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Daily ration of Antarctic silverfish (*Pleuragramma antarcticum* Boulenger, 1902) in the Eastern Weddell Sea*

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SUMMARY: The daily ration of *Pleuragramma antarcticum* in the Eastern Weddell Sea was investigated from midwater and bottom trawl samples collected in the Antarctic in the summer of 1998. Using a gastric evacuation model that takes into account Weddell Sea temperature below zero and information on the prey type daily ration estimates were: 1.133% BW for immature fish of 10-16 cm and 0.484% BW for mature fish of 17-24 cm. The low daily ration intake was influenced by the low temperatures that limited the rate of gastric evacuation. This model seems more realistic than results from the classic Elliot & Persson and Eggers models that are also used in this paper, since their assumptions on feeding regularity are more rigid and they do not consider data of energy density of the prey.

Key words: daily ration, evacuation rate, Antarctic, pelagic fish, temperature.

RESUMEN: PROPORCIÓN DIARIA DE ALIMENTO DEL DIABLILLO ANTÁRTICO (*PLEURAGRAMMA ANTARCTICUM* BOULENGER, 1902) EN EL ESTE DEL MAR DE WEDDELL. – La ración diaria de alimento de *Pleuragramma antarcticum* en el mar de Weddell es investigada en muestras de arrastres de fondo y pelágicas recogidas durante diferentes horas del día en el verano antártico de 1998. Utilizando un modelo de evacuación gástrica que tiene en cuenta la temperatura bajo del Mar de Weddell e información sobre el tipo de presa, las estimaciones de consumo diario fueron: 1.133% BW para peces inmaduros entre 10 -16 cm y 0.484% BW para peces maduros entre 17-24 cm. La baja ración diaria ingerida estuvo influida por las bajas temperaturas que limitan la tasa de evacuación gástrica. Este modelo parece más realista que los resultados de los modelos clásicos de Elliot & Persson and Eggers también empleados, ya que sus asunciones sobre su periodicidad de alimentación son más rígidas y no consideran datos de densidad energética de las presas.

Palabras clave: proporción diaria de alimento, tasa de evacuación gástrica, Antártica, pez pelágico, temperatura.

INTRODUCTION

The Antarctic silverfish has circum-Antarctic distribution (DeWitt, 1970; Williams, 1985; Hubold and Ekau, 1987; Wöhrmann *et al.*, 1997, Fogg, 1998). It is the most abundant pelagic fish species (DeWitt, 1970; DeWitt and Hopkins, 1977), being important in the diet of other vertebrates that feed in the water column (Schultz, 1945; Andriashev, 1965). It is a key water column species in the Antarctic shelf food web (Hubold, 1984). It is a pelagic planktivore (DeWitt and Hopkins, 1977; Gorelova and Gerasimchuk, 1981; Daniels, 1982; Eastman, 1985; Hubold, 1985; Moreno *et al.*, 1986; Hubold and Ekau, 1990; Hubold and Hagen, 1997). According to these authors it is a zooplanktophagous species in all the phases of its life cycle, varying its feeding between copepods and different

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sizes of krill as it grows from postlarva to adult.

The water of the eastern Weddell Sea is approximately -1.8°C (Hubold, 1991) and the rate of gastric evacuation is highly dependent on temperature (Elliot, 1972; Dos Santos and Jobling, 1990; Salvatore *et al*., 1987; Smith *et al*., 1989). Almost all estimates of fish consumption rates, carried out both in the field and in the laboratory, have been made at temperatures much higher than 0°C (Elliott and Persson, 1978; Grove and Crawford, 1980; Jobling, 1981; Gwyther and Grove, 1981; Dos Santos and Jobling, 1990; Tanasichuck *et al*., 1991; Bromley, 1994). Experiments on gastric evacuation on any fish at water temperatures close to or less than 0°C are rare (Tyler, 1970; Tarverdieva, 1972; Jones, 1974; Crawford, 1979; Targett, 1981; Montgomery *et al*., 1989; Hop and Tonn, 1998). Also, there is very little information available on the daily consumption rate of *P. antarcticum* (Gorelova and Gerasimchuk, 1981). In this paper the daily ration of *P. antarticum* is estimated using three different gastric evacuation models and the results are discussed.

MATERIALS AND METHODS

Field sampling

During the ANT XV/III cruise carried out in the eastern Weddell Sea on board the RV Polarstern in the southern summer of January and February of 1998 (Arntz and Gutt, 1999), stomach contents of *P. antarcticum* were analysed. Sampling was carried out at different hours of the day and night, and using bottom and midwater trawls to obtain information on the patterns of daily migration of the fish in relation to the picnocline (Dieckmann and Thomas, 1999). The samples were caught at different depths in the water column (50 and 150 m) and also on the seafloor, and when there was a sufficient number of specimens a maximum of 10 were selected at random from each haul to carry out the stomach content analysis. In summer on the eastern Weddell Sea shelf, the temperature in the upper part of the water column ranges between -1.8 and -1.2°C, and between -1.8 and +0.5°C close to the bottom (Gerdes *et al*., 1992). If there was evidence of feeding in the net during the haul by *P. antarcticum*, the predator was rejected and, whenever possible, another specimen of the same length was selected. The state of the gall bladder was examined (Robb, 1992) in order to separate the empty stomachs of specimens that had regurgitated food shortly before being caught from those that were truly empty. Weight, length to the lowest cm and sex were recorded for each Antarctic silverfish sampled. The stomach contents of each fish were analysed individually on board the research vessel. The volume of total stomach contents (cc) was measured using a trophometer, Olaso (1990) and Olaso *et al*. (1998).

Crustacean and fish prey were identified to the lowest possible taxa, whereas other invertebrates were classified to higher taxonomic levels. For each prey type, percentage contribution to the volume of stomach contents and number of items per stomach were recorded. The approximate percentage of the total volume made up by the individual identified prey categories was then determined, and the relationship between estimated volume and actual weights of the stomach contents was estimated as described in Olaso (1990) derived from a power model (a=0.932735, b=0.99324, r^2= 0.99; p<0.01).

Quantitative diet analysis and daily ration

Food data are presented in terms of the mean weight of stomach contents and percentage of empty stomachs. To allow comparison of prey quantities in *P. antarcticum* of various sizes, stomach contents were expressed as a percentage of the body weight (%BW). The relationship between the body weight and the size was estimated by means of a power model estimated on board from the sample of 588 specimens of *P. antarcticum* (a = 0.01109, b = 3.381545, r^2 = 0.979; p<0.01). Empty stomachs were considered in all analyses.

The feeding rate of fish in natural populations can be estimated by means of gastric evacuation models (Bajkov, 1935). In these models, the rate of gastric evacuation is affected mainly by the size of the body and the physiological condition of the predator, as well as by the food type and the degree of stomach fullness, and increases with temperature following an exponential or potential curve (Fange and Grove, 1979; Salvatore *et al*., 1987; Vondracek, 1987). To avoid the effect of predator size on the rate of gastric evacuation, R, one solution is to express the stomach content as a percentage of the predator body weight (%BW) instead of using total stomach weight. Therefore, the mean stomach content per sample, WT, used in all the consumption estimates carried out was expressed as %BW, and to consider the changes that occurred in the feeding habits with growth, two size groups were used: immature fish (10-16 cm) and mature fish (17-24 cm).

Given the temperatures in the depth ranges studied, we assumed that the digestion processes were carried out at a mean temperature of -1.4°C. Considering these low temperatures and the limited food data for *P. antarticum*, estimates of daily ration were determined using three different exponential models of gastric evacuation (Elliott and Persson, 1978; Eggers, 1977; Dos Santos and Jobling, 1995) and the results are compared and discussed for each one. In the three models empty stomachs were considered when mean stomach contents and daily rations were calculated, given that they reflect the frequency of food intake.

For the Elliot and Persson model, in order to obtain a more complete image of the 24 h cycle, stomach content samples that had been collected were artificially grouped at intervals of time *t*; for the mature specimens they were: 0-3 h, 3-6 h, 6-9 h, 9-12 h, 12-15 h, 15-18 h and 18-24 h, whereas for the immature ones the reduced sample size made it necessary to use six-hour intervals (e.g. 12-18, 18-24). The Eggers model was used given the lack of data in some time intervals of the daily cycle. The value of the evacuation rate, R (in the two models), was not determined experimentally by these authors, since the existing formula $R = 0.0406\ e^{0.111T}$ was used (Durbin *et al.*, 1983), where T is the temperature; this value was determined experimentally by these authors at temperatures ranging from 2 to 20°C in different fish species. Since *P. antarcticum* is adapted to lower temperatures we extrapolated the value of R using a T of -1.4°C.

The Dos Santos Model is formed from the reformulation of a function that describes the gastric evacuation of different preys (Dos Santos and Jobling, 1992) determined by the energy contents of such preys. According to the model, the evacuated quantity depends on the initial food size, the water temperature (T, °C) and the fish body size. This model gives the consumption of the most characteristic prey types (i.e. copepods, euphausiids, prawns and fish) and the total consumption is estimated from the sum of the consumptions of each characteristic prey. The consumption estimates from the equation are not defined when the stomach content is zero, and in this case the consumption estimate is also zero.

RESULTS

It was observed that *P. antarcticum* preys mainly on copepods and euphausiids. To facilitate the calculations, only four general prey groups were considered, so that each one contained similar prey taxa in size and biological characteristics. These groups were:

Pisces: (*P. antarcticum*, *Trematomus lepidorhinus*, undetermined Myctophidae and undetermined fish)

Crustaceans A: (*Euphausia superba*, undetermined *Euphausia*, undetermined Peracarida, undetermined Crustacea, undetermined Hyperiidae, *Themisto gaudichaudii*, undetermined Amphipoda).

Crustaceans B: (*Nematocarcinus longirostris*, *Notocrangon antarcticus*)

Crustaceans C: (*Rhincalanus gigas*, *Calanus propinquus*, undetermined Calanoida, Copepoda undetermined, Ostracoda).

The mean stomach contents for each size group and time period as percentage body weight are

TABLE 1. – Mean of food (% BW) present in the stomach of *Pleuragramma antarcticum* (x/ ± 95% of confidence limits) and estimated mean amount of food ingested during each 3 h period. BW=body weight. % BW: including the fish with empty stomachs.

	No. of predators	Empty %	Mean ±95% C.L. (%BW)	Minimum (%BW)	Maximum (%BW)	Ingestion (%BW)
10-16 cm						
24 - 03	7	14.3	0.871 ± 0.838	0.193	3.276	0.064
03 - 06	6	0.0	1.211 ± 0.265	0.771	1.518	0.449
06 - 09	7	14.3	0.664 ± 0.462	0.193	1.765	-0.450
09 - 12	13	61.5	0.211 ± 0.180	0.262	1.030	-0.408
12 - 18	10	30.0	0.698 ± 0.455	0.517	1.983	0.584
18 - 24	2	0.0	0.899 ± 0.250	0.771	1.026	0.368
17-24 cm						
24 - 03	32	15.6	0.491 ± 0.133	0.107	1.516	0.203
03 - 06	6	16.7	0.779 ± 0.633	0.184	1.829	0.354
06 - 09	21	52.4	0.290 ± 0.184	0.089	1.671	-0.434
09 - 12	27	48.1	0.188 ± 0.093	0.132	0.823	-0.077
12 - 15	13	38.5	0.204 ± 0.129	0.149	0.582	0.036
15 - 18	18	50.0	0.403± 0.234	0.131	1.085	0.231
18 - 21	2	50.0	0.147 ± 0.288	0.294	0.294	-0.228
21 - 24	8	0.0	0.331 ± 0.098	0.184	0.608	0.209

TABLE 2. – Daily ration Dos Santos model (% body weight / day) in the two selected size ranges of *Pleuragramma antarcticum*. C.L.: confidence limits.

	10-16 cm Daily ration ±95% C.L.	17-24 cm Daily ration ±95% C.L.
Fish prey	0.010 ± 0.053	0.014 ± 0.083
Crustaceans A prey	0.358 ± 0.295	0.257 ± 0.057
Crustaceans C prey	0.735 ± 0.419	0.209 ± 0.213
Crustaceans B prey	0.004 ± 0.126	
Total Food	1.103 ± 0.280	0.484 ± 0.083
No. Full stomachs	31	77
No. Empty stomachs	13	45
No. Regurgitated	1	5

shown in Table 1. In order to estimate the mean feeding rate for periods of three hours during the day, the mean weight of the fish stomach contents that contained food (%BW) was used. The mean weight of food in the stomachs was 1.3% BW, but the range of values observed in the individual fish varied from 0 to 3.3% BW.

The rate of gastric evacuation (*R*) was estimated as 0.0348 g/h, by extrapolation from the formula of Durbin *et al*. (1983) at a temperature of -1.4°C. The estimates of the daily ration from the Elliot and Persson model are summarised in Table 2, and show that the ingestion estimates in each time interval fluctuated considerably, with both positive and negative values being obtained. The overall daily ration values obtained were 0.607 ± 0.139% BW for the immature specimens and 0.295 ± 0.096% BW for the mature ones. Eggers's method showed very similar values of daily ration repletion to the previous method, 0.663 ± 0.129% BW in the immature specimens, and 0.295 ± 0.096 %BW in the mature specimens.

The method of Dos Santos and Jobling gave higher mean consumption values than the methods of Eggers and Durbin; 0.484 ± 0.083% BW in the mature Antarctic silverfish and 1.103 ± 0.280% BW in the inmature ones. The data showed that the crustaceans C (copepods) were the food base in the immature fish and represented more than double the quantity of crustaceans A (Table 2). On the other hand, the crustaceans A (euphausiids) were the prey most ingested by the mature fish.

DISCUSSION

The estimates on the consumption of Antarctic or Arctic fish that live at very cold water temperatures give low results, and are always based on laboratory experiments (Crawford, 1978; 1979; Montgomery *et al*., 1989; Targett, 1981; Targett *et al*., 1987). In other works gastric evacuation rates at sub-zero temperatures have been predicted by extrapolation from experiments conducted at higher temperatures (Fange and Grove, 1979), given that only a few studies have investigated gastric evacuation rates at sub-zero temperatures, presumably because of the high expense required to sustain fish at sub-zero temperatures in the laboratory. The rate of evacuation of Durbin *et al*. (1983) is based on data of generally higher temperatures, and extrapolation to temperatures below zero should be carried out with caution (Hop and Graham, 1995). We assumed that this extrapolated R provides a good fit to obtain the ingestion rates of *P. antarcticum* and our estimates of daily consumption do not even reach 0.7% BW in immature Antarctic silverfish of 105 g either with the model of Elliot and Persson (1978) or with the model of Eggers (1979). Nevertheless, the gastric evacuation rates found in the experiments on Arctic cod (*Boreogadus saida*) carried out by Hop and Tonn (1998), R=0.0149 g/h, are lower than the R estimated by Durbin *et al*. (1983), but the daily ration estimate at -1.42°C is 1.13% BW for fish of 50 g. Therefore, it is necessary to consider that the adaptation to polar temperatures (metabolism cold adaptation) involves an increase in metabolic rate (Wohlschlag, 1964; Holeton, 1974), as we discuss in the following paragraphs.

Kock (1992) undertook a summary of several authors that work on the daily ration ingested by notothenioids and indicated that, as an estimation for the majority of the species, the most probable rates are 0.5-2.5% of the body weight, and that these values can increase in summer when the krill is locally very abundant; these differences are logical if we consider that the fish from any single environment differ enormously in metabolic rate according to lifestyle (Somero, 1991). Even in winter and at -1.7°C, Targett *et al*. (1987) observed that the notothenioid *Harpagifer* had a daily consumption of 1.46%. The relatively high values of *Harpagifer* and *Boreogadus* (species which grow and move fast at very low temperatures) show that these species may have high metabolisms and are not in the same category as fishes like *P. antarcticum*. Steffensen (2002) discovered that some Antarctic fish species do not show high resting aerobic oxygen consumption values or standard metabolic rates, and hence it is concluded that metabolic cold adaptation in the traditional sense is an artefact.

The pelagic *P. antarcticum* has adapted over a million years to cold water, achieving neutral buoyancy through a combination of lack of swim bladder buoyancy (Eastman and DeVries, 1982; Clarke and Johnston, 1996), skeletal reduction and lipid deposition (DeVries and Eastman, 1978), cold-adapted gastric enzymes (Härtling, 1991), and big mitochondrial volume densities (Pörtner, 2002). Hence, these adaptations to pelagic life make *P. antarcticum* a rather sluggish fish with a low scope of activity and low metabolic demands (Wöhrmann *et al.*, 1997), and logically its consumption is lower than that of other more active polar species.

On the other hand, in the model of Dos Santos and Jobling (1995), the evacuated quantity is dependent on the initial food size, the water temperature, the fish body size and the prey type. We think that with this model there is less bias and, besides appearing more consistent when using the energy density of the preys, the results of the daily consumption show higher values closer to those of other studies. Our values of daily consumption obtained from the Dos Santos and Jobling model (1995), 1.1% BW for immature fish between 10-16 cm and 0.5% BW for mature fish between 17-24 cm, agree with those found for these low temperatures in other fish of polar environments, and specifically with the only estimate of daily ration for *P. antarcticum* that was carried out in summer by Gorelova and Gerasimchuk (1981), with ranges of 0.5-1.2% BW. Fonds *et al.* (1992) indicate that at water temperatures of less than 0°C, the low evacuation rates can limit daily food intake when the food is seasonally abundant. Nevertheless, we have to bear in mind that the differences in evacuation time can be attributed to numerous factors, such as feeding rhythm, digestion rates and abundance of prey types (Durbin *et al.*, 1983; Tanasichuk *et al.*, 1991). Also, the values used to obtain the gastric evacuation rates are usually based on fish stimulated to eat at specific time intervals and on certain prey types (Jobling, 1980; Basimi and Grove, 1985), and this artificial feeding stimulation may result in overestimates of daily ration.

Therefore, we wish to stress the importance of the fact that we used field data, and although these estimates are taken from a limited set of data, they bring out some information on the food consumption of *P. antarticum*, an issue that has not been addressed before in this Antarctic area and that is very important from an ecological point of view.

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