Reconstruction of original body size and estimation of allometric relationships for the longfin inshore squid (*Loligo pealeii*) and northern shortfin squid (*Illex illecebrosus*)

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Quantification of predator-prey body size relationships is essential to understanding trophic dynamics in marine ecosystems. Prey lengths recovered from predator stomachs help determine the sizes of prey most influential in supporting predator growth and to ascertain size-specific effects of natural mortality on prey populations (Bax, 1998; Claessen et al., 2002). Estimating prey size from stomach content analyses is often hindered because of the degradation of tissue and bone by digestion. Furthermore, reconstruction of original prey size from digested remains requires species-specific reference materials and techniques. A number of diagnostic guides for freshwater (Hansel et al., 1988) and marine (Watt et al., 1997; Granadeiro and Silva, 2000) prey species exist; however they are limited to specific geographic regions (Smale et al., 1995; Gosztonyi et al., 2007). Predictive equations for reconstructing original prey size from diagnostic bones in marine fishes have been developed in several studies of piscivorous fishes of the Northwest Atlantic Ocean (Scharf et al., 1998; Wood, 2005). Conversely, morphometric relationships for cephalopods in this region are scarce despite their importance to a wide range of predators, such as finfish (Bowman et al., 2000; Staudinger, 2006), elasmobranchs (Kohler, 1987), and marine mammals (Gannon et al., 1997; Williams, 1999).

As with the bones and otoliths of prey fish, cephalopod beaks are often recovered from predator stomachs and may be used for identification of prey species and the reconstruction of original prey body size (Clarke, 1986). Many predators (e.g., marine mammals) cannot digest the chitinous beaks and thousands of beaks may accumulate in the stomachs until they are regurgitated (Clarke, 1980). Predictive equations for estimating body size in the two most common species of cephalopods in the Northwest Atlantic Ocean (Bowman et al., 2000) are either based on few observations ($n=25$) as seen in the longfin inshore squid (*Loligo pealeii*) (Gannon et al., 1997), or are nonexistent as is true for the northern shortfin squid (*Illex illecebrosus*).

Trophic niche breadth is the range of relative prey sizes consumed ontogenetically by a predator (Scharf et al., 2000). In previous diet studies, trophic niche breadth has been used to predict shifts in foraging modes and physical limitations on feeding patterns (Bethea et al., 2004; Beauchamp et al., 2007). Calculation of trophic niche breadth requires measurements of the total lengths of predators and prey. Depending on how a species is traditionally 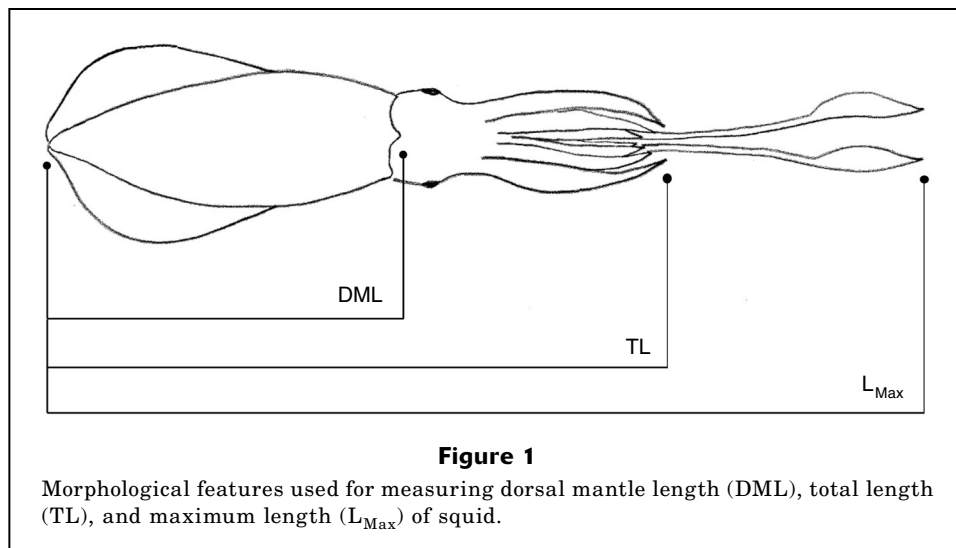measured (e.g., fork length in fish, mantle length in squid) in population and other types of surveys, information on total length may not always be readily available. Therefore, knowledge of allometric relationships may be useful to accurately assess trophic interactions and predator-prey relationships. For the majority of cephalopod species, there are currently no predictive equations to estimate total length from mantle length and to account for variability in growth. To improve descriptions of the feeding habits of teuthophagous predators and to increase the number of evaluations of size-based predation on cephalopod prey we present 1) predictive equations for reconstructing original prey size and 2) allometric relationships of mantle length to total body length for the two most common species of cephalopods in the Northwest Atlantic Ocean, *L. pealeii* and *I. illecebrosus*.

Materials and methods

Loligo pealeii were collected by otter trawl from coastal waters off Massachusetts during the months of May through September of 2006 and 2007. *Illex illecebrosus* were collected from outer shelf waters from New Jersey to North Carolina during February 2007 on both the winter and spring bottom trawl surveys conducted by the National Marine Fisheries Service (Northeast Fisheries Science Center) (Azarovitz, 1981). All squid were preserved by freezing until they were processed in the laboratory. Specimens were thawed to room temperature and then measured for dorsal mantle length (DML), total length (TL), and maximum length (L_{Max}) to the nearest 1.0 millimeter. Dorsal mantle length was measured as the distance between the posterior

Figure 1

Morphological features used for measuring dorsal mantle length (DML), total length (TL), and maximum length (L_{Max}) of squid.

and anterior tips of the dorsal side of the mantle, total length was measured as the distance between the posterior tip of the mantle to the end of the longest arm, and maximum length was measured as the distance between the posterior tip of the mantle to the end of the longest tentacle (Fig. 1). Beaks were extracted from the buccal mass and the lower rostrum length (LRL) of the lower beak was measured to the nearest 0.01 millimeter. Lower beaks were held so that the rostrum tip was facing the observer and then turned to a left-facing orientation (Fig. 2); the lower beak was best viewed when held against a white background for contrast. The LRL of *L. pealeii* was measured by placing the tip of the moving arm of the calipers inside the jaw angle of the lower beak and extending it to the tip of the rostrum (Clarke, 1986) (Fig. 2A). The LRL of *I. illecebrosus* was measured from the tip of the rostrum to the jaw angle. In *I. illecebrosus* the shoulder forms a tooth which facilitates location of the jaw angle (Fig. 2B). Beaks from both species were measured either under a dissecting microscope or a magnifying glass.

Least squares regression analysis was used to estimate the relationship between mantle length and total length, mantle length and maximum length, and LRL and mantle length for both squid species. Using the PROC UNIVARIATE command in SAS, vers. 9.1 (SAS Institute Inc., Cary, NC), we found that all variables were in compliance with assumptions of normality and no outliers were detected. Linear models were used to develop predictive equations for all pairings of morphological structures. All statistical analyses were performed by using the PROC REG command in SAS.
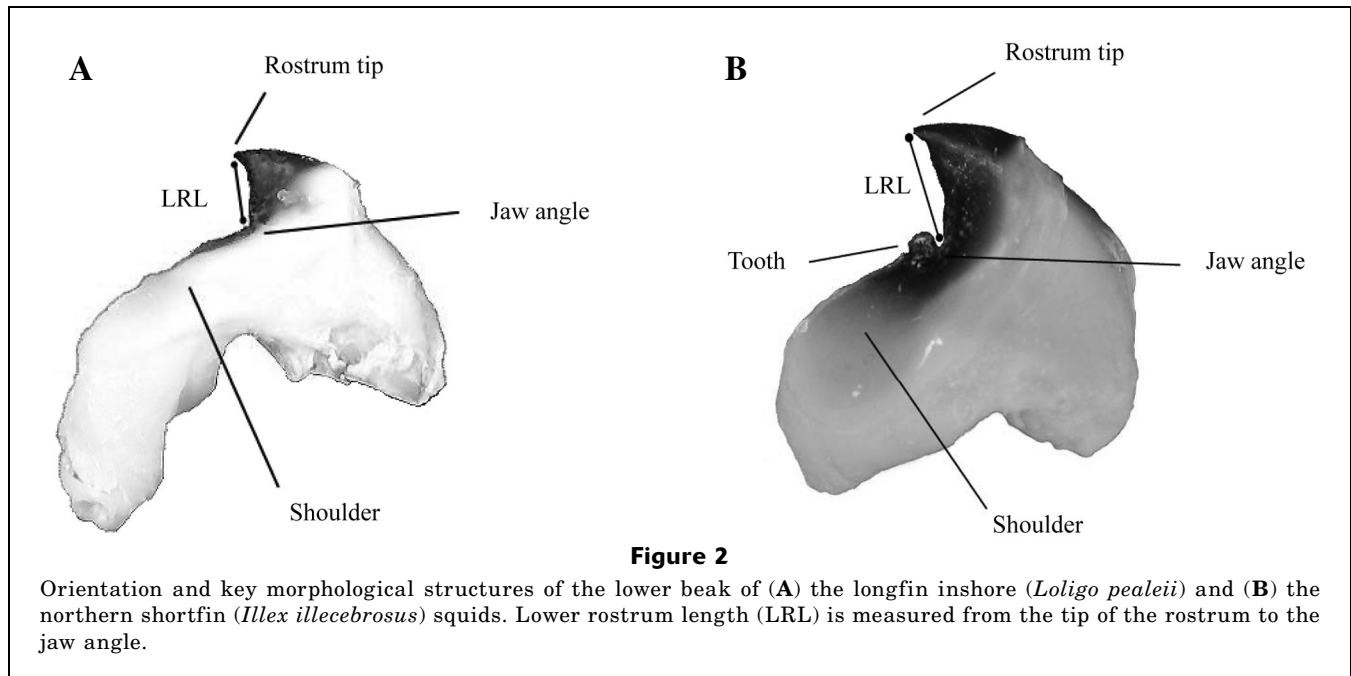
Results

Total length (TL) and maximum length (L_{Max}) were strongly related to dorsal mantle length (DML) in both

L. pealeii and *I. illecebrosus*. The r^2 values for all body size relationships ranged from 0.88 to 0.98 and were highly significant ($P<0.0001$) (Table 1). A total of 434 *L. pealeii* ranging in size from 1.9 to 28.0 cm (DML) and 158 *I. illecebrosus* ranging in size from 4.4 to 28.4 cm (DML) were measured to develop allometric relationships between DML, TL, and L_{Max}.

Equations for reconstructing original squid size (DML) from lower rostrum lengths (LRL) were highly significant ($P<0.0001$) in both *L. pealeii* and *I. illecebrosus* (Table 1). The model developed for *L. pealeii* improved the only known equation for this species by expanding the sample size from $n=25$ and the coefficient of determination (r^2) of 0.73 (Gannon et al., 1997) to $n=144$ and an r^2 of 0.83 (Table 1). Lower rostrum lengths (LRL) were measured from *L. pealeii* ranging from 2.6 to 24.7 cm (DML). The predictive model for estimating DML from LRL in *I. illecebrosus* was developed from 89 specimens ranging from 4.4 to 28.4 cm (DML). The relationship between LRL and DML in *I. illecebrosus* was stronger and less variable ($r^2=0.94$, coefficient of variation [CV]=8.15) in comparison to *L. pealeii* ($r^2=0.83$, CV=15.94). Measurement of the lower rostral length in *I. illecebrosus* is greatly facilitated by the presence of a tooth located in the angle point. This structure is absent in the lower beak of *L. pealeii*, and may make measuring beaks from this species more difficult and prone to error.

Discussion

The results of the present study are intended to assist and encourage quantitative assessments of cephalopod prey in the diets of a broad range of finfish, elasmobranch, marine mammal, and seabird predators. Although methods for identification and reconstruction of original body size from cephalopod beaks have

Figure 2

Orientation and key morphological structures of the lower beak of (**A**) the longfin inshore (*Loligo pealeii*) and (**B**) the northern shortfin (*Illex illecebrosus*) squids. Lower rostrum length (LRL) is measured from the tip of the rostrum to the jaw angle.

Table 1

Least squares regression equations for describing the relationship of total length (TL) to dorsal mantle length (DML) and maximum length (L_{Max}), and the relation of DML to the lower rostral length of the lower beak (LRL) in longfin inshore (*Loligo pealeii*) and northern shortfin (*Illex illecebrosus*) squids. All measurements are given in centimeters. n=sample size, r^2=coefficient of determination, F=the F-statistic, and P-value=significance of each model.

Species	Equation	n	r^2	F	P-value
Loligo pealeii	$TL = 1.29DML + 3.11$	434	0.97	14,818.7	<0.0001
	$L_{Max} = 1.52DML + 6.17$	434	0.88	3018.05	<0.0001
	$DML = 92.29LRL - 2.12$	144	0.83	639.2	<0.0001
Illex illecebrosus	$TL = 1.76DML - 1.43$	158	0.98	6624.16	<0.0001
	$L_{Max} = 2.05DML - 0.44$	158	0.97	4409.64	<0.0001
	$DML = 48.92LRL + 0.82$	89	0.94	1364.18	<0.0001

been available for several decades (Clarke, 1980, 1986), information on body-size relationships in the two most common species of squid found in the Northwest Atlantic Ocean has been lacking. Results presented here improved the fit of the only known model for reconstructing mantle length from the rostral length of the lower beak in *L. pealeii*. Clarke (1986) provided an equation for reconstructing body mass from the LRL in *I. illecebrosus*; however, to the best of our knowledge, an equation for reconstructing body length was not previously available for this species.

Mantle length is the universally measured characteristic to assess squid size in population and commercial surveys because it is easy to measure and exhibits less variation in comparison to other structures. We do not advocate changing the current method because, as shown here, morphological relationships for total length (TL) and maximum length (L_{Max}) can be reliably predicted from dorsal mantle length (DML). However, for the purposes of evaluating relative predator-prey body-size relationships, mantle length does not accurately represent total size. Squid swim with their arms extended in front of them or bent slightly downwards and rarely extend their two tentacles, which are longer than their eight arms, except during feeding and mating (Hanlon and Messenger, 1996). Therefore, when a predator attacks a squid it likely perceives the total body size of the squid as the sum of the arms and mantle, thus, making TL the appropriate measure for calculating relative body size. In response to predator

presence in laboratory conditions, squid have occasionally been observed swimming with their tentacles extended, perhaps to appear bigger and to deter attacks. Maximum length (L_{Max}) therefore could be used as an upper limit of predator-perceived squid size. Conversely, in studies where squid is considered the predator rather than the prey, maximum length may be useful to investigators interested in estimating the reach or striking distance of a squid.

All of the morphological relationships measured in this study were found to be highly accurate predictors of body size. The proposed models to back-calculate original size from the lower rostral length of squid beaks provide coefficients of determination similar to those found in previous studies where fish bones and eye lenses were used to calculate original prey size (Scharf et al., 1997, 1998; Wood, 2005). Although it appears that cephalopod beaks are less susceptible to digestion than fish bones, it is still possible that erosion may lead to some measurement bias (Tollit et al., 1997; Santos et al., 2001). The rostrum and shoulder are the sections of the beak formed earliest in development; they are most resistant to digestion and erosion and therefore ideal structures for reconstructing body lengths (Clarke, 1980). As is true with all allometric relationships, the techniques presented here are species specific and may not be reliable estimators of squid body size if applied to lengths beyond the ranges used to develop the predictive equations. Both longfin and shortfin squids attain body sizes larger than were included in the present study; however, our analyses include the most commonly observed lengths of squid found in predator diets and should be adequate for most diet studies. For example, <5% of longfin and shortfin squid prey sizes reported in Kohler (1987), Gannon et al., (1997), Williams (1999), Chase (2002), and Staudinger (2006) exceeded the largest mantle lengths measured here. It should also be noted that specimens collected for the present study were from a portion of the total distributional range of each species and were collected on a limited temporal scale (Macy and Brodziak, 2001; Hendrickson, 2004). If there is variation in squid allometry due to seasonal, interannual, and regional differences in population structure, our sampling regime may not have fully encapsulated these deviations.

Knowledge of size-selective feeding behaviors is fundamental to assessing trophic relationships and defining ecological niches (Bax, 1998). Some of the greatest consumers of cephalopods are large apex predators such as pelagic sharks, tunas, swordfish, and marine mammals; however, the majority of diet data collected on these and many other teuthophagous predators has been qualitative (Smale, 1996). Further, although it has been well established that marine predators are size-selective when feeding on piscine prey (Juanes and Conover, 1994, 1995; Juanes et al., 2001), evaluation of size-based predation on cephalopods has not been well explored. Perhaps the reason for this paucity of information, especially in the Northwest Atlantic Ocean, is the lack of available tools and techniques (Scharf

et al., 1998). In previous studies where squid size has been taken into consideration, mantle length was used to calculate relative prey size and to evaluate trophic niche breadths (MacLeod et al., 2006; Ménard et al., 2006), or total length was estimated from anatomical drawings (Chancollon et al., 2006). These approaches are not recommended because they either considerably underestimate total squid size or fail to capture variation in size with growth, thereby introducing error into subsequent calculations.

To gain a complete understanding of the energetic demands of marine predators, it will be necessary for this key prey group to be accurately assessed. Discerning the squid sizes that are most important to supporting predator growth will improve evaluations of age- and size-based consumption rates of squid predators, natural mortality rates of squid populations, competition among species, and resource sharing between the commercial fishing industry and marine predators.

Acknowledgments

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