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SIGNS OF PREY-SIZE SELECTIVITY IN THE FEEDING BEHAVIOUR OF *Todaropsis eblanae* (CEPHALOPODA: OMMASTREPHIDAE)

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ABSTRACT

The stomach contents of 334 *Todaropsis eblanae* caught by commercial trawlers fishing off Galician coast (NW Spain) were weighed and examined. The most abundant prey was blue whitting (*Micromesistius poutassou*).When possible (n=69), weight of prey was estimated.

A line which express the maximum stomach content in relation to predator weight was calculated (curve MSC). The line relating maximum prey weigth and weigth of the predator was also adjusted (curve MPW). After plotting both curves, two facts were observed: i) Maximum prey size was similar to predator size in *T. eblanae* individuals < 100 g of body weight. A flattening out in prey sizes was observed for larger sized predators. ii) Values reached by the line MPW were at least four or five times those reached by the line MSC.

According to these results, *T. eblanae* almost never captured prey larger than 100 g, although larger preys were available in the habitat. To explain this event, a working hypothesis is proposed: Since prey smaller than 100 g are big enough to fill the stomach of any *T. eblanae*, the individuals of this species would not be energetically rewarded capturing larger preys.

INTRODUCTION

Cephalopods are fast growing carnivorous molluscs which play a vital role in the food webs of marine ecosystems (Amaratunga, 1983). Due to their importance from the viewpoint of ecology and fisheries in the world seas, the loliginids (squids) and the ommastrephids (short-finned squid) are the most studied nektonic cephalopods and knowledge of their trophic ecology is relatively extensive, although fractionary and incomplete. Ommastrephid diet is mainly based on 3 zoological groups: teleosts, crustaceans and cephalopods (Nixon, 1987).

Ommastrephids are among the most voracious cephalopods. Adult *I.illecebrosus* may consume in captivity a daily ration between 10 and 15% its own weight (O'Dor et al., 1980), the average daily rate of ingestion ranging from 3.6 to 6.7% of the predator's weight, increasing with temperature. In another member of the Ommastrephidae family (*Todarodes pacificus*), the maximum daily ration consumed in aquarium ranged from 7 to 13% of its own weight (Sakurai et al., 1991).

Few studies have reported calculations of the size of ingested preys. An occasional tendency towards increasing prey size as the predator grows has been observed (Collins et al., 1994; Froerman, 1984; Breiby and Jobling, 1985). Nevertheless, it is unclear whether this indicates a general pattern, since other evidences contradict this behaviour (Dawe et al., 1983;

Rocha et al., 1994).

In the case of *Illex illecebrosus* no prey-predator size relationship was found, except that the maximum size of prey attacked was roughly equal to predator size (O'Dor et al., 1980). This, together with the variability in the size range of available preys, with the possible non-ingestion of hard structures from larger prey (Rocha et al., 1994), and with the intra- and inter-specific variation in predator behaviour, may, at least partly, explain the apparent contradictions alluded to. Calculation of the size of preys is interesting not only from the viewpoint of the preying behaviour of the species, but also for the study of population biology and ecology (i.e. estimating on which fraction of the prey population the predator is most intensely acting on).

This paper, which is complementary to a larger study on the trophic ecology of ommastrephids (Rasero et al., in press), analyzes the possible prey-size selectivity by *Todaropsis eblanae* , from the study of the prey-predator size relationship.

MATERIAL AND METHODS

A total of 334 stomach contents of *T.eblanae* from both sexes, comprising a wide range of sizes and stages of maturity, were identified. Specimens were taken monthly (between November, 1992 and November, 1993) from trawl fishing on the Galician (NW Spain) shelf and slope (100-500 m depth). Further details of the sampling, materials and methodology used are found in Rasero et al., (in press). When possible, the weight of preys was calculated (n=69). The method used was as follows: in most teleosts (all the *Micromesistius poutassou* and *Gadiculus argenteus*, and some *Merluccius merluccius*), fish length was estimated using the equations given by Pierce et al., (in press), based on the foremost caudal vertebrae in a perfect state of preservation, as recommended in that paper. After calculating length, fish weight was estimated using the equations by Meixide (pers.comm.) for *M.poutassou*, Pereda and Villamor (1991) for *G.argenteus*, and Bedford et al., (1986) for *M.merluccius*. In the case of *Argentina sphyraena* and some *M.merluccius*, weight was obtained directly from the weight of otoliths using equations by Harkönen (1986) and Hislop (pers.comm.), respectively.

Cephalopod weight was estimated from mandibular measurements, using equations by Pérez-Gándaras (1986).

A curve was calculated to estimate the maximum weight of the stomach content in relation to the body weight of the predator (BW = Total weight - Stomach content weight (SCW)). This curve is defined as "maximum stomach content curve" (MSC). It was calculated applying the following method:

1) By dividing the SCW data by squid BW classes. These BW classes were as follows: One class each 40 g, for specimens between 0 and 440 g.

2) By obtaining the average of the 3 maximum SCW values in each BW class. Only the classes with at least 3 SCW values were considered.

3) By extracting the successive maxima (n=6) of these SCW averages, from the lesser to the greater BW class. The highest maximum was obtained in the class 281-320 g BW.

4) By adjusting a regression line to these successive maxima, taking the average value of each BW class as the abscissa value.

RESULTS AND DISCUSSION

The curve estimating the maximum weight of stomach content (MSC) was SCW=2.05+0.067 BW (r^2=0.88, n=6). Figure 1 shows the MSC and the curve indicating maximum prey weight (MPW), fitted by eye through the interval 0-300 g. A line (bisectrix) indicating the equality between prey and predator weight is also shown.

It was observed that individuals smaller than 100 g may ingest prey of their same weight. From that weigth on, prey size practically stabilizes and there is hardly any visible increase except for one isolated point, a *M.merluccius* weighing 251 g captured by a *T.eblanae* weighing 314 g.

The estimated sizes of blue whiting (*M.poutassou*) consumed by *T.eblanae* basically range from 20 to 26 cm in standard length, which is perfectly matched to the sizes of *M.poutassou* more frequently found throughout the year in Galician waters (Robles, 1970). Likewise, blue whiting is an extremely abundant resource in these waters, comprising over 40% of the diet of *T.eblanae* (Rasero et al., in press), and representing 48.3% of the biomass of fishes available to trawl fishing (Sánchez and Pereiro, 1992).

The equality between the maximum weights of prey and the weights of the predator, as observed in the small individuals, gives an idea of the high predatory capacity of the subadults of this species.

The existence of a maximum limit in the size of preys captured by subadults, a limit which approximately coincides with the size of the predator, has already been observed in *Illex illecebrosus* by O'Dor et al. (1980).

Stabilization in the sizes of preys, evident in *T.eblanae* with a body weight of over 100 g (excepting the aforesaid isolated point), has already been observed in, among others, *Illex illecebrosus* (Dawe et al, 1983) and in *Loligo vulgaris* and *L. forbesi* (Rocha et al., 1994). There are several hypotheses in the literature to explain this stabilization:

i) The Behavioural hypothesis: the two works cited above point out the possibility that the species might capture other larger sized preys, whose vertebrae and otoliths are not ingested. Thus, this behaviour would make it impossible to estimate their sizes. The non-ingestion of the hard parts of their preys (head, vertebrae and tail, and, occasionally, the internal organs) is a behaviour which has been repeatedly observed in *Illex illecebrosus* (O'Dor et al., 1980; Wallace et al., 1981; Dawe et al., 1983; Dawe, 1992). A similar behaviour to that observed in *I.illecebrosus* may explain the low number of otoliths found in the stomachs of *T.eblanae* (Rasero et al., in press). However, the ingestion of other hard parts, such as vertebrae (on which the sizes of the majority of preys were estimated), appears to be somewhat common in this species. This leads us to consider that this behavioural hypothesis, although it cannot be totally ruled out, is not altogether adequate for explaining this particular case.

ii) The Ecological hypothesis: a further explanation for the stabilization in prey sizes has been pointed out by Dawe et al. (1983). In this case, it would be the non-availability of larger sized preys in the habitat which would cause the lack of increase in the sizes of preys ingested as the predator grows. This explanation is untenable in this case, since some species present in significant amounts in the *T.eblanae* diet, such as *M.merluccius* (Rasero et al., in press), attain much greater weights in the area (Sánchez and Pereiro, 1992), as is also shown by this single hake specimen weighing 251 g appearing in the illustration.

iii) The authors wish to propose a third hypothesis, the Energetical hypothesis: since prey smaller than 100 g are big enough to fill the stomach of any *T. eblanae*, the individuals of this species would not be energetically rewarded capturing larger preys. This hypothesis is based in the comparison between MSC (Maximum Weight of Stomach Content Curve) and MWP (Maximum Weight of Preys Curve). Even considering MSC as a slight infraestimate of the maximum potential fill of the stomach (as a result of the partial digestion of some of the stomach contents used for the calculation), the larger preys found in the stomachs would be big enough to fill several times the stomach of a*T.eblanae* of any size. If we assume that preys had been ingested in their entirety, the individual ration (Ration = 100 x Estimated Weight of the prey/Body Weight (BW) of the predator) would lie between 0.009% and 112.4%, with an average value of 36.9±25.13% (an average of 31.1±17.89%, if we only consider the *T.eblanae* with a body weight of over 100 g). The last average value is by far greater than the highest rations per food intake estimated for other sub-adult and adult ommastrephid squids: between 5 and 7% in *Todarodes pacificus* (Sakurai et al., 1991), 3 and 11% in *Illex illecebrosus* (Wallace et al., 1981), with a maximum of 21% in *Illex illecebrosus* (Hirtle et al., 1981). As regards the daily ration, the most reliable estimates show average values between 2.6 and 3.7% in *Todarodes pacificus* (Sakurai et al., 1991), an average value of 13.14% in *Dosidicus gigas* (Ehrhardt, 1991), and maximum values of 10-15% in *Illex illecebrosus* (O'dor et al., 1980). These data support the hypothesis above, as it does not appear reasonable for the average ration of *T.eblanae* to be at least three times higher than that of any other ommastrephid.

Consequently, it would be logical to consider that this squid does not capture larger sized preys, since it does not need to capture them. It is probable that the capture of larger preys involves a greater energetic cost, whereas the energetic yield is smaller, due to the limited stomach capacity.

This Energetical hypothesis would also explain the extremely low occurrence of otoliths and cranial remains in the stomach contents (Rasero et al., in press), since a large proportion of each prey captured is probably not ingested by the predator, being the less fleshy body parts (head, tail, etc) commonly rejected.

As a conclusion, the hypothesis of a certain degree of selectivity in the sizes captured seems reasonable. This selectivity can be caused by a commitment between the availability of preys of certain sizes in the environment, the feeding energetic yield, and the filling capacity of the stomach. This agrees with the predictions of the "optimal foraging theory" (Schoener, 1971).

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Figure 1: Prey-predator weigth relationships for *T. eblanae*. Points: estimated weigth of the preys (Other teleosts include *Merluccius merluccius, Gadiculus argenteus* and *Argentina sphiraena*; Other cephalopods include *Illex coindetii, Alloteuthis subulata* and *Loligo vulgaris*). MPW = Curve of the maximum weight of preys. MSC = Curve of the maximum weight of stomach content.