BEAKS OF THE MARKET SQUID, *LOLIGO OPALESCENS*, AS TOOLS FOR PREDATOR STUDIES

JERRY KASHIWADA AND CONRAD W. RECKSIEK
Moss Landing Marine Laboratories
P.O. Box 223, Moss Landing, CA 95039

KONSTANTIN A. KARPOV
The Resources Agency
California Department of Fish and Game
California State Fisheries Laboratory
350 Golden Shore, Long Beach, CA 90802

INTRODUCTION

Studies of feeding habits of predators are greatly complicated since digestive processes often leave prey items unrecognizable and unmeasurable. Items in such a state are of no value in determining the importance of prey species in the diet of the predator. Hard structures that resist digestion have allowed many researchers to identify and quantify prey items despite the deterioration of softer tissues.

Squid remains are found in the stomachs of many marine predators. Unfortunately, squid have few hard parts that resist digestion well enough to be used for stomach analyses. Dragovich and Wise (1969) chose to use the pen (gladius) for estimating body length and volume of ingested squid. The pen is not always a useful tool for stomach analyses of predators, since it can be easily fragmented and is seldom found intact. The chitinous beaks, however, are more resistant to fragmentation and are often found in the stomachs of predators. Beaks have proven to be valuable in many studies of cephalopod predators. Clarke (1962) used beaks to distinguish families and to estimate the weight of squid eaten by predators. He found that the lower beaks were more useful for identification. Clarke and MacLeod (1974) were able to distinguish species of cephalopods by various beak characteristics. The pictorial guide to cephalopod beaks developed by Iverson and Pinkas (1971) provides a method for distinguishing the beaks of *Loligo opalescens* from other squids found in the North Pacific Ocean. In addition to food habit information, Clarke and Stevens (1974) deduced possible migration patterns in blue sharks (*Prionace glauca*) by identifying the squid species eaten.

Although weights and volumes are essential measurements in feeding studies of specific predators, an estimate of body length is sufficient for our studies of the predators of *Loligo opalescens*. Spratt (1975) used a linear regression to estimate body size of northern anchovy (*Engraulis mordax*) from otolith measurements. A similar regression of dorsal mantle (body) length on beak dimensions could be used for estimating the size of *L. opalescens* from measurements of the beaks alone. Differences in sex, geographical location, and size may affect the accuracy of the estimates produced by regression. There is a noticeable difference in the size of the head and arms of males and females (Fields 1965). Clarke (1962) mentions possible differences in the amount of darkening of the beaks of the same species which are found in different geographical locations. The possible effects of these factors and their extent need to be examined. In this report we investigate the relationship between body size and various beak dimensions to develop a technique for estimating body sizes by measuring beaks of *L. opalescens* taken from predator stomachs. We also examine variability introduced by differences in size, sex, and geographical origin. We were especially interested in determining whether beak morphology could be used to detect the presence of subpopulations of *L. opalescens*.

METHODS

Loligo opalescens used for this study were captured in southern and central (Monterey Bay) California waters during a cruise of the California Department of Fish and Game research vessel *Alaska* (Cruise 76A4). Additional samples from the Monterey Bay area were taken from Moss Landing Marine Laboratories research vessel *Oconostota* cruises and from the catches of commercial fishermen.

The body of the squid was measured from the posterior tip to the anteriormost point of the mantle along the dorsal side (dorsal mantle length). The sex of the squid was recorded when such determination was possible. The buccal mass which contains the beak was extracted from a wide size range of squid from the two geographical locations. The beaks were extracted after the surrounding tissue was allowed to decay in a vial of water for a day or two. On each upper beak (Figure 1), four dimensions were measured: upper hood length (UHL), rostral darkening (URD), rostral length (URL), and rostral width (URW). Four measurements were also made on each lower beak (Figure 2): lower rostral darkening (LRD), hood length (LHL), crest length (LCL), and rostrum-wing length (LRW). Names of the beak structures were taken from Clarke (1962).

A dissecting microscope with an ocular micrometer was used to take the measurements. The measurements were plotted against dorsal mantle length (DML). Least square regressions of the measurements on dorsal mantle length were calculated (Sokal and Rohlf 1969, p. 410). Selected regressions were calculated for the beaks of Monterey Bay males, Monterey Bay females, southern California males, and southern California females. An

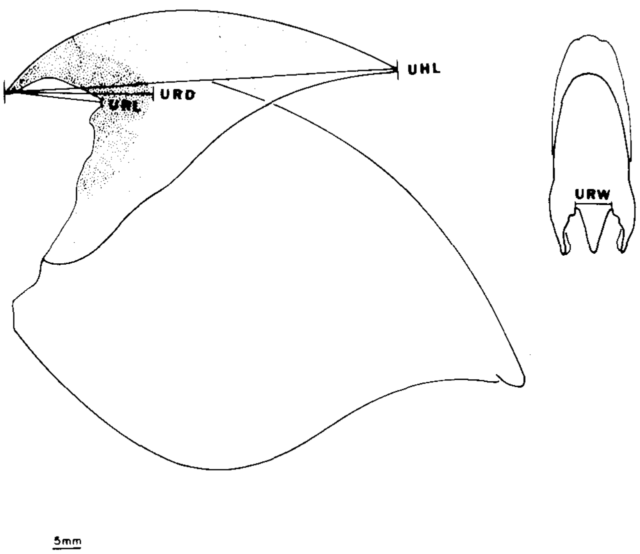

Figure 1. Illustration of upper beak showing the dimensions measured: URL (Upper Rostral Length), URD (Upper Rostral Darkening), UHL (Upper Hood Length), URW (Upper Rostral Width).

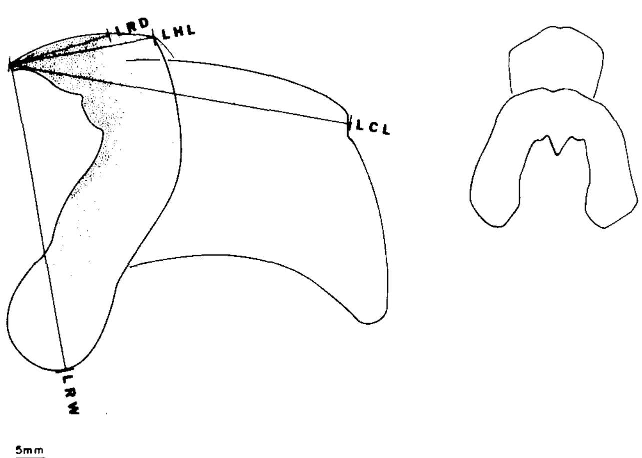

Figure 2. Illustration of lower beak showing dimensions measured: LRD (Lower Rostral Darkening), LHL (Lower Hood Length), LCL (Lower Crest Length), LRW (Lower Rostrum-Wing Length).

F-value was calculated to compare the significance of the regression lines (Sokal and Rohlf 1969, p. 420) of each dimension on dorsal mantle length for Monterey Bay males.

Differences in both sex and geographic origin were examined as sources of variation about the regression lines. To test for differences attributable to geographical location, the slopes and variances of the regression of upper hood length (UHL) on dorsal mantle length (DML) for Monterey Bay and southern California male squid were compared (Snedecor and Cochran 1967, p. 435). The same comparisons were made for Monterey Bay male and female squid to test for sexual differences.

In determining which beak dimensions would be most useful in predator studies, both the significance of the regression lines and the durability of the dimensions in resisting digestion were considered. The significance of the regression lines was compared by using the *F*-values mentioned above. One dimension was chosen for both the upper beak and lower beak. A regression of these dimensions on dorsal mantle length was calculated by combining all available data without regard to sex or geographical origin. Equations for estimating dorsal mantle length from measurements of these dimensions were calculated. Analysis of variance tables were calculated to allow the placement of confidence limits on estimates made from the equations. The slopes of the regression lines for southern and central (Monterey Bay) California squid were compared (Snedecor and Cochran 1967, p. 435) to determine whether separate regression lines for the two areas would be required for these beak dimensions.

The ratio of upper rostral length (URL) to upper rostral width (URW) was calculated to investigate possible proportional differences in size, sex, and geographical location. A 3-way analysis of variance was performed using a library computer program (Nie et al. 1975) to compare sources of variation attributable to these three effects. Three size groups, small (20-80 mm), medium (81-135 mm), and large (136-195 mm), were used. Central and southern California squid were used to test the effects of differences in geographical location.

RESULTS AND DISCUSSION

The calculated *F*-values show that the most significant regression lines for the upper and lower beak measurements are upper hood length (UHL) and lower crest length (LCL), respectively (Table 1). Upper rostral length (URL) and lower rostral darkening (LRD) had the least significant regression lines.

TABLE 1

Regression Statistics of Beak Dimensions (mm) on Dorsal Mantle Length (mm) for Male *Loligo opalescens* from Monterey Bay.

Beak Dimension	Regression Coefficient	Intercept	Error *df*	*F*
URL	0.0104	0.184	60	479.4
UHL	0.0481	0.243	58	2147.8
URW	0.0103	0.247	60	752.3
URD	0.0169	0.295	60	547.6
LHL	0.0178	0.212	60	645.1
LCL	0.0399	0.159	60	2096.1
LRW	0.0311	0.486	58	552.9
LRD	0.0124	−0.066	60	308.7

Since the slope of the regression lines is important in estimating body length from beak measurements, comparisons of slope and variance of the regression lines were made. The upper hood length dimension was chosen to test for differences due to geographical location because the high significance of its regression line makes it more sensitive to possible differences. No significant differences in slopes and variances of the regressions were found. Since the slope of the regression line for southern California male squid is not significantly different from that for Monterey Bay male squid (Figure 3; Table 2), a single regression equation can be used to represent the relationship between upper hood length and dorsal mantle length for southern and central California *Loligo opalescens.* We believe similar comparisons of the other beak dimensions would also show no significant differences; these dimensions show more scattering about their regression lines and would be less sensitive in demonstrating differences in slopes.

TABLE 2
Comparison of Slopes of the Regressions of Upper Hood Length (mm) on Dorsal Mantle Length (mm) for Monterey Bay and Southern California Male *Loligo Opalescens.*

Location	*df*	*B* (Slope)	*MS*res
Monterey Bay . . .	59	0.0481	0.161
Southern California	53	0.0509	0.243

Comparison of slopes: $F = 2.17$ N.S.

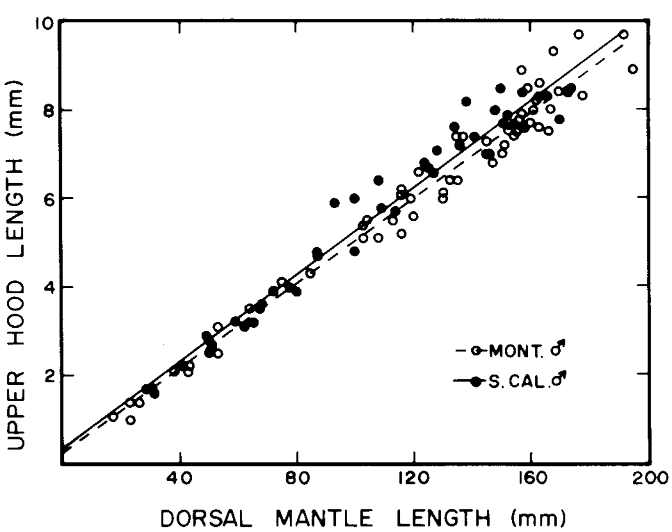

Figure 3. Regressions of upper hood length on dorsal mantle length for male *Loligo opalescens* from Monterey Bay and southern California.

No significant difference was found between the residual variances of the regressions of upper hood length on dorsal mantle length of central California male and female squid; however, a significant difference was found in the slopes of these regressions (Figure 4; Table 3). Although the difference was highly significant, it was not great enough to impair the usefulness of a regression line combining measurements of both males and females (*F*-values, Table 3).

The lower crest length and upper hood length dimensions would be the most useful dimensions for estimating the size of squid from beak measurements since they

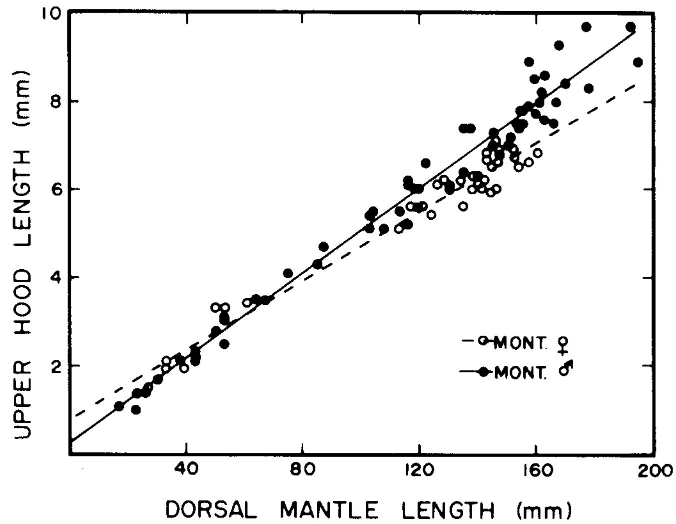

Figure 4. Regressions of upper hood length on dorsal mantle length for male and female *Loligo opalescens* from Monterey Bay.

TABLE 3
Comparison of Slopes of the Regressions of Upper Hood Length (mm) on Dorsal Mantle Length (mm) for Male and Female *Loligo opalescens* from Monterey Bay.

Sex	*df*	*B* (Slope)	*MS*res	*F*
Males	59	0.0481	0.1615	2147.8
Females	41	0.0393	0.0956	1417.1
Pooled . . .	101	0.0451		2121.6

Comparison of slopes: $F = 32.0$ *** ($P < .001$)

exhibit the least scatter about their regression lines. Unfortunately, both these dimensions often cannot be measured because the beak structures involved are fragile and freqeuntly damaged. For beaks taken from the stomachs of predators captured in Monterey Bay, the lower hood length and upper rostral width dimensions were found to be the most durable (James Harvey, personal communication). Although the regressions for these two latter dimensions have more error, these dimensions are usually undamaged and are, therefore, more valuable as tools for stomach analysis.

All available data were used in plotting regressions of lower hood length and upper rostral width on dorsal mantle length (Figure 5 and 6). These dimensions did not show a significant difference between the regression lines for southern and central California *Loligo opalescens* (Tables 4 and 5). The combined regressions should therefore be useful for predator studies in both areas and presumably for the entire range of *L. opalescens.* To estimate dorsal mantle length from a given beak, regression analyses and analyses of variance for these two combined regression lines were performed (Tables 6 and 7). Confidence limits for estimates made from these equations can be calculated using a method described by Sokal and Rohlf (1969, p. 446).

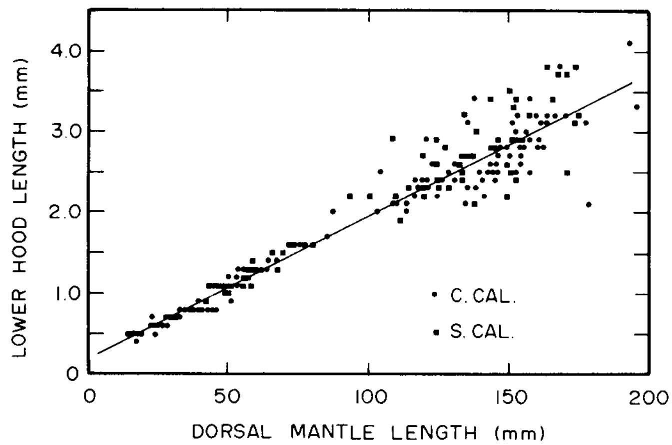

Figure 5. Regression of lower hood length on dorsal mantle length combining data for *Loligo opalescens* of both sexes and from both southern California and Monterey Bay.

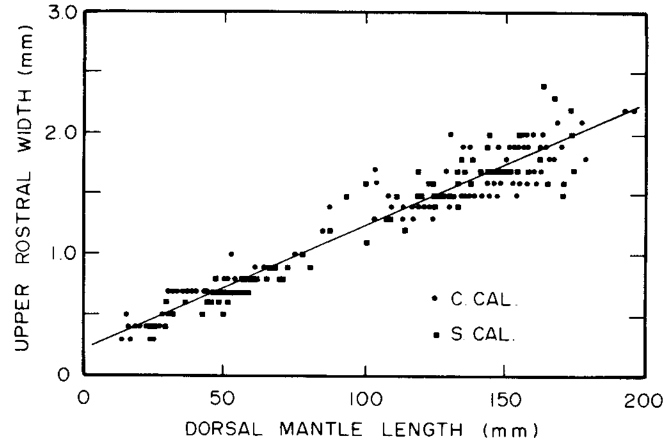

Figure 6. Regression of upper rostral width on dorsal mantle length combining data for *Loligo opalescens* of both sexes and from both southern California and Monterey Bay.

TABLE 4

Comparison of Slopes of the Regressions of Lower Hood Length (mm) on Dorsal Mantle Length (mm) for *L. opalescens* of Both Sexes from Monterey Bay and Southern California.

Location	*df*	*B* (Slope)	*MS*res
Monterey Bay ...	117	0.0169	0.0583
Southern California	96	0.0183	0.0705

Comparison of slopes: $F = 2.59$ N.S.

TABLE 5

Comparison of Slopes of the Regressions of Upper Rostral Width (mm) on Dorsal Mantle Length (mm) for *L. opalescens* of Both Sexes from Monterey Bay and Southern California.

Location	*df*	*B* (Slope)	*MS*res
Monterey Bay ...	117	0.0099	0.0187
Southern California	96	0.0107	0.0225

Comparison of slopes: $F = 3.76$ N.S.

TABLE 6

Regression Equation of Lower Hood Length (mm) on Dorsal Mantle Length (mm) and Analysis of Variance Table Combining Data for Both Sexes and Both Geographic Locations.

LHL = 0.01760 x DML + 0.21763

Source of Variation	*df*	*SS*	*MS*	*Fs*
Explained ...	1	164.015	164.015	2495.51
Unexplained	213	13.999	0.065723	
Total	214	178.014		

$y^2 = 178.014$
$x^2 = 528{,}614.321$
$xy = 9{,}311.31953$

TABLE 7

Regression Equation of Upper Rostral Width (mm) on Dorsal Mantle Length (mm) and Analysis of Variance Table Combining Data for Both Sexes and Both Geographic Locations.

URW = 0.01023 × DMP + 0.21648

Source of Variation	*df*	*SS*	*MS*	*Fs*
Explained ...	1	55.2338	55.2338	2674.11
Unexplained..	213	4.3994	0.020655	
Total	214	59.6332		

$y^2 = 59.6332$
$x^2 = 527{,}473.953$
$xy = 5{,}397.63256$

TABLE 8

Model 1 Analysis of Variance Table for the Effects of Size, Geographic Location and Sex on the Upper Rostral Length/Upper Rostral Width Ratio.

Source of Variation	Sum of Squares	*df*	Mean Square	*F*	Significance of *F*
Main effects					
Size	0.43415	2	0.21707	13.848	0.001
Location	0.00001	1	0.00001	0.001	0.999
Sex	0.00013	1	0.00013	0.008	0.999
2-way interactions					
Size-Location...	0.01587	2	0.00793	0.506	0.999
Sex-Size	0.06981	2	0.03490	2.227	0.110
Location-sex ...	0.07413	1	0.07413	4.729	0.030
3-way interactions ..	0.08746	2	0.04373	2.790	0.064
Residual	1.88100	120	0.01567		
Total	2.56660				

The analysis of variance results for the upper rostral length (URL) / upper rostral width (URW) ratio (Table 8) shows there is a highly significant difference between the size of the squid, whereas no differences can be detected for sex or geographical location. The difference is caused by an increase in the value of the ratio for the medium and large size groups. The 2-way treatment interaction of location and sex was significant at the .05 level (Table 8). The implications of this interaction are difficult to resolve since neither location nor sex was found to have a significant effect by itself. The interaction may have occurred because the squid in the Monterey Bay female small division were smaller than their southern California counterparts.

Aside from quantifying the relationships between body size and various beak dimensions, this research uncovered little evidence for variation in beak morphology with geographic location. Positive results in this area of investigation may have served as evidence for population- or climate-related differences. Our impression is that beak morphology by itself will not show such differences.

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