RC* 121.9	0.76	*ln *W* = 4.5 + ln *RC* 2.7	0.92
giardi	*ML* = 6.2 + *RL* 331.6	0.41	ln *W* = 7.6 + ln *RL* 2.6	0.70
Ommastrephes	**ML* = 44.6 + *RC* 103.5	0.99	*ln *W* = 4.4 + ln *RC* 2.3	0.99
bartramii	*ML* = 52.7 + *RL* 276.1	0.96	ln *W* = 6.6 + ln *RL* 2.07	0.98
Loligo	**ML* = 6.0 + *RW* 240.9	0.87	*ln *W* = 4.4 + ln *RC* 1.95	0.76
opalescens	*ML* = 32.4 + *RL* 607.8	0.74	ln *W* = 6.0 + ln *RL* 1.4	0.58

damaged margins (e.g., RW, WW upper beak) were excluded from consideration when constructing the key, even though they might show very good separation between species' means when used in a ratio (e.g., RL/RW upper beak). Larger dimensions which have easily damaged margins (e.g., CL/HL) can still provide a reliable dimension within the variability of the sample simply because the eroded margin represents less of the overall dimension compared with the smaller dimension with similar properties.

Accurately determining which cephalopods are abundant in an area and which of these might be important in a predator's diet are difficult problems to solve. The abundance of a species in a trawl sample is not necessarily an accurate reflection of its relative abundance in the field (Wormuth 1976) or in a predator's stomach (Clarke 1977). In an attempt to reduce this sampling bias the cephalopods in this study were chosen on the basis of their abundance in trawl samples (Young 1972; Okutani 1974), in collections using alternate sampling devices (e.g., dip nets and jigs (Wormuth 1976)), and in stomach content studies of cephalopod predators in the same area (Pinkas et al. 1971; Perrin et al. 1973).

The eastern tropical Pacific is the area for which these beak characterizations were constructed. In many cases, large, pelagic cephalopod predators in this area will contain a large percentage of the species described in this study. As one moves away from this area, however, less can be said about the potential usefulness of this key, since the species composition and morphological characteristics, including beak dimensions, can change. As an example, 28 specimens of *O. bartramii* from the Gulf of Mexico and northwestern Atlantic have an upper rostral length to jaw width ratio mean (RL/JW) of 1.22 (CI_{05} = ±0.02); considerably greater than the eastern tropical Pacific mean of *O. bartramii* ($\bar{x}$ = 1.06, CI_{05} = ±0.03). This higher ratio value also holds for three specimens from southeastern Australia.

Such geographical variation in species with disjunct distributions is not uncommon and has been noted in other body measurements for *O. bartramii* by Young (1972). Additional measurements must be made on remaining cephalopod species in this key, particularly those with disjunct distributions, before this key can be reliably used outside the eastern tropical Pacific area.

There will be cephalopods in the stomachs of predators which are not included in this work. In order to reduce misidentifications, therefore, full use should be made of the alternate ratio means, the beak figures, and the descriptive characteristics.

In most beaks, the dimensions which resulted in the best regression equations for mantle length and body weight were those that were close to the overall length of the beak (CL, HL, RC). In badly damaged beaks, however, these dimensions are often in poor conditon. The pairs of regression equations for each of the eight species represent an effort to increase the flexibility of estimating the size of a cephalopod. The regression equations which use the RL dimension variable will give less accurate estimates, but can be used in all but the most severely damaged beaks, as the RL is a very durable dimension.

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